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Diversity among New World microhylid frogs (Anura: Microhylidae): morphological and osteological comparisons between *Nelsonophryne* (Günther 1901) and a new genus from Peru

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A new genus and species of microhylid frogs are described from localities at elevations of 2500–2960 m on the eastern slopes of the Andes in central Peru. These are the first microhylids recorded from the Peruvian Andes and they differ from all other neotropical microhylids by their lack of a tympanum, tympanic annulus and stapes. *Phrynopus carpish* is removed from Leptodactylidae and placed in Microhylidae. Several novel morphological characters for microhylids are described, among them dermal body spines, expanded nuptial pads in males and heterotopic cartilages. Osteological descriptions and comparison of the new genus with *Nelsonophryne* revealed a number of intriguing characters that may prove to be useful in phylogenetic studies. Among these are the presence of a double, rather than single, wall between the olfactory capsules in one genus and the presence of a pair of previously undescribed bones in the nasal capsules of one species in each genus. In addition, some of these taxa have spinous projections on the ventral surface of the hyoid plates, and one species has only seven presacral vertebrae, owing to the fusion of Presacrals I and II. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **149**, 583–609.

ADDITIONAL KEYWORDS: amphibians – Andes – osteology – *Melanophryne* gen. nov. – systematics.

INTRODUCTION

Microhylid frogs occur on all continents except Ant-

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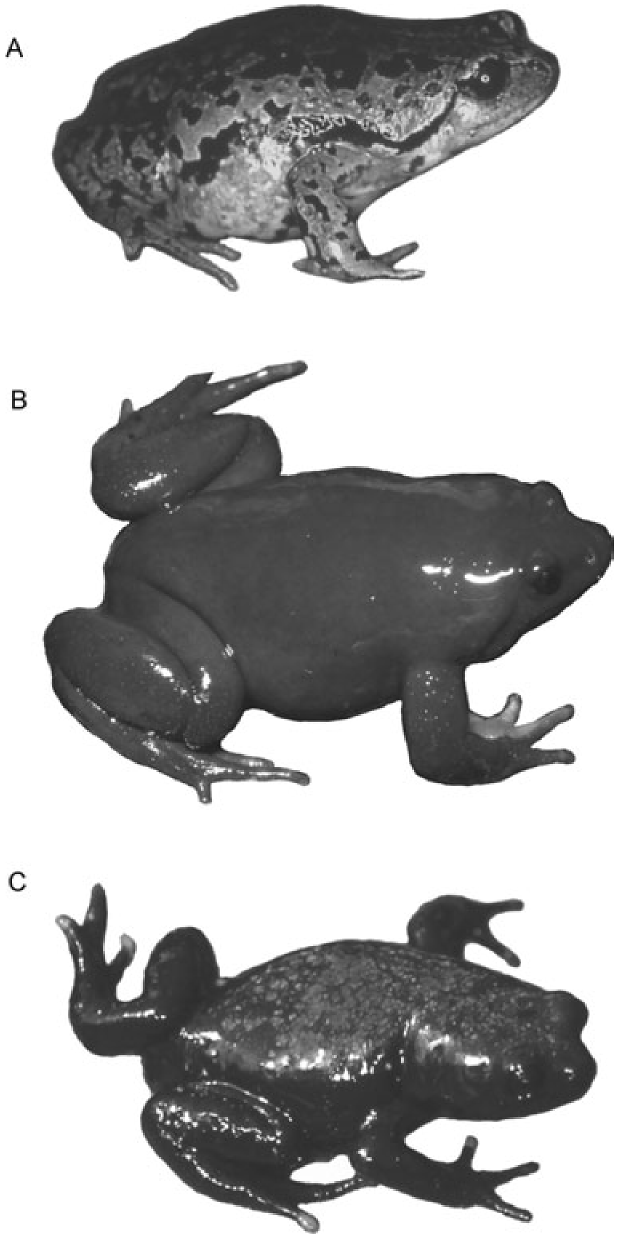

Figure 1. A, *Nelsonophryne aequatorialis* (KU 121056, SVL 36.5 mm), photo by J. D. Lynch. B, *N. aterrima*, photo by K.-H. Jungfer. C, *Melanophryne carpish* (MTD 45614, SVL 33.7 mm), photo by E. Lehr.

leptodactylids to microhylids (da Silva & Meinhardt, 1999).

Ten species and six genera of microhylids are known from the Amazonian lowlands of Peru (Lehr, 2002). These are: *Altigius alios* Wild, *Chiasmocleis anatipes* Walker & Duellman, *C. bassleri* Dunn, *C. ventrimaculata* (Andersson); *Ctenophryne geayi* Mocquard, *Elachistocleis bicolor* (Valenciennes), *Hamptophryne boliviana* (Parker), *Syncope antenori* Walker, *S. carvalhoi* Nelson and *S. tridactyla* (Duellman & Mendelson).

Lehr, Rodríguez & Córdova (2002) described *Phrynopus carpish* (Leptodactylidae) based on a single adult female from the Cordillera de Carpish in eastern central Peru. This species resembles species of central Peruvian *Phrynopus* in lacking a tympanic membrane and annulus, and in having slender, non-dilated digits, feet with basal webbing and a stout body. However, the presence of numerous, pigmented ovarian eggs in *P. carpish* was considered unusual, because the terrestrial eggs of *Phrynopus* undergo direct development from terrestrial eggs (Lehr *et al*., 2002). In 2002, an additional specimen of *P. carpish* was found and tissue samples were taken for phylogenetic analysis based on 12S and 16S mitochondrial rDNA. These results (Lehr, Fritzsch & Müller, 2005) revealed that *P. carpish* is not a member of the genus *Phrynopus* nor is it a leptodactylid frog. Examination of the skeletons of *P. carpish* and an unidentified series of '*Phrynopus*' from Cordillera Yanachaga in Peru revealed microhylid characteristics – namely a firmisternal pectoral girdle and a sacrum with expanded diapophyses – in both taxa. Comparison of these Andean taxa with the New World microhylines revealed so many differences that an affiliation with the existing genera was not possible. Herein we describe the new genus and compare it with the only other known genus of Andean microhylid frogs, *Nelsonophryne.*

Extensive osteological descriptions are provided for the new taxa and *Nelsonophryne aequatorialis* and *N. aterrima.* Since Parker's (1934) seminal work, osteological features of the palate and pectoral girdle, in particular, and to a lesser extent, characters of the vertebral column and terminal phalanges have appeared in the microhylid systematic literature. Commentary and literature summaries were provided by Zweifel (1986), Wu (1994) and Wild (1995). Despite the application and apparent utility of osteological characters, the microhylid literature is notably bereft of comprehensive skeletal descriptions; thus, comparisons of features among taxa usually are impossible based on reports in the literature. There is only one reasonably complete account of the skeletal development and adult skeleton in microhylids, and this describes *Hamptophyrne boliviana* (de Sá & Trueb, 1991). It is our intent to provide comparable data in this study with baseline descriptions of the adult osteology of two additional genera and four species of microhylid frogs.

MATERIAL AND METHODS

The generic description is based on the characters used by Zweifel (1986) as modified by Wild (1995), who referred to neopalatines instead of palatines and an anterior vomer instead of prevomer. We distinguish between the absence of a quadratojugal and an incomplete maxillary arcade, which can occur when the quadratojugal and maxilla do not articulate with one another. We refer to terminal phalanges as being Y-shaped instead of bilobed.

Specimens collected in 1994 were preserved in 4% formalin, whereas those collected in 2001 and 2003 were preserved in 96% ethanol; all were stored in 70% ethanol. The frogs were dissected to determine sex based on the presence or absence of ovaries. Measurements taken with digital calipers and rounded to the nearest 0.1 mm are as follows: snout–vent length (SVL), tibia length, foot length (distance from proximal margin of inner metatarsal tubercle to tip of Toe IV), head length (from angle of jaw to tip of snout), head width (at level of angle of jaw), eye diameter, interorbital distance, upper eyelid width, internarial distance and eye–nostril distance (straight line distance between anterior corner of orbit and posterior margin of external nares). We measured spines and eggs to the nearest 0.1 mm with a stereomicroscope equipped with an ocular micrometer.

Specimens were cleared-and-double stained for cartilage and bone following the methods of Taylor & Van Dyke (1985) with few modifications. Terminology of cranial osteology follows that of Trueb (1973, 1993) and Duellman & Trueb (1994); terminology of hyoid apparatus follows that of Trewavas (1939) and that of heterotopic bones is adopted from Nussbaum (1982). Drawings were made using a stereomicroscope equipped with a camera lucida (Nikon SMZ 1000). Codes for museum collections are taken from Leviton *et al*. (1985) and Frost (2004), with the addition of MTD (Museum für Tierkunde Dresden) following Fritz (2002). For specimens examined, see Appendix 1.

RESULTS

TAXONOMY

MELANOPHRYNE GEN. NOV.

Type species: *Phrynopus carpish* Lehr, Rodríguez & Córdova, 2002.

Content: Two species.

Diagnosis: A genus of the family Microhylidae (presence of firmisternal pectoral girdle and palatal ridges) and subfamily Microhylinae (characterized by edentate maxillary arcade and small vomers). The olfactory capsules do not share a common medial wall. *Melanophryne* is easily distinguished from all other New World microhylid genera by its lack of a tympanum, tympanic annulus and stapes.

Description: Occipital fold absent. Clavicles and procoraoid cartilage present in pectoral girdle. Hyoid corpus lacking recurved ventral projections. Maxillary arcade complete. Paired vomers single, each consisting of small corpus with short pre- and postchoanal processes associated with anteromedial and medial margins of choana. Prootic not ossified posterolaterally; venter of otic capsule mineralized, but not ossified. Neopalatine covering posteroventral, posterior and posterodorsal margins of planum antorbitale. Anterior end of the cultriform process of the parasphenoid truncate and with an irregularly excised margin.

Melanophryne differs from Andean *Nelsonophryne* in the following features (characters of *Nelsonophryne* in parentheses; Table 1): clavicles and procoracoid cartilage present (absent); hyoid plate flat with or without simple, conical ventral projection (spinous, recurved projections present); double-walled (single-walled) septum nasi separating olfactory capsules; tympanic annulus and stapes absent (present); occipital fold absent (present); and Carpal 2 fused with Carpals 3 and 4 (Carpal 2 discrete).

Spines are present on the ventral surfaces of the jaws in males of the following genera: *Chiasmocleis*, *Ctenophryne*, *Dasypops* (restricted to chin), *Dermatonotus*, *Elachistocleis*, *Gastrophryne*, *Hypopachus*, *Melanophryne* (except *M. carpish*), *Nelsonophryne*, *Relictovomer* and *Stereocyclops*. Of the latter, *Melanophryne*, *Chiasmocleis* and *Stereocyclops* lack an occipital fold. Male *Melanophryne barbatula* have a large nuptial pad covering the dorsal surfaces of Fingers II and III, and the inner dorsolateral surface of Finger IV, whereas the nuptial pad is limited to Fingers II and III in *Stereocyclops*, and *Chiasmocleis* lacks a nuptial pad.

Etymology: The generic name *Melanophryne* is feminine and is composed of two nouns derived from the Greek, *melano*, meaning black, and *phryne*, meaning toad. The name refers to the black or dark brown colour of the skin in combination with *phryne*, which is a commonly used ending for microhylid generic names.

MELANOPHRYNE CARPISH (LEHR, RODRÍGUEZ & CÓRDOVA, 2002) COMB. NOV.

FIGS 1–3

Diagnosis: (1) Female SVL to 34.5 mm, male SVL to 29.4 mm. (2) Females and males lacking spines; males without vocal sac, vocal slits and nuptial pad. (3) Dorsal skin in females smooth; in males, finely areolate. (4) Dorsum black with green blotches; venter black with orange blotches on throat and chest. (5) Tongue oval. (6) Terminal phalanges irregularly T-shaped or knobbed; lacking prominent heterotopic cartilage at tibiofibular-tarsal joint; seven presacral vertebrae with Presacrals I and II fused; clavicles curved and

Table 1. Summary and comparison of morphological features among species of *Melanophryne* and *Nelsonophryne*

	Melanophryne		*Nelsonophryne*	
Character	*M. barbatula*	*M. carpish*	*N. aequatorialis*	*N. aterrima*
Occipital fold	Absent	Absent	Present	Present
Tympanum	Absent	Absent	Absent	Absent
Vocal slit	Absent	Absent	Absent	Absent
Spines:				
Females	Present in region of tympanum	Absent	A few small spines present on dorsum	A few small spines present on dorsum, and on dorsolateral surfaces of hind limbs and in cloacal region
Males	Present on chin and on dorsal and lateral surfaces of body; absent on forearms and hands; absent on feet except for venter of Toe V	Absent	Present on chin and on dorsum and dorsolateral surfaces of upper fore- and hind limbs; present on lateral edges of fingers and toes and ventral surfaces of feet	Present on chin; a few minute spines on dorsum, on fore- and hind limbs, on lateral edges of fingers and toes, and beneath cloaca
Nuptial pad	Covering Fingers II and III, and inner lateral margin of Finger IV	Absent	Covering Fingers II and III, and inner lateral margin of Finger IV	Covering Fingers II and III, and inner lateral margin of Finger IV
Heterotopic cartilage	Present at tibiofibular-tarsal joint	Absent	Absent	Absent
Medial prenasal process	Absent	Poorly developed	Well developed	Well developed
Septum nasi	Double walled	Double walled	Single	Single
Precerebral fenestra	Present	Absent	Absent	Absent
'Laminar' nasal bone	Present	Absent	Present	Absent
Nasals	Large; narrowly separated; covering lateral and anterior parts of olfactory capsule	Small; broadly separated; not covering lateral parts of olfactory capsule	Large; broadly separated; not covering lateral and anterior parts of olfactory capsule	Large; narrowly separated; not covering lateral and anterior parts of olfactory capsule
Vomer	Small, triangular	Small, triangular	Moderate with expanded corpus	Moderate with expanded corpus

Maxilla-premaxilla	Abut	Maxilla overlaps premaxilla	Abut	Abut
Neopalatine	Covering posteroventral, posterior, and posterodorsal margins of planum antorbitale	Covering posteroventral, posterior, and posterodorsal margins of planum antorbitale	Covering posteroventral, posterior, and posterodorsal (only at lateral extreme) margins of planum antorbitale	Covering posteroventral and posterior margins of planum antorbitale
Middle third of braincase	Cartilaginous	Cartilaginous	Cartilaginous	Mostly ossified
Terminus of cultriform process of parasphenoid	Truncate, but irregularly excised	Truncate, but irregularly excised	Bifurcate	Bifurcate
Prootic	Not ossified posterolaterally	Not ossified posterolaterally	Ossified	Ossified
Floor of otic capsule	Mineralized, not ossified	Mineralized, not ossified	Ossified	Ossified
Crista parotica	Triangular; not mineralized	Triangular; not mineralized	Quadrangular; mineralized	Quadrangular; mineralized
Stapes and tympanic annulus	Absent	Absent	Present	Present
Exoccipitals	Fused dorsomedially, but not ventromedially	Not fused dorsomedially or ventromedially	Not fused dorsomedially or ventromedially	Fused dorsomedially and ventromedially
Frontoparietal, orbital margin	Straight; orientated anteromedially	Straight; orientated anteromedially	Curved	Curved
Maxillary arcade	Complete	Complete	Complete	Incomplete; quadratojugal reduced
Hyoid corpus	Flat	Elevations; projections absent	Anterior and posterior projection present	Single, central projection
Carpal fusion	Carpals 2, 3, and 4	Carpals 2, 3, and 4	Carpals 3 and 4	Carpals 3 and 4
Terminal phalanges	Y-shaped	Irregularly knobbed	Irregularly knobbed	Acuminate
Clavicles	Straight; narrow; not reaching coracoids	Curved; narrow; not reaching coracoids	Absent	Absent
Procoracoid cartilage	Reduced, not in contact with coracoid	Reduced, in contact with coracoid	Absent	Absent
Presacral vertebrae	Eight	Seven; I and II fused	Eight	Eight
Presacral VIII	Procoelous	Amphicoelous	Amphicoelous	Amphicoelous

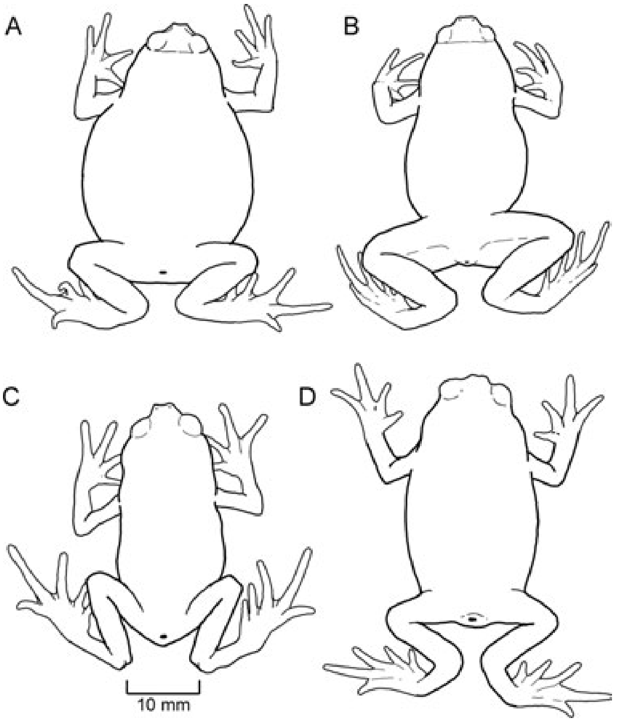

Figure 2. Body shapes of *Nelsonophryne* and *Melanophryne* in dorsal aspect. A, *Nelsonophryne aequatorialis* (KU 178289). B, *N. aterrima* (KU 30775). C, *Melanophryne barbatula* (MTD 45944). D, *M. carpish* (MHNSM 20699).

nearly reaching coracoid. (7) Hyoid corpus with simple, conical projection. (8) Laminar nasal bone absent.

In *Syncope*, Presacrals I and II also are fused; however, *M. carpish* has seven free presacral vertebrae, whereas *Syncope* has only six. In addition, the urostyle bears a basal transverse process; there is digital reduction in the hand and foot, and the quadratojugal is absent in *Syncope* (Walker, 1973; Walker & Duellman, 1974; da Silva & Meinhardt, 1999).

Remarks: Chromosome number, call and tadpole unknown.

Distribution and ecology: *Melanophryne carpish* is known from cloud forests at elevations between 2750 and 2960 m in central Peru (Departamento de Huánuco: Cordillera de Carpish), and in northern Peru (Departmento de Amazonas: Laguna de los Cóndores: 6°50′49″S, 77°41′40″W; Fig. 4), where P. Venegas heard the frog's advertisement call at an elevation of 2870 m in 2005. The distance between the two localities is 364 km (airline). The holotype was caught in a pitfall trap near terrestrial bromeliads in February; the second specimen (MTD 45614, a gravid female) was found in July in the centre of a water-filled bromeliad about 1 m above ground during the afternoon. In northern Peru, *M. carpish* was found in November on the ground below a terrestrial bromeliad (Venegas, 2005). *Melanophryne carpish* is restricted to primary cloud forests with (terrestrial) bromeliads, which are used as hiding places and presumably for deposition of eggs. The ovary of MTD 45614 contained 83 pigmented eggs that have an average diameter of 1.6 ± 0.14 mm ($n = 10$).

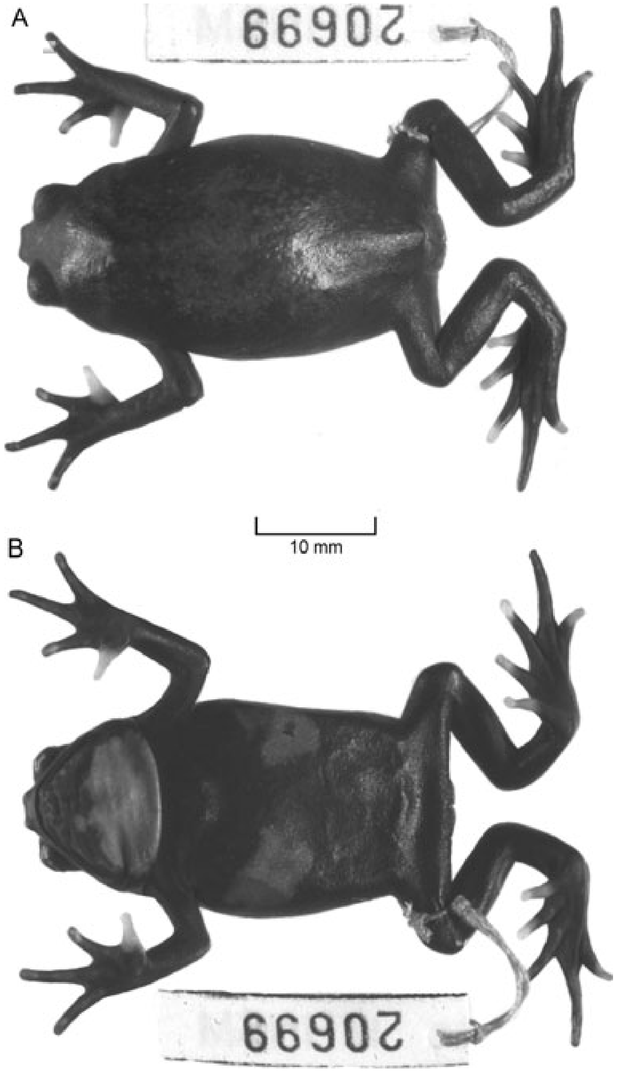

Figure 3. Adult female *Melanophryne carpish* (MHNSM 20699, holotype) in dorsal (A) and ventral (B) views. Photos by B. Bastian.

The stomach of *Melanophryne carpish* (MTD 45614) contained arthropods belonging to the following orders/families: Coleoptera, Juliaformes, Formicidae and Staphylinidae.

MELANOPHRYNE BARBATULA SP. NOV.

FIG. 5

Holotype: MHNSM 19904, male, collected in 1994 at Parque Nacional Yanachaga-Chemillen, at approxi-

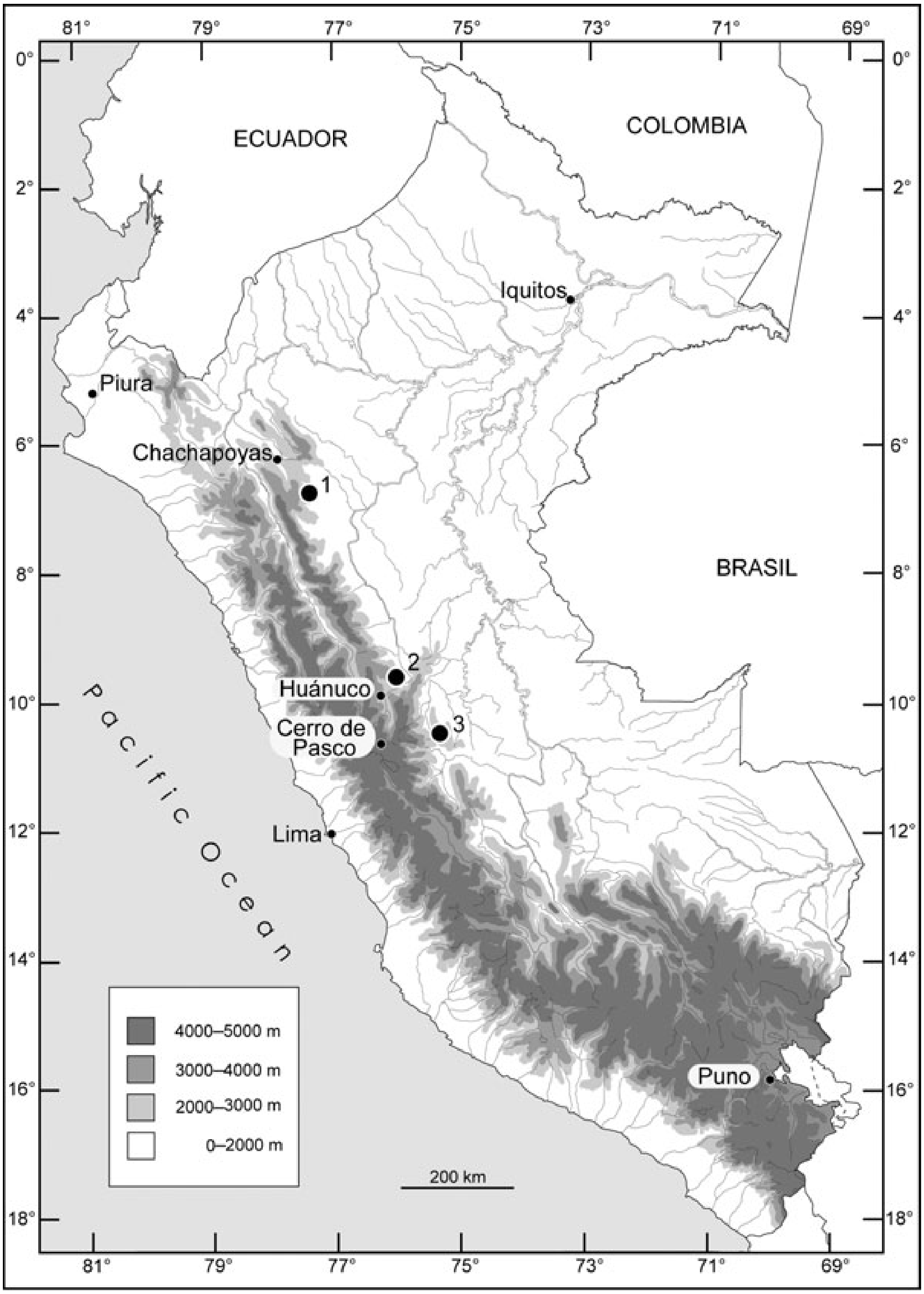

Figure 4. Map of Peru showing distribution of *Melanophryne carpish* (1, Departamento de Huánuco: Cordillera de Carpish: 09°43′19″S, 76°05′67″W, 2750–2960 m; 2, Departamento de Amazonas: Laguna de los Cóndores: 06°50′49″S, 77°41′40″W, 2870 m), and *M. barbatula* (3, Departamento de Pasco: Parque Nacional Yanachaga-Chemillén, *c*. 2500 m).

mately 2500 m, Distrito de Oxapampa, Provincia de Oxapampa, Departamento de Pasco, Peru, by J. Icochea.

Paratypes: MHNSM 19903 (female, cleared-and-stained), MHNSM 19905 (male), MTD 45944 (female), MTD 45945 (male), all collected with the holotype.

Diagnosis: (1) Female SVL to 27.0 mm, male SVL to 24.9 mm. (2) Females with spines only in region of tympanum; males with spines on ventral surface of lower jaw, dorsal and lateral surfaces of head, dorsum, body flanks, dorsal surface of upper arms, on ventral surface on tarsus, on lateral surface of Toe V, and ventral surface of Toe V; vocal sac and vocal slits absent, large nuptial pad present. (3) Dorsal skin of males and females smooth except for regions covered by spines. (4) Dorsum and venter uniform brown and lacking pattern. (5) Tongue oval. (6) Terminal phalanges Y-shaped; prominent heterotopic cartilage at tibiofibular-tarsal joint; eight presacral vertebra with Presacrals I and II separate; clavicles straight, narrow and not reaching coracoids. (7) Hyoid corpus flat, lacking projections. (8) Laminar nasal bone present.

Description of holotype: Adult male (Fig. 5); SVL 23.7 mm; tibia length 9.2 mm; foot length 10.8 mm; head length 7.6 mm; head width 8.5 mm; eye diameter 2.2 mm; interorbital distance 2.8 mm; upper eyelid width 1.9 mm; internarial distance 1.8 mm; eye–nostril distance 1.8 mm. Ventral skin smooth, dorsal skin with numerous small (0.05 mm in diameter) conical, white spines; large conical spines (up to 0.25 mm in diameter and 0.15 mm in height) on ventral surface of lower jaw (Fig. 6A), dorsal and lateral surfaces of head, dorsum, body flanks, dorsal surface of upper arms, on ventral surface of tarsus, on lateral surface of Toe V, and ventral surface of Toe V. Head nearly as broad as body; occipital fold absent. Snout truncate in dorsal and lateral profiles (Fig. 6B); nostrils positioned laterally close to tip of snout, equidistant from each other and from the eyes; loreal region nearly vertical, slightly concave; supratypmanic fold moderate, extending to insertion of arm, broad and thick above arm insertion; canthus rostralis slightly angular; eyes relatively large, eye diameter 29% of head length; width of upper eyelid 68% of interorbital distance; pupil round in preserved specimen. Tympanic annulus and tympanic membrane absent. Tongue large, oval, posterior half free. One palatal ridge visible when mouth open. Relative lengths of fingers: IV > V > III > II; digital tips rounded, flattened and slightly expanded, terminal grooves, lateral fringes and webbing absent; subarticular tubercles prominent, round, elevated; inner metacarpal tubercle ovoid, elongate, elevated, one-third size of outer metacarpal tubercle; outer metacarpal tubercle ovoid, elongate, elevated (Fig. 7); prominent nuptial pad covering dorsal surfaces of Fingers II, III and inner dorsolateral surface of Finger IV (Fig. 8A). Relative lengths of toes: IV > III > V > II > I, tips rounded, flattened and slightly expanded, terminal grooves and lateral fringes absent, webbing basal; subarticular tubercles prominent, ovoid, elongate, more prominent on Toes II and III than on others; inner metatarsal tubercle prominent, oval, elevated; outer metatarsal tubercle absent (Fig. 7); prominent heterotopic cartilage at tibiofibular-tarsal joint (Fig. 9).

Coloration of holotype in preservative: Dorsal, lateral and ventral surfaces dark brown with no pattern. Conical spines white to pale grey. Nuptial pad pale brown.

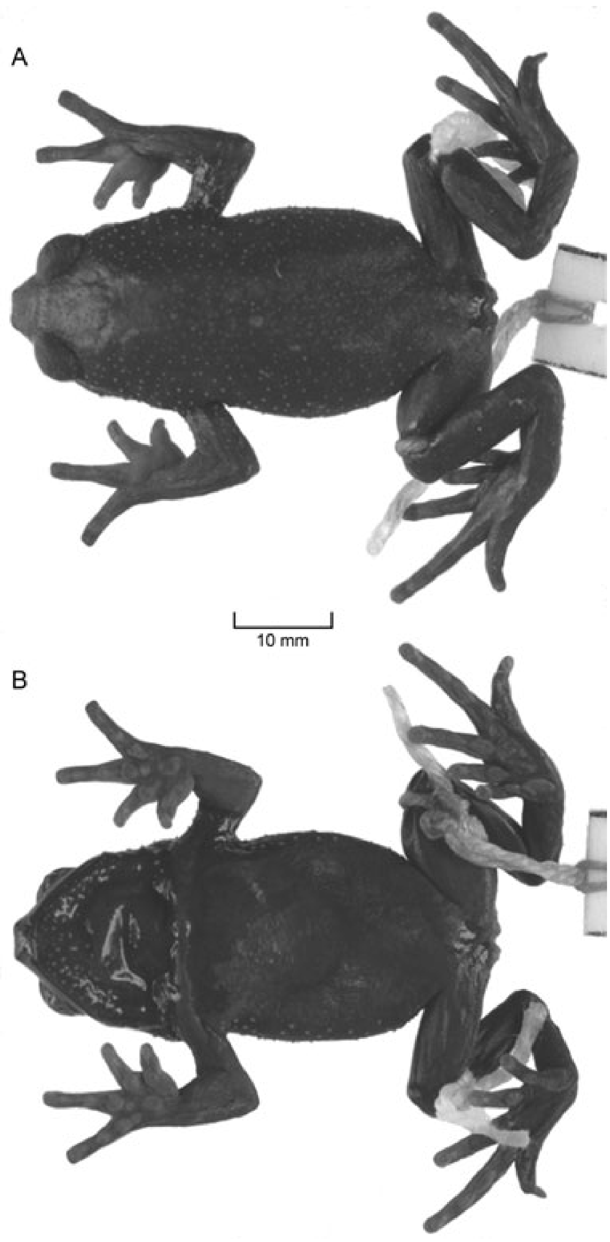

Figure 5. Adult male *Melanophryne barbatula* (MHNSM 19904, holotype) in dorsal (A) and ventral (B) views. Photos by F. Höhler.

Coloration of holotype in life: Unknown.

Variation: No variation in respect to coloration and external morphology was observed. For variation in meristic characters, see Table 2.

Etymology: The specific name *barbatula* is the diminutive of the Latin word *barbatus*, meaning bearded. The name is used in reference to the large spines of the ventral surface of the lower jaw, which resemble a beard.

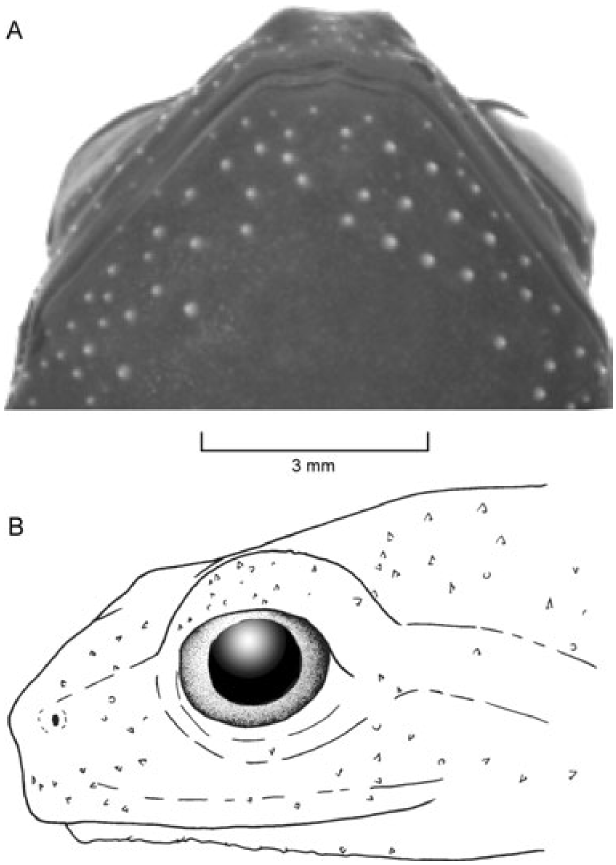

Figure 6. Ventral (A) and lateral (B) views of head of adult male *Melanophryne barbatula* (MHNSM 19905) to show distribution of spines on head.

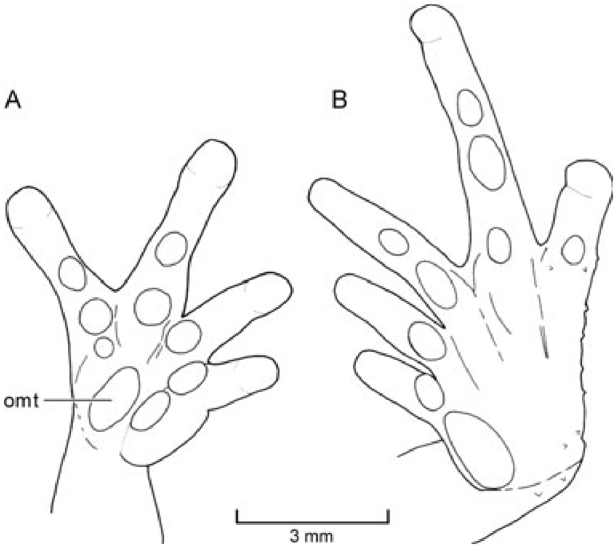

Figure 7. Ventral views of hand (A) and foot (B) of *Melanophryne barbatula* (MHNSM 19005). omt, outer metatarsal tubercle.

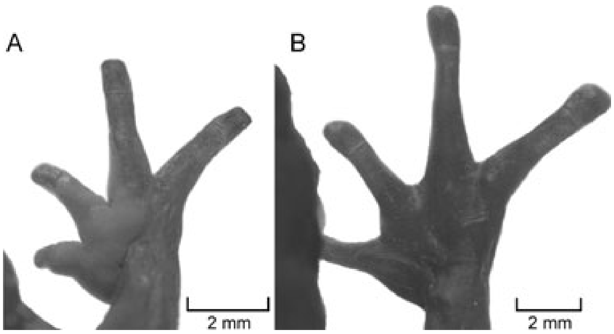

Figure 8. Dorsal views of hand of (A) male *Melanophryne barbatula* (MHNSM 19904) and (B) female *M. barbatula* (MTD 45944).

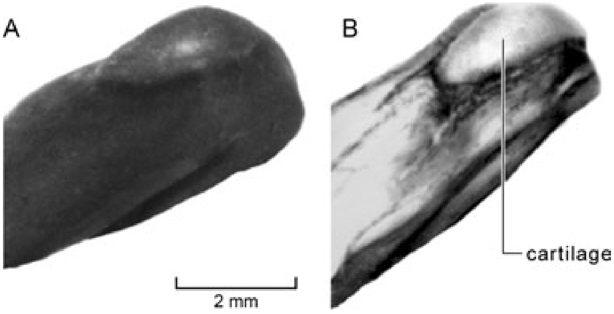

Figure 9. Prominent heterotopic cartilage at tibiofibular–tarsal joint (heel) in *Melanophryne barbatula* (MHNSM 19903, A, right heel; B, left heel with skin removed).

Remarks: Chromosome number, call, and tadpole unknown.

Distribution and ecology: *Melanophryne barbatula* is known only from Parque Nacional Yanachaga-Chemillén, which is located in the valley of the Río Palcazu in the Amazon Basin of central Peru. The park is 122 000 ha in area and consists primarily of the Cordillera de Yanachaga, which reach an elevation of 3643 m. On the eastern side of the park, the Cordillera de Yanachaga descends gradually into the valley of the Río Palcazu. On the western flank, the Cordillera de Santa Barbara reaches an elevation of 3400 m and is separated from the Cordillera de Yanachaga by the deep Huancabamba Canyon. The zoological collection of the Parque Nacional Yanachaga-Chemillén administration (INRENA) contains one unnumbered specimen of *M. barbatula* collected along with specimens of *Eleutherodactylus sagittulus* Lehr, Aguilar & Duellman at San Alberto (*c*. 10°32′53″S, 75°22′17″W, 2200 m).

The ovary of MHNSM 19903 contained 22 pigmented eggs with an average diameter of 1.6 ± 0.09 mm ($n = 10$).

Table 2. Morphometric data describing *Melanophryne*. Ranges (in mm) are followed by the mean and one standard deviation in parentheses

	M. barbatula		*M. carpish*	
Character	Females (*n* = 2)	Males (*n* = 3)	Females (*n* = 3)	Males (*n* = 1)
SVL	26.2–27.0 (26.6 ± 0.57)	21.8–24.9 (23.5 ± 1.56)	33.7–34.5 (34.0 ± 0.42)	29.4
Tibia length	9.3–10.6 (10.0 ± 0.92)	8.0–9.7 (9.0 ± 0.87)	10.9–11.7 (12.0 ± 1.08)	11.0
Foot length	12.9–14.0 (13.0 ± 1.41)	10.3–11.3 (10.8 ± 0.50)	13.2–15.9 (14.6 ± 1.36)	14.5
Head length	9.1–10.1 (9.6 ± 0.71)	7.3–8.8 (7.9 ± 0.79)	10.2–11.4 (10.7 ± 0.61)	10.2
Head width	10.1–10.3 (10.2 ± 0.14)	7.4–8.6 (8.2 ± 0.67)	11.5–12.6 (12.2 ± 0.61)	11.0
Eye diameter	2.2–2.3 (2.3 ± 0.07)	2.1–2.2 (2.1 ± 0.06)	2.6–3.1 (2.9 ± 0.26)	2.6
Interorbital distance	2.8–3.3 (3.1 ± 0.35)	2.7–3.0 (2.8 ± 0.15)	2.5–3.2 (2.9 ± 0.36)	3.4
Upper eyelid width	2.0–2.1 (2.1 ± 0.07)	1.8–1.9 (1.9 ± 0.06)	2.1–2.4 (2.2 ± 0.15)	2.2
Internarial distance	1.9–2.0 (2.0 ± 0.07)	1.3–1.8 (1.6 ± 0.29)	2.2–2.3 (2.3 ± 0.26)	2.4
Eye-naris distance	1.9–2.2 (2.1 ± 0.21)	1.7–1.9 (1.8 ± 0.10)	2.1–2.7 (2.4 ± 0.25)	1.9
Head width/SVL	0.38–0.39	0.34–0.36	0.33–0.37	0.37
Head length/SVL	0.35–0.37	0.32–0.35	0.30–0.33	0.35
Tibia length/SVL	0.34–0.40	0.37–0.39	0.32–0.35	0.37
Eye-naris distance/Eye diameter	0.07–0.08	0.81–0.90	0.58–0.95	0.73
Upper eyelid width/Interorbital distance	0.61–0.75	0.63–1.06	0.80–0.92	0.65

One stomach of *Melanophryne barbatula* (MHNSM 19903) contained arthropods belonging to the following families: Blattelidae, Carabidae, Cryptorhynchinae, Galumnidae, Oribatidae and Formicidae, and an unidentified insect larva. The arthropod composition indicates a leave litter habitat for *M. barbatula*.

OSTEOLOGY

Cranium of Nelsonophryne (Fig. 10)

Shape and proportions: The greatest widths of the skulls are at the angles of the jaws, and in both *Nelsonophryne aequatorialis* and *N. aterrima*, the skulls are wider than their medial lengths – about 21% in *N. aequatorialis* and 31% in *N. aterrima*. The rostrums of both species are large, occupying between one-quarter and one-third of the medial length of the skull in *N. aequatorialis* and more than one-third of the length in *N. aterrima*. The jaws are relatively short in both taxa, with the angle of the jaw lying anterior to the level of the fenestra ovalis in each.

Nelsonophryne aequatorialis differs from its congener in having a broadly rounded snout (vs. angular) viewed in dorsal profile. Owing to the shape of the braincase and the proportions of the skull, *N. aequatorialis* has a kidney-shaped orbit (delimited by the neurocranium and medial margin of the pterygoid) when viewed in dorsal aspect, whereas that of *N. aterrima* is quadrangular. The jaw of *N. aterrima* is markedly shorter than that of its congener. A transverse line projected across the skull between the ends of the upper jaw intersects the midportions of the cristae paroticae and traverses the frontoparietals at a level about one-quarter of their length forward (i.e., well anterior to the posterior margins) in *N. aterrima*, whereas the same line lies along the posterior margins of the cristae paroticae at about the midlength of the otic capsules and only slightly anterior to the posterior edges of the frontoparietals in *N. aequatorialis.*

Neurocranium: The anterior neurocranium, composed of the large olfactory capsules and anterior part of the braincase, is predominantly cartilaginous in both *N. aequatorialis* and *N. aterrima*. The internasal septum is robust in each taxon and terminates anteriorly in a distinct median prenasal process. The species possess complex septomaxillae, with each bone being lodged in the cartilaginous crista intermedia between the planum terminale at the ventral end of the oblique and alary cartilages, which form the anterior and posterior margins of the external naris, respectively.

The plana antorbitalae are robust, cartilaginous structures with a transverse orientation in *Nelsonophryne*. Each is invested by a simple, unadorned neopalatine along the posteroventral margin of the planum. The neopalatine is broadly separated from the maxilla laterally, but articulates with the anterior margin of the sphenethmoid medially. Sphenethmoid ossification is limited to the lateral and ventrolateral

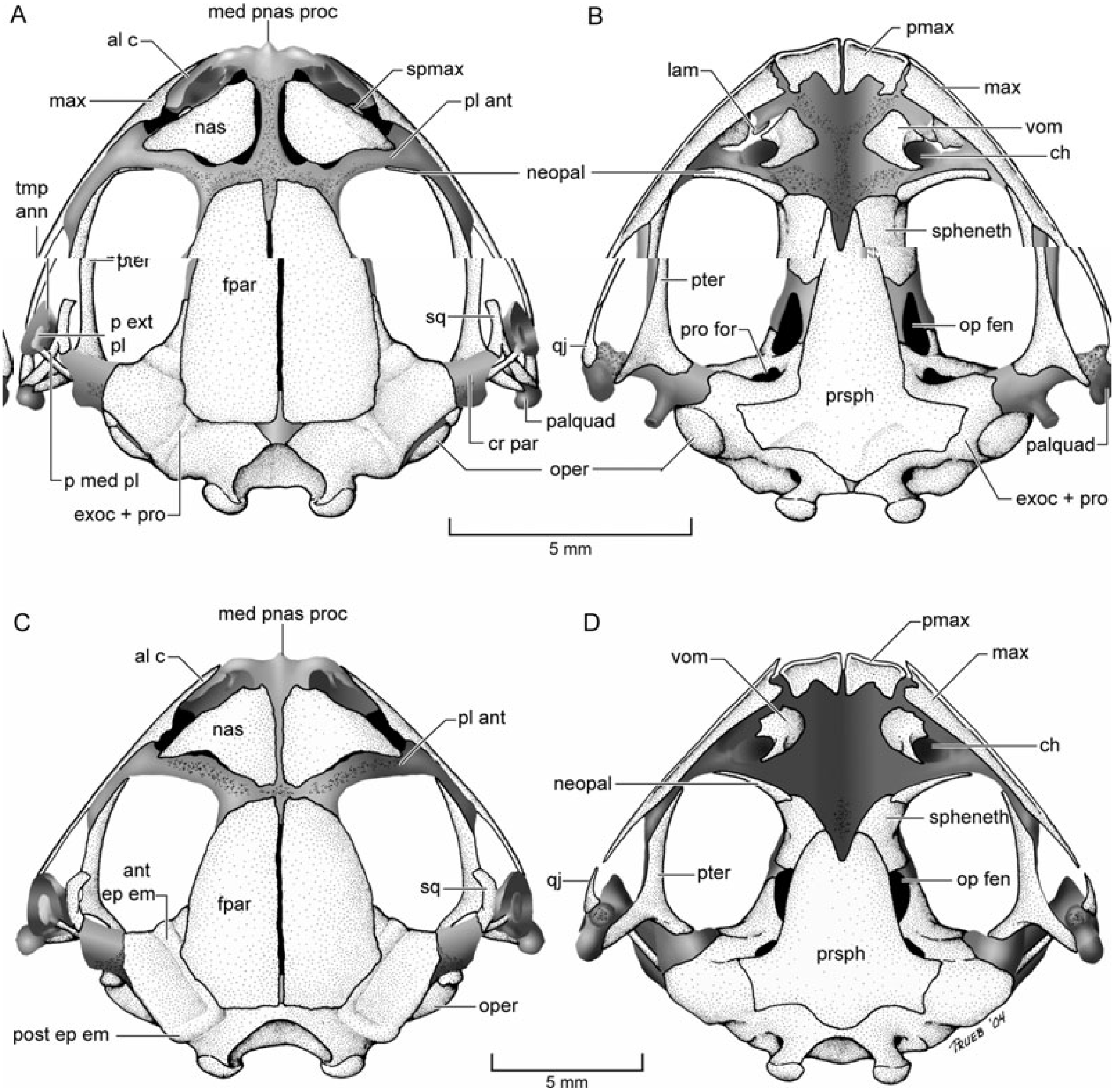

Figure 10. Crania of *Nelsonophryne*. *Nelsonophryne aequatorialis* (KU 178288) in dorsal (A) and ventral (B) aspects. *Nelsonophryne aterrima* (KU 30773) in dorsal (C) and ventral (D) aspects. Black and white stipple represents bone, whereas grey tone is cartilage; stippling in grey represents mineralization of the cartilage. al c, alary cartilage; ant ep em, anterior epiotic eminence; ch, choana; cr par, crista parotica; exoc, exoccipital; fpar, frontoparietal; lam, laminar bone; max, maxilla; med pnas proc, medial prenasal process; nas, nasal; neopal, neopalatine; op fen, optic fenestra; oper, operculum; p ext pl, pars externa plectri; p med pl, pars media plectri; palquad, palatoquadrate; pl ant, planum antorbitale; pmax, premaxilla; post ep em, posterior epiotic eminence; pre cer tect, precerebral tectum; pro for, prootic foramen; pro, prootic; prsph, parasphenoid; pter, pterygoid; qj, quadratojugal; spheneth, sphenethmoid; spmax, septomaxilla; sq, squamosal; tym ann, tympanic annulus; vom, vomer.

portions of the braincase; thus, the roof anterior to the frontoparietals and the ventromedial parts of the anterior braincase anterior to the parasphenoid are cartilaginous. The sphenethmoids are short, but nonetheless form the anterior margin of the optic fenestra in *N. aterrima*.

The exoccipitals and prootics are fused. Each otic capsule is well ossified and bears a broad, cartilaginous crista parotica that is associated with the exceedingly short otic process of the squamosal. The operculum is large and bony and located on the posterolateral surface of the otic capsule. The stapes lies anteriorly adjacent to the operculum in the fenestra ovalis. The pars media plectri is a long, slender, ossified element that extends anterolaterally beneath the crista parotica and behind the palatoquadrate and ventral ramus of the squamosal to terminate in the plate-like, cartilaginous pars externa plectri located in the middle of the incomplete tympanic annulus.

There are several significant differences in the neurocrania of *Nelsonophryne aequatorialis* and *N. aterrima*. In *N. aequatorialis*, the sidewall (paries nasi) of the nasal capsule is elaborated posterior to the septomaxilla and planum terminale. The lamina inferior extends posteriorly as a cartilaginous plate; as a consequence, this complex of nasal cartilages lies relatively close to the posterior nasal wall. The posterior end of what we infer to be the lamina inferior is associated with a small, flat, oval ossification that lies slightly dorsal and anterolateral to the prechoanal ramus vomer and the anterolateral margin of the choana (Fig. 10B). Herein, we refer to this pair of olfactory elements as laminar bones. These elements do not occur in *N. aterrima*, and among anurans, are known only in *Melanophryne barbatula*.

Patterns of mineralization of the cartilage differ in the species. In *Nelsonophryne aequatorialis*, disorganized mineralization of the ethmoid and olfactory cartilages is visible dorsally in the region of the septum nasi, ethmoid plate and medial portions of the plana antorbitale. Similar mineralization is visible ventrally anterior to the sphenethmoid, medially between the vomers and along the anteromedial margins of the vomers toward the premaxillae. In *N. aterrima*, mineralization is less extensive, with the ethmoid plate and dorsal parts of the plana antorbitale being only partially mineralized and mineralization of the floor of the braincase being limited to a small amount between the sphenethmoid bones.

Some of the most trenchant differences between these taxa involve the shape, proportions, and ossification of the orbital region of the braincase. The central braincase is longer and more slender in *Nelsonophryne aequatorialis* than in *N. aterrima*. Thus, the short sphenethmoids in *N. aequatorialis* comprise less than half the orbital length of the braincase and the middle third of the orbital walls are cartilaginous; the anterior two-thirds of the optic fenestra is cartilaginous, whereas the posterior third is formed by the prootic. The width of the braincase at the posterior part of the orbit (between anterior ends of anterior epiotic eminences) is less than twice the width of the braincase at the anterior margin of the orbit. The braincase is relatively shorter in *N. aterrima*. The sphenethmoids form the anteroventral margin of the optic fenestra; the posterior three-quarters of the optic fenestra is formed by the prootic and parasphenoid. There is only a narrow dorsal bridge of cartilage between the sphenethmoid and prootic bones. The width of the braincase at the posterior part of the orbit (between anterior ends of anterior epiotic eminences) is less than twice the width of the braincase at the anterior margin of the orbit.

The posterior neurocranium is more completely ossified in *Nelsonophryne aterrima* than in *N. aequatorialis*; in the former, the margin of the foramen magnum is complete in bone, whereas in the latter, the exoccipitals are separated by cartilage dorso- and ventromedially. The crista parotica of *N. aequatorialis* bears a distinct process associated with the otic ramus of the squamosal, whereas in *N. aterrima*, the otic process is associated with the anterolateral corner of the crista. The configuration of the otic capsules, as defined by the epiotic eminences, differs in these taxa. In *N. aequatorialis*, the anterior and posterior arms are about equal in length, whereas in *N. aterrima*, the anterior epiotic eminence is about twice as long as the posterior epiotic eminence. The frontoparietal overlaps the medial union of the epiotic eminences in *N. aequatorialis*, but in *N. aterrima*, the frontoparietal overlies the medial edge of the anterior eminence and terminates at the union of the anterior and posterior eminences. Although both taxa possess large, bony opercula, these are visible only in dorsal view, and in both dorsal and ventral aspects of *N. aequatorialis*.

Dorsal investing bones: Both species of *Nelsonophryne* have large, well-developed nasals and frontoparietals. Despite the expansive sizes of the nasals, the bones only partially roof the rostrum, and do not articulate with one another, the maxillae laterally or the frontoparietals posteriorly; most of the planum antorbitalae is exposed in each species. The frontoparietals are narrowly separated from one another in both taxa, and extend from the ethmoid plate to about the middle of the otic capsules posteriorly. The lateral margins of the bone in the orbital region are slightly convex in both species.

The nasals of *Nelsonophryne aequatorialis* are proportionally much smaller than those of *N. aterrima*. In the former, the bones are broadly separated from one another medially (narrow separation in *N. aterrima*) and neither completes the roof (tectum) of the olfactory capsules nor bridges the gap posteromedially to the ethmoid plate. The frontoparietals differ in their relationships with the otic capsules (described above) and with the orbital part of the neurocranium. Thus, the frontoparietal of *N. aequatorialis* has a rounded posterolateral corner, whereas the margin of the bone is at and parallel to the anterior epiotic eminence in *N. aterrima.* In *N. aequatorialis*, the cartilaginous margin of the orbital neurocranium is visible along the lateral margin of the frontoparietal in dorsal view, whereas in *N. aterrima*, the frontoparietal completely covers the underlying neurocranium.

Ventral investing bones: The parasphenoid is robust in both species of *Nelsonophryne* and the end of the cultriform process bears a deep, V-shaped incision. The parasphenoid is proportionally longer in *N. aequatorialis* than it is in *N. aterrima*; it extends from near the margin of the foramen magnum anterior to near the anterior margins of the sphenethmoids, whereas in *N. aterrima*, the bone reaches only the midlength of the sphenethmoids. At its greatest width (between right and left alar margins), the parasphenoid covers the medial half of each otic capsule in *N. aequatorialis*, but only the medial third of the capsule in *N. aterrima*. The lateral margins of the cultriform process converge anteromedially and are almost straight in *N. aequatorialis*, whereas they describe a shallow, sigmoid curve in *N. aterrima.*

The neopalatines are slender, unornamented, and in articulation with the anterolateral margins of the sphenethmoids in *Nelsonophryne.* In both taxa, the bone extends along the ventral and posterior margins of the planum antorbitale and is broadly separated from the maxilla. The neopalatine of *N. aequatorialis* is more extensive than that of *N. aterrima*, because in the former, the lateral part of the bone is visible along the posterior margin of the planum in dorsal aspect and can be seen to articulate with the anterior ramus of the pterygoid.

The vomers of *Nelsonophryne* are moderate in size; they lack dentigerous processes, are broadly separated from one another medially and do not articulate or fuse with any other palatal element. The body of the vomer is rectangular in *N. aequatorialis*, but subcircular in *N. aterrima*; in both taxa, the body of the vomer lies anteromedially adjacent to the choana. A short, stout prechoanal process is present along the anteromedial margin of the choana in *N. aequatorialis*, whereas in *N. aterrima*, the prechoanal process is present, but short and indistinct. In both species, a postchoanal process, which is longer and more robust than the prechoanal process, supports the posteromedial margin of the choana.

Maxillary arcade: In *Nelsonophryne*, the edentate maxillary arcade is composed of paired premaxillae, maxillae, and quadratojugals. Whereas the upper jaw is complete in *N. aequatorialis*, it is incomplete in *N. aterrima*, in which the quadratojugal is reduced and lacks an articulation with the maxilla. The maxillae and premaxillae have broad, well-developed partes palatinae. The pars palatina of the premaxilla bears acuminate medial processes and lateral processes that are blunt in *N. aequatorialis* and acuminate in *N. aterrima.* The pars facialis of the maxilla is poorly developed in both taxa. Although the maxillae lack a preorbital process, each bears a dorsal expansion in the region between the planum antorbitale and the anterior nasal cartilages. In *N. aterrima*, the anterior end of the pars facialis of the maxilla overlaps slightly the lateral margin of the premaxillae; the elements do not overlap in *N. aequatorialis*. The alary processes of the premaxillae differ in these species. In *N. aequatorialis*, the alary process is short, straight, and orientated more or less perpendicular to the horizontal plane of the skull in lateral view. In frontal aspect, the medial space between the premaxillae has a broad U-shape, owing to the parallel margins of the medial edges of the processes. In *N. aterrima*, the alary process is short, curved and orientated more or less perpendicular to the horizontal plane of the skull in lateral view. The curved alary processes diverge dorsolaterally from one another in frontal view.

Suspensory apparatus: The triradiate pterygoid is a robust bone with an anterior ramus that is nearly straight and parallel to the longitudinal axis of the skull in *Nelsonophryne.* The anterior ramus is distinctly separate from the pars palatina of the maxilla in *N. aterrima*, but laterally articulating with it in *N. aequatorialis*; in addition, the anterior ramus articulates with the dorsolateral end of the neopalatine in *N. aequatorialis.* Both species have robust medial rami that articulate with the anteroventral corner of the cartilaginous otic capsule in the extreme posterolateral region of the orbit. The medial and posterior rami are about the same length in *N. aequatorialis*, but in *N. aterrima*, the posterior ramus is distinctly longer than the medial ramus.

In *Nelsonophryne*, the T-shaped squamosals have exceedingly short otic rami that are associated with the anterolateral corner of the crista parotica. The zygomatic rami are about twice the length of the otic ramus and curved slightly anteromedially in dorsal view. The ventral rami invest the lateral surface of the palatoquadrate and articulate ventrally with the quadratojugals.

Hyoid apparatus (Fig. 11)

The hyoid corpus of both species of *Nelsonophryne* is as broad (at its waist between the anterolateral and posterolateral processes), or slightly broader, than its medial length. The cartilaginous corpus is partially mineralized in both species, with mineralization being more widespread in *N. aequatorialis* than in *N. aterrima.* Both taxa bear projections on the midventral surfaces of the hyoid corpora. In *N. aequatorialis*, there is a pair of projections, with the anterior one being located in the middle of the hyoid body and the posterior projection lying between the posteromedial processes. In *N. aterrima*, the single, large projection is located in the middle of the corpus. The anterolateral processes are broad, flat, hemispherical structures, whereas the posterolateral processes are slender, posteriorly curved projections. The bony posteromedial processes are expanded proximally and distally. Whereas the proximal expansion is symmetrical, the distal expansion produces peculiar thickenings or lumps along the distomedial margins of the processes. The hyoglossal sinus of *N. aequatorialis* is relatively larger than that of *N. aterrima*, and bears a hyoglossal membrane. The hyoids of both species bear flat, shelf-like extensions along the anterior curves of the hyalia.

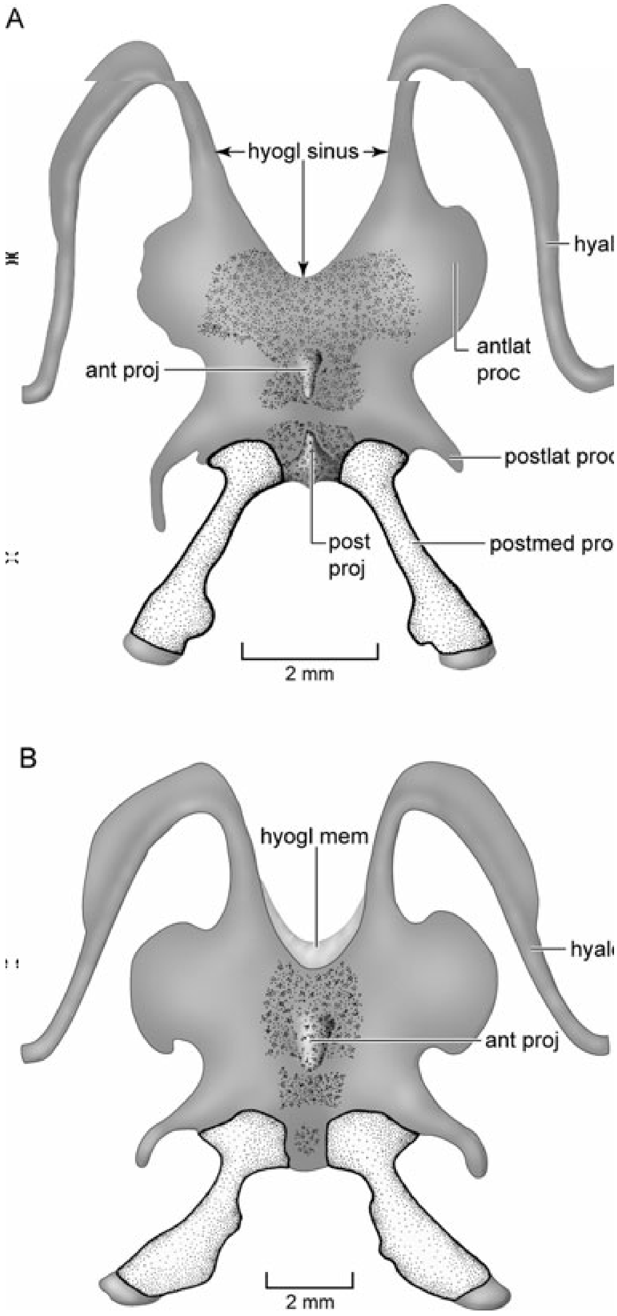

Figure 11. Hyoids of *Nelsonophryne* in ventral view. A, *Nelsonophryne aequatorialis* (KU 178288). B, *Nelsonophryne aterrima* (KU 30773). Black and white stipple represents bone, whereas grey tone is cartilage; stippling in grey represents mineralization of the cartilage. ant proj, anterior projection; antlat proc, anterolateral process; hyogl mem, hyoglossal membrane; hyogl sinus, hyoglossal sinus; post proj, posterior projection; postlat proc, posterolateral process; postmed proc, posteromedial process.

Postcranium of Nelsonophryne

Vertebral column (Fig. 12): There are eight presacral vertebrae of which the first seven are procoelous. In *Nelsonophryne aequatorialis*, Presacral VIII is biconcave. However, in *N. aterrima*, the articular surfaces of Presacral VIII are obscured by partially mineralized cartilage; the transverse profiles of these articulations appear to be more or less flat, as opposed to distinctly convex or concave.

The neural arches of the vertebrae are broad in both taxa, with each vertebra being wider than it is long. *Nelsonophryne aterrima* has a robust vertebral column, with all presacrals being imbricate. Imbrication is best developed on Presacrals I–IV; the neural arch of Presacral I bears blunt parasagittal processes, whereas the remaining vertebrae have dorsomedial neural spines that overlap the posteriorly adjacent vertebra. The presacrals are about equal in size to one another except for Presacral II, which is only about half as long as it is broad. In *N. aequatorialis*, Presacrals I–IV are not imbricate, V and VI are weakly imbricate, and VII and VIII are non-imbricate. Presacrals II and III are distinctly shorter than the remaining vertebrae, with II being substantially shorter than III.

The character of the transverse processes is similar in both species of *Nelsonophryne*, with Presacrals II–IV bearing moderately stout processes, and Presacrals V–VIII having much shorter, less robust processes. The vertebral profile of *N. aterrima* in decreasing order of overall width of bony parts is: III > IV ≅ sacrum > II > V > VI > VII = VIII; that of *N. aequatorialis* is: III > IV = sacrum = II = IV > VII > VI = VII = VII. The width of the bony sacral diapophyses in both taxa is unusually narrow. The diapophyses are symmetrically and only moderately dilated, with the

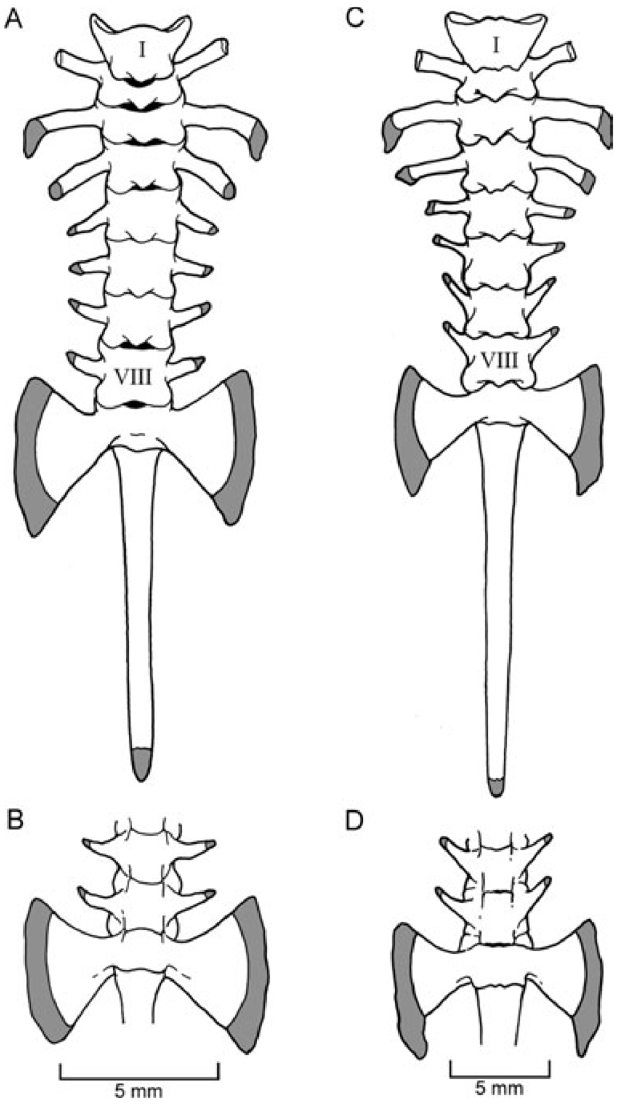

Figure 12. Vertebral columns of *Nelsonophyrne*. *Nelsonophryne aequatorialis* (KU 178288) in dorsal (A) aspect and sacral region in ventral (B) aspect. *Nelsonophryne aterrima* (KU 30773) in dorsal (C) aspect and sacral region in ventral (D) aspect. Presacrals I and VIII are numbered. Note the conditions of the centra of Presacral VIII, amphicoelous in *N. aequatorialis* and apparently notochordal in *N. aterrima.* Grey areas are cartilage.

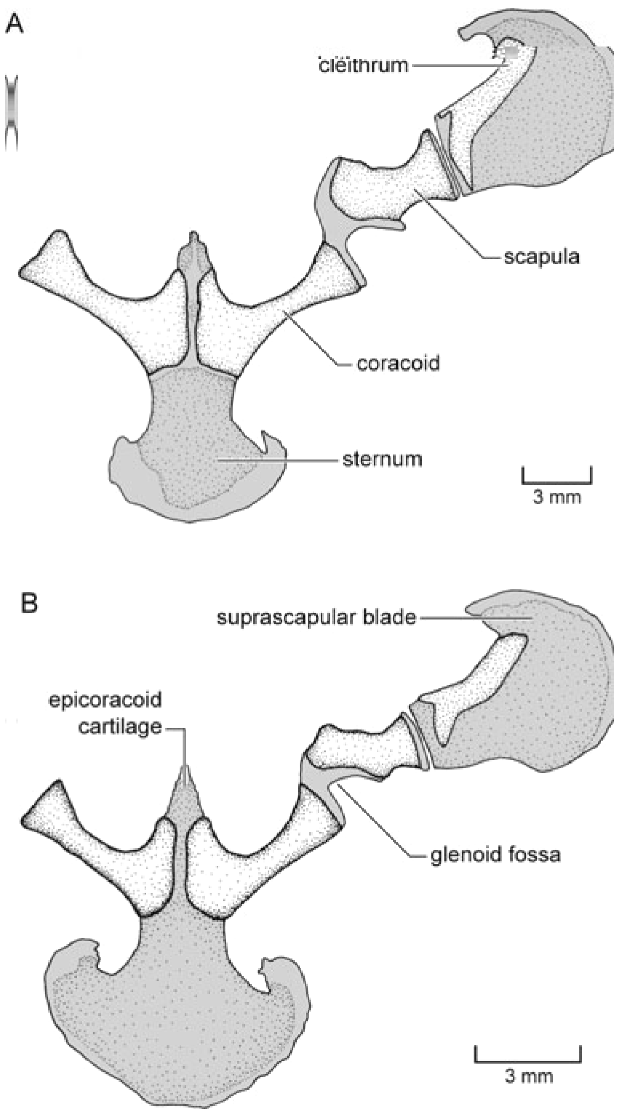

Figure 13. Pectoral girdles of *Nelsonophrыne* in ventral view. A, *Nelsonophryne aequatorialis* (KU 178288). B, *Nelsonophryne aterrima* (KU 30773). Note the absence of a clavicle and procoracoid cartilage in both species. Only the left scapula and suprascapula are shown, and these structures have been deflected into the ventral plane for the purposes of illustration. Black and white stipple represents bone, whereas grey tone is cartilage; stippling in grey represents mineralization of the cartilage.

width of the lateral margin being 2–2.5 times the width of the base; the diapophyses are slightly more dilated in *N. aequatorialis* than in *N. aterrima.* In each species, the urostyle articulates with the sacrum via a bicondylar articulation. The urostyle of *N. aequatorialis* is proportionally shorter (*c.* 87% of the length of the presacral vertebral column) than that of *N. aterrima*, in which the urostyle is approximately the same length as the presacral portion of the column.

Pectoral girdle (Fig. 13): The pectoral girdles of *Nelsonophryne* lack clavicles and procoracoid cartilages, and have only a median vestige of the epicoracoid cartilage. The coracoids are robust bones that are narrowly separated medially by cartilage. The glenoid end of the coracoid is symmetrically expanded to about twice the width of the midshaft width of the bone. The sternal end is about twice the width of the glenoid end and is asymmetrical, being more expanded anteromedially than posteromedially. The sternum is robust and mineralized in both species, but proportionally much larger in *N. aterrima* than in *N. aequatorialis.*

The scapulae are poorly developed in *Nelsonophryne.* The glenoid fossa is cartilaginous and the scapula is unicapitate, lacking a distinct partes acromialis and glenoidalis. The leading edge of the ossified scapula is anteriorly convex and about 2.5 times the posterior margin of the bone adjacent to the glenoid fossa. The suprascapular cartilage is well developed and heavily mineralized. The dorsal border is rounded and bears a distinct anterodorsal process or hook in each species. The cleithrum is better developed in *N. aequatorialis* than in *N. aterrima.* It invests the leading edge of the suprascapula in each species, but has a more extensively developed posteroventral process in *N. aequatorialis* than in *N. aterrima.*

Pelvic girdle (Fig. 14). In both species of *Nelsonophryne*, the ilial shafts are long, slender and lacking dorsolateral crests. The overall length of each girdle is about 2.5 times the width between the anterior ends of the ilial shafts. Both have low ilial prominences and pubes that are heavily mineralized, but not ossified.

In *Nelsonophryne aequatorialis*, the halves of the pelvic girdle are not fused; thus, cartilage separates the ilia and ischia medially and forms the preacetabular margin. In addition the posterior margins of the ischia are cartilaginous. The acetabulum is subcircular and eccentric, and the preacetabular angle (between the ilial shaft and the anterior margin of the acetabular ilium in lateral view) is approximately 90°. The acetabular portion of the girdle is longer than it is high.

The pelvic girdle of *Nelsonophryne aterrima* differs from that of *N. aequatorialis* in being more extensively ossified; both the ilia and the ischia are completely ossified. The acetabulum is round and the preacetabular angle acute.

Manus and pes (Fig. 15). *Nelsonophryne* has the standard anuran phalangeal formulae for the hand and foot of 2-2-3-3 and 2-2-3-4-3, respectively. In increasing order of length, the order of the digits on the hand is: II–III–V–IV, and that of the foot is: I–II–V–III–IV. In both species the carpus is composed of a radiale, ulnare, Element Y, separate Carpals 1 and 2, and a large postaxial element assumed to represent a fusion of Carpals 3 and 4. Element Y seems to be slightly larger in *N. aterrima* than in *N. aequatorialis*, and the prepollex is composed of three elements in *N. aterrima*, and only two bones in *N. aequatorialis.* The tarsus is composed of Tarsals 1–3 in each species. Although the prehallux comprises two bones in both species, the element is markedly larger in *N. aterrima* than in *N. aequatorialis.* The most distinctive difference between the hand and foot morphology of these two species is the shape of the terminal phalanges; they are expanded and slightly bilobed in *N. aequatorialis*, whereas they are simple and unexpanded in *N. aterrima.*

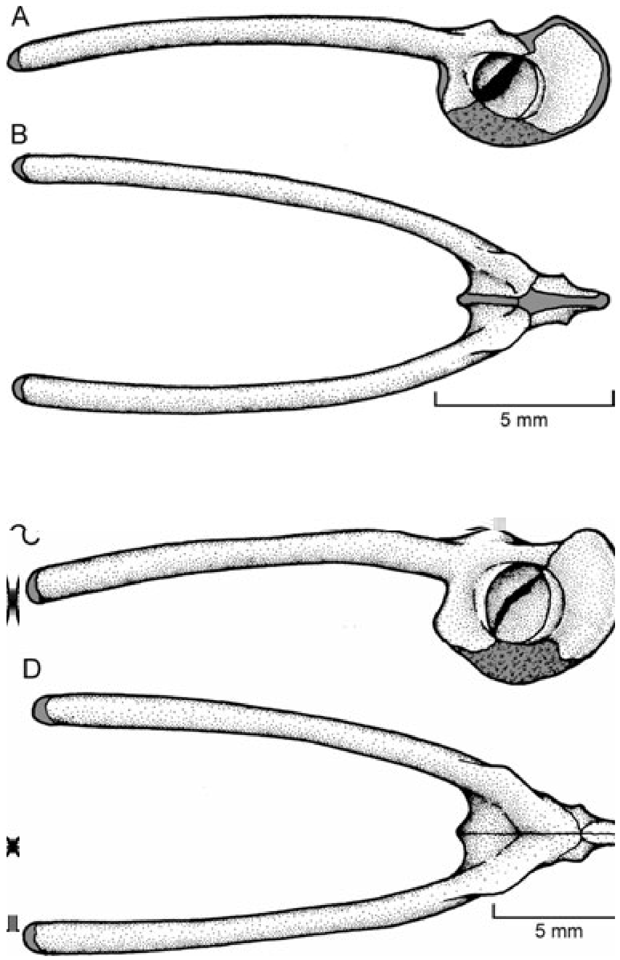

Figure 14. Pelvic girdles of *Nelsonophryne. Nelsonophryne aequatorialis* (KU 178288) in lateral (A) and dorsal (B) aspects. *Nelsonophryne aterrima* (KU 30773) in lateral (C) and dorsal (D) aspects. Grey denotes cartilage, and grey with stipples, mineralized cartilage.

Cranium of Melanophryne (Fig. 16)

Shape and proportions: The greatest widths of the skulls are at the angles of the jaws, and in both *Melanophryne carpish* and *M. barbatula*, the skulls are wider than their medial lengths – about 35% in *M. carpish* and 42% in *M. barbatula.* The rostrums of both species are large and angular to blunt terminally when viewed in dorsal profile. The rostrum occupies between one-quarter and one-third of the medial length of the skull in *M. barbatula* and about one-

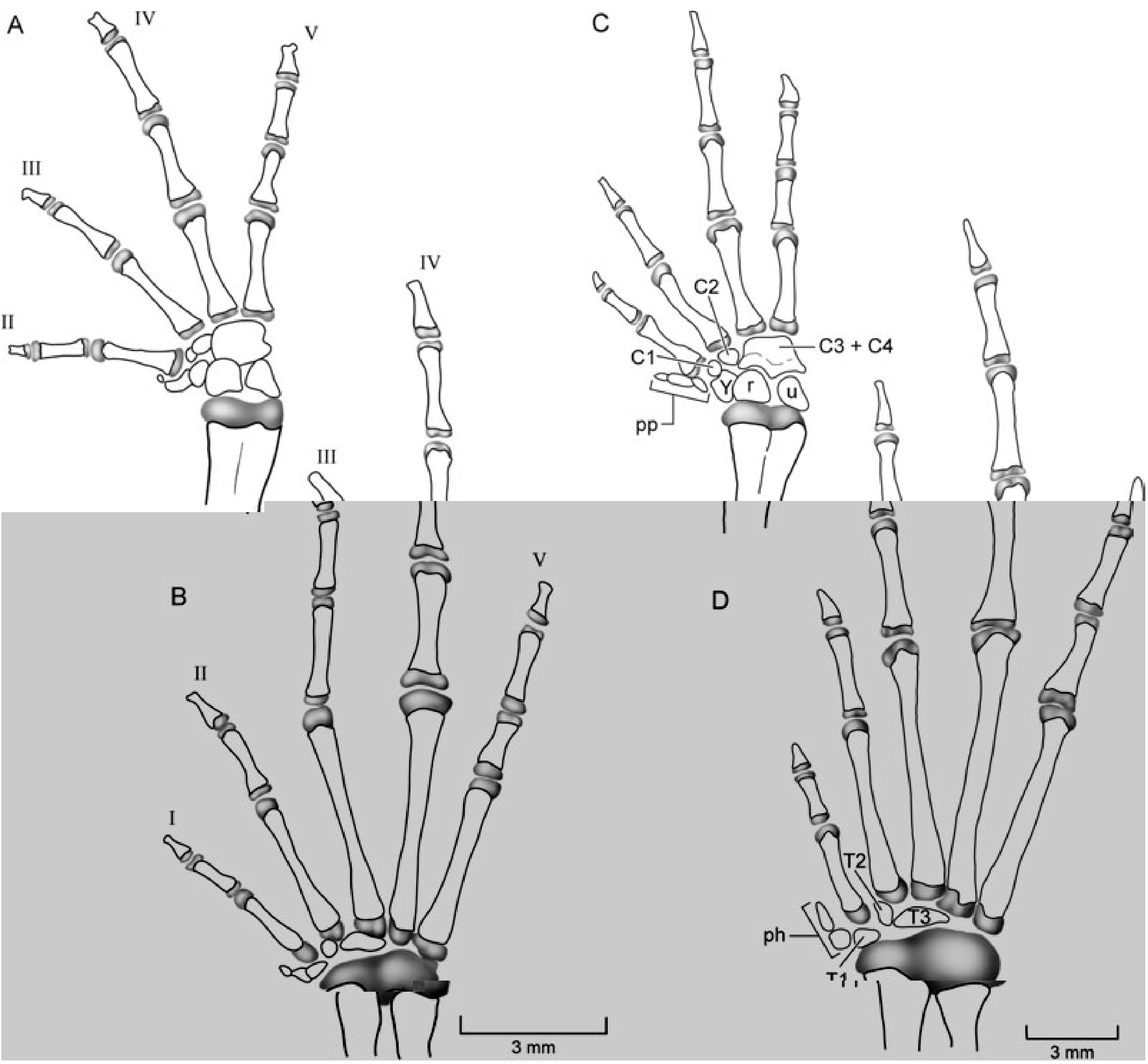

Figure 15. Dorsal views of right hands and feet of *Nelsonophryne. Nelsonophryne aequatorialis* (KU 178288) hand (A) and foot (B). *Nelsonophryne aterrima* (KU 30773) hand (C) and foot (D). Bones are shown in white and grey denotes cartilage. C1–4, Carpals 1–4; ph, prehallux; pp, prepollex; r, radiale; T1–3, Tarsals 1–3; u, ulnare; Y, Element Y.

third of the length in *M. carpish.* The jaws are relatively long in both taxa, with the angle of the jaw lying lateral to the level of the fenestra ovalis in each. The posterior position of the angles of the jaws is reflected by the projection of a transverse line projected across the skull between the ends of the upper jaw; in both species, such a line lies posterior to the cristae paroticae, traversing the otic capsules in the posterior quarter of their lengths along the posterior margin of the frontoparietals.

The most notable difference in cranial shape and proportions in *Melanophryne* is in the orbit. In *M. carpish*, the dorsal shape of the orbit, as circumscribed by the pterygoid and neurocranium, is ovoid, with the midorbital width being slightly more than half the length (60%). In *M. barbatula*, the orbit is narrowly oval, with the midorbital width being less than half the length (40%).

Neurocranium: In *Melanophryne*, the anterior neurocranium comprising the large olfactory capsules and anterior part of the braincase is mostly cartilaginous, but some mineralization is apparent in the medial wall of each capsule. Although the internasal area is

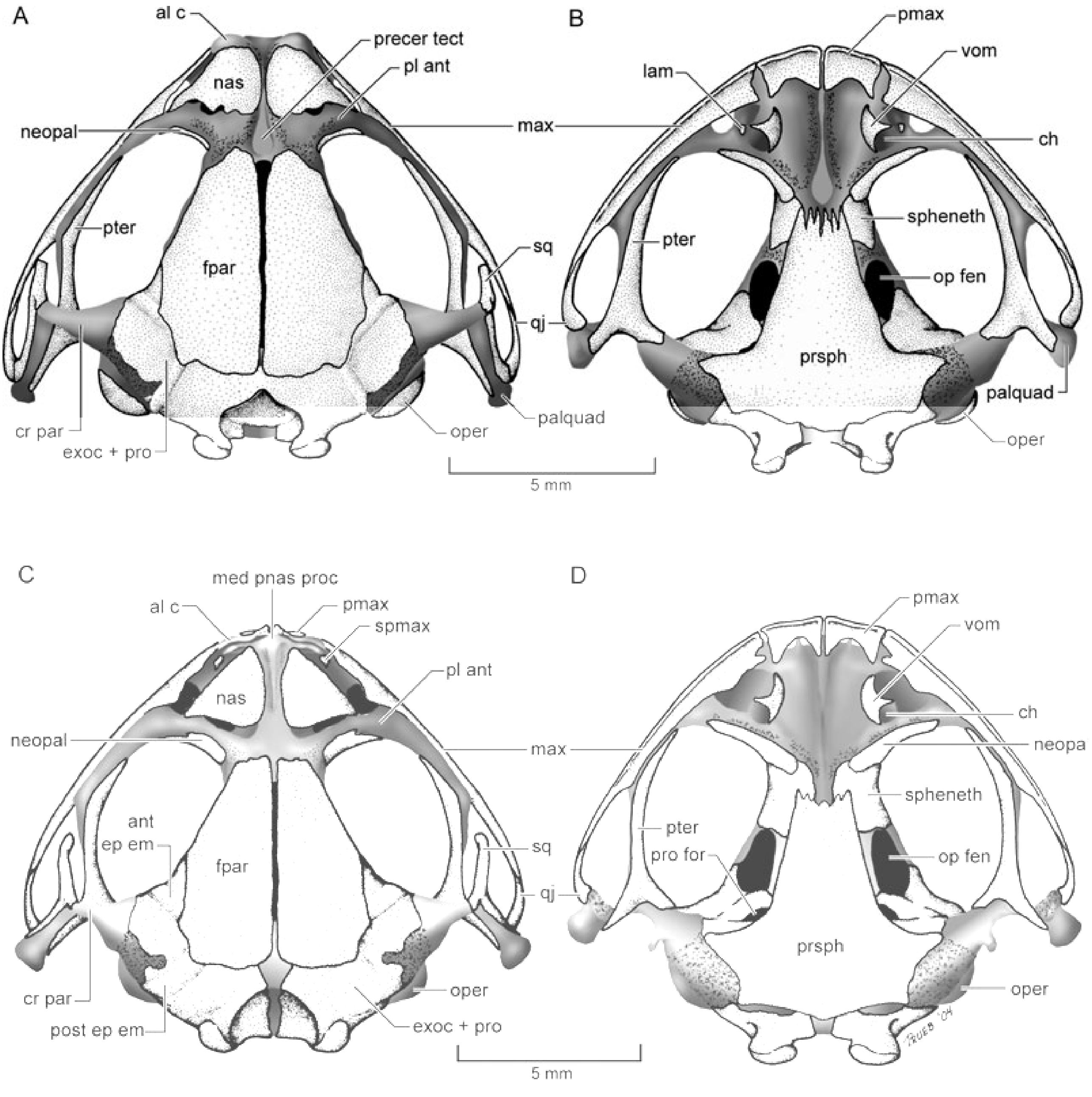

Figure 16. Crania of *Melanophryne*. *Melanophryne barbatula* (MHNSM 19903) in dorsal (A) and ventral (B) aspects. *Melanophryne carpish* (KU 45614) in dorsal (C) and ventral (D) aspects. Black and white stipple represents bone, whereas grey tone is cartilage; stippling in grey represents mineralization of the cartilage. Abbreviations as in Figure 10.

continuous in cartilage, there is a pair of medial walls separated by a thinner area of cartilage. In dorsal aspect, mineralization of these medial nasal capsule walls is visible; ventrally, the walls can be seen to diverge slightly from one another anteromedially. The complex septomaxilla is located in the cartilaginous crista intermedia between the planum terminale at the ventral end of the oblique cartilage and alary cartilage.

The olfactory capsules of *M. carpish* and *M. barbatula* differ in several respects. In *M. barbatula*, a prenasal process is absent, whereas in *M. carpish* a small process is present. The presence of a distinct medial wall for each olfactory capsule is more readily apparent in *M. barbatula* than in *M. carpish*. *Melanophryne barbatula* is further characterized by having a teardrop-shaped precerebral space at the front end of the braincase between the pair of olfactory capsules.

Although both taxa have complex septomaxillae, only *M. barbatula* has a pair of laminar bones, as described in *Nelsonophryne aequatorialis.*

The plana antorbitalae are robust, cartilaginous structures that have an oblique, anterolateral orientation in *Melanophryne*. Each planum is invested by the neopalatine; this bone broadly overlaps the anterior margins of the sphenethmoids medially and extends along the ventral, posterior and dorsal margins of the planum. The neopalatine is broadly separated from both the maxilla and the anterior ramus of the pterygoid. The dorsomedial portions of the plana antorbitalae are partially mineralized, along with the ventral parts of the plana along the anterior margins of the neopalatines in both species. Ventrally, the floor of the braincase is lightly mineralized between the sphenethmoids in *M. carpish*, but mineralization is absent in this area in *M. barbatula*. Sphenethmoid ossification is limited to the lateral and ventrolateral portions of the braincase in both taxa; thus, the roof anterior to the frontoparietals and the ventromedial parts of the anterior braincase anterior to the parasphenoid are cartilaginous. The sphenethmoids comprise less than half of the orbital portion of the braincase in *M. carpish*, and only about one-quarter of the braincase in *M. barbatula*. In *M. carpish*, most of the margin of the optic fenestra is cartilaginous, but the posterior edge is formed by the bony prootic. In *M. barbatula*, less of the margin of the fenestra is cartilaginous (*c.* the anterior two-thirds), with more of the fenestra being bony (i.e. *c.* posterior third formed by the prootic). The width of the braincase at the posterior part of the orbit (between the anterior ends of the anterior epiotic eminences) is distinctly greater than twice the width of the braincase at the anterior margin of the orbit in both species of *Melanophryne.*

Although the exoccipitals and prootics are fused, the otic capsules are not synostotically united in *Melanophryne carpish*, and only partially united in *M. barbatula*; thus, in *M. carpish*, the foramen magnum has broad areas of cartilage dorso- and ventromedially between the exoccipitals, and in *M. barbatula*, there is a broad area of cartilage ventromedially between the exoccipitals. The otic capsules are poorly ossified in both species, with most of the ventral parts and the posterolateral dorsal parts bearing irregular mineralization. *Melanophryne carpish* is distinguished by a cartilaginous gap in the floor of the otic capsule between the bony exoccipital and the parasphenoid. In both species, the crista parotica is moderately narrow and bears a slender anterolateral process that is associated with the squamosal via an exceedingly short otic ramus. The anterior and posterior epiotic eminences are about equal in length in both species, but the canals seem proportionally narrower in *M. barbatula* than in *M. carpish. Melanophryne carpish* has a large, cartilaginous operculum on the posterolateral surface of the otic capsule; equal parts of the operculum are visible in dorsal and ventral views. By contrast, the large operculum in *M. barbatula* is about half ossified and located on the posterolateral surface of the otic capsule; more of the operculum is visible from the dorsal than from the ventral aspect. Both taxa lack stapes and tympanic annulae.

Dorsal investing bones: The nasals are relatively small and broadly separated from one another medially in *Melanophryne carpish*, whereas they are moderately sized and narrowly separated from one another medially in *M. barbatula*. The bones are triangular in *M. carpish*, but blunt anteriorly and with an irregularly scalloped posterior margin in *M. barbatula.* A posteroventral maxillary process lies dorsal to the planum antorbitale in both taxa, but is better developed in *M. barbatula.* The nasals are broadly separated from the frontoparietals in both species, but the separation is proportionally greater in *M. barbatula* than in *M. carpish.* The frontoparietals extend from the ethmoid plate to about the middle of the otic capsules posteriorly; they overlap the union of the anterior and posterior epiotic eminences in both species. The length of the bone is about 2.5 times its greatest width. In *M. carpish*, the supraorbital margins of the frontoparietals are straight and anteromedially convergent to a relatively narrow, truncate anterior margin; they completely conceal the lateral walls of the braincase in the orbital region. However, in *M. barbatula*, the anterior margin of the frontoparietal is not truncate and the cartilaginous dorsolateral walls of the braincase are visible along the margins of the frontoparietals in the orbital region. Medially, the frontoparietals are narrowly separated in both species; their posterior margins are widely separated from the dorsal margin of the foramen magnum.

Ventral investing bones: The parasphenoid is moderate in size, extending from near the margin of the foramen magnum anterior to the midlength of sphenethmoids in *Melanophryne carpish.* In *M. barbatula*, the cultriform process of the parasphenoid nearly reaches the anterior margins of the sphenethmoids and is closer to the neopalatines than in *M. carpish*. At its greatest width (between anterolateral corners of alae), the parasphenoid covers about half of each otic capsule in both taxa. The bone is wider than it is long and has extraordinarily broad (anterior to posterior) alae in both species. The lateral margins of the cultriform process are straight and slightly convergent anteriorly in both *M. carpish* and *M. barbatula*. The anterior end of the process has an irregularly excised, truncate anterior margin in both species of *Melanophryne*.

The neopalatine in *Melanophryne* is a large, blunt-ended bone that invests the ventral, posterior and posterodorsal margins of the planum antorbitale. It is visible in both dorsal and ventral views. The medial end overlaps the sphenethmoid in both taxa, but the overlap is broader in *M. carpish* than in *M. barbatula.* In both species of *Melanophryne*, the lateral end of the neopalatine is broadly separated from both the maxilla and the anterior ramus of the pterygoid.

The vomers of *Melanophryne* are small, isolated bones that are broadly separated from one another medially. The body of the vomer is crescentic and lies anteromedially adjacent to the choana. A short, distinct prechoanal process lies along the anterior-anteromedial margin of the choana, and a longer postchoanal process supports the medial margin of the choana. A dentigerous process is absent in both species.

Maxillary arcade: The edentate maxillary arcade consists of paired premaxillae, maxillae, and quadratojugals, and is complete in *Melanophryne*. The maxillae have moderately well developed partes palatinae. In *M. carpish*, the pars palatina broadens abruptly in the choanal region, whereas in *M. barbatula*, the lingual margin of the pars palatina forms a smooth arc, gradually becoming wider in the choanal region. In both taxa, the pars palatina of the premaxilla is well developed and elaborated into acuminate medial and lateral processes; the lateral processes are slightly larger than the medial processes. The posterior margin is deeply concave in *M. carpish* and shallowly concave in *M. barbatula.* The maxilla lacks a preorbital process, but bears a low dorsal expansion in the region between the planum antorbitale and the anterior nasal cartilages. The anterior end of the pars facialis of the maxilla does not overlap the lateral margin of the premaxilla. In *M. carpish*, each premaxilla bears a relatively tall, curved alary process that is orientated approximately perpendicular to the horizontal plane of the skull in lateral view; in frontal view, the curved alary processes diverge dorsolaterally from one another. However, in *M. barbatula*, the alary processes of the premaxillae are tall, slender and straight, rather than curved.

Suspensory apparatus: The triradiate pterygoid is slender in *Melanophryne carpish* and more robust in *M. barbatula.* The long, slightly curved anterior ramus nearly reaches the planum antorbitale anteriorly in both taxa. In *M. carpish*, the medial ramus is short and blunt, and invests the anteroventral margin of the cartilaginous otic capsule in the posterolateral region of the orbit. In *M. barbatula*, the medial ramus is about the same length as the posterior ramus of the pterygoid, but markedly more stout, whereas in *M. carpish*, the posterior ramus is about twice the length of the medial ramus.

The squamosal otic ramus that is associated with the anterolateral corner of the crista parotica is so abbreviated that the bone has more of an inverted and reflected L-shape than a T-shape. The zygomatic ramus is curved slightly anteromedially in dorsal view in *Melanophryne carpish* and is substantially longer than the short straight zygomatic ramus in *M. barbatula*. In both species, the ventral ramus of the squamosal invests only the anterolateral edge of the palatoquadrate and articulates ventrally with the quadratojugal.

Hyoid apparatus (Fig. 17): The hyoid corpus is slightly longer than broad (at its waist between the anterolateral and posterolateral processes) in *Melanophryne carpish*, and about equal in length and breadth in *M. barbatula.* The cartilaginous corpus is partially mineralized in both species of *Melanophryne* – centrally and peripherally in *M. carpish*, but symmetrically distributed across the corpus between the anterolateral alary processes in *M. barbatula.* Only *M. carpish* bears a pair of hyoid projections on the midventral surface of the hyoid corpus. The anterolateral processes are narrow and flat, and bear a short anterior process in both taxa. The posterolateral processes are slender, posteriorly curved projections that are longer in *M. barbatula* than in *M. carpish*. In *M. carpish*, the bony posteromedial processes are expanded proximally; the distal end is relatively slender, but there is a thickening along the distomedial margin of each process. In *M. barbatula*, the posteromedial processes are reminiscent of bowling pins; they are slightly expanded proximally and the distal ends are bulbous. The hyoglossal sinuses of both species are V-shaped, and that of *M. barbatula* is deeper than the hyoglossal sinus of *M. carpish.* This difference reflects the differences in the shapes of the anterior hyalia, which are sharply curved in *M. barbatula* and broadly curved in *M. carpish*; a hyoglossal membrane also is present in the latter. The hyalia of the two species also differ by *M. barbatula* possessing a short anterior process and *M. carpish* having a broad, shallow shelf along the anterior margin.

Postcranium of Melanophryne

Vertebral column (Fig. 18): *Melanophryne barbatula* has eight procoelous, non-imbricate presacral vertebrae. The column is unusual in having anterior presacrals that are less imbricate than the posterior presacrals. Presacrals II and III are shorter than the posterior presacrals. The vertebral profile in decreasing order of width of the bony parts is: III > sacrum > II ≅ IV > V ≅ VII ≅ VIII > VI. The sacral diapophyses

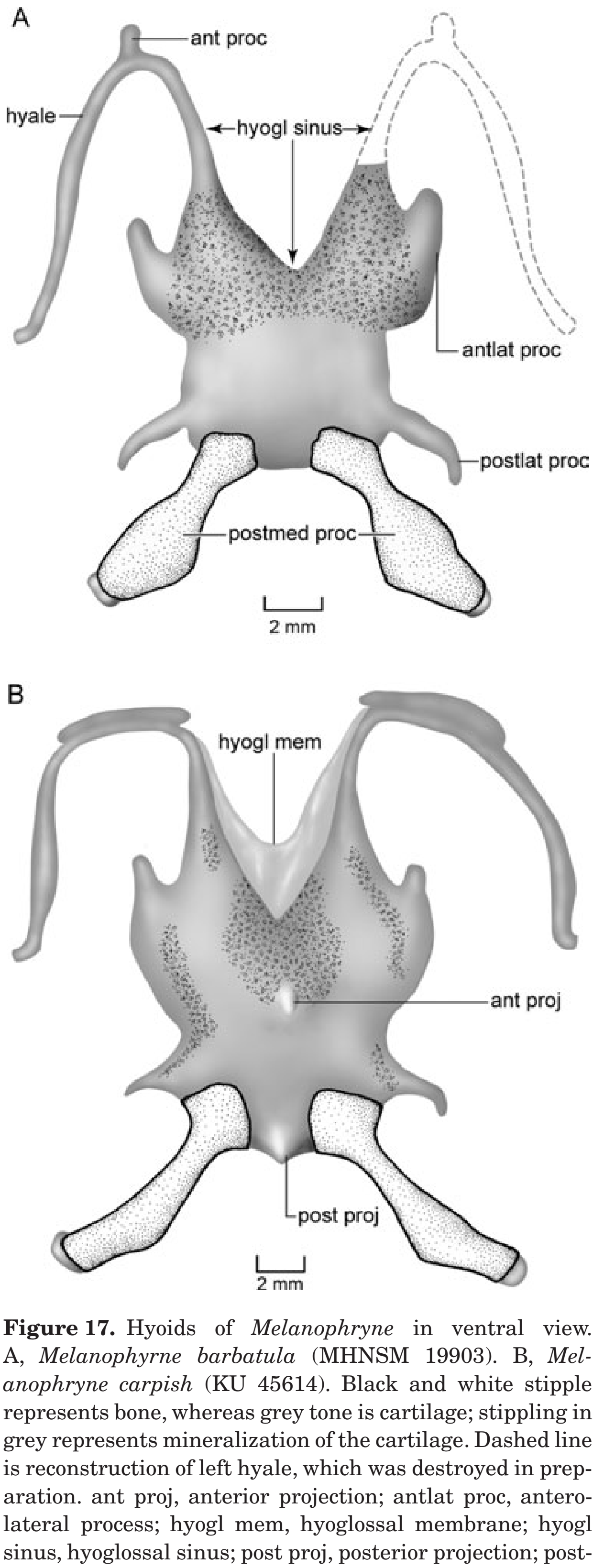

Figure 17. Hyoids of *Melanophryne* in ventral view. A, *Melanophyrne barbatula* (MHNSM 19903). B, *Melanophryne carpish* (KU 45614). Black and white stipple represents bone, whereas grey tone is cartilage; stippling in grey represents mineralization of the cartilage. Dashed line is reconstruction of left hyale, which was destroyed in preparation. ant proj, anterior projection; antlat proc, anterolateral process; hyogl mem, hyoglossal membrane; hyogl sinus, hyoglossal sinus; post proj, posterior projection; postlat proc, posterolateral process; postmed proc, posteromedial process.

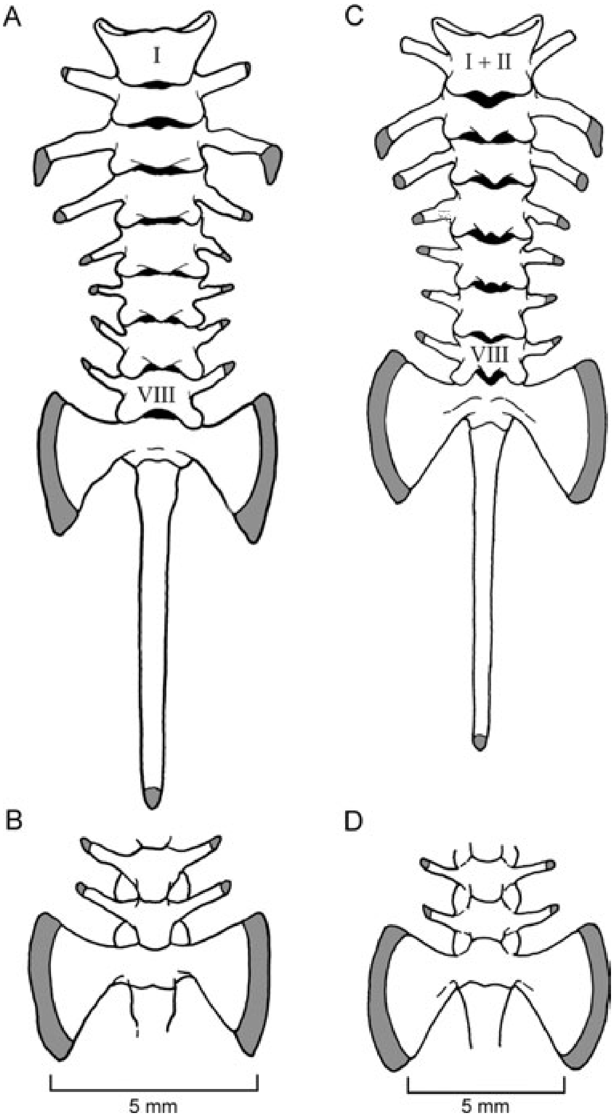

Figure 18. Vertebral columns of *Melanophryne*. *Melanophryne barbatula* (MHNSM 19903) in dorsal (A) aspect, and sacral region of vertebral column in ventral (B) aspect. *Melanophryne carpish* in dorsal (C) aspect and sacral region in ventral (D) aspect. Presacrals I, I +II and VIII are numbered. Note the conditions of the centra of Presacral VIII, procoelous in *M. barbatula* and amphicoelous in *M. carpish.* Grey areas are cartilage.

are moderately dilated with the lateral margin being about 3 times the width of the base of the diapophysis, and the posterior half of the diapophysis being slightly larger than the anterior half. The urostyle bears a bicondylar articulation with the sacrum and is slightly shorter (*c.* 90%) than the presacral vertebral column.

Melanophryne carpish has seven non-imbricate presacral vertebrae; Presacrals I and II seem to be fused; although developmental data are unavailable to confirm this assumption, the configuration of the first presacral (length with well-developed transverse processes) suggests this to be the case. Presacrals I + II–VII are procoelous, and Presacral VIII is biconcave. Presacral III is slightly shorter than the posterior presacrals. The vertebral profile in decreasing order of width of the bony parts is: sacrum > III > I + II > V ≅ VIII > VI ≅ VII. The sacral diapophyses are more broadly dilated in *M. carpish* than in *M. barbatula*, with the width of the lateral margin of the diapophysis being about 4.5 times the width of the base. The diapophysis is asymmetrical, with the posterior half being broader and significantly larger than the anterior half. The urostyle, which has a bicondylar articulation with the sacrum, is only about 87% the length of the presacral part of the vertebral column.

Pectoral girdle (Fig. 19): The girdles of *Melanophryne* have reduced clavicles that are broadly separated medially and that are associated with moderately well developed procoracoid cartilages, and an epicoracoid cartilage between the coracoids. The procoracoid cartilages and clavicles of *M. carpish* are more extensively developed than those of *M. barbatula.* In *M. carpish*, the slender clavicle has a concave anterior margin, whereas in *M. barbatula*, the clavicle is straight to slightly convex anteriorly. *Melanophryne carpish* is distinguished by the association of the distal end of the procoracoid with a spur of bone from the coracoid; the margin of the pectoral fenestra is complete and has a characteristic comma shape. *Melanophryne barbatula* lacks the connection between the coracoid and procoracoid and thus has an incomplete pectoral fenestra, which is oval in contrast to the condition in *M. carpish.*

The coracoids are robust bones that are narrowly separated medially by cartilage. The glenoid end of the coracoid is symmetrically expanded to about twice the width of the midshaft width of the bone. The sternal end is about twice the width of the glenoid end and is more symmetrical in *Melanophryne* than in *Nelsonophryne*. The sternum is relatively shorter in *Melanophryne* than in *Nelsonophryne.* Nonetheless, the element is well developed and mineralized in both species of *Melanophryne*, but proportionally larger in *M. barbatula* than in *M. carpish.*

Pelvic girdle (Fig. 20): The proportions of the girdles in *Melanophryne* differ from those of *Nelsonophryne* in the relative width of the girdle between the anterior ends of the ilial shafts and the total length of the pelvis; the girdle is wider and shorter in *Melanophryne* than in *Nelsonophryne.* In addition, the posteroventral margin of the ischium is cartilaginous in *Melanophryne*, and both species have oval acetabula.

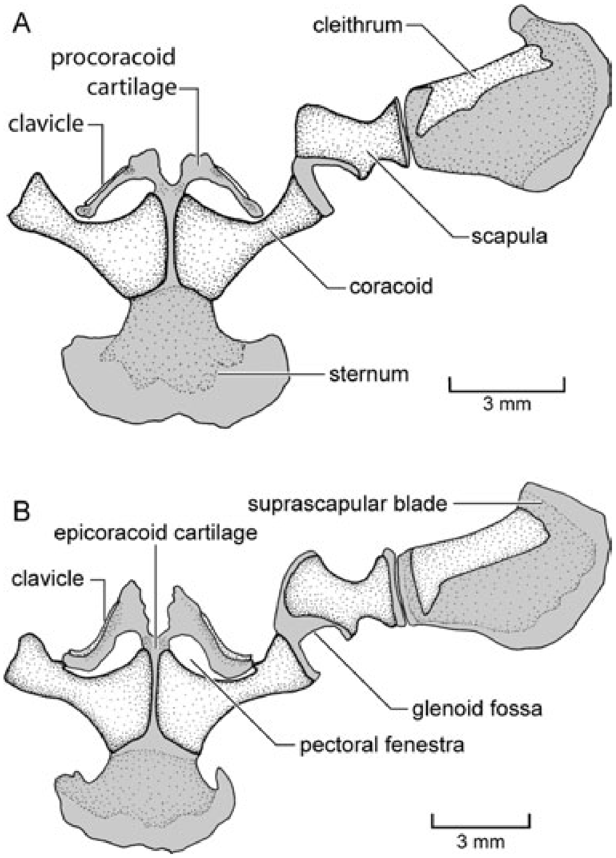

Figure 19. Pectoral girdles of *Melanophryne* in ventral view. A, *Melanophryne barbatula* (MHNSM 19903). B, *Melanophryne carpish* (KU 45614). Only the left scapula and suprascapula are shown, and these structures have been deflected into the ventral plane for the purposes of illustration. Note the presence of a reduced clavicle and procoracoid cartilage in both species. Black and white stipple represents bone, whereas grey tone is cartilage; stippling in grey represents mineralization of the cartilage.

The pectoral girdle of *Melanophryne barbatula* more nearly resembles those of *Nelsonophryne* than does that of *M. carpish.* In *M. barbatula*, the ilial shafts are long and slender and lacking any crests. The ilial prominence is low – lower than those of *Nelsonophryne.* The pubes are heavily mineralized, and the anterior acetabular angle is approximately 90°.

In *Melanophryne carpish*, the ilial shafts are markedly curved in lateral profile and bear a poorly developed dorsolateral crest along the distal half of each shaft. The ilial shafts are more robust than in *M. barbatula* and *Nelsonophryne.* By contrast, the pubes are less mineralized than in the other taxa, with mineralization limited to the margin of the acetabulum.

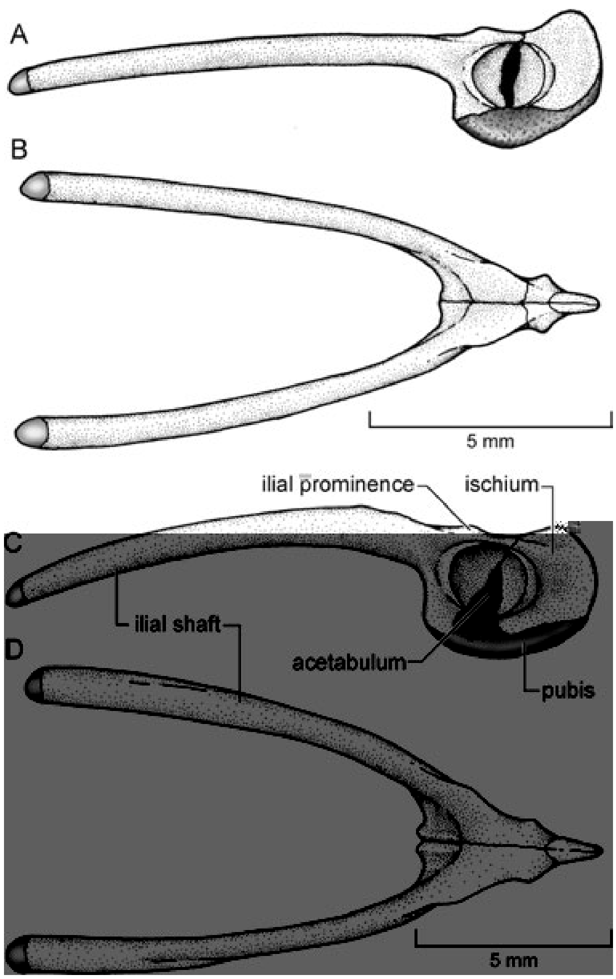

Figure 20. Pelvic girdles of *Melanophryne*. *Melanophryne barbatula* (MHNSM 19903) in lateral (A) and (B) dorsal aspects. *Melanophryne carpish* (KU 45614) in lateral (C) and (D) dorsal aspects. Grey denotes cartilage, and grey with stipples, mineralized cartilage.

Manus and pes (Fig. 21): *Melanophryne* has the standard anuran phalangeal formulae for the hand and foot of 2-2-3-3 and 2-2-3-4-3, respectively. In increasing order of length, the order of the digits on the hand is: II–III–V–IV, and that of the foot is: I–II–V–III–IV. In both species, the carpus is composed of a radiale, ulnare, Element Y, Carpal 1, and a large postaxial element assumed to represent a fusion of Carpals 2, 3 and 4. Element Y is slightly larger in *M. carpish* than in *M. barbatula.* The prepollex is composed of two elements in both species. The tarsus is composed of Tarsals 1–3 and the prehallux of three bones in both species. The terminal phalanges of the hands and feet are expanded and bilobed in both species. The expansion is more marked in the terminal phalanges of the hand than of the foot, and the condition is more exaggerated in *M. barbatula* than in *M. carpish.*

DISCUSSION

For many decades, microhylids were thought to be restricted to lowland habitats, with only one genus represented in the Andes of Ecuador (Lynch, 1986; Duellman, 1999). The discovery of a new genus with two species from the Peruvian Andes suggests a greater diversity of species in the eastern Andes than previously supposed. A summary of the morphological diversity among these four species is given in Table 1.

The first researcher to present comparative data on New World microhylines in the last 50 years was Walker (1973), who compiled an abbreviated table of morphological characters for the 17 genera then recognized. Largely, Walker's selection of characters seems to reflect the morphological suites examined by previous authors such as Parker (1934) and Carvalho (1948, 1954), such as the nature and number of presacral vertebrae, the presence/absence of a tympanum (as an indication of the presence of an ear), the condition of the clavicle, the nature of the palate and the completeness of the maxillary arcade. Wild (1995) speculated that this emphasis on certain parts of the skeleton resulted from the morphological uniformity of external characters of microhyline frogs. In his description of a new genus and species (*Adelastes hylonomos*) from Venezuela, Zweifel (1986) compared data derived from karyology and vocalizations, in addition to the traditional morphological features, and Donnelly, de Sá & Guyer (1990) analysed larval data in an attempt to resolve phylogenetic relationships of New World microhylines. Wu (1994) conducted a large-scale phylogenetic study of Microhylidae based on traditional microhylid morphological characters, in addition to features used by Lynch (1973) and Ford (1989), and a few myological characters of his own; he sampled 105 species in 56 genera. Wild (1995) described *Altigius alios* from Peru and presented an analysis of 18 New World microhyline genera based on characters provided by Zweifel (1986) and Donnelly *et al*. (1990).

Our findings suggest additional morphological features that should be examined in adult microhylines with the objective of assessing their potential value to phylogenetic studies. External morphological characters include the presence and distribution of spines and other dermal modifications, and the nature of the nuptial pad (if it is present) in males. Dermal spines are common in microhylids; the size and distribution of the spines on the bodies of the frogs vary sexually and taxonomically. When spines are present, males usually have more, larger spines that are more widely distributed on the body than they are in females. For example, males may bear spines between their fingers and toes, and on the throat, whereas in females, the spines may be restricted to the dorsum, the region of the tympanum, on the fore- and hind limbs (but not between

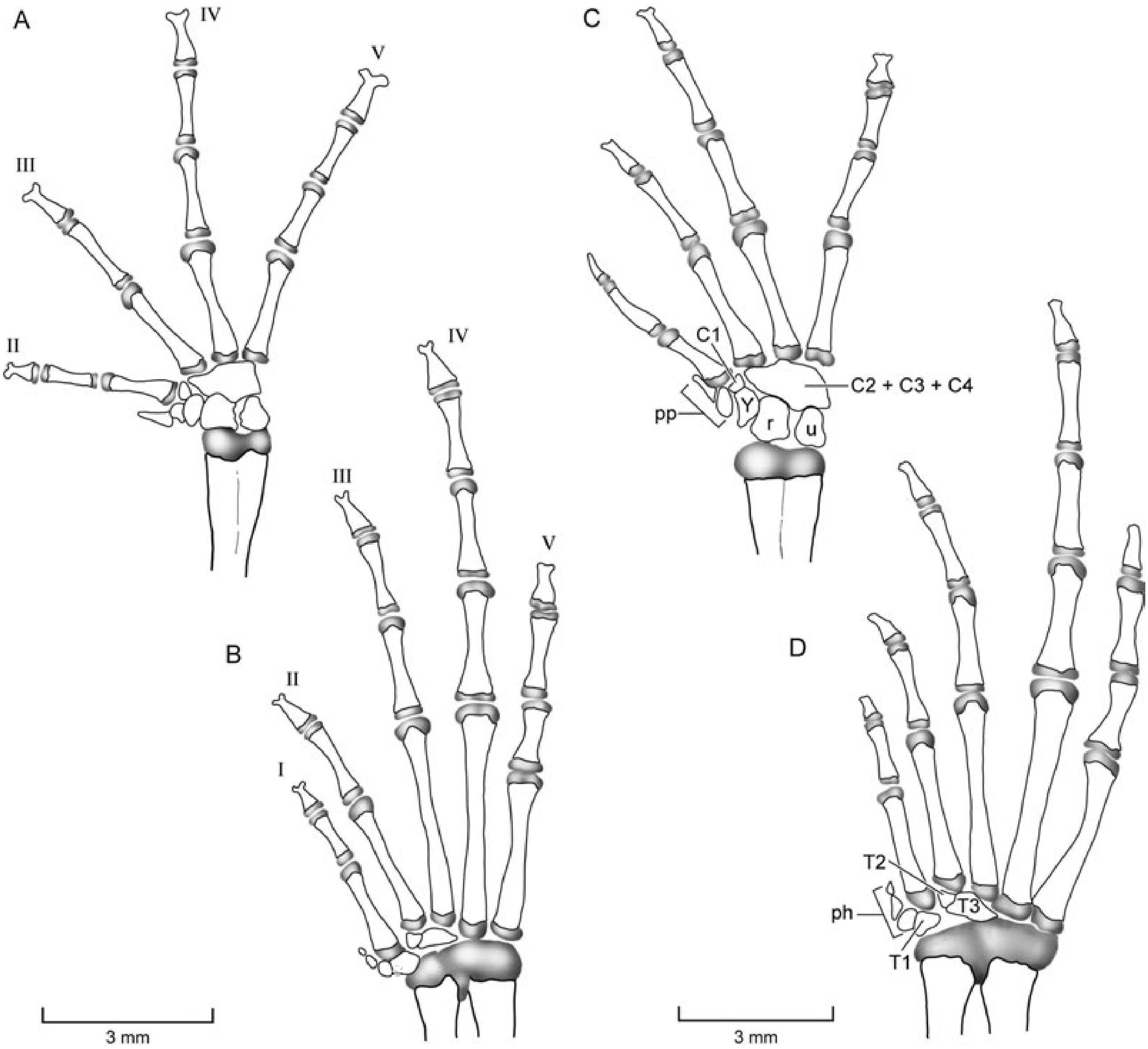

Figure 21. Dorsal views of right hands and feet of *Melanophryne*. *Melanophryne barbatula* (MHNSM 19903) hand (A) and foot (B). *Melanophryne carpish* (KU 45614) hand (C) and foot (D). Bones are shown in white and grey denotes cartilage. C1–4, Carpals 1–4; ph, prehallux; pp, prepollex; r, radiale; T1–3, Tarsals 1–3; u, ulnare; Y, Element Y.

the toes), and in the cloacal region. The function of these spines is unknown; however, it is possible that they discourage predators or play a role in courtship behaviour. Such speculation needs to be confirmed by observation, and our knowledge of the natural history of microhylids is limited – especially for *Melanophryne* and *Nelsonophryne*. The only tadpole that has been described in these two genera is that of *N. aterrima* (Donnelly *et al*., 1990). The habits of *M. barbatula* are unknown, but *M. carpish* is known to climb into bromeliads, and *Nelsonophryne aequatorialis* and *N. aterrima* are exclusively terrestrial.

The list of osteological features is more extensive than those of soft morphology. Beginning with the cranium, we note that there seem to be fundamental differences in the structure of the nasal capsules that result in some taxa having widely separated olfactory organs, whereas others have nasal capsules that are medially adjacent and share a relatively thin, common medial wall (septum nasi). Jurgens (1971) reported that in *Hypopachus cuneus* and *Elachistocleis ovalis*, the nasal capsules and the nasal sacs extend posteriorly beneath the forebrain to a level coincident with the middle of the eye; so far as is known, this condition is unique among microhylines and anurans as a whole, in which the nasal capsules usually lie forward and ventrolateral to the anterior braincase. Jurgens (1971) also noted that in some microhylids, the premaxillae are located below, rather than in front of, the nasal capsule. This condition usually is associated with extension of the maxilla over the premaxilla, and in its most extreme condition, the maxillae are symphygnathine (i.e. dentaries articulate with one another anterior to premaxillae). The 'laminar' nasal bone that we describe has not been reported before; however, examination of illustrations of some Old World taxa in Zweifel (1972) leads us to suspect that the same, or a similar, element may be present in other microhylids. There is more variation in the anterior end of the cranium comprising the sphenethmoids, the plana antorbitalae, neopalatines, vomers, maxillae and premaxillae in microhylids than is represented in all other anurans. The diversity of palatal design is overwhelming; its systematic and functional significance will elude us until taxa have been carefully compared, and the ontogenetic development of this part of the cranium is documented in several taxa. The hyoid is also a source of character variation. Zweifel (1986) reported a strange parahyoid bone in *Adelastes* and illustrated a ventral projection from the bone that resembles the hyoid projections that we describe in *Nelsonophryne.*

The postcranial skeleton offers several other suites of characters, the most familiar of which is the pectoral girdle. Fusion of Presacrals I and II seems to be a relatively rare phenomenon among microhylines, occurring only in *Melanophryne carpish* and *Syncope*, and deletion of a presacral vertebra apparently has occurred only in *Syncope.* However, there is considerable variation in the condition of the last presacral; the vertebra may be amphicoelous or procoelous in congeners. It is unknown whether this feature varies intraspecifically or ontogenetically. With few exceptions, the pelvic girdle has been ignored. We assume that the heterotopic sesamoid cartilage in the ligamentum calcanei at the tibiofibular–tarsal joint in *M. barbatula* serves the same function in the broad taxonomic diversity of anurans in which it has been noted to occur – to strengthen the tendon of the M. plantaris longus around the 'heel' joint for walking, swimming, jumping and swimming (Nussbaum, 1982). Although differences in the relative lengths of digits and the shapes of the terminal phalanges have been reported, researchers have not documented the differences in the skeletal features of the manus and pes.

The absence of a tympanum in anurans from the Andes in central Peru seems to be relatively common and has been recorded for species belonging to various genera in Hylidae, Leptodactylidae and Microhylidae; this might be an adaptation to high-altitude habitats. Morphological convergences (e.g. narrow toes and fingers without or with reduced pad, reduction or absence of the ear) between leptodactylids (*Phrynopus*, *Eleutherodactylus*, *Phyllonastes*) and microhylids mainly occur in frogs inhabiting the Andes. These morphological similarities have complicated species diagnoses based on external features and resulted in taxonomic errors. For example, *Adelophryne tridactyla*, which was described by Duellman & Mendelson (1995), subsequently was shown to be a member of the genus *Syncope* (Da Silva & Meinhardt, 1999) and *Phrynopus carpish* described by Lehr *et al*. (2002) is placed in the new microhylid genus *Melanophryne* in this paper.

Phylogenetic studies of New World microhylids based on genetic data are being conducted by Rafael de Sá (University of Richmond) and Eli Greenbaum (University of Kansas), both of whom have access to tissue samples of *Melanophryne* (MTD 45614). Our results have uncovered many fascinating morphological features. The evolutionary histories and the value of these characters to our understanding of the relationships of these frogs await a combined analysis of morphological and molecular data. In the meantime, similar morphological data, including ontogenetic histories, remain to be gathered on other microhylids from around the world.

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APPENDIX 1

Specimens examined

Altigius alios: PERU: Madre de Díos: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m: KU 216021. *Arcovomer passarellii:* BRAZIL: Rio de Janeiro: Itaguai: KU 93232–36. *Chiasmocleis anatipes:* ECUADOR: Sucumbíos: Santa Cecilia, 340 m: KU 146034, 146037–39, 158521–24, all paratypes. *Chiasmocleis bassleri:* PERU: Loreto: junction Río Sucusari and Río Napo: KU 220478. *Chiasmocleis bicegoi:* BRAZIL: Rio de Janeiro: Itaguai: KU 93238–41. *Chiasmocleis ventrimaculata:* PERU: Huánuco: Río Llullapichis, 4–5 km upstream from Río Pachitea, Finca Panguana, 200 m: KU 178997; Loreto: Río Curanja, Balta, 300 m: KU 197047; Madre de Díos: Cocha Cachu, Río Manú between Río Panagua and Río Cachiri, *c*. 400 m: KU 154750–51; Cusco Amazónico, 15 km E Puerto Maldonado, 200 m: KU 206632–35. *Ctenophryne geayi:* PERU: Madre de Díos: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m: KU 205775, 215543, 215545; VENEZUELA: Bolívar: 13 km S, 1 km E Puente Cuyuni, 140 m: KU 167374–84. *Dasypops schirchi:* BRAZIL: Espirito Santo: Sooretama: KU 93247–51. *Dermatonotus muelleri:* ARGENTINA: Formosa: Laguna Garay, Ingenero Juárez: KU 128951–54. *Elachistocleis bicolor:* BRAZIL: Rondonia: Porto Velho: KU 74312, 93256–60; Río Grande do Sul: 18 km E Porto Alegre: KU 154617. *Elachistocleis ovalis*: PERU: Loreto: Río Curanja, Balta, 300 m: KU 197049–56. *Gastrophryne carolinensis:* U.S.A.: Florida: Marion County: Silver Springs: KU 90962–67. *Gastrophryne olivacea:* MEXICO: Sinaloa: 3 mi N Los Mochis: KU 73922–27; 5.7 mi NE Villa Unión: KU 75451–60. *Gastrophryne usta:* EL SALVADOR: San Salvador: 3 km SE Ilopango: KU 184825–52. *Hamptophryne boliviana:* PERU: Madre de Díos, 15 km E Puerto Maldonado, 200 m: KU 205780–97, 207751–63, 209193, 215554–74. *Hypopachus barberi:* HONDURAS: Ocotepeque: Belén Gualcho, 1470 m: KU 194230; El Chaguitón, 1870 m: KU 194231–32; Intibuca: Zacate Blanco, 2020 m: KU 94233; 11 km WNW La Esperanza, 1860 m: KU 194234; La Paz: 5 km S Santa Elena, 2020 m: KU 194235. *Hypopachus variolosus:* MEXICO: Chiapas: 14.4 km SW Las Cruces, 700 m: KU 65323–49. *Melanophryne carpish:* PERU: Huánuco: Huánuco: Cordillera de Carpish (09°43′19″S, 76°05′76″W), 2960 m: MHNSM 20699 (holotype); Cordillera de Carpish (09°43′58.2″S, 76°06′41.9″W), 2750 m: MTD 45614 (cleared-and-stained); Cordillera de Carpish: MTD 46334; San Martín: Huallaga: Juanjui: Laguna de los Cóndores (06°50′49″S, 77°41′40″W), 2870 m: MHNSM 19471. *Myersiella microps:* BRAZIL: Río de Janeiro: Terezopolis, São Paulo: 10 km NW Caraguatatuba: KU 93262–63. *Nelsonophryne aequatorialis:* ECUADOR: Azuay: Cuenca, 2540 m: KU 121056–85; Cuenca, 2600 m: KU 202911–913; NW edge Cuenca, 2650 m: KU 178325–334; 4 mi E Cuenca, 2540 m: KU 135271–76; Cutchil, 3.6 km S Sigsig, 2530 m: KU 141588; 5.7 km SW La Paz, 3000 m: KU 202914–918; Cañar: Biblián, 2615 m: KU 141587: Loja: Saraguro, 2500 m: KU 135277; 2 km SSW Saraguro, 2560 m: KU 178283–324; 3.7 km S Saraguro, 2800 m: KU 202919–920; 3.5 km WSW Urdaneta, 2550 m: KU 202921. *Nelsonophryne aterrima*: COSTA RICA: Alajuela: Cinchona, *c*. 1600 m: KU 65319; Isla Bonita: KU 32728; Volcán Póas, 6 mi E Isla Bonita: KU 28173; Cartago: Moravia: KU 30773–77, 30779–86, 32721–23; Moravia de Turrialba, 1200 m: KU 65320; Heredia: Isla Bonita, 1450 m: KU 103820; San José: San Isidro del General: KU 32725–26; 10–20 mi W San Isidro del General: KU 32727; ECUADOR: Pichincha: Estacíon Biológica Río Palenque, 56 km N Quevedo, 220 m: KU 152588; PANAMA: Bocas de Toro: Río Claro c. Junction with Río Changena, 910 m: KU 116504; Darién: Laguna, 820 m: KU 77574–75; Tacarcuna, 550 m: KU 77576. *Relictovomer pearsei:* VENEZUELA: Bolívar: Km 144, El Dorado–Santa Elena de Uairén Road, 1210 m: KU 167409–428. *Stereocyclops incrassatus:* BRAZIL: Espirito Santo: Sooretama: KU 93265–69. *Synapturanus rabus:* ECUADOR: Napo: Río Yasuni, 200 km upstream from Río Napo: KU 175217. *Syncope antenori:* COLOMBIA: Amazonas: Puerto Nariño: KU 153398; ECUADOR: Sucumbíos: Puerto Libre, Río Aguarico, 570 m: KU 124001–002, 124004–006, 124010–011, all paratypes; PERU: Huánuco: S slope Serrania Sira, 'Laguna', 1280 m: KU 154756. *Syncope carvalhoi:* PERU: Loreto: lower Río Napo region, E bank Río Yanayacu, *c*. 90 km N Iquitos, 120 m: KU 206164. *Syncope tridactyla:* PERU: Loreto: 1.5 km N Teniente López: KU 221992.