



Original investigation

The description of a new species of *Myzopoda* (Myzopodidae: Chiroptera) from western Madagascar

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Abstract

A new species of *Myzopoda* (Myzopodidae), an endemic family to Madagascar that was previously considered to be monospecific, is described. This new species, *M. schliemanni*, occurs in the dry western forests of the island and is notably different in pelage coloration, external measurements and cranial characters from *M. aurita*, the previously described species, from the humid eastern forests. Aspects of the biogeography of *Myzopoda* and its apparent close association with the plant *Ravenala madagascariensis* (Family Strelitziaceae) are discussed in light of possible speciation mechanisms that gave rise to eastern and western species.

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Introduction

Recent research on the mammal fauna of Madagascar has and continues to reveal remarkable discoveries. A considerable number of new small mammal and primate species have been described in recent years (Goodman et al. 2003), and numerous other mammals, known to taxonomists, await formal description. Much of this recent information is based on renewed interest in biological inventories of the remaining forested zones of the island and the associated systematic studies of specimens obtained during these surveys. In some cases these animals can be recognized as new to science when first handled in the field by specialists, while in cases of cryptic

speciation molecular studies have been very informative to resolve questions of species limits (e.g., Olson et al. 2004; Yoder et al. 2005). The bat fauna of the island is no exception – until a decade ago these animals remained largely under studied and ongoing surveys and taxonomic work have revealed that they may be something on the order of 30% richer in species than noted in the most recent treatment of this group (Peterson et al. 1995). As with other mammals, in certain cases new species of bats are immediately recognizable (e.g., Goodman and Cardiff 2004) and in other cases molecular tools help in defining species limits (Goodman et al. 2006).

The chiropteran family Myzopodidae is endemic to Madagascar and as currently understood is monospecific, represented by *Myzopoda aurita* (Milne-Edwards and Grandidier, 1878). After the creation of the Myzopodidae for this species (Thomas 1904), it was proposed, based on morphological grounds, to be part of the Vespertilionoidea, which included the families Natalidae, Furipteridae, Thyropteridae, Vespertilionidae, Mystacinidae and Molossidae (Koopman 1994). More recently, using molecular studies, the Myzopodidae has been placed in the Noctilionoidea (Teeling et al. 2005), which also comprises the Furipteridae, Thyropteridae, Mystacinidae, Noctilionidae, Mormoopidae and Phyllostomidae. Only two families of bats in the world are currently considered monospecific (Simmons 2005): the Craseonycteridae and the Myzopodidae.

With regard to *Myzopoda*, Thomas (1904) referred to it as “exceedingly rare and remarkable”, the latter point certainly associated with the large flat adhesive organs, or suckers, attached to the thumb and hind foot; hence its vernacular name sucker-footed bat. These structures have been the subject of detailed morphological studies (Schliemann 1970, 1971).

Until about 15 years ago few observations or specimens were available of *Myzopoda*. However, on the basis of recent field surveys it has been recorded at a variety of sites in the eastern humid forests of Madagascar (Schliemann and Goodman 2003; Fig. 1). There was one previously collected specimen from Mahajanga, on the dry western side of the island (Schliemann and Maas 1978), which indicated that the ecological breadth of this genus was greater than previously recognized. Over the past few years we have captured individuals of *Myzopoda* at three different localities in the west. These animals are notably different in pelage coloration than those of the east, which lead us to investigate their taxonomic status. Using data on external, cranial and dental morphology we are able to document that the western population of *Myzopoda* is different than that of the east, and it is described herein as a new species.

Material and methods

In order to examine patterns of morphological variation in *Myzopoda* we have consulted specimens housed in several natural history museums. The acronyms of these institutions are: AMNH – American Museum of Natural History, New York; BMNH – The Natural History Museum, London (formerly The British Museum [Natural History]); FMNH – Field Museum of Natural History, Chicago; MNHN – Muséum national d’Histoire naturelle, Paris; PBZT – Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; RMNH – Rijksmuseum van Natuurlijke Historie, Leiden; UADBA – Université d’Antananarivo, Département de Biologie Animale, Antananarivo; UADP – Université d’Antananarivo, Département de Paléontologie, Antananarivo; USNM – National Museum of Natural History (formerly United States National Museum of Natural History), Washington, DC; ZMB – Museum für Naturkunde, Humboldt Universität zu Berlin [formerly Zoologisches Museum], Berlin; and ZMH – Zoologisches Museum Hamburg, Hamburg. A list of *Myzopoda* specimens used in this study is presented as Table 1.

We recorded five external measurements in millimeters using a ruler from collected specimens before preparation. These included: total length, tail length, hind foot length (not including claw), ear length and forearm length. Further, we measured body mass in grams using a spring balance. For certain specimens these data were obtained directly from museum labels or field catalogues, and in other cases they were measured from liquid preserved specimens. SMG also took 10 wing and two foot measurements using a dial callipers from liquid preserved specimens: 3rd digit – metacarpal, 3rd digit – 1st phalanx, 3rd digit – 2nd phalanx, 3rd digit – 3rd phalanx, 4th digit – metacarpal, 4th digit – 1st phalanx, 4th digit – 2nd phalanx, 5th digit – metacarpal, 5th digit – 1st phalanx, 5th digit – 2nd phalanx, tibia and calcar. Seven cranial or mandibular and four dental measurements were made by SMG using digital calipers, accurate to the nearest 0.1 mm: occipitonasal length, from occipital condyles to anterior-most point of nasal bone; greatest zygomatic breadth, width taken across zygomatic arches at the widest point; interorbital breadth, dorsal width at most constricted part of skull; mastoid width, greatest width across skull at mastoid processes; greatest braincase width, breadth at widest portion of braincase; lacrimal width, greatest width across rostrum at lacrimal projections; anterior palatal width (C^1-C^1), taken across the outer alveolar borders of the upper canines; maxillary toothrow (C^1-M^3), length from anterior alveolar border of upper canine to posterior alveolar border of the

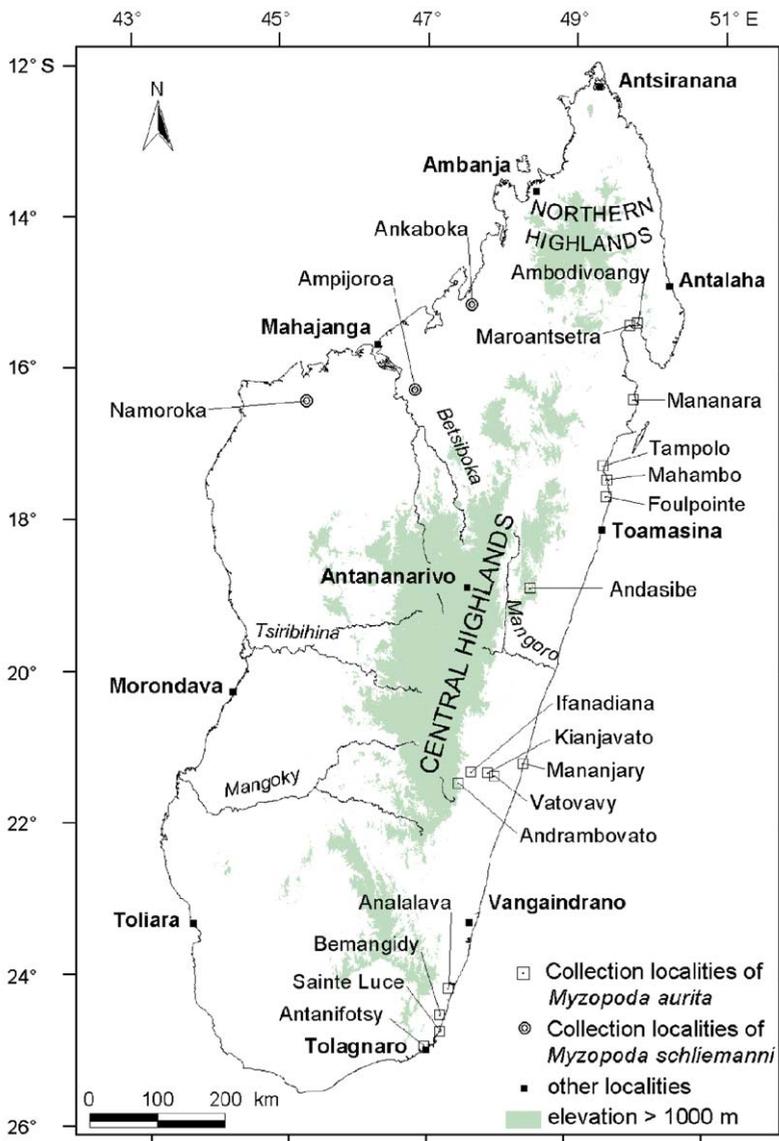


Fig. 1. Map of Madagascar, showing the sites specimens of *Myzopoda* spp. are known from and used in this study. The grey shading represents portions of the island over 1000 m in elevation. The general limits of the Central and Northern Highlands are noted. (Map prepared by Lucienne Wilmé.)

third upper molar; upper molariform toothrow, length from anterior alveolar border of PM^3 to posterior alveolar border of M^3 ; width M^3 , greatest lateral-medial width of tooth; and mandible length, from the posterior-most portion of the condyles to anterior-most point of lower incisors.

Results

Using information from morphological analyses we can demonstrate that the populations of *Myzopoda* inhabiting the western

Table 1. List of *Myzopoda* specimens examined (see Material and methods for a listing of museum acronyms).Specimens of *Myzopoda aurita*

Province de Fianarantsoa: Andrambovato (USNM 449282); Ifanadiana (USNM 449315); Kianjavato (AMNH 257130; FMNH 185227; UADP 226; USNM 448886, 448929, 448930, 448931, 448932, 449283, 449285); Mananjary (MNHN 1907.618)

Province de Toamasina: Ambodivoangy (MNHN 1985.434), Andasibe (FMNH 184490); Foulpointe (FMNH 183990); Mahambo (RMNH 26117); Mananara (ZMB 5866); Maroantsetra (MNHN 1985.654); Tampolo (FMNH 165454, 179203, 179204, 179273), "Tamatave" [= Toamasina] (BMNH 99.11.3.5; ZMH T1488, T1489, T1840, ZMB 23584)

Province de Toliara: Analalava (USNM 577065); Bemangidy (FMNH 85237, 92832); Sainte Luce (UADBA RBJ-200); USNM 578740, 578742, 578743, 578856, 578857, 578858)

No precise locality: "Madagascar" (MNHN 1997.770, holotype; ZMB 22843; ZMH T1487).

Specimens of *Myzopoda schliemanni*

Province de Mahajanga: SF d'Ampijoroa (FMNH 177327, holotype); Ankaboka (FMNH 185790, 185791, 185793, 185794); Parc National de Namoroka (UADBA RBJ 203, RBJ 204); "Majunga [= Mahajanga], sur la côte ouest" (MNHN 1947.292).

and eastern portions of Madagascar are different from one another. Even though the type specimen of *M. aurita* (MNHN 1997.770) bears the vague designation of being from "Madagascar", with no further details in the type description (Milne-Edwards and Grandidier 1878), this specimen, based on color and external measurements (see Comparisons section), is from the east. Hence, the western individuals represent a new species that is described here.

***Myzopoda schliemanni* new species**

Holotype: FMNH 177327, male specimen prepared as skin, skull and partial post-cranial skeleton. Field number SMG 13624. Collected by S. M. Goodman on 18 April 2003 at Province de Mahajanga [Parc National d'Ankarafantsika], SF [Station Forestière] d'Ampijoroa, Jardin Botanique A, 16°19.4'S, 46°48.4'E, 160 m (Fig. 1). The skin specimen is in good condition; although as it had considerable subcutaneous fat, there was some seepage of grease onto the dorsal and lower ventral pelage. The basisphenoid-basioccipital suture is fully ossified and it has a full permanent dentition. The left portion of the rostrum is partially broken at the level of the lacrimal canal and the winged-portions of the pterygoids are broken (Fig. 2).

Paratypes: Three males and four females and all are adult, except as noted. MNHN 1947.



Fig. 2. Different views of holotype of *Myzopoda schliemanni* (FMNH 177327). Upper left – dorsal view of cranium, upper right – ventral view of cranium and lower – lateral view of cranium and mandible. (Photograph taken by John Weinstein, Field Museum image number Z94433-05d.)

292, female, "Majunga, sur la côte ouest", 12 June 1940; UADBA RBJ 203 and 204, female and male (respectively), Province de Mahajanga, Parc National de Namoroka, Andriabe, about 5 km south of Namoroka (village), 16°24'30.6" and 45°18'39.5", 110 m,

13 October 2004; FMNH 185790, 185791, male and sub-adult female (respectively), Province de Mahajanga, Ankaboka, 15°02.24'S, 47°47.13'E, 200 m, 4 June 2000; FMNH 185793, 185794, male and female (respectively), Province de Mahajanga, Ankaboka, 15°02.24'S, 47°47.13'E, 200 m, 5 June 2000.

Etymology: The species name has been chosen to honor Professor Dr. Harald Schliemann, University of Hamburg, in recognition of his long interest in sucker-footed bats, including several important anatomical studies (e.g., Schliemann 1970, 1971). Professor Schliemann has recently retired from his university post after a long and fruitful career, including being the Director of the Zoologisches Institut und Zoologisches Museum, Hamburg. We suggest Schliemann's sucker-footed bat as the vernacular name of this species and eastern sucker-footed bat for *M. aurita*.

Distribution: *Myzopoda schliemanni* is known from three precise localities in the dry deciduous forest zone of western Madagascar from Ankaboka at the northern limit of its distribution to Namoroka at the southern limit (Fig. 1). These localities are approximately 300 km apart and in lowland habitat. The holotype was obtained at Ampijoroa, which is also a lowland site and about 80 km inland direct distance from the coastal town of Mahajanga. The fourth collection locality, of the Paris specimen (MNH 1947. 292), is vague. On the basis of extrapolation of its preferred habitat type (see below), it is likely that this species has a broader distribution in the dry deciduous zones of the west, particularly further north to perhaps at least the Sambirano region in the vicinity of Ambanja.

Measurements of holotype: Measurements are in mm and the body mass in g. Total length, 107; tail length, 44; hind foot length, 6; ear length, 30; forearm, 47; weight, 9.9; occipitonasal length, 14.9; greatest zygomatic breadth, 11.7; interorbital breadth, 4.1; mastoid width, 9.8; greatest braincase width, 8.8; lacrimal width, 5.9; anterior palatal width (C^1-C^1), 4.0; maxillary tooththrow (C^1-M^3), 5.9; upper molariform tooththrow, 4.3; width M^3 , 2.0; mandible length, 11.0; 3rd digit –

metacarpal length, 37.2; 3rd digit – 1st phalanx length, 16.5; 3rd digit – 2nd phalanx length, 16.6; 3rd digit – 3rd phalanx length, 11.7; 4th digit – metacarpal length, 36.0; 4th digit – 1st phalanx length, 13.6; 4th digit – 2nd phalanx length, 14.0; 5th digit – metacarpal length, 37.2; 5th digit – 1st phalanx length, 11.5; 5th digit – 2nd phalanx length, 8.5; tibia length, 15.0; calcar length, 10.9.

Description: *Myzopoda schliemanni* is a relatively small microchiropteran bat with a forearm length of 45–49 mm. Like the other member of this genus it has very prominent funnel-shaped ears, which are not joined at their base, and the external ear conch attaches close to the base of the mouth. There is an odd mushroom-shaped process at the base of each ear that is probably the tragus (Thomas 1904; cf. Koopman 1994). Distinct large flat adhesive organs, or suckers, are attached to the thumb and hind foot. Second digit of wing reduced to the metacarpal and a small phalanx. Tail elongated and reaches terminus of extensive uropatagium.

The hairs of the dorsum have buff-brown distal tips merging to moderate mouse-gray bases. The venter is a uniform light mouse-gray. The posterior portion of the braincase tends to be less bulbous than in *M. aurita*, the palatine foramen is constricted and with a narrow “v-shape”, the nasal sulcus is shallow and relatively broad, the nasals are narrow and rectangular in shape and the frontals are not notably inflated. Dental formula in adults is $2/3-1/1-3/3-3/3$. It is notably smaller in several external measurements than *M. aurita*.

Variation: *t*-Tests were conducted of the external, cranial and dental measurements of adult *M. aurita* (maximum $n = 36$) and *M. schliemanni* (maximum $n = 7$), and neither species was found to be sexually dimorphic. In all subsequent comparisons the sexes are combined for each species. Considerable variation, as reflected by standard deviation, was found in certain external measurements for *M. aurita* (Tab. 2). When the measurements are restricted to a single collector there is a notable reduction in the standard deviation of total length and hind foot length, while other measurements, such

Table 2. External measurements (in mm) and body mass (in g) of *Myzopoda* spp. Samples are of adults and divided between eastern and western localities. Descriptive statistics presented as mean \pm standard deviation, minimum–maximum, *n*. Samples measured by a single field collector (SMG) are in italics. *t*-Test comparisons are presented between the complete western and eastern samples. Measurements of *M. aurita* holotype were measured directly from liquid preserved specimen.

	Total length	Tail length	Hind foot length	Ear length	Forearm length	Body mass
<i>Myzopoda schliemannii</i>						
Holotype FMNH 177327	107	44	6	30	47	9.9
Combined samples	102.3 \pm 8.96 92–107, <i>n</i> = 3	45.6 \pm 1.36 44–47, <i>n</i> = 7	5.7 \pm 0.58 5–6, <i>n</i> = 6	30.9 \pm 0.75 30–32, <i>n</i> = 7	47.4 \pm 1.30 45–49, <i>n</i> = 7	9.3 \pm 1.34 7.8–10.3, <i>n</i> = 3
<i>Myzopoda aurita</i>						
Holotype MNHN 1997.770	—	51	6	35	48	—
Combined samples	110.3 \pm 4.47 101–118, <i>n</i> = 26	46.9 \pm 3.03 40–53, <i>n</i> = 36	7.4 \pm 1.70 5–10 ¹ , <i>n</i> = 30	33.9 \pm 1.45 31–39, <i>n</i> = 27	48.8 \pm 1.37 46–52, <i>n</i> = 31	8.6 \pm 0.85 7.2–10.5, <i>n</i> = 26
	112.7 \pm 1.53 111–114, <i>n</i> = 3	47.3 \pm 3.06 44–50, <i>n</i> = 3	5.3 \pm 0.58 5–6, <i>n</i> = 3	32.7 \pm 1.15 32–34, <i>n</i> = 3	47.7 \pm 1.52 46–49, <i>n</i> = 3	9.3 \pm 0.25 9.0–9.5, <i>n</i> = 3
	<i>t</i> = 2.05, <i>df</i> = 27 <i>P</i> = 0.01	n.s.		<i>t</i> = 2.07, <i>df</i> = 32 <i>P</i> = 5.7 ^{–6}	<i>t</i> = 2.03, <i>df</i> = 36 <i>P</i> = 0.007	n.s.
	3rd digit – metacarpal	3rd digit – 1st phalanx	3rd digit – 2nd phalanx	3rd digit – 3rd phalanx	4th digit – metacarpal	4th digit – 1st phalanx
<i>Myzopoda schliemannii</i>						
Holotype FMNH 177327	37.2	16.5	16.6	11.7	36.0	13.6
Combined samples	36.0 \pm 1.08 34.2–37.2, <i>n</i> = 8	16.8 \pm 0.57 16.1–17.8, <i>n</i> = 8	18.2 \pm 0.74 16.6–18.7, <i>n</i> = 8	11.8 \pm 1.91 10.6–13.8, <i>n</i> = 7	35.6 \pm 1.44 33.5–37.7, <i>n</i> = 8	14.1 \pm 0.39 13.6–14.7, <i>n</i> = 8
<i>Myzopoda aurita</i>						
Holotype MNHN 1997.770	38.2	18.0	20.5	12.3	38.7	14.7

Combined samples	37.5 ± 1.01 35.6–39.0, <i>n</i> = 17 <i>t</i> = 2.07, <i>df</i> = 23 <i>P</i> = 0.005	17.3 ± 0.59 16.3–18.6, <i>n</i> = 19 n.s.	18.6 ± 0.92 17.0–20.5, <i>n</i> = 19 n.s.	12.4 ± 0.81 11.0–13.7, <i>n</i> = 18 n.s.	36.9 ± 1.11 34.9 ± 38.7, <i>n</i> = 17 <i>t</i> = 2.07, <i>df</i> = 23 <i>P</i> = 0.02	14.5 ± 0.39 13.5–16.5, <i>n</i> = 19 <i>t</i> = 2.06, <i>df</i> = 25 <i>P</i> = 0.04
	4th digit – 2nd phalanx	5th digit – metacarpal	5th digit – 1st phalanx	5th digit – 2nd phalanx	Tibia	Calcus
<i>Myzopoda schiemanii</i>						
Holotype FMNH 177327	14.0	37.2	11.5	8.5	15.0	10.9
Combined samples	15.5 ± 0.77 14.0–16.6, <i>n</i> = 8	36.7 ± 1.56 34.7–38.9, <i>n</i> = 8	11.6 ± 0.48 10.8–12.4, <i>n</i> = 8	10.3 ± 0.99 8.5–11.6, <i>n</i> = 8	16.2 ± 1.21 14.8–18.4, <i>n</i> = 8	13.2 ± 1.77 10.9–16.1, <i>n</i> = 8
<i>Myzopoda aurita</i>						
Holotype MNHN 1997.770	16.3	38.4	12.7	10.8	16.4	14.0
Combined samples	15.0 ± 0.87 13.5–16.5, <i>n</i> = 19 n.s.	38.1 ± 1.13 36.0–40.0, <i>n</i> = 17 <i>t</i> = 2.07, <i>df</i> = 23 <i>P</i> = 0.02	11.6 ± 0.50 10.7–12.7, <i>n</i> = 19 n.s.	10.3 ± 0.62 8.9–11.7, <i>n</i> = 19 n.s.	17.2 ± 0.61 16.0–17.9, <i>n</i> = 15 <i>t</i> = 2.08, <i>df</i> = 21 <i>P</i> = 0.01	14.0 ± 1.08 12.6–16.1, <i>n</i> = 14 n.s.

¹On the basis of this range and associated variance it can be assumed that these measurements are a mixture of those with and without the hind claw. Statistical tests not conducted.

as tail length, continue to show the same level of variation (Tab. 2). Within *M. schliemanni* there is little variation in the dorsal buff-brown and ventral mouse-gray pelage coloration or in cranial and dental measurements amongst the specimens obtained at several different localities. The pelage coloration of *M. aurita* is a consistent dark brown.

Comparisons: In the holotype skin specimen of *M. schliemanni* (FMNH 177327) from Ampijoroa, the dorsum fur, which is longer and shaggier than in *M. aurita*, has buff-brown distal tips merging to moderate mouse-gray bases. The ventrum is a uniform light mouse-gray (Fig. 3). In contrast, the pelage of *M. aurita* is characterized by being a uniform dark brown, bordering on blackish, on both the ventrum and dorsum (Fig. 3); although a few individuals have a dark golden-brown tinge to the pelage. In the specimens of *M. schliemanni* from Ankaboka and Namoroka, all of which were preserved in formaldehyde and subsequently transferred to ethanol, the pelage coloration is consistent with the holotype of *M. schliemanni* and distinctly lighter than in individuals of eastern *M. aurita*.

Even though the holotype of *M. aurita* has been stored in alcohol for over 130 years, the pelage is not completely foxed and the color remains notably darker than individuals of this genus from western Madagascar. Further, the specimen's external measurements fall within the range of the eastern species (Tab. 2). Hence, we conclude that the holotype represents *M. aurita* as defined herein.

The external measurements of *M. schliemanni* are distinctly smaller than *M. aurita* (Tab. 2). For total length, hind foot length, ear length and forearm length these differences are statistically significant. Perhaps most notable in this regard is ear length, which shows less overlap between the two species than the other external measurements. Several of the wing bone measurements show statistically significant differences between the two species, and in each case it is *M. schliemanni* that is smaller than *M. aurita* (Tab. 2).

The two species show broad overlap in cranial and dental measurements (Tab. 3) and none of these comparisons are statisti-

cally significant. The tooth formula is identical in both species. Further, no notable difference was found in tooth or cusp shape. In *M. schliemanni* the cranium tends to be slightly less bulbous in appearance than in *M. aurita*. The palatine foramen in *M. schliemanni* is notably more constricted and a narrow "v-shape" as compared to the more open and broad "U-shape" in *M. aurita* (Fig. 4). Further, there are distinct differences in aspects of the rostral morphology in the two species (Fig. 5). In *M. aurita* the nasal sulcus is distinctly narrower and deeper than in *M. schliemanni*. Further, in *M. schliemanni* the nasals form a largely parallel structure, while in *M. aurita* they are expanded posteriorly and then constricted. The frontals are notably more inflated in *M. aurita* than in *M. schliemanni*. The holotypes of *M. schliemanni* and *M. aurita* were directly compared and these differences are consistent between all adult specimens of the two taxa.

Principal component analyses were conducted on external, wing bone, cranial, and dental measurements of the specimens of *Myzopoda* spp. Of these four comparisons it was only the external measurements that showed a clear separation of *M. schliemanni* and *M. aurita* (Fig. 6), in which the first two factors explained 69.7% of the variance. Ear length and forearm length had the heaviest loadings (Tab. 4). These results are concordant with the univariate analyses.

Natural history: It has been noted in the literature that *Myzopoda aurita* is a denizen of moist tropical forests and is often found associated with the large broad-leaf plants, most notably *Ravenala madagascariensis* of the Family Strelitziaceae (Schliemann and Maas 1978; Koopman 1994; Göpfert and Wasserthal 1995). This tree with banana-like leaves, reaching 10–15 m tall, often grows naturally in areas with moist ground. *Ravenala* is also one of the more important pioneering plants in heavily degraded habitats, particularly the eastern biome, after forest clearing and the successive passage of fire (Blanc et al. 2003). It is presumed that the sucker-like structures on this bat's wrists and ankles are used to adhere to slick flat leaf-surfaces, aiding the bat in climbing up the leaves or adhering to a roosting position. In



Fig. 3. Image above, photograph ventral view of holotype of *Myzopoda schliemanni* (FMNH 177327) obtained on 18 April 2003 in the Station Forestière d'Ampijoroa, Parc National d'Ankarafantsika. (Photograph taken by Steven M. Goodman.) Image below, photograph ventral view of typical eastern *M. aurita* captured at Tampolo. (Photograph taken by Achille P. Raselimanana.)

Table 3. Cranial and dental measurements (in mm) of *Myzopoda* spp. Samples are of adults and divided between eastern and western localities. Descriptive statistics presented as mean \pm standard deviation, minimum–maximum, *n*. No significant differences were found between the two geographic samples based on *t*-Test comparisons.

	Occipito-nasal length	Greatest zygomatic breadth	Interorbital breadth	Mastoid width	Greatest Braincase breadth	Lacrimal width
<i>Myzopoda schliemannii</i>						
Holotype FMNH 177327	14.9	11.7	4.1	9.8	8.8	5.9
Combined samples	15.1 \pm 0.23 14.9–15.5, <i>n</i> = 6	11.5 \pm 0.13 11.4–11.7, <i>n</i> = 5	4.1 \pm 0.08 4.0–4.2, <i>n</i> = 7	9.3 \pm 0.56 8.5–9.8, <i>n</i> = 7	9.0 \pm 0.17 8.8–9.2, <i>n</i> = 4	5.9 \pm 0.10 5.7–5.9, <i>n</i> = 4
<i>Myzopoda aurita</i>						
Holotype MNHN 1997.770	15.2	11.8	4.0	9.6	9.0	5.9
Combined samples	15.3 \pm 0.42 14.6–16.2, <i>n</i> = 22	11.7 \pm 0.36 11.2–12.3, <i>n</i> = 16	4.2 \pm 0.17 3.9–4.5, <i>n</i> = 23	9.5 \pm 0.56 8.6–10.3, <i>n</i> = 21	8.9 \pm 0.21 8.6–9.2, <i>n</i> = 14	5.9 \pm 0.19 5.4–6.1, <i>n</i> = 16
	C ¹ –C ¹	C ¹ –M ³	Upper molariform	Width M ³	Mandible length	
<i>Myzopoda schliemannii</i>						
Holotype FMNH 177327	4.0	5.9	4.3	2.0	11.0	
Combined samples	3.8 \pm 0.14 3.6–4.0, <i>n</i> = 7	5.9 \pm 0.19 5.6–6.1, <i>n</i> = 7	4.2 \pm 0.12 4.0–4.3, <i>n</i> = 4	1.8 \pm 0.08 1.7–2.0, <i>n</i> = 4	11.3 \pm 0.28 11.0–11.8, <i>n</i> = 7	
<i>Myzopoda aurita</i>						
Holotype MNHN 1997.770	3.9	5.9	4.1	1.8	11.6	
Combined samples	3.9 \pm 0.16 3.6–4.1, <i>n</i> = 24	6.0 \pm 0.14 5.7–6.2, <i>n</i> = 24	4.2 \pm 0.12 4.0–4.5, <i>n</i> = 15	1.8 \pm 0.08 1.7–2.0, <i>n</i> = 16	11.6 \pm 0.36 11.0–12.6, <i>n</i> = 19	

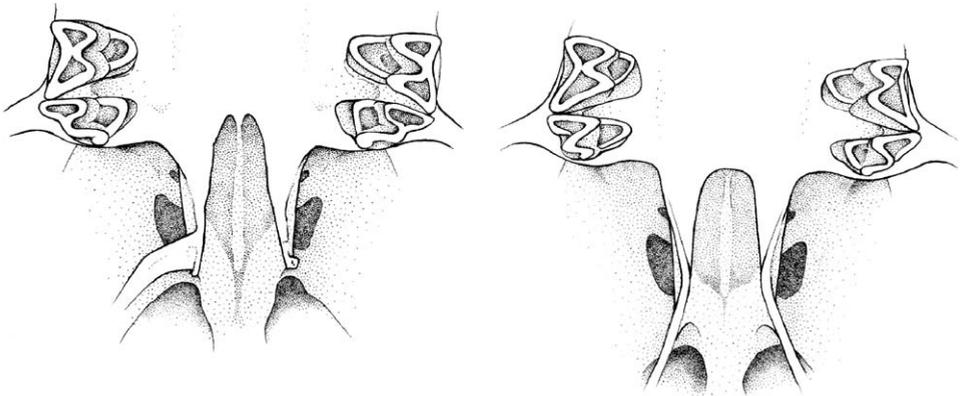


Fig. 4. Views of the palatine foramen in (left) *Myzopoda schliemanni* (Holotype FMNH 177327) and (right) *M. aurita* (FMNH 179273). The difference in the foramen shape in these two specimens is consistent between the two species. The left pterygoid (as viewed here) of *M. schliemanni* is broken and bent laterally and the right one is completely missing. (Drawing by Rebecca Kramer.)

1948, the late Harry Hoogstraal found this species in a *Ravenala* leaf in southeastern Madagascar, in this case a young uncoiled one (Schliemann and Goodman 2003; field catalogue in the FMNH), and although numerous field researchers have subsequently searched the leaves of this plant for *Myzopoda*, this is the only direct observation of which we are aware to support this association. Captive individuals readily climb up *Ravenala* leaves (Göpfert and Wasserthal 1995).

An interesting plant–bat relationship occurs in the genus *Thyroptera*, a member of the New World family Thyropteridae, that shows remarkable parallel development of suction discs on the wrists and ankles as found in *Myzopoda*. *Thyroptera*, composed of three distinct species, are known to use their suckers to grip the slick leaves of *Heliconia* (Family Musaceae) and *Calathea* (Family Marantaceae), which they use as day roosts in often heavily degraded forest (Findley and Wilson 1974; Vonhof and Fenton 2004). Analyses of the functional morphology of these appendage structures and molecular studies of the phylogenetic relationships of *Thyroptera* and *Myzopoda* (Schliemann 1970, 1971; Teeling et al. 2005) reveal that these remarkable adaptations are convergent between the two genera. Even though there is only one direct published observation of

Myzopoda roosting in *Ravenala* leaves, context and inference would imply that the axiom about the association of this bat and plant is correct. Thus, we assume that the preferred natural day roost sites of *Myzopoda* are plants with broad and smooth leaves, such as *Ravenala* or other plants such as *Pandanus* (Family Pandanaceae), certain species of palms and ferns, introduced *Musa* (Family Musaceae), and *Typhonodorum* (Family Araceae).

For the specimens of *M. aurita* obtained in the eastern biome and for which we have details on the specific situation where they were captured, the majority were within or close to stands of *Ravenala* and generally at elevations below 50 m. In a vast portion of the east, from at least Vangaindrano to Maroantsetra, much of the former extensive lowland forests have been cleared and dense stands of *Ravenala* are the dominant pioneering species in the resulting secondary habitat. *Myzopoda* has been recorded in this zone at several different sites and based on extrapolation presumably has a broad distribution in heavily degraded lowland eastern areas, particularly those dominated by *Ravenala*. Our records of *Myzopoda* from western Madagascar are associated with locally mesic conditions and for most cases in close proximity to *Ravenala* or other plants with broad and smooth leaves. The holotype of

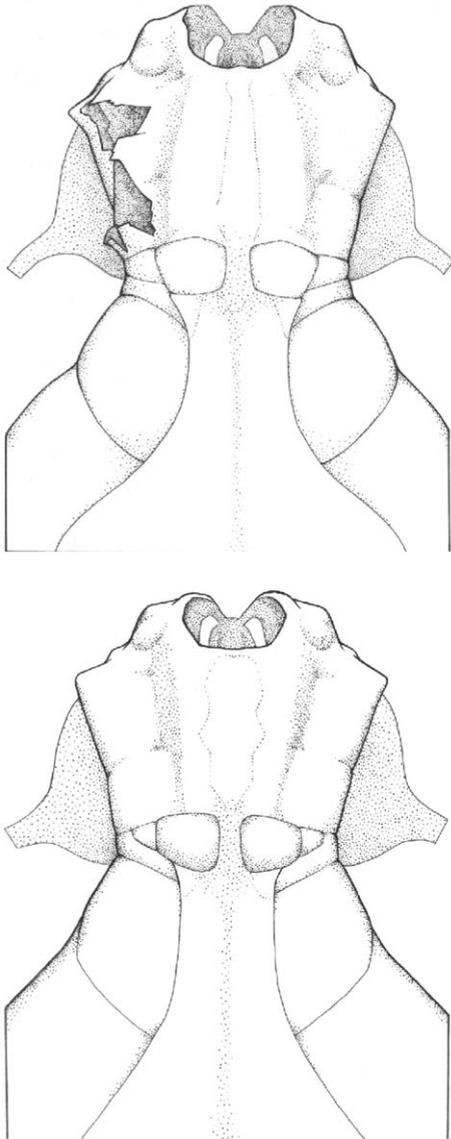


Fig. 5. Views of the upper rostrum in (left) *Myzopoda schliemanni* (Holotype FMNH 177327) and (right) *M. aurita* (FMNH 179273). The differences in the nasal sulcus, nasal shape and frontals in these two specimens are consistent between the two species. (Drawing by Rebecca Kramer.)

M. schliemanni was captured in a mist net at the edge of a marsh, near the Station Forestière d'Ampijoroa, which included *Ravenala* and *Raphia* palms, albeit the former

not a common member of the local plant community. The Ankaboka sites where this species was netted contain highly degraded lowland areas and the animals were captured over streams in gallery forest. Although *Ravenala* was not specifically noted in this zone, it can be found in the general vicinity. Finally, at Namoroka both specimens were captured by hand while roosting in a cave (Kofoky et al. 2006) and an additional individual was netted over a stream in a mixed marsh woodland area. The habitat immediately surrounding the cave site was dry deciduous forest, and about 750–1000 m deeper in the forest was a permanent river system with *Raphia* palms and large strap-leaf *Pandanus*. A third individual captured at Namoroka and released was obtained in habitat heavily modified by human activities and included an extensive marsh system with *Raphia*, *Pandanus* and a few examples of *Ravenala*, and mango trees on slightly higher ground.

The holotype of *M. schliemanni* was obtained on 18 April and had notably large deposits of yellow sub-cutaneous fat. Further, the testicles were scrotal, measured 5×3 mm, and the epididymides were convoluted. The scrotum coloration was noted as being, “dull yellow with dark spots”. Amongst the four specimens obtained at Ankaboka in early June there was one sub-adult with an unossified skull and partial non-permanent dentition. One of the animals handled at Namoroka in mid-October was a female with developed mammae. Nothing definitive can be stated about the reproductive season in this species, but it would appear that it is not confined to a narrow period of the year.

Several male specimens of *M. aurita* were noted as having scrotal testes, including one individual on 14 March in which they measured 4×3 mm and individuals on 14 April and 24 May that measured 5×4 mm and with convoluted epididymides. Thus, it would appear that reproductive males retain their testicles in a descended position for at least 3 months per year.

In two cases of male *M. aurita* with enlarged testes it was recorded in the field catalogue that the scrotum was “light beige in coloration with black spots around testicles”. It has

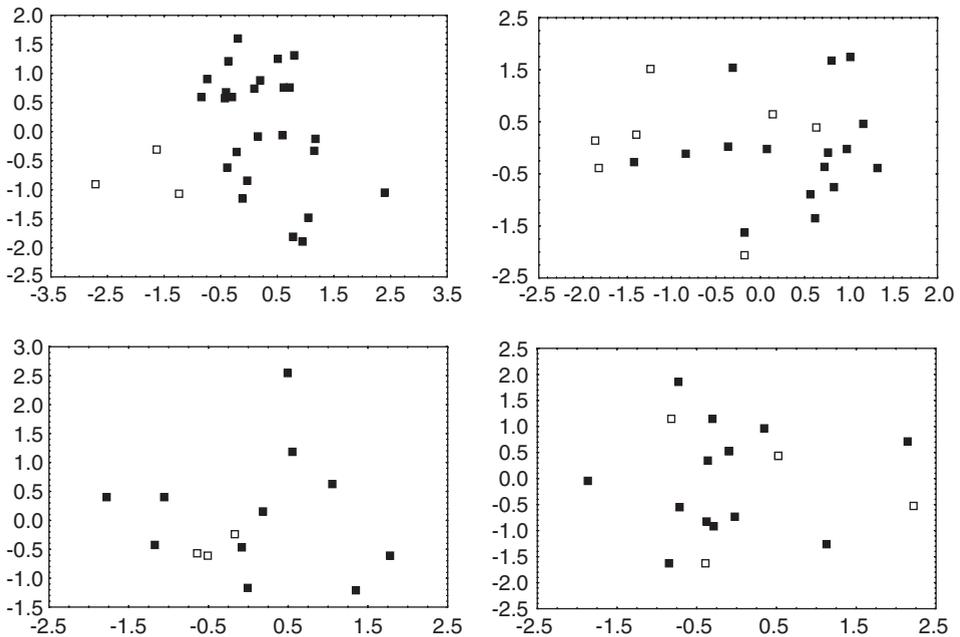


Fig. 6. Projection of factor 1 (x-axis) and factor 2 (y-axis) in principal component analysis of external (upper left), wing bone (upper right), cranial (lower left) and dental (lower right) measurements of *Myzopoda aurita* (black squares) and *M. schliemanni* (light squares). Loading contributions of variables to each axis are shown in Table 4.

already been noted in the literature that male Myzopodidae have pigmented portions of their external sexual organs (Kermott and Timm 1988), which in this case was scattered dark brown pigment to the tunica vaginalis surrounding the epididymis. The function of the colored testicular pouch is uncertain, but may be associated with thermoregulation, visual communication, or a shield against ultraviolet radiation. Given that the pigmentation in *Myzopoda* forms an irregular pattern, rather than being equally distributed across the scrotal region and seems confined to adult males in breeding condition, this would indicate a probable social communication function, rather than related to temperature regulation or a radiation shield.

Discussion

Given the putative association mentioned above between *Ravenala* and *Myzopoda*, we

examine this relationship in finer detail to understand potential speciation mechanisms in *Myzopoda*. Blanc et al. (2003) indicated that the upper elevational limit of *Ravenala* is somewhere between 1000 and 1100 m. The results of elevational transects of plant communities in the eastern humid forests are concordant with this assessment. *Ravenala*, as a member of non-disturbed forest, drops out between 800 and 1000 m, and this pattern is relatively consistent across the 12° latitudinal range of the eastern forests (Lewis et al. 1996; Messmer et al. 2000). However, *Ravenala* can be found in isolated patches, particularly in wet valley bottoms associated with degraded habitats (*savoka*), up to about 1300 m (Humbert 1965). This plant is common along the complete length of the eastern lowland area, with a distinctly more clumped distribution in drier zones at the northern end of the island near Antsiranana, where it can be found in wet valley bottoms, and then west to the Sambirano region near Ambanja, and then becomes distinctly less common

Table 4. Factor loadings of principal component analysis for a series of analyses of *Myzopoda* spp. Graphic presentations of these comparisons are given in Fig. 6.

Variable	Factor 1	Factor 2
External measurements		
Total length	0.748	-0.125
Tail length	0.475	-0.676
Hind foot length	0.261	0.850
Ear length	0.824	0.051
Forearm length	0.855	0.145
Eigenvalues	2.27	1.22
% total variance	45.3	24.4
Wing bone measurements		
3rd digit - metacarpal	0.926	0.247
3rd digit - 1st phalanx	0.438	0.607
3rd digit - 2nd phalanx	0.219	0.833
3rd digit - 3rd phalanx	0.646	-0.071
4th digit - metacarpal	0.917	0.243
4th digit - 1st phalanx	0.551	0.474
4th digit - 2nd phalanx	-0.127	0.853
5th digit - metacarpal	0.920	0.043
5th digit - 1st phalanx	0.280	0.702
5th digit - 2nd phalanx	0.046	0.866
Eigenvalues	3.60	3.32
% total variance	36.0	33.2
Cranial measurements		
Occipitonasal length	0.950	-0.125
Greatest zygomatic breadth	0.791	0.372
Interorbital breadth	0.067	0.987
Mastoid width	0.775	0.472
Lacrima width	0.842	0.203
Eigenvalues	2.84	1.39
% total variance	56.9	27.8
Dental measurements		
Anterior palatal width	0.533	0.429
Maxillary tooththrow	-0.046	0.906
Upper molariform tooththrow	0.396	0.510
Width M ³	0.908	-0.048
Eigenvalues	1.28	1.27
% total variance	31.7	31.7

along the west coast south to at least Namoroka. On the basis of our joint bat inventory data in humid forests of the east, using direct capture and acoustic sampling, the highest elevation *Myzopoda* has been recorded is at around 970 m, in the vicinity of Andasibe. Thus, there is considerable concordance between the upper altitudinal limits

in the eastern biome of *Ravenala* and *M. aurita*.

Given the considerable morphological similarity between *M. aurita* and *M. schliemanni*, and the fact they are the only members of this endemic genus, it is assumed that one of the two represent a speciation event after dispersal. Further, given their apparent propensity for roosting in *Ravenala*, which is notably more common in the east than the west, we assume that the species group originated in the east and then dispersed to the west. (However, a priori the dispersal event and subsequent speciation could have been in the opposite direction.) Here, we propose two different scenarios on how this event may have taken place.

The first hypothesis is dispersal directly across the Central Highlands, for example, at the latitudinal level of Antananarivo (Fig. 1). This seems unlikely given that this zone rises notably higher than 1000 m and the east-west hiatus of several hundred kilometers for even moderate size patches of *Ravenala* habitat. However, one cannot rule out a hypothesis of cataclysmic dispersal, such as cyclone winds that physically blew the animals across the Central Highlands.

The second hypothesis is an east to west dispersal event across the region falling between the Central Highlands and Northern Highlands, which comprises a vast zone with potential corridors of less than 1000 m in elevation (Fig. 1). Across the northern portion of central Madagascar, in the zone linking Toamasina and Mananara on the east coast to Mahajanga on the west coast, *Ravenala* is patchy in its distribution and hence stepping-stone dispersal across this region is plausible.

Comparisons between the genera *Myzopoda* and *Thyroptera* show a remarkable number of convergent parallels in certain morphological adaptations and aspects of reproduction. It would appear that females of *T. tricolor* are polyoestrous, with perhaps two breeding cycles per year, and that adult males have multiple spermatogenic rounds or produce sperm continuously (Wimsatt and Enders 1980; Krutzsch 2000). Further, *T. tricolor* is known to have a complex social system (Vonhof et al. 2004). Members of this

genus also have relatively complex geographical ranges (Gregorin et al. 2006). Given all of the interesting repeated convergent patterns between *Myzopoda* and *Thyroptera*, research on the natural history and reproductive system in the former genus is almost certain to uncover some fascinating details.

On the basis of limited information, *M. schliemanni* lives in portions of the central lowland west where there are relatively mesic conditions, associated with marshes, rivers or transitional humid-dry forests. Although two of the three sites this species is known from are protected areas (Parc National d'Ankarafantsika and Parc National de Namoroka), it appears, based on our inventory work, to be sparsely dispersed in the central western portions of the island (Goodman et al. 2005). The forest habitat at the Ankaboka sites, as well as one of the two sites at Namoroka, were notably disturbed by human activities and by extrapolation this species appears to be resilient to certain levels of anthropogenic perturbation. Across its known range, measuring about 300 km in length, there is considerable non-continuous habitat similar to sites in which it has been found, and we suspect that the threats to this species' long-term existence are not notably severe.

In their assessment of the conservation status of the world's Microchiroptera, Hutson et al. (2001) considered *M. aurita* to be a species of special concern, largely associated with it being the sole member of an endemic family and that little information was available about its distribution. Over the course of the past decades, largely as a result of biological inventories, we now know that this species is more broadly distributed than previously realized and inhabits areas of extensive secondary habitats of *Ravenala*. While it is true that *M. aurita* is currently only known from in or around three protected areas (Parc National de Marojejy, Parc National de Masoala and Réserve Spéciale d'Andasibe; Pont and Armstrong 1990; Russ et al. 2001; Schliemann and Goodman 2003; Tab. 1), inferred levels of threat may be less severe than previously assumed given its ability to live in highly disturbed areas. Finally, based on the description of a

second species of *Myzopoda* herein, the family Myzopodidae is no longer monospecific and the sole family of bats with this level of uniqueness in the world is the Craseonycteridae.

The discovery of *M. schliemanni* and new information on the distribution and conservation status of *M. aurita* are based on recent survey work. In a few years considerable progress has been made on numerous aspects of the chiropteran fauna of the island. This underlines the importance of basic scientific research for establishing the priorities for conservation programs and assessments of presumed rare and possibly endangered animals.

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Zusammenfassung

Beschreibung einer neuen Art von *Myzopoda* (Myzopodidae: Chiroptera) von West-Madagaskar

Die Myzopodidae, eine endemische Familie von Fledermäusen auf Madagaskar, galt bisher als monospezifisch. In Madagaskar wurde eine neue Art, *M. schliemanni*, gefunden. Diese Art aus den Trockenwäldern West-Madagaskars unterscheidet sich in der Fellfärbung, externen morphologischen Maßen und Schädelmerkmalen von *M. aurita*, der bisher einzig beschriebenen Art der Familie. *Myzopoda aurita* ist aus den immergrünen Regenwäldern des Ostens Madagaskars bekannt. Biogeographische Muster der Verteilung von *Myzopoda* und ihre enge Assoziation mit dem "Baum des Reisenden (*Ravenala madagascariensis*; Strelitziaceae)" werden in Zusammenhang mit Speziationsmechanismen diskutiert, die zur Entstehung der westlichen und östlichen Art beigetragen haben.

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