

THE MALE NUPTIAL CHARACTERISTICS OF *ARTHROLEPTIDES*
MARTIENSSENI NEIDEN, AN ENDEMIC TORRENT FROG FROM TANZANIA'S
EASTERN ARC MOUNTAINS

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Recent field work in the Udzungwa Mountains of Tanzania has resulted in the discovery of the hitherto unreported nuptial characters of male *Arthroleptides martiensseni* which are described and illustrated in this contribution. These newly described characters are compared with the nuptial characters of male *Arthroleptides dutoiti*, a supposedly extinct species from Mount Elgon (Kenya) as well as with members of the West African genus *Petropedetes*, which exhibit some remarkable morphological and ecological similarities with *Arthroleptides martiensseni*.

INTRODUCTION

The montane rainforests of Cameroon and Tanzania contain a remarkable diversity of anurans, characterized by a high degree of endemism (Perret, 1966; Howell, 1993; Lawson, 1993). Two genera, *Petropedetes* (Reichenow, 1874) and *Arthroleptides* (Neiden, 1910) contain species that are highly specialized for living on wet cliff faces, often in and immediately adjacent to waterfalls and cascades. These adaptations include tadpoles that have evolved a distinctive suite of morphological characters that allow for their development on mossy, wet rock faces, as well as a distinctive "T-shaped" terminal expansion of the digits in adults, which allow these frogs to adhere to the slippery rock surfaces as described by Boulenger (1905) and Loveridge (1925).

Reichenow (1874) described the genus based on *Petropedetes cameronensis* sp. nov. from "Bimbia in the Cameroon foothills." Boulenger (1887) described *Cornufer* (= *Petropedetes*) *johnstoni* from "Rio del Rey, Cameroons District." This description was based on a single, sub-adult male (Amiet, 1983). Subsequently Boulenger (1900) placed *Cornufer johnstoni* in the genus *Petropedetes*. Bocage (1895) described *Tympanoceros* (= *Petropedetes*) *newtonii*, from "Fernaõ do Pó" (= Fernando Po), noting that the large tympanum was "surmonté tout près de son bord supérieur par un tubercule cylindrique." Boulenger (1905) described *P. natator* from "Sierra Leone at 800 feet" and *P. palmipes* from "Efulen, South Cameroon." Ahl (1924) described *P. obscurus* from "Tscharra Dana-Fluss" in Kenya. *P. obscurus* was synonymized with *P. cameronensis* by Perret (1984) who found the two species morphologically indistinguishable, and considered Ahl's Kenya locality data to be erroneous. Amiet (1973) described *P. perreti* from "Nsoung, 1400-1500 m., Cameroon" and *P. parkeri* (Amiet,

1983) from "d'Atolo (région de Mamfé), Cameroon." Six of the eight species of the genus *Petropedetes* occur in the western and southern portions of Cameroon, including Fernando Po. *P. cameronensis* has also been collected in eastern Nigeria, and *P. newtoni* in Equatorial Guinea, which indicates a remarkable center of speciation in the region of the Bight of Biafra (Perret, 1984).

Neiden (1910) described the genus *Arthroleptides* based on *Arthroleptides martiensseni* sp. nov. from "Amani, Deutschostafrika", now Tanzania. This species has a restricted distribution, endemic to the Eastern Arc Mountains of Tanzania, reported from the East and West Usambaras, the Ulugurus, and the Udzungwas (Howell, 1993). Neiden considered *Arthroleptides* to be intermediate between *Petropedetes*, with which it shared the distinctive "T-shaped" terminal phalanges and *Arthroleptis*, with which it shared the absence of vomerine teeth and the reduction of webbing between the toes. The second member of the genus, *A. dutoiti* was described by Loveridge (1935) from two adults (male and female) and an immature specimen from the eastern slopes of Mt. Elgon, Kenya. This species is considered extinct by Baillie & Groombridge (1996). *Petropedetes* and *Arthroleptides* share many morphological and ecological similarities. However, certain members of the genus *Petropedetes* possess a suite of morphological characters unique to breeding males. These include enlarged femoral glands, the presence of a bony, metacarpal projection, tympanic and brachial hypertrophy, and most distinctive, the presence of a nipple-like projection on the tympanum. Perret (1984) summarized the characters of breeding male *Petropedetes*, reporting that the tympanic projection occurred in four of the seven recognized species (i.e. *perreti*, *newtoni*, *parkeri*, and *johnstoni*). Perret also noted that the location of the projection varied by species, from the centre of the tympanum to the upper

margin. An examination of Perret's data also shows that these four species have larger tympani than the three species (i.e. *cameronensis*, *natator* and *palmipes*) that lack tympanic projections. All four species that have tympanic projections also possess a bony, metacarpal projection; however, this character is also shared with *P. palmipes*.

Considerable confusion exists in the literature as to the structure of the tympanic projection, undoubtedly the most distinctive sexually dimorphic character of male *Petropedetes*. This was illustrated by Noble (1931) and by Duellman & Trueb (1994). These authors concluded that the projection was the columella thrust through the eardrum, covered by dermis. Duellman & Trueb (1994) stated that this projection would diminish the vibratory capacity of the tympanum, thereby reducing its sensitivity to high frequencies. However, du Toit (1943) in his anatomical monograph on *Petropedetes* stated that "*Petropedetes* is unique in possessing a seasonal secondary sexual characteristic in the form of a so-called tympanic papilla. The latter, which Noble (1931) mistook for the *pars externa plectri* thrust through the drum is in reality a thickened portion of the outer dermal part of the tympanic membrane." He further explains the structure of the papilla to be quite complex, consisting of epidermal and cutis components, with a concentration of glands, collagenous fibres in its basal portion, a subepidermal pigment layer that is better developed in the papilla than other portions of the tympanum, as well as a superficial cornified layer that is produced into tiny, wart-like asperities. This paper reports the discovery of an equivalent suite of nuptial characteristics in breeding male *Arthroleptides martienseni*, and discusses the taxonomic relationships between *Petropedetes* and *Arthroleptides* in the light of this new discovery.

MATERIALS AND METHODS

In December 1995, an intensive, multi-taxa biodiversity inventory of two sites in the Udzungwa Mountains National Park was conducted at the beginning of the several-month long rainy season. Nine days were spent at a single site at the foot of the Udzungwa Escarpment, along the Mwaya River at 350 m. This locality included a mixture of riverine forest, miombo, and disturbed edge and agricultural habitats near Man'gula village. Nine days were spent at a single upland site (1100-1200 m) along the upper reaches of the Njokomoni River, in primary, undisturbed rainforest. Sampling was conducted in a systematic, repeatable manner. Herpetological samples were collected using 200 meter-long drift fences, with 20-litre buckets (ca. 0.5 m depth) placed at 5 m intervals, and were checked in the morning and evening each day. Hundreds of litter-dwelling amphibians and reptiles, as well as invertebrates and small mammals, were collected using this technique. These were counted to gain a crude measure of relative abundance and, with the exception of a small percentage that were preserved, released.

Additional data were collected by conducting time-constrained transect searches, along trails and river-edge, both during the day and at night; by opportunistic examination of fallen trees and rotten logs; and by making several excavations, to exhume fossorial species.

Specimens were collected to document the diversity of species, and whenever possible, the range in variation, sexual dimorphism, and life history stages of each species of amphibian and reptile found. These voucher specimens were anaesthetized, individually labelled, and fixed in formalin. Tissue samples for DNA analysis were collected prior to fixation, and stored in ethyl alcohol. Colour photographs were taken of selected specimens prior to preservation and tape recordings of frog calls were made. All specimens were exported to the American Museum of Natural History (AMNH) for follow-up identification and study. Preparation of this paper required examining specimens of *Petropedetes* and *Arthroleptides* deposited in both the AMNH and the Natural History Museum (London). As preserved frogs are quite pliable, all measurements reported on Tables 1 and 2 were made with calipers and rounded to the nearest 0.5 mm. Great care was exercised to be consistent in measuring technique, i.e. the application of pressure to the specimen from the caliper's jaws. Unless otherwise noted, the sex of all specimens examined was verified by internal examination through a slit cut through the abdomen wall.

RESULTS AND DISCUSSION

On 8 December 1995, a series of eleven frogs (AMNH 151340-50) was collected at night by the author and A. M. Nikundiwe in primary rainforest, perched on large boulders in cascades on the Njokomoni River, near where the river drops off of the edge of the Udzungwa Escarpment in Tanzania's Udzungwa Mountains National Park, 7°48'57"S, 36°51'15"E, 1100 m. That afternoon the dry weather had broken with an exceptionally heavy thunderstorm. Two of the largest individuals of this series were mature males (AMNH 151342-43). They were quite remarkable in that they possessed several of the distinctive breeding characteristics of male *Petropedetes*, including the unique tympanic projection which was located between the center and upper rim of the tympanum, as well as tympanic and brachial hypertrophy, and a large, metacarpal knob. Although we remained at this location until 16 December, these large adult frogs were found only once, on this single night that had been preceded by heavy rains.

Juveniles and sub-adults were found consistently along the Njokomoni River, up to its headwaters at 1200 m. During the day they remained hidden under stones along the river bank; at night they were active on the forest floor and in the river, and one was found perched in a small tree 1 m above the ground. Several voucher specimens were collected along the length of the river (AMNH 151351-55). A single sub-adult

TABLE 1. Measurements/nuptial characters of *Arthroleptides martiensseni* from the Eastern Arc Mountains of Tanzania. 0, not present; 1, weakly developed; 2, strongly developed; ?, data not available. AMNH, American Museum of Natural History, New York; BM, Natural History Museum, London; KMH, Kim Howell field series (to be deposited at the Natural History Museum, London).

(1) MALES								
Museum No.	Length (mm)	Papilla	Metacarpal knob	Tympanic hypertrophy	Brachial hypertrophy	Chin+ gular spines	Femoral glands	Month collected
AMNH 151342	73	2	2	2	2	2	not visible	12
AMNH 37281	58.5	2	2	2	2	2	? visible	09
AMNH 151343	55	2	2	2	2	0	not visible	12
KMH 13571	52	1	2	1	0	0	not visible	07
BM 1982.543	43	0	?	0	0	0	not visible	01
AMNH 151347	42	0/1	0/1	0/1	0	0	not visible	12
AMNH 151339	41.5	0	0/1	0	0	0	not visible	12
BM 1994.794	39	0	?	0/1	0	0	not visible	?
BM 1980.363	38	0	?	1	0	0	not visible	10
BM 1994.647	37.5	0	?	0/1	0	0	not visible	10
BM 1974.57	37	0	?	1	0	0	not visible	10
BM 1994.795	36	0	?	1	0	0	not visible	?
BM 1974.58	33.5	0	?	1	0	0	not visible	10

(2) FEMALES								
Museum No.	Length (mm)	Papilla	Metacarpal knob	Tympanic hypertrophy	Brachial hypertrophy	Chin+ gular spines	Femoral glands	Month collected
BM 1986.483	60	0	?	0/1	0	0	not visible	10
AMNH 151341	58	0/1	1	1	0	0	not visible	12
BM 1980.199	58	0	?	1	0	0	not visible	11
AMNH 151344	57	0	1	1	0	0	not visible	12
AMNH 151345	57	0	1	1	0	0	not visible	12
BM 1982.542	55.5	0	?	1	0	0	not visible	01
BM 1994.719	50	0	?	0/1	0	0	not visible	?
AMNH 151340	42.5	0/1	0/1	0/1	0	0	not visible	12
AMNH 151346	39.5	0/1	0/1	0/1	0	0	not visible	12
AMNH 151355	39	0	0	0/1	0	0	not visible	12

specimen was collected at a lowland site, in riverine forest, at the foot of the Udzungwa Escarpment, in the Udzungwa Mountains National Park, Man'gula Camp Site No. 3 on the Mwaya River, 7°50'51"S, 36°53'00"E, 350 m (AMNH 151339).

Initially, these specimens were identified as *Petropedetes* based on the morphology of the breeding males. However, upon comparison with specimens at the Natural History Museum (London) it became apparent that these were referable to *Arthroleptides martiensseni*. In his anatomical study of *Arthroleptides dutoiti*, du Toit (1938) examined a presumably mature male of 25 mm (the type specimen is a gravid 31 mm female) and although making note of some unusual features, such as the "*annulus tympanicus* has an additional ventromedially directed process not met with in other forms", makes no reference to any tympanic projections. How had such a distinctive anatomical feature of *Arthroleptides martiensseni* escaped detection for nearly a century? Examination of

the extensive Tanzanian holdings of the Natural History Museum began to shed some light on this puzzle. Juvenile and sub-adult *Arthroleptides* were well represented in this collection, as were adult females, but large males were absent (see Table 1).

The largest male in the Natural History Museum collection was an uncatalogued specimen, K.M. Howell Field Number 13571, collected during the early dry season on 29 July 1996 in the Mtai Forest Reserve, Tanzania (38°46'E, 4°51'S), measuring 52 mm snout-urostyle length. The left tympanum was slightly hypertrophic with a tiny tympanic projection. The right tympanum showed no signs of hypertrophy or tympanic projection. The secondary sexual characteristics of this specimen were so subtle, they could easily be overlooked. This contrasts markedly with AMNH 151343, measuring 55 mm snout-urostyle length, but collected at the beginning of the rainy season. This specimen had well-defined tympanic papillae and hypertrophied tympani surrounded by a raised ring of

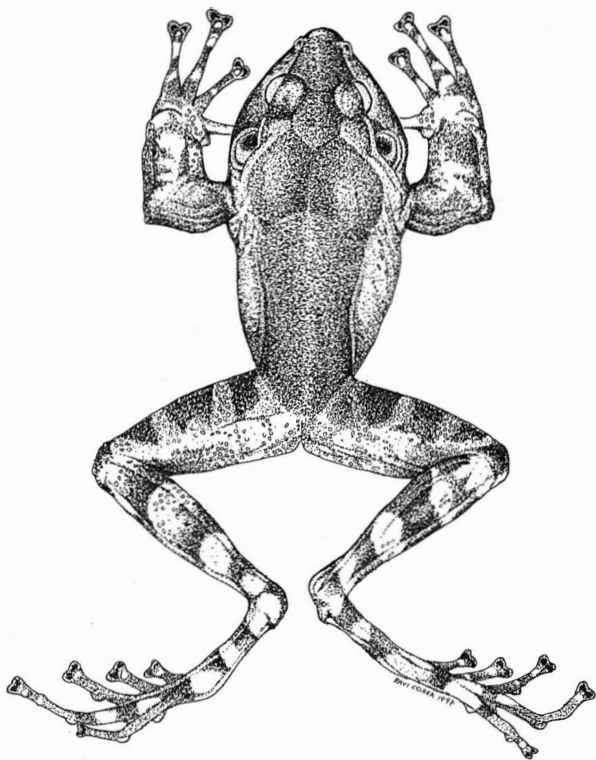


FIG. 1. Dorsal view of AMNH 151342 (M.W. Klemens Field No. 11003), *Arthroleptides martiensseni*, illustrating the distinctive nuptial characteristics of the breeding male. Note the variation in shape of the tympanic papilla. (x 0.75).

knobs. Brachial hypertrophy was also well-developed in this specimen as was the metacarpal knob.

The most spectacular development of these secondary sexual characteristics are found on AMNH 151342 (Figs. 1 & 2). This specimen measures 73 mm snout-urostyle length, far larger than any specimen reported in the literature. It has well-developed, strongly protruding tympanic papillae; the papilla on the right tympanum has a curved surface, whereas the papilla on the left tympanum is distinctly squared-off. The tympani are hypertrophied, both surrounded by a ring of knobs. There are well-defined spines on the chin and throat and the forelimbs exhibit marked brachial hypertrophy. There is a strongly protruding metacarpal knob. Another specimen, a 58.5 mm male collected by Arthur Loveridge in the Uluguru Mountains on 19 September 1926 (AMNH 37281) exhibits all the distinctive characteristics of AMNH 151342 but, due to the extremely soft preservation, accompanied by some minor tissue

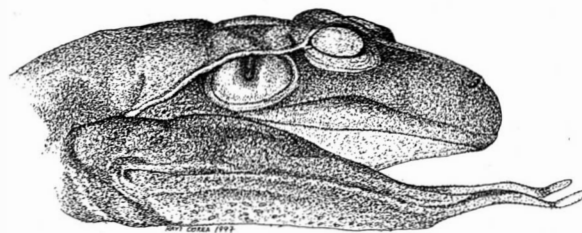


FIG. 2. Lateral view of AMNH 151342 (M.W. Klemens Field No. 11003), *Arthroleptides martiensseni*, illustrating the squared-off tympanic papilla referred to in the text. (x 1.5).

deterioration, the presence of what appear to be a pair of deeply imbedded femoral glands were noted.

I also examined a series of eight *Arthroleptides dutoiti* collected by R. Keith on 6 April 1962 (except AMNH 68677 collected on 17 May 1962) along the Suan River, NE Mt. Elgon, Kenya, 7000 feet (AMNH 68670-77). Two of these were quite small and presumed to be juveniles. The remaining six specimens could be divided into two morphologically distinct groups. As this species is presumed to be extinct, and these specimens irreplaceable, their sex was not verified by dissection. Three frogs (AMNH 68672-73, 68675) range from 23.5-25.5 mm snout-urostyle length. They possess none of the distinctive breeding characteristics of male *A. martiensseni*, however all three of these specimens possessed large, conspicuous femoral glands (see Table 2) and are presumed to be males. The remaining three specimens (AMNH 68670-71, 68677) are larger (i.e. 30-31.25 mm snout-urostyle length). They do not possess any of the distinctive breeding characteristics of male *A. martiensseni*, nor any trace of femoral glands and are presumed to be females. The ventral colouration varies markedly between these two groups. The females have a strongly marbled violet/black and grey/white ventral pattern, which is consistently uniform from head to thigh. The males have a weaker pattern, strong on the thighs, but dissipating on the venter, and becoming very weak in the gular region. Loveridge (1935) made no reference to the presence of enlarged femoral glands on his single male paratype. Possibly he overlooked these glands, but as Loveridge had a keen eye, I suspect that it is more likely that the male paratype was not in full breeding condition. Loveridge's male paratype measured 25 mm and the type, a gravid female, measured 31 mm.

TABLE 2. Measurements of presumed male *Arthroleptides dutoiti* from Mt. Elgon, Kenya. All measurements in mm.

Museum Number	Length	Right thigh	Right femoral gland	Left thigh	Left femoral gland
AMNH 68675	23.5	13.5	6.5	13.5	7.0
AMNH 68672	25.5	12.5	6.0	12.5	6.5
AMNH 68673	25.5	13.0	6.5	13.5	7.0

Both these specimens, as well as a 10.5 mm juvenile paratype, were collected on 8 January 1934. Loveridge noted differences in ventral colouration which do not agree with my observations on the AMNH series, stating that "below and posterior aspect of thighs light violet brown slightly flecked with white in the type, rather more abundantly flecked and mottled in the paratypes."

CONCLUSIONS

Mature *Arthroleptides martiensseni* males possess many of the same secondary sexual characters that were considered unique to *Petropedetes*. These include the presence of a tympanic papilla, brachial and tympanic hypertrophy, an enlarged metacarpal knob, and spines on the chin and gular region. In fact, *Arthroleptides martiensseni* bears more than a superficial resemblance to *Petropedetes parkeri* as described by Amiet (1983). Breeding males of both species are characterized by rudimentary digital webbing; larger body size than females; gular granulations topped with a tiny, dark spine; cutaneous spinosity, especially in the area between the tympanum and the forelimbs; marked brachial hypertrophy; large tympanum with papilla located toward the top of the tympanic rim; metacarpal knob; and reduced (possibly absent in the case of *A. martiensseni*) femoral glands. Breeding male *A. dutoiti* do not resemble *A. martiensseni*. However, they share, with breeding males of several species of *Petropedetes*, a prominent, enlarged femoral gland.

The marked similarities in both morphology and ecology of these two genera of specialized frogs, their distribution in the western and extreme eastern portions of the equatorial African rainforest bloc, and the apparent absence of any similar taxa in between raises many interesting biogeographical and evolutionary questions which remain to be resolved. Although it is premature to extrapolate from these data, a systematic analysis of the relationships between the various constituent taxa of *Petropedetes* and *Arthroleptides* is fertile ground for future investigation. These frogs may all be referable to *Petropedetes*, with *parkeri* and *martiensseni* sharing a close relationship, i.e. they may be sister-taxa. *Arthroleptides dutoiti* closely resembles *Petropedetes cameronensis*, warranting a re-evaluation of Perret's (1984) synonymy of *Petropedetes obscurus* and re-examination of Ahl's syntypes, as Perret may not have considered the possibility that Ahl's specimens were *Arthroleptides* (this possibility only became apparent after I had returned Ahl's syntypes to Berlin). The need for additional herpetological inventory across the African rainforest bloc should be a high priority, not only for basic scientific knowledge, but to develop a scientifically-informed strategy for designating priority areas for conservation within this vast expanse of rainforest, second in size only to Amazonia. Possibly the "missing link" that will bridge the gap between the torrent frogs of west and east Africa awaits discovery behind a waterfall on an as-of-yet unexplored inselberg in the Congo basin.

ACKNOWLEDGMENTS

Field work in the Udzungwa Mountains National Park was part of a joint biodiversity program between the Wildlife Conservation Society (New York), Tanzania National Parks (TANAPA), and the University of Dar es Salaam. Specimens from these surveys are held at the American Museum of Natural History with duplicates on long-term loan from the Department of Zoology and Marine Biology, University of Dar es Salaam, Tanzania. Research was conducted under clearance provided through the offices of the Tanzanian Commission for Science and Technology (COSTECH) and the Serengeti Wildlife Research Institute. For their companionship and assistance in the field I am most grateful to Professor A.M. Nikundiwe, Mr. P. Kihale, Mr. S. Chuwa, and Mr. Agricola, as well as the logistical support and encouragement provided by Dr. P. Moehlman.

For fruitful discussions, and access to both specimen and bibliographic collections, I am most grateful to Dr. B. Clarke and Professor J. Poynton (Natural History Museum, London), Dr. L. S. Ford and Dr. C. W. Myers, Ms. M. G. Arnold, Ms. R. Johnston, Mr. D. Dickey, and Mr. T. Trombone (American Museum of Natural History). Dr. R. Günther of the Museum für Naturkunde, Berlin allowed me to borrow the syntypes of *Petropedetes obscurus* and provided important information concerning Neiden's type material. Mr. J. Buskirk translated several of the important *Petropedetes* papers that are cited and Mr. R. Corea prepared Figs 1 and 2. Financial support for this research was provided by the Bay Foundation and the John D. and Catherine T. MacArthur Foundation.

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Accepted: 28.7.97