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Morphological Assessments and Phylogenetic Relationships of the Seychellean Frogs of the Family Sooglossidae (Amphibia: Anura)

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Ronald A. Nussbaum and Sheng-Hai Wu (2007) Morphological assessments and phylogenetic relationships of the Seychellean frogs of the family Sooglossidae (Amphibia: Anura). *Zoological Studies* **46**(3): 322-335. The frog family Sooglossidae is endemic to the Seychelles Is. in the Indian Ocean, and consists of 2 genera and 4 species, the monotypic *Nesomantis* and *Sooglossus* (3 species). Many previous studies have suggested that *Sooglossus sechellensis* is more similar to *Nesomantis thomasseti* than to its congener, *S. gardineri*. Based on an extensive dataset of 188 morphological characters, we concluded that *Nesomantis* and *S. sechellensis* form a monophyletic group with the exclusion of *S. gardineri* (and *S. pipilodryas*). We therefore have established a new genus, *Sechellophryne*, to accommodate the latter 2 species.
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Key words: *Nesomantis thomasseti*, *Sooglossus gardineri*, *Sooglossus pipilodryas*, *Sooglossus sechellensis*, *Sechellophyrne* gen. nov.

The granitic Seychelles Is. lie in the western Indian Ocean between 4° and 5°S latitude and 55° and 56°E longitude, about 1600 km east of Africa (Mombasa), 926 km northeast of Madagascar (Antsiranana), and 2900 km southwest of India (Mumbai). These islands have fascinated biogeographers and geologists since the late 19th century when Darwin (1859) and Wallace (1880) pointed out that they are continental in character in spite of their great distance from large continental blocks.

Among the unusual features of the Seychelles is the presence of endemic amphibians. Wallace (1880) recognized amphibians as a group with very limited means of transoceanic dispersal, and their presence in the Seychelles was an important factor that prompted him to classify the Seychelles as "continental" as opposed to "oceanic" islands. However, the means by which amphibians and other sedentary groups may have populated the granitic Seychelles remained mysterious until the late 20th century when continental drift gained respectability, and the formation of the western Indian Ocean through the breakup of Gondwanaland began to be understood.

The amphibian fauna of the Seychelles consists of 13 species (6 caecilians and 7 frogs), 12 of which are endemic. The single non-endemic species, the ranid frog, *Ptychadena mascareniensis*, is widespread in sub-Saharan Africa, Madagascar, and the Mascarene Is. It may have been introduced to the Seychelles by humans (Mertens 1934, Vences et al. 2004, but see Nussbaum 1984).

The 6 species of caecilians (in 3 endemic genera) in the Seychelles are monophyletic (Nussbaum and Ducey 1988, Haas et al. 1993, Hedges and Maxson 1993, Nussbaum unpubl. data), and molecular data (Haas et al. 1993) suggest that the lineage has been present in the Seychelles for at least 30 million yrs. Wilkinson et al. (2002 2003) suggested that the nearest relative

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of Seychellean caecilians is the Indian genus *Gegeneophis*.

Of the 6 endemic species of frogs, *Tachycnemis seychellensis* belongs to a monotypic (Nussbaum and Wu 1995) hyperoliid genus. It is placed either in a monotypic subfamily (Tachycneminae) (Channing 1989), sister to the remaining hyperoliids or to the Malagasy *Heterixalus* (Frost et al. 2006).

The remaining 4 Seychellean frogs constitute the 2 genera of *Nesomantis* (*thomasseti*) and *Sooglossus* (*gardineri*, *pipilodryas*, and *sechellensis*) of the endemic family, the Sooglossidae. At the time of their discovery at the end of the 19th century, the sooglossids were assigned to the families Ranidae and Bufonidae. Noble (1926) placed them together as a distinctive group of the Pelobatidae, which he later (Noble 1931) formally named the Sooglossinae; but this was viewed with skepticism based on biogeographic considerations (e.g., Darlington, 1957).

Griffiths (1963) defined the family Sooglossidae and placed it among the ranoids, and this was accepted by most subsequent authors (e.g., Savage 1973, Duellman 1975). However, other phylogenetic hypotheses also abound, mainly as the result of using different characters and species (as a myobatrachid: Lynch 1973, Nussbaum 1979 1980, Duellman and Trueb 1986, Ford and Canatella 1993; as a leptodactylid: Laurent 1975, Tyson 1987; as a group including dendrobatids and microhyloids: Blommers-Schlösser 1993; as basal to the Hyloidea: Hoegg et al. 2004; as basal in the Hyloides: Frost et al. 2006; as basal to the ranoids: Tyler 1985; or as a sister to the recently described Indian Nasikabatrachidae: Biju and Bossuyt 2003).

Although the phylogenetic position of the sooglossids is unresolved, Noble's (1926) contention that they are monophyletic has not been refuted (Griffiths 1959 1963, Nussbaum 1979 1980 1982, Tyler 1985, Green et al. 1988).

It appears that the classification of the 3 species (prior to the description of *S. pipilodryas*) did not accurately reflect their phylogenetic relationships. Comparisons of chromosomes (Nussbaum 1979), advertisement calls (Nussbaum et al. 1982), and isozymes (Green et al. 1988) all suggested that *Sooglossus gardineri* is the most divergent species and that it, and not *Nesomantis thomasseti*, should be placed in a separate genus. This conclusion, based on phenetics, needs to be confirmed using cladistic methods.

The purposes of this paper were to (1) use a cladistic methodology applied to a broad morphological database to confirm or refute the monophyletic status of the sooglossids; and (2) determine the cladistic relationships within the family.

Taxonomic history

Boettger (1896) described the first sooglossid as *Arthroleptis sechellensis*, thereby assigning the species to a group of African ranids. Boulenger (1906) transferred *Arthroleptis sechellensis* to a new genus, *Sooglossus*, on the basis of tongue morphology (entire and elliptical), but retained the species among the ranids. Boulenger (1909) described *Nesomantis thomasseti* as a new frog genus and species from Mahé I., Seychelles. He wrote that *Nesomantis* is allied to *Sooglossus*, but unlike the latter genus, *Nesomantis* has vomerine teeth and lacks a claw-like, dermal tip to the digits. Boulenger viewed *S. sechellensis* as a dwarf *Nesomantis*. He did not comment on its relationships to other frogs, although he apparently assumed it was a ranid close to *Arthroleptis* and other African ranoids. Shortly afterwards, Boulenger (1911) described a 3rd Seychellean frog as *Nectophryne gardineri*, believing it to belong to an African bufonid genus, because of webbing at the base of the toes.

Noble (1926) noted pelobatid characteristics in all three of these Seychellean frogs, and consequently, he (1931) established a new pelobatid subfamily, the Sooglossinae, to accommodate all 3 species.

Noble (1926) stated that the differences between *S. sechellensis* and *Nesomantis* "are very trivial", but that it is "well to utilize these generic names until the anatomy of *N. thomasseti* and *S. sechellensis* is better known." He indicated that a separate genus might be justified for *Nec. gardineri*, but instead he opted for expanding the definition of *Sooglossus* and placing it in the latter genus as *Soo. gardineri*.

The recently described Nasikabatrachidae from the Western Ghats of India is considered to be the sister group of Sooglossidae based on molecular evidence (Biju and Bossuyt 2003). However, based on the limited morphological evidence from their description, it is more like the African Hemisotidae in the unique pectoral girdle architecture, external morphology, and life history (Scott 2005). However, Frost et al. (2006) found further support for a sooglossid-nasikabatrachid relationship and considered Nasikabatrachidae to

be a junior synonym of the Sooglossidae.

Gerlach and Willi (2002) described *Soo*. *pipilodryas* from the island of Silhouette as a new cryptic species closely related to *S*. *gardineri*. If *Soo*. *pipilodryas* proves to be a valid species (distinct from *S*. *gardineri*), then it is clearly the sister species of *S*. *gardineri*, and its existence will not affect the phylogenetic analysis that follows.

MATERIALS AND METHODS

We recorded morphological characters from 36 frog species representing 12 families (Appendix 1). The data set include 188 characters and is part of a larger project on the phylogeny of advanced frog families (Wu 1994). Characters and character states are listed in appendix 2. The data matrix can be obtained from the corresponding author upon request.

Cladistic analyses were performed using PAUP for McIntosh, vers. 4.0b 10 (Swofford 2002). All 33 non-sooglossid taxa were used as outgroups. All characters were treated as unordered. Phylogenetic trees were obtained using maximum parsimony (MP) methods with heuristic search options. The following settings were used in the analyses: collapsing 0 length branches; starting trees obtained by stepwise addition and only minimal trees being swapped; and swapping options including the TBR (tree-bisection reconnection) algorithm, MULPARS, and steepest descent. Two hundred random additions were performed, and the 50% consensus cladogram was used in the results.

Branch supports were evaluated using bootstrapping methods with 1000 replicates and 10 random additions. The same search options used in the MP analysis were used in the procedure.

Character optimization was based on both the ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) methods. Only synapotypies obtained in both optimizing methods were listed as synapotypies in the final diagnoses of the clades. This is a more-conservative estimate of the synapotypies because there is no a priori reason to assume whether convergences or reversals are more-common processes in evolution.

RESULTS

The majority rule (50%) consensus tree from 1119 equally parsimonious cladograms had a consistency index of 0.243. Sooglossidae monophyly was supported by parsimony and bootstrapping (Fig. 1).

Twenty-four synapotypies diagnose the family, and bootstrap support for the clade was strong. *Nesomantis thomasseti* and *Soo*. *sechellensis* share 7 synapotypies, and bootstrap support for the grouping was moderately strong, thus supporting the monophyly of the 2 species with the exclusion of *Soo*. *gardineri*.

The family Sooglossidae is grouped with the Dendrobatidae and Leptodactylidae, but the bootstrapping support was low. Firmsternal families (Arthroleptidae, Microhylidae, and Petropedetidae) were highly supported by the MP and bootstrapping methods.

DISCUSSION

The cladistic results strongly support the conclusions of all students of the sooglossids beginning with Noble (1926) that this group is monophyletic. Noble's (1926 1931) attempt to assign the sooglossids to the Pelobatidae was based on too-few characters and too-few taxa. Griffith's (1959 1963) assignment of sooglossids broadly to ranoids resulted from errors in recording morphology, and subsequent workers who also argued for a ranoid association, (e.g., Savage 1973, Duellman and Trueb 1986,Blommers-Schlösser 1993) were misled by Griffith's erroneous morphological data. The discovery of some relatively plesiotypic character states for sooglossids also led various authors (Lynch 1973, Nussbaum 1980, Ford and Cannatella 1993) to hypothesize a myobatrachid affiliation for sooglossids.

DNA sequence data from the mitochondrial 12S ribosomal RNA gene suggested a closer relationship between myobatrachids and sooglossids than between bufonids and sooglossids (Hedges and Maxson 1993), as did a combined dataset using both mitochondrial 12S and 16S rRNA gene sequences (Hay et al. 1995). Both analyses indicated that sooglossids are more basal than myobatrachids and bufonids and closer to the former. With current knowledge, it is not possible to resolve the discrepancies between the cladograms based on morphology and rRNA gene sequencing.

Our results are consistent with earlier data on karyology (Nussbaum 1979), vocalization (Nussbaum et al. 1982), and allozymes (Green et al. 1988) which indicate that *Nes*. *thomasseti* and

Soo. *sechellensis* are closer cladistically than are *Soo*. *sechellensis* and *Soo*. *gardineri*. Additionally, the color patterns of *Nes*. *thomasseti* and *Soo*. *sechellensis* are similar and differ from the pattern of *Soo*. *gardineri*. The former 2 species have a generalized, camouflage color pattern consisting of a brownish ground color with scattered, small, dark markings; whereas *Soo*. *gardineri* has a more-specialized color pattern with a highly variable dorsal coloration and a bold black lateral band on the head and body. The color pattern of *Soo*. *pipilodryas* is nearly identical to that of *Soo*. *gardineri* (Gerlach and Willi 2002). Clearly a new taxonomic arrangement is needed, which includes 3 possible solutions. All 4 species could be placed in a single genus with the genus name *Sooglossus* having

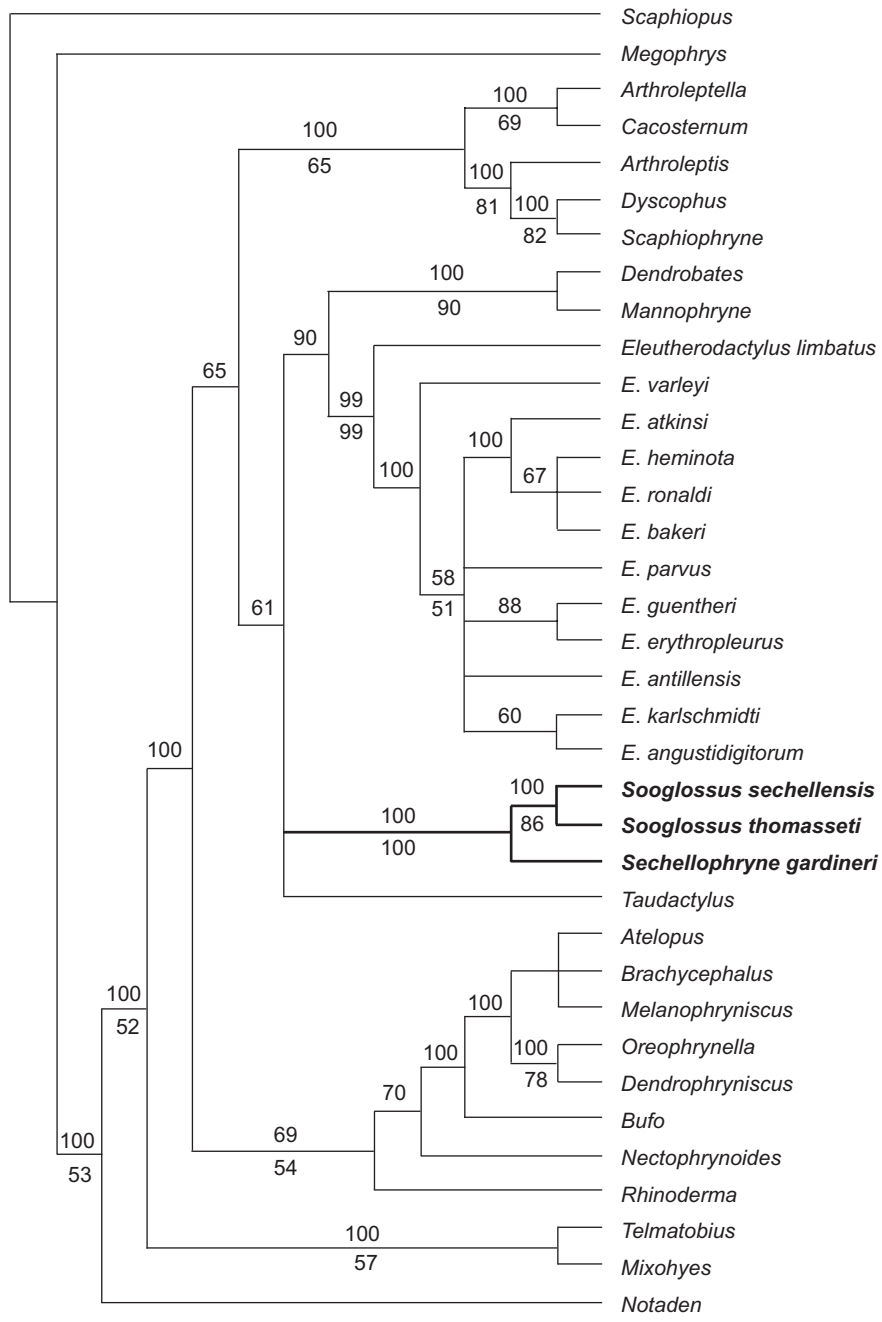

Fig. 1. Majority rule (50%) consensus cladogram of 937 steps (CI = 0.2467) with 161 informative morphological characters. Numbers above the branches indicate the percent support from 1119 equally parsimonious trees, while the numbers below the branches are bootstrap support for the clades. Only values > 50% are shown.

priority, or all 3 could be placed in monotypic genera, or *Soo. gardineri* and *Soo. pipilodryas* could be placed in a new genus and *Nes. thomasseti* placed in *Sooglossus* along with *Soo. sechellensis*. The latter option more reasonably reflects the cladistic relationships and acknowledges the great differences among the species, and is the solution we propose.

While sooglossids are undoubtedly monophyletic, the differences among the 4 species are great, which suggests long isolation in association with Seychellea. Our results do not resolve the issue of ex-Seychellean biogeographic relationships of the sooglossids. Bufonids occur in Africa and India, but are conspicuously absent from Madagascar, the continental land mass currently closest to Seychellea. Similarly, while caecilians occur in the granitic Seychelles, Africa, and India, none occurs in Madagascar. However, differences between sooglossids and bufonids, and between sooglossids and other possible sister groups (including *Nasikabatrachus*), are great; and it seems increasingly unlikely that a definite solution to the biogeographic origins of the sooglossids will be found.

For the moment, we do not include the Nasikabatrachidae within the Sooglossidae as suggested by Frost et al. (2006). This is because we lack comparative morphological data and because we suspect that *Nasikabatrachus* may prove to be a hemisotid or at least a microhyloid.

SYNOPSIS

Sooglossidae Noble

Sooglossinae Noble 1931: 494.
Sooglossidae Griffiths 1963: 273.

Diagnosis: Phaneroglossal anuran with modified arciferal pectoral girdles with small epicoracoid horns that are free posteriorly and with small musculus (m.) epicoracodeii; inguinal amplexus; 26 haploid chromosomes, the smaller of which are telocentric.

Twenty-four synapotypies diagnose the family based on our phylogenetic results. Even though none of the synapotypies is uniquely derived on a global scale, the combination of these character states is sufficient for diagnosing the family among advanced frog families. The character states are (numbers refer to characters listed in appendix 2): (20) 3rd toe shorter than 5th; (36) left and right m. sternohyoideus dorsalis inserting on each other rather than on hyoid plate; (38) a cutaneous slip of m. pectoralis present; (39) m. rectus abdominis pars anteroreflecta present; (40) a type I iliosacral articulation; (41) m. iliolumbaris insertion on 1 or 2 transverse processes; (48) insertion of m. sartoriosemitendinosus dorsal to m. gracilis minor; (50) accessory ligament of m. gluteus magnus present; (66) tympanic ring absent; (67) stapes absent; (91) choanal portion of prevomer wider than choanal diameter; (101-104) mentomeckelian bone absent; (119) cricoid ring with a mid-ventral gap; (123) bronchial process of cricoid absent; (141) monocondylar articulation between sacrum and coccyx; (145) transverse processes on coccyx present; (152) clavicle curved; (154) procoracoid curved; (177) tips of fingers pointed; (179) sesamoid bone at tibio-metatarsal joint present; and (187) tips of toes pointed.

Content: Two genera, *Sooglossus* (2 species), and a new genus (*Sechellophryne*)described below.

Distribution: Two islands, Mahé and Silhouette, of the granitic Seychelles, western Indian Ocean.

Sechellophryne gen. nov.

Type species: *Nectophyrne gardineri* Boulenger 1911: 377.

Diagnosis: Sooglossid anuran with slightly webbed toes. A black lateral stripe from eye region to hindlimbs. Ten synapotypies: (19) webbing between toes at base; (53) posterolateral process of nasal absent; (64) braincase component of sphenethmoid contacting anterior border of optic foramen; (65) sphenethmoid forming anterior and medial border of orbit; (95, 96) palatine absent; (99) length of cultriform process of parasphenoid short, not reaching anterior border of optic foramen; (112) alary process of hyoid narrow base with lateral expansion; (166) dorsal protuberance of ilium absent; and (184) sesamoid on ventrolateral surface of tarsometatarsal joint present.

Content: Two species.

Distribution: As for the family.

Etymology: The generic name is derived from "Sechelles" (French) and "phryne" (Greek, feminine, toad), meaning the "Seychelles toad".

Sechellophryne gardineri (Boulenger) comb. nov.

(Fig. 2)

Nectophryne gardineri Boulenger 1911: 377. Syntypes: BM 1910.3.18.73-79, collected in 1908 by J. Stanley Gardiner during the Second Percy Sladen Expedition to the Seychelles. Type locality : "Mahé: Morne Pilot, 2700 ft. Silhouette: highest jungle."

Sooglossus gardineri: Noble 1926: 12. First use of combination.

Identification: Characters of the genus. Smallest sooglossid and close to smallest known frog, 75 adult females averaging 11.5 mm in snout-vent length with a maximum of 13 mm; sample of 91 males averaging 10.2 mm with a maximum of 11 mm; 20 subadults averaging 7.9 mm. Coloration of upper surfaces highly variable, some individuals uniformly reddish-brown, others uniformly light tan, others reddish-brown with white middorsal stripe, others with dark or light blotches on contrasting background. Sides of head and body always darker than upper and lower surfaces. Undersurfaces dark, but not as dark as sides. Vocalization, high-pitched "peep" or whistle reminiscent of cricket, calls in isolation almost always during daytime. *Sooglossus sechellensis* and *Soo. thomasseti* are much larger, the former up to 25 mm, and the latter up to 55 mm in snout-vent length. These 2 species often with a black triangular spot on top of head just behind eyes, which is lacking in *Sec. gardineri* comb nov. Dark lateral bands of latter missing in the 2 *Sooglossus* species.

Distribution: As for the family.

Etymology: Named for J. Stanley Gardiner

Remarks: Embryos of *Sec. gardineri* comb. nov. directly develop in terrestrial nests (in litter, under stones, in hollow stems of fallen tree fern branches, etc.). The embryos are attended by the mother.

Sechellophryne pipilodryas (Gerlach and Willi)

Sooglossus pipilodryas: Gerlach and Willi 2002: 452. Holotype: UMZ 2001.1.1, collected on 8 Sept. 2000 by J. Gerlach, R. Gerlach, and J. Willi. Type locality: "Mon Plaisir (in *Phoenicophorium borsigianum* axil, below Mt. Dauban at approximately 700 m altitude), Silhouette" .

Identification: Characters of genus. Small sooglossid, slightly larger than *Sec. gardineri*, females averaging 14.3 mm in snout-vent length with a maximum of 15.8 mm; males 10.0-12.6 mm. Compared to *Sec. gardineri*, *Sec. pipilodryas* with larger eyes, shorter tibia, and shorter fingers I and II. Coloration of upper surfaces variable, all with a mid-dorsal hastate mark running from a point halfway between eyes and forelimbs to vent. Vocalization, high-pitched squeak, similar to *Sec. gardineri*, but with more repetitions.

Distribution: Silhouette I. (Mon Plaisir, Jardin Marron).

Etymology: Refers to the calls, from *pipilo* (Latin, meaning a chirp), and *dryas* (Latin, for a forest spirit).

Sooglossus Boulenger

Sooglossus Boulenger 1906: 321. Type species: *Arthroleptis sechellensis* Boettger, by monotypy.

Nesomantis Boulenger 1909:293. Type species: *Nesomantis thomasseti* Boulenger, by monotypy. New synonymy.

Diagnosis: Sooglossid frogs lacking webbing at base of toes. Diagnostic characters: (44) origin of m. coccygeosacralis on urostyle along its full length; (51) nasals with median contact; (54) posterior margin of nasal touching frontoparietal; (61) anterior margin of frontoparietal straight; (70) premaxilla and maxilla in contact and overlapping; (133) spinal processes on vertebrae II to IV present; and (164) posterior plate of xiphisternum slightly expanded.

Content: Two species, *Sooglossus sechellensis* (Boettger) and *Soo. thomasseti* (Boulenger).

Distribution: As for the family.

Etymology: Refers to the shape of the tongue, which is entire (no posterior notch).

Sooglossus sechellensis (Boettger) comb. nov.

(Fig. 3)

Arthroleptis sechellensis Boettger 1896: 350. Lectotype: SMF 7179, designated by Mertens 1967: 43, collected approximately during 1895 by August Brauer. Type locality: "Auf den Seychellen."

Sooglossus sechellensis: Boulenger 1906: 321. First use of combination.

Identification: A small *Sooglossus*. Females averaging about 20 mm in snout-vent length (maximum about 25 mm); males averaging about 15 mm (19 mm maximum). Golden-brown dorsolateral ground color with bands and spots of black on back, sides, and upper surfaces of legs; no dark band on sides of head and body as in *Sec. gardineri*; large, often triangular, black spot on top of head just behind eyes, not present in *Sec. gardineri*; venter white, but chin and chest with light-brown spots. Most similar in coloration to young of

Soo. thomasseti, but latter usually with a thin white vertebral stripe. Vocalization typically a croak followed by four "tocking" notes: "rrraackkk-toc-toc-toc-toc", produced in isolation, mainly during the day.

Eight uniquely derived characteristics are found in this species: (6) supratympanic fold oblique; (96) lateral margin of palatine not in contact with maxilla; (100) posterior projection of parasphenoid entering foramen magnum; (106) pseudo-teeth on dentary present; (127) orientation of posterior margin of transverse process II horizontal; (130) transverse process VI posteriorly directed; (143) sacral diapophysis expanded; and (188) ventral surface of terminal phalanges with knob-like projection.

Distribution: As for family and genus.

Etymology: The specific name "*sechellensis*" (French spelling) refers to the group of islands where the species is found.

Remarks: *Sooglossus sechellensis* exhibits female parental care of embryos in terrestrial nests and has direct development with non-feeding larvae transported on the dorsum of the female parent. They call night and day and more frequently during wet weather. During dry weather, they seem to call more frequently during the day than at night.

***Sooglossus thomasseti* (Boulenger) comb. nov.**

(Fig. 4)

Nesomantis thomasseti Boulenger 1909: 293. Holotype: BM 1907.10.15.111, collected in 1905 by H. P. Thomasset. Type locality: "Cascade, Mahé, at an altitude of 1500 feet."

Identification: Thomasset's frog the largest of the 3 sooglossid species and the rarest frog in the Seychelles. Full-grown females larger (about 55 mm in snout-vent length) than adult males (45 mm). Upper surfaces golden to reddish-brown with scattered black markings. Some few individuals with a broad, brown middorsal stripe. With black bars across tops of toes and legs. Many with a thin white or yellow line down middle of back and across backs of thighs. Most with a white line behind each eye which extends backwards to a point on back just above front legs. With a double row of 2-6 small, light-colored bumps down back, beginning behind each eye. Large eyes golden except for black pupils. Undersurfaces brown with some light mottling. Tips of toes slightly expanded, apparently for increased friction useful in climbing. Thomasset's frog a rock climber, and found most often at night sitting on rocks and large boulders. Rarely found climbing on low branches of trees and shrubs. Call similar to that of Seychelles

Fig. 2. *Sechellophryne gardineri* comb. nov. (Boulenger). Photo by Ronald A. Nussbaum.

Fig. 3. *Sooglossus sechellensis* comb. nov. (Boettger). Photo by Ronald A. Nussbaum.

Fig. 4. *Sooglossus thomasseti* comb. nov. (Boulenger). Photo by Ronald A. Nussbaum.

frog, but notes produced at a slower rate, call is longer, and 1st gutteral note repeated 3 or 4 times rather than once. Entire song sounds like "rraack-rraack-rraack-toc-toc-toc-toc."

Fifteen uniquely derived character states were found in this species:(11) tips of fingers expanded into discs; (15) fleshy tips of toes expanded into discs; (45) origin of m. tensor fascia latae on ilium on posterior 1/3 of ilium; (59) crest on posterior 1/2 of frontoparietal present; (80) angle between horizontal process of squamosal and prootic greater than 45°; (81) squamosal bending posteroventrally; (92) dentary process of prevomer posterior to choana; (93) dentary processes of prevomer not in contact medially; (94) prevomerine teeth present; (97) palatine and prevomer fused; (111) hyoglossal sinus of hyoid deep; (113) posterolateral process of hyoid bifurcated; (128) length of transverse process IV longer than III; (156) lateral edge of procoracoid reduced; and (160) omosternum with distal expansion.

Distribution: As for family and genus.

Etymology: Named for Mr. H. P. Thomasset, who collected the holotype.

Remarks: The mode of development and the presence or absence of parental care is unknown for *Soo*. *thomasseti* comb. nov. However, this species is likely to have direct terrestrial development with female egg-guarding. This is based on the observation (RAN) that females have large yolky eggs (typical of direct development) in their ovaries, and that no unidentified larvae which might be young of *Soo*. *thomasseti* comb. nov. have been found in streams or small ponds in the Seychelles. The prediction of female egg-guarding is based on the observations (RAN) that females of *Soo*. *sechellensis* and *Sec*. *gardineri* comb. nov. guard their eggs.

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APPENDIX I. Specimens examined

ARTHROLEPTIDAE: *Arthroleptis stenodactylus*, UMMZ 190671. **BUFONIDAE:** *Atelopus* varius, UMMZ 167396; *Bufo bankorensis*, UMMZ 199143, 199144; *Dendrophryniscus* brevipillicatus, UMMZ 127926; *Melanophryniscus stelzneri*, UMMZ 166797; *Nectophrynoides viviparus*, UMMZ 70290; *Oreophrynella quelchii*, UMMZ 85141. **DENDROBATIDAE:** *Dendrobates auratus*, UMMZ 184022, 184021; *Mannophryne herminae*, UMMZ 113914(2). **LEPTODACTYLIDAE:** *Eleutherodactylus antillensis*, UMMZ 80669; *E. atkinsi*, UMMZ 63981; *E. augustidigitorum*, UMMZ 112799; *E. bakeri*, UMMZ 123080; *E. erythropleurus*, UMMZ 121457; *E. guentheri*, UMMZ 204763; *E. heminota*, UMMZ 136452; *E. karlschmidti*, UMMZ 73433; *E. limbatus*, UMMZ 65032; *E. parvus*, UMMZ 127919; *E. ronaldi*, UMMZ 80910; *E. varleyi*, UMMZ 63978; *Telmatobius marmoratus*, UMMZ 68179. **LIMNODYNASTIDAE:** *Mixophyes schevilli*, UMMZ 132692; *Notaden nichollsi*, UMMZ 124498. **MEGOPHRYIIDAE:** *Megophrys* sp., no tag. **MICROHYLIDAE:** *Dyscophus antongilii*, UMMZ 191162, 191167; *Scaphiophryne calcaratum*, UMMZ 191138; **MYOBATRACHIDAE:** *Taudactylus diurnus*, UMMZ 132731; **PETROPEDETIDAE:** *Arthroleptella lightfooti*, UMMZ 190668; *Cacosternum bottgeri*, UMMZ 190653. **RHINODERMATIDAE:** Rhinoderma darwini, UMMZ 123886. **SCAPHIOPODIDAE:** *Scaphiopus couchii*, UMMZ 200821, 200822. **SOOGLOSSIDAE:** *Nesomantis thomasseti*, UMMZ 144476, 177110, 177111, 179597; *Sooglossus gardineri*, UMMZ 183079, 183080; *Soo. sechellensis*, UMMZ 179624, 183077, 183078.

APPENDIX II. Characters and character states

External morphology

1. Position of nostril relative to level of eye. 0: nostril at or above ventral margin of eye; 1: nostril above dorsal margin of eye. **2.** Position of nostril relative to tip of jaw. 0: nostril located anterior to tip of jaw; 1. nostril located at level or posterior to level of tip of jaw. **3.** Pupil shape. 0: round; 1: horizontal; 2: vertical. **4.** Tympanic membrane. 0: tympanum distinct; 1: tympanum indistinct, covered by skin, or absent. **5.** Lateral skin fold. 0: dorsolateral fold absent; 1. dorsolateral fold present. **6.** Oblique skin fold. 0: oblique supratympanic fold absent; 1: oblique supratympanic fold present. **7.** Posterior margin of tongue. 0: free; 1: attached. **8.** Anterior palatal fold. 0: absent; 1: simple; 2: papillated. **9.** Posterior palatal fold. 0: absent; 1: simple; 2: papillated. **10.** Relative length of 1st and 2nd fingers. 0: 1st finger shorter than 2nd; 1: 1st finger longer than 2nd. **11.** Fleshy tip of phalanges on forelimb. 0: simple; 1: expanded into discs. **12.** Webbing between fingers. 0: absent; 1: present. **13.** Relative length between 2nd and 4th fingers. 0: 2nd finger longer than 4th; 0: 2nd finger shorter than 4th. **14.** Lateral metacarpal tubercle. 0: entire; 1: divided. **15.** Fleshy tip of toes. 0: simple; 1: expanded into discs. **16.** Shape of inner metatarsal tubercle. 0: simple; 1: large and elevated, skin keratinized. **17.** Outer metatarsal tubercle. 0: absent; 1: present, oval in shape; 2: present, elevated into a spade-like shape. **18.** Tarsometatarsal tubercle. 0: absent; 1: present, spine-shaped; 2: present: spade-shaped. **19.** Webbing between toes. 0: web at least at base; 2: absent. **20.** Relative length between 3rd and 5th toes. 0: 3rd toe longer than 5th; 1: 3rd toe shorter than 5th. **21.** Maxillary and premaxillary teeth. 0: present; 1: absent.

Myology

22. Aponeurosis on midline of m. intermandibularis. 0: absent; 1: present. **23.** Lateral slip of m. intermandibularis. 0: absent; 1: 1 lateral slip; 2: 2 lateral slips. **24.** Origin of lateral slip of m. intermandibularis. 0: from jaw angle; 1: midway on mandible; 2: absent. **25.** Orientation of anterior fibers of m. intermandibularis. 0: anteromedio-posterolaterally; 1: posteromedio-anterolaterally. **26.** Position of cranial nerve V relative to m. adductor mandibulae longus. 0: muscle absent; 1: muscle medial to nerve; 2: muscle lateral to nerve; 3: muscle penetrated by nerve. **27.** Position of cranial nerve V relative to m. adductor mandibulae internus. 0: nerve anterior to muscle; 1: nerve posterior to muscle; 2: nerve penetrating muscle. **28.** Insertion of m. adductor mandibulae internus. 0: by muscle fiber; 1: by ligament. **29.** M. adductor mandibulae externus superficialis. 0: muscle absent; 1: cranial nerve V medial to muscle; 2: cranial nerve V lateral to muscle. **30.** Origin of m. depressor mandibulae. 0: on dorsal fascia and skull; 1: on skull only; 2: on dorsal fascia only. **31.** Insertion of m. petrohyoideus posterior III. 0: on posteromedial process of hyoid; 1: on posteromedial process and on cricohyoid membrane. **32.** Origin of m. cucularis relative to that of m. petrohyoideus posterior III. 0: dorsal and lateral; 1: ventral. **33.** Insertion of m. constrictor laryngis anterior. 0: on medial margin of posteromedial process; 1: on ventral hyoid plate. **34.** Number of slips of m. petrohyoideus posterior. 0: 2; 1: 3. **35.** M. omohyoideus. 0: present; 1: absent. **36.** M. sternohyoideus dorsalis. 0: originating on lateral hyoid. 1: fibers connecting to each other. **37.** Insertion of m. pectoralis and m. deltoideus. 0: insertion converge; 1: pectoralis dorsal and medial to deltoideus; 2: insertion separated by deltoid crest of humerus; 3: pectoralis inserting on axillary spine. **38.** Cutaneous slip of m. pectoralis. 0: absent; 1: present. **39.** M. rectus abdominis pars anteroreflecta. 0: absent; 1: present. **40.** Iliosacral articulation. 0: type I; 1: type II. **41.** M. iliolumbaris insertion on transverse process. 0: on 1 or 2 transverse processes; 1: on 3 or more transverse processes. **42.** Origin of m. coccygeoiliacus on urostyle. 0: on posterior tip; 1: on posterior 1/2 of urostyle. **43.** Origin of m. iliacus externus. 0: covering the dorsal surface of ilium; 1: ilium exposed. **44.** Origin of m. coccygeosacralis on urostyle. 0: on anterior 1/2 of urostyle; 1: along full length of urostyle. **45.** Origin of m. tensor fascia latae on ilium. 0: on posterior 1/3 length of ilium; 1: on anterior 1/2 length of ilium; 2: muscle absent. **46.** Anterior insertion of m. iliacus externus. 0: on margin of diapophysis; 1: not to diapophysis. **47.** M. adductor longus. 0: absent; 1: present. **48.**

APPENDIX II. (Cont.)

Insertion of m. sartorio-semitendinosus relative to m. gracilis minor. 0: ventral; 1: penetrating; 2: dorsal. **49.** Cutaneous slip of m. gracilis minor. 0: absent; 1: present. **50.** Accessory ligament of m. gluteus magnus. 0: absent. 1: present.

Osteology of the head

51. Median contact of nasals. 0: in contact; 1: separate. **52.** Nasal shape. 0: club-shaped; 1: wide, triangular; 2: square, rhomboidal, or rectangular. **53.** Posterolateral process of nasal. 0: absent; 1: present. **54.** Posterior margin of nasal. 0: touching frontoparietal; 1: separated from frontoparietal. **55.** Posterolateral process of frontoparietal. 0: absent; 1: present. **56.** Ossification of frontoparietal. 0: well-ossified, separate; 1: well-ossified, in contact with each other; 2: poorly ossified, frontal fontanelle exposed. **57.** Posterior margin of frontoparietal. 0: forming dorsal border of foramen magnum; 1: exposing exoccipital; 2: frontoparietal on lateral side, not to midline. **58.** Frontoparietal posterior process. 0: straight; 1: with process; 2: frontoparietal restricted on lateral side, not to midline. **59.** Crest on posterior 1/2 of frontoparietal. 0: absent; 1: present. **60.** Frontoparietal ossification center. 0: 2; 1: 1. **61.** Anterior margin of frontoparietal. 0: medial side extending beyond lateral side; 1: anterior margin straight; 2: lateral part extending beyond medial part. **62.** Cranial exostosis. 0: absent; 1: present. **63.** Fusion of sphenethmoid on mid-ventral portion. 0: separate; 1: fused. **64.** Braincase component of sphenethmoid. 0: contacting anterior border of optic foramen; 1: not in contact. **65.** Sphenethmoid. 0: on medial margin of orbit; 1: forming anterior and medial border of orbit. **66.** Ear, tympanic ring. 0: present; 1: absent. **67.** Ear, stapes. 0: absent; 1: present, proximal end simple; 2: present, proximal end enlarged. **68.** Premaxilla, alary process. 0: projecting forward; 1: vertical; 2: backward. **69.** Height of premaxillary alary process. 0: > width of pars dentalis; 1: ≤ width of pars dentalis. **70.** Premaxilla and maxilla. 0: contacting and overlapping; 1: not in contact. **71.** Premaxilla, pars palatina. 0: with a recess in middle; 1: with a straight edge; 2: absent. **72.** Premaxilla, angle between alary process and horizontal process. 0: perpendicular; 1: inclined laterally away from midline. **73.** Premaxilla, pars dentalis width of lateral and medial flanges. 0: lateral wider or equal to medial flange; 1: medial wider than lateral. **74.** Maxilla, anterior border. 0: separate; 1: fused anteriorly. **75.** Maxilla, articulation with quadratojugal. 0: in contact; 1: not in contact; 2: quadratojugal absent. **76.** Pars facialis of maxilla. 0: pars absent; 1: pars triangular; 2: pars square. **77.** Maxilla, articulation with zygomatic ramus of squamosal. 0: not in contact; 1: in contact. **78.** Quadratojugal. 0: present; 1: absent. **79.** Quadratojugal articulation with zygomatic ramus of squamosal. 0: not in contact; 1: in contact. **80.** Alignment of horizontal process of squamosal with prootic. 0: parallel; 1: < 45°; 2: > 45°. **81.** Squamosal shape. 0: straight; 1: bending posteroventrally; 2: bending posterodorsally. **82.** Squamosal, angle between ventral ramus and mandible. 0: nearly perpendicular; 1: > 45°, < 90°; 2: about 45°. **83.** Squamosal, articulation with quadratojugal. 0: fused or abutting each other; 1: separate; 2: quadratojugal absent. **84.** Zygomatic ramus of squamosal. 0: absent; 1: present. **85.** Otic ramus of squamosal. 0: absent; 1: present. **86.** Pterygoid, anterior ramus. 0: in contact or fused with maxilla; 1: separated by cartilage. **87.** Pterygoid medial ramus. 0: absent; 1: separated from otic capsule by cartilage; 2: in contact with otic capsule. **88.** Prevomer, odontoid. 0: absent; 1: present. **89.** Prevomer, anterior process. 0: absent; 1: present. **90.** Size of prechoanal process of prevomer relative to choanal diameter. 0: smaller than 1/2 choanal diameter; 1: larger than 1/2 choanal diameter. **91.** Width of choanal portion of prevomer relative to choanal diameter. 0: wider; 1: narrower. **92.** Dentary process of prevomer. 0: posterior to choana; 1: medial to choana; 2: absent. **93.** Dentary process of prevomer median contact. 0: separate; 1: meeting at midline; 2: process absent. **94.** Prevomerine teeth. 0: present; 1: absent. **95.** Medial margin of palatine. 0: meeting at midline; 1: not in contact at midline; 2: palatine absent. **96.** Lateral margin of palatine. 0: not in contact with maxilla; 1: in contact; 2: palatine absent. **97.** Palatine and prevomer. 0: separate; 1: fused; 2: palatine or prevomer absent. **98.** Anterior margin of cultriform process of parasphenoid. 0: serrated; 1: rounded or square; 2: forked. **99.** Length of cultriform process of parasphenoid. 0: reaching level of palatine or sphenethmoid; 1:

APPENDIX II. (Cont.)

short, not reaching anterior border of optic foramen. **100.** Posterior projection of parasphenoid. 0: entering foramen magnum; 1: not entering foramen magnum. **101.** Mentomeckelian bone. 0: a separate bone; 1: absent. **102.** Medial constriction of mentomeckelian bone. 0: none; 1: constriction present; 2: mentomeckelian bone absent. **103.** Relative height of medial and lateral edges of mentomeckelian bone. 0: medial edge wider; 1: lateral edge higher; 2: mentomeckelian absent. **104.** Shape of mentomeckelian bone. 0: L-shaped; 1: straight; 2: mentomeckelian bone absent. **105.** Length of lateral process of mentomeckelian bone. 0: absent; 1: shorter; 2: longer. **106.** False teeth on dentary. 0: absent; 1: present.

Osteology of the hyoid and larynx

107. Coronoid process of angulosplenial. 0: absent; 1: pointed dorsally; 2: pointed medially. **108.** Width of hyoid. 0: wide; 1: narrow. **109.** Lateral process on anterior hyale. 0: absent; 1: present. **110.** Medial process on anterior hyale. 0: absent; 1: present. **111.** Hyoglossal sinus of hyoid. 0: shallow; 1: deep. **112.** Alary process of hyoid. 0: absent; 1: narrow throughout; 2: narrow base with lateral expansion; 3: greatly expanded. **113.** Posterolateral process of hyoid. 0: absent; 1: simple; 2: bifurcated. **114.** Stalk medial to posteromedial processes of hyoid. 0: absent; 1: present. **115.** Medial expansion at base of posteromedial processes of hyoid. 0: absent; 1: present. **116.** Expanded flange on medial side of posteromedial processes of hyoid. 0: absent; 1: present. **117.** Expanded flange on medial side of posterolateral processes of hyoid. 0: absent; 1: present. **118.** Fibrous gap separating hyoid plate horizontally. 0: absent; 1: present. **119.** Cricoid ring. 0: ring complete; 1: with mid-ventral gap; 2: with mid-dorsal gap. **120.** Esophageal process of cricoid. 0: absent; 1: present. **121.** Ventromedial process of cricoid. 0: absent; 1: present. **122.** Cricoid ring connection to posteromedial process of hyoid. 0: absent; 1: present. **123.** Bronchial process of cricoid. 0: absent; 1: present. **124.** Apical cartilage on dorsal arytenoid cartilage. 0: absent; 1: present.

Osteology of the vertebral column

125. Atlantal intercotylar distance relative to cotylar width. 0: narrower; 1: wider. **126.** Anterior margin of atlas. 0: straight; 1: with median process; 2: concave. **127.** Orientation of posterior margin of transverse process II. 0: anteriorly; 1: horizontally; 2: posteriorly. **128.** Length of transverse process IV. 0: longer than III; 1: significantly shorter than III. **129.** Orientation of transverse process V. 0: anteriorly; 1: horizontally; 2: posteriorly. **130.** Orientation of transverse process VI. 0: anteriorly; 1: horizontally; 2: posteriorly. **131.** Orientation of transverse process VII. 0: anteriorly; 1: horizontally; 2: posteriorly. **132.** Orientation of transverse process VIII. 0: anteriorly; 1: horizontally; 2: posteriorly. **133.** Spinal processes on vertebrae II to IV. 0: absent; 1: present. **134.** Accessory process on transverse process of vertebra III. absent; 1: present. **135.** Length of transverse processes V to VIII relative to width of vertebral body. 0: < 1/2; 1: between 1/2 and 1; 2: > 1. **136.** Imbricateness of neural arch. 0: imbricate; 1: non-imbricate. **137.** Fusion of vertebrae I and II. 0: separate; 1: fused. **138.** Fusion of sacrum and coccyx. 0: not fused; 1: fused. **139.** Number of presacral vertebrae. 0: 8; 1: 7. **140.** Shape of last presacral vertebral centrum. 0: procoelous; 1: diplasiocoelous; 2: amphicoelous; 3: opisthocoelous. **141.** Articulation between sacrum and coccyx. 0: monocondylar; 1: bicondylar; 2: fused. **142.** Orientation of anterior margin of diapophysis. 0: anteriorly; 1: posteriorly; 2: horizontally. **143.** Expansion of sacral diapophysis. 0: not expanded; 1: expanded; 2: greatly expanded. **144.** Fan-shaped expansion between sacrum and coccyx. 0: absent; 1: present. **145.** Transverse processes on coccyx. 0: absent; 1: present.

Osteology of the pectoral and pelvic girdles

146. Medial coracoid. 0: straight; 1: bifurcated. **147.** Coracoid, posterior margin. 0: curved; 1:

APPENDIX II. (Cont.)

straight. **148.** Curvature of coracoid. 0: straight; 1: bent anteriorly. **149.** Dilation of coracoid. 0: not dilated; 1: dilated medially. **150.** Lateral edge of clavicle. 0: reaching glenoid fossa; 1: reduced, not to fossa; 2: clavicle absent. **151.** Medial edge of clavicle. 0: to coracoid near midline; 1: medial edge free; 2: clavicle absent. **152.** Curvature of clavicle. 0: curved; 1: straight; 2: clavicle absent. **153.** Middle portion of clavicle. 0: not touching coracoid; 1: touching coracoid; 2: clavicle absent. **154.** Curvature of procoracoid. 0: curved; 1: straight; 2: absent. **155.** Procoracoid, middle portion. 0: not touching coracoid at middle; 1: touching coracoid; 2: procoracoid absent. **156.** Procoracoid, lateral edge. 0: to glenoid fossa; 1: lateral edge reduced; 2: procoracoid absent. **157.** Medial edge of procoracoid. 0: reaching midline; 1: medial edge reduced; 2: procoracoid absent. **158.** Epicoracoid. 0: overlapping; 1: fused. **159.** Base of omosternum. 0: absent; 1: simple. 2: forked. **160.** Omosternum shape. 0: absent; 1: simple; 2: with distal expansion. **161.** Stalk of omosternum. 0: absent; 1: cartilaginous; 2: ossified. **162.** Xiphisternum. 0: absent; 1: cartilaginous; 2: ossified. **163.** Posterior margin of xiphisternum. 0: absent; 1: rounded; 2: with a recess. **164.** Posterior plate of xiphisternum. 0: absent; 1: pointed; 2: expanded slightly; 3: greatly expanded. **165.** Crest on dorsal surface of ilium. 0: absent; 1: present. **166.** Dorsal protuberance of ilium. 0: absent; 1: present. **167.** Preacetabular region of puboilium. 0: V-shaped; 1: U-shaped with straight medial edge; 2: U-shaped with pointed edge.

Osteology of the appendicular skeletons

168. Dorsal carpal sesamoid. 0: absent; 1: present. **169.** Fusion of carpal II to postaxial centrale. 0: separated; 1: fused. **170.** Fusion of preaxial centrale and distal carpal I. 0: separate. 1: fused. **171.** Condition of prepollex carpale. 0: separate from other elements; 1: fused to carpal I and preaxial centrale; 2: fused to prepollex. **172.** Shape of prepollex. 0: expanded; 1: slender. **173.** Articular surface between 2 distal carpal phalanges. 0: of equal width; 1: penultimate phalanx wider; 2: penultimate phalanx narrow. **174.** First finger. 0: normal; 1: reduced. **175.** Fourth finger. 0: normal; 1: reduced. **176.** Articular condyles on terminal phalanges. 0: 1; 1: 2. **177.** Tip of finger. 0: bifurcate; 1: knob-like; 2: pointed. **178.** Intercalary elements. 0: absent; 1: present. **179.** Sesamoid bone at tibio-metatarsal joint. 0: absent; 1: present. **180.** Tarsalia II. 0: present; 1: fused to others. **181.** Number of prehallical elements. 0: 2; 1: 3; 2: 4. **182.** Shape of prehallux. 0: expanded; 1: simple. **183.** Sesamoid on ventromedial tarsometatarsal joint. 0: absent; 1: present. **184.** Sesamoid on ventrolateral surface of tarsometatarsal joint. 0: absent; 1: present. **185.** First toe. 0: normal; 1: reduced. **186.** Fifth toe. 0: normal; 1: reduced. **187.** Tip of toes. 0: bifurcate; 1: knob-like; 2: pointed. **188.** Terminal phalanges, ventral surface. 0: smooth; 1: knob-like projection present.