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A new miniature Melanesian Forest Frog (Ceratobatrachidae: *Cornufer*) from New Britain Island, constituting the first record of the subgenus *Batrachylodes* from outside of the Solomon Archipelago

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Abstract

We describe a new species of *Cornufer*, subgenus *Batrachylodes*, from high-elevation forests of New Britain Island in the Bismarck Archipelago of Eastern Melanesia. The new species, *Cornufer exedrus* **sp. nov.**, is a biogeographically disjunct member of the *Batrachylodes* clade, representing the first record of the subgenus from outside of the Solomon Archipelago. The new species is a small terrestrial form from dense, closed-canopy forests above 1500 meters elevation in the Nakanai Mountains of eastern New Britain. It differs from its closest relatives, the other members of the subgenus *Batrachylodes*, on the basis of its minute body size, degree of digital disc expansion, reduced subdigital tuberculation, color pattern, and other traits related to its small size. We also provide a description of the new species' simple advertisement call. The diversity of ceratobatrachid frogs of the Bismarck Archipelago is most likely still underestimated despite several recent surveys. Our understanding of evolutionary trends and species boundaries in the subgenus *Batrachylodes* currently is hampered by lack of genetic samples and call recordings corresponding to voucher specimens of the endemic species of Bougainville Island.

Key words: Bismarck Archipelago, Papua New Guinea, Southwest Pacific, Sticky-toed frogs, advertisement calls

Introduction

The subgenus *Batrachylodes* (*sensu* Brown *et al.* 2015) is a modest assemblage of directly-developing, small-bodied, terrestrial and scansorial forest frogs (genus *Cornufer*) from the Solomon Archipelago (consisting of the country of Solomon Islands and the nearby islands of Bougainville and Buka, politically part of Papua New Guinea; Fig. 1). Eight species were previously arranged to constitute their own genus due to their phenotypic distinctiveness (Boulenger 1887; Brown 1952; Brown & Parker 1970), most included species are small terrestrial to scansorial frogs that are triangular in overall body shape, with small heads, pointed protuberant snouts, countersunk lower jaws, and near vertical lores similar in appearance to many semifossorial frogs of the family Microhylidae (Menzies 2006; Pough *et al.* 2016). Additionally, members of this subgenus are set apart from most other *Cornufer* by the lack of vomerine teeth and an unforked omosternal style, and many with the shared possession of a distinctive color pattern (Brown 1952; Brown & Parker 1970). Common elements of this coloration consist of a diagonally oriented, stratified lateral pigmentation pattern, with sharp demarcation between light (above) and dark (below) colors, with or without a bright line extending from the tip of the snout, over the eyelid, then posteroventrally to the groin (Fig. 2).

Imbedded within the genus *Cornufer*, species of *Batrachylodes* are thought to be related to a few poorly known, small-bodied species formerly of the genus *Platymantis* from New Guinea, eastern Indonesia, and the

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Bismarck Archipelago. However, the phylogenetic relationships of *Batrachylodes* to the other members of the *Cornufer* clade remain poorly resolved (Brown *et al.* 2015). Nevertheless, *Batrachylodes* itself has consistently been interpreted as a phenotypically cohesive unit (Brown & Parker 1970; Menzies 2006), with a distribution restricted to the islands that make up the biogeographically and geologically cohesive Solomon Archipelago (Fig. 1; Allison 1996; Brown 1997).

In the Solomon Archipelago, species of *Batrachylodes* exhibit a nested distributional pattern with the highest diversity and endemism on the northwestern island of Bougainville and decreasing diversity in the islands to the southeast (Fig. 1). Three species of *Batrachylodes* are known only from Bougainville proper: *C. gigas* and *C. montanus* are restricted to Bougainville's montane rainforests, while *C. mediodiscus* occurs at lower elevations on Bougainville as well as the adjacent smaller island of Buka (Brown & Parker 1970; Menzies 2006). *Cornufer minutus* is known from Bougainville and Choiseul (see discussion; Brown & Parker 1970). *Cornufer trossulus* and *C. wolfi* are known from Bougainville, Choiseul, Isabel, and nearby smaller islands (Sternfeld 1920; Brown & Myers 1949; Brown & Parker 1970; Pikacha *et al.* 2008), a group of landmasses that largely composed the previously contiguous Greater Bukida aggregate island during Pleistocene glacial periods of lower sea levels (Mayr & Diamond 2001). *Cornufer elegans* was at first described as a montane Bougainville endemic (Brown & Parker 1970), but later listed as more widespread throughout the Solomon Archipelago (Pikacha *et al.* 2008). However, additional work is needed to clarify the distribution of *C. elegans* outside of Bougainville, and here we restrict it to the Greater Bukida island group. Finally, *C. vertebralis* is known from all major islands in the Solomon Archipelago except Makira (Boulenger 1887; Brown 1952; Brown & Parker 1970; Pikacha *et al.* 2008). Although there are records of *C. vertebralis* from smaller islands (Ugi and Santa Ana) near Makira, these records need further verification given the absence of this taxon on Makira (Brown 1952).

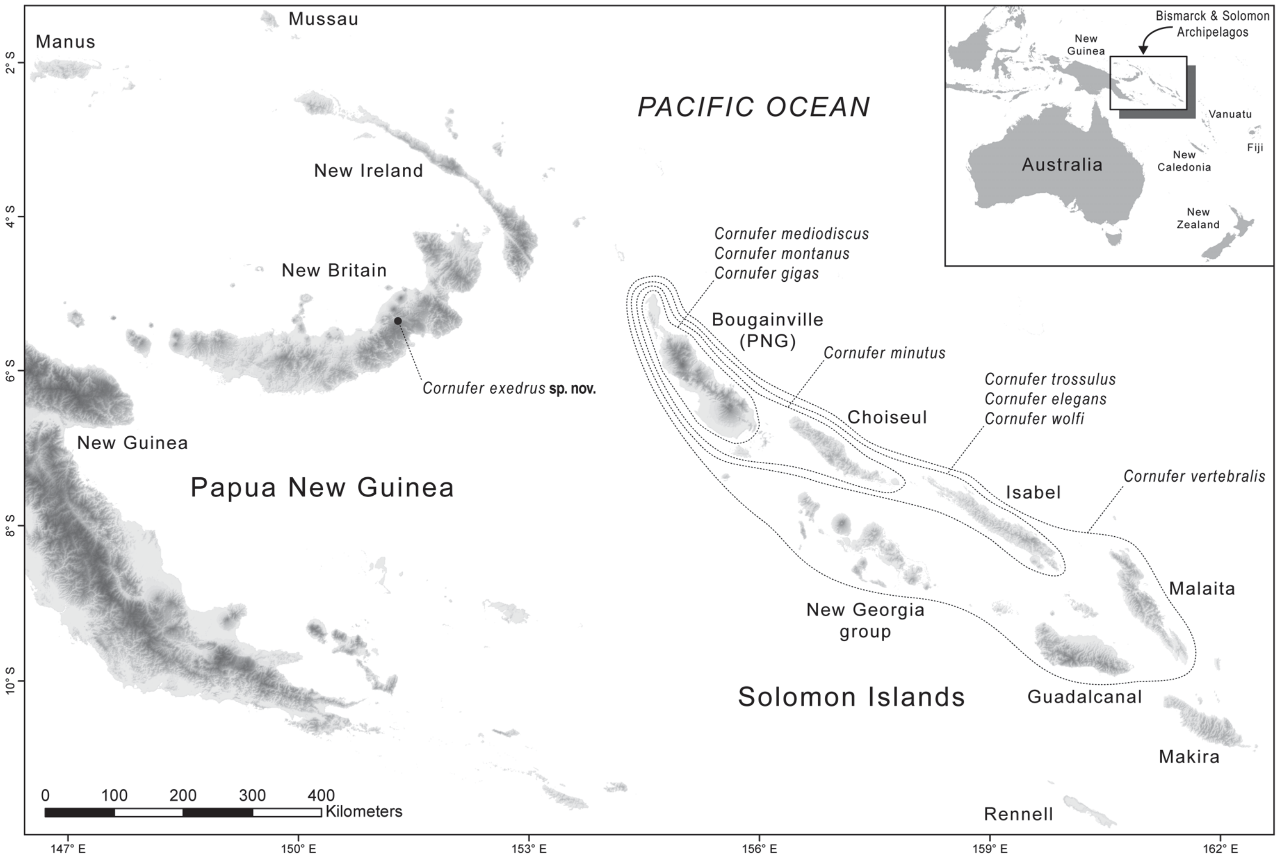

FIGURE 1. Map of the Bismarck and Solomon Archipelagos showing the distributions of all species of *Cornufer* within the subgenus *Batrachylodes*, including the type locality of *Cornufer exedrus* (black circle) at Tompoi Camp (~1,600 m above sea level) in the Nakanai Mountains of eastern New Britain.

Biodiversity survey work in the Bismarck Archipelago has increased in the last two decades, resulting in numerous discoveries and descriptions of *Cornufer* species from New Britain (Foufopoulos & Brown 2004; Brown *et al.* 2006a,b, 2013; Kraus & Allison 2007, 2009), New Ireland (Allison & Kraus 2001), and Manus (Kraus & Allison 2009; Richards *et al.* 2007, 2014; Richards & Aplin 2015). The majority of these discoveries have recently been placed in the newly described subgenus *Aenigmanura* (sister to the clade containing the subgenus *Batrachylodes*; Brown *et al.* 2015:figs. 2–3), but *C. bufonulus* (New Britain) and *C. caesiops* (New Britain) belong to the unresolved clade containing *Batrachylodes* (Brown *et al.* 2015). Still, to date, none of these discoveries has been identified as possessing phenotypic similarities with described *Batrachylodes* taxa (Boulenger 1887; Brown & Parker 1970) and, in fact, were originally described as *Platymantis* (Kraus & Allison 2007, 2009).

In April 2009, while conducting biodiversity surveys at around 1600 m elevation in the Nakanai Mountains of eastern New Britain, SJR discovered a strikingly distinct, minute leaf litter frog resembling the "typical" morphology of frogs of the subgenus *Batrachylodes*. The conspicuous phenotypic similarity would be sufficient to confidently assign this new species to *Batrachylodes*, but we confirmed this relationship with phylogenetic analysis of DNA sequence data and here describe the first member of this *Cornufer* (*Batrachylodes*) clade from outside of the geologically and biogeographically cohesive Solomon Archipelago.

Materials and methods

Morphology. Morphological data were taken from specimens (Appendix I) preserved in 10% formalin and later transferred to 70% ethanol (see Specimens Examined section). Morphometric data were recorded by RMB and SLT with digital calipers (to the nearest 0.1 mm). Sex was determined by inspection of gonads (females and males), by direct observations of vocalizing behavior (males), or by confirmation of vocal slits in the floor of the buccal cavity (males). Character definitions follow Zweifel (1960, 1969, 1975) as well as Foufopoulos & Brown (2004), Brown *et al*. (2006a, b, 2013), and Brown & Richards (2008) and we recorded: snout–vent length (SVL), head length (HL), eye diameter (ED), midpoint interorbital distance (IOD), snout length (SNL), tympanic annulus horizontal diameter (TD), widest point head width (HW), hand (manus) length (ML), foot (pes) length (PL), femur length (FL), tibia length (TBL), tarsus length (TSL), forearm length (FA), Toe-IV length (Toe4L), Finger-I length (Fin1L), Finger-III length (Fin3L), Finger-I disk width (Fin1DW), Finger-III disk width (Fin3DW), Toe-IV disk width (Toe4DW), and widths of penultimate phalanges of Finger-III (PpFin3) and Toe-IV (PpToe4). Other qualitative external phenotypic characters assessed include color pattern, dermal ornamentation, and size and shape of subdigital tubercles.

Acoustic analysis. Advertisement calls were recorded by SJR at a sampling rate of 44.1 kHz with a Marantz PMD-661 Solid-state Recorder and Sennheiser ME66 microphone. Calls were recorded at distances of 1–2 m and (ambient temperatures were noted during recordings). Because our calls all were recorded within a range of 1.5°C, we undertook no temperature correction before analysis. Calls were analyzed with Raven© Pro 1.5 alpha (Bioacoustics Research Group, Cornell Lab of Ornithology, 2012) software set to default spectrogram parameters (256 samples and 50% overlap). We examined audiospectrograms (sonograms), oscillograms (waveforms), and power spectra for a variety of spectral and temporal characters (Foufopoulos & Brown 2004; Brown *et al.* 2006a, b, 2013; Kraus & Allison 2007; Brown & Richards 2008; Richards *et al.* 2014).

Genetic analyses. We sequenced a fragment of the mitochondrial 16S rRNA gene (16S; ~875-bp) for molecular phylogenetic analysis. New sequences were generated for six individuals of the undescribed species along with the following representatives from the *Batrachylodes* subgenus: *Cornufer minutus* (3), *Cornufer trossulus* (3), *Cornufer wolfi* (1), *Cornufer vertebralis* (3). We also incorporated preexisting ceratobatrachid 16S sequence data available on GenBank that were generated by Brown *et al.* (2015), which include all *Batrachylodes* taxa that have been sequenced for 16S, several more distantly related *Cornufer* representatives, and two *Platymantis* species as outgroup taxa. A complete list of sampling for molecular analyses and GenBank numbers is provided in Appendix II.

Molecular techniques for DNA extraction, PCR amplification, and sequencing follow Brown *et al.* (2015). For PCR amplification and sequencing, we used the 16SC (5′-GTRGGCCTAAAAGCAGCCAC-3′) and 16SD (5′-CTCCGGTCTGAACTCAGATCACGTAG-3′) primers (Darst & Cannatella 2004). Sequences were assembled in Geneious v.5.3.6 (Kearse *et al.* 2012), aligned using the MUSCLE algorithm in Geneious, and alignments were visually inspected and edited for accuracy. Phylogenetic analyses were performed using maximum likelihood (ML) with the program RAxML v.8.2.10 (Stamatakis 2014) using the rapid bootstrap algorithm (-f a function) to run 1,000 bootstrap replicates and 200 ML tree searches under the GTR+G nucleotide substitution model as selected by the model selection program jModelTest v.2.0 (Darriba *et al.* 2012) and the recommendations in the RAxML manual (Stamatakis 2014). Additionally, 16S genetic divergences (uncorrected *p*-distances) between *Batrachylodes* taxa were calculated using MEGA v.7.0.20 (Kumar *et al.* 2016).

Results

Both molecular and morphological data support this diminutive New Britain taxon as a new, divergent species of *Cornufer* within the subgenus *Batrachylodes*. As in previous phylogenetic analyses (Brown *et al.* 2015), many of the basal relationships among *Cornufer* species included here remain poorly resolved in our analyses, but all taxa within the subgenus *Batrachylodes* form a well-supported clade (Fig. 3). We recover the undescribed species to be nested within this subgenus but highly divergent from all other taxa (Fig. 3). Uncorrected *p*-distances between the new species and other *Batrachylodes* taxa included here range from 7.3–12.3% genetically divergent based on the 16S mtDNA locus, well above the level of divergence among other species pairs within this subgenus (e.g., *C. trossulus* and *C. wolfi* 16S *p*-distances = 4.7%) (Table 1). Examination of morphology with comparisons to other species recover a suite of characters that both unite this new taxon with the *Batrachylodes* clade yet diagnose it from other described members of this subgenus. We highlight these morphological characters and describe this biogeographically disjunct new species of *Cornufer* (*Batrachylodes*) below.

TABLE 1. Summary of the average between- and within- (diagonal) species *p*-distance values for the mitochondrial 16S rRNA marker in the genus *Cornufer*, focusing on the subgenus *Batrachylodes* (numbers 5–12). *Cornufer* sp. 1 and sp. 2 respectively correspond to LSUMZ 94038 and LSUMZ 94039, specimens of unclear species identity from Bougainville Island (see Appendix II).

		1	2	3	4	5	6	7	8	9	10	11	12
1	*C. heffernani*	–											
2	*C. cheesemanae*	0.144	–										
3	*C. parkeri*	0.168	0.144	–									
4	*C. bimaculatus*	0.162	0.129	0.153	–								
5	*C. minutus*	0.172	0.148	0.177	0.146	0.004							
6	*C. exedrus* **sp. nov.**	0.165	0.134	0.168	0.143	0.123	0.002						
7	*C. trossulus*	0.158	0.150	0.156	0.145	0.120	0.084	0.003					
8	*C. wolfi*	0.155	0.142	0.160	0.151	0.116	0.073	0.047	0.008				
9	*C. cf. vertebralis*	0.175	0.138	0.163	0.151	0.126	0.084	0.080	0.078	0.019			
10	*C. sp. 1*	0.161	0.135	0.162	0.146	0.116	0.084	0.073	0.076	0.059	–		
11	*C. sp. 2*	0.176	0.151	0.169	0.166	0.130	0.088	0.079	0.085	0.069	0.044	–	
12	*C. vertebralis*	0.169	0.149	0.169	0.156	0.132	0.085	0.091	0.084	0.073	0.054	0.078	0.035

Species Description

Cornufer (Batrachylodes) exedrus sp. nov.

Figs. 2a–c, 4, 5

Holotype. South Australia Museum (SAMA) R64760 (SJR Field No. 10784), adult male, collected by S. J. Richards at Tompoi Camp, 1590 m above sea level (05°20.623'S, 151°18.873'E; WGS-84), Nakanai Mountains, East New Britain Province, Papua New Guinea, 19 April 2009.

Paratypes. SAMA R64762 and R64764 (SJR Field Nos. 10815 and 10820 respectively), two adult males, and SAMA R64763 (SJR 10819), adult female, all collected at the type locality, 21 April 2009; SAMA R64761 and

R71008 (SJR 10798 and 10821 respectively), two adult males, same locality, 20 and 21 April 2009, respectively; SAMA R64765 (SJR 10843), juvenile, and SAMA R71007 (SJR 10846), adult male, same locality, 23 April 2009.

Etymology. The specific epithet is derived from the masculine formation of the Greek adjective *exedros*, meaning away from home, strange, or extraordinary. The surprising discovery of *Cornufer* (*Batrachylodes*) *exedrus* from a high elevation site in New Britian is a taxonomic and biogeographic enigma, given that all other species in the subgenus are restricted to the Solomon Archipelago.

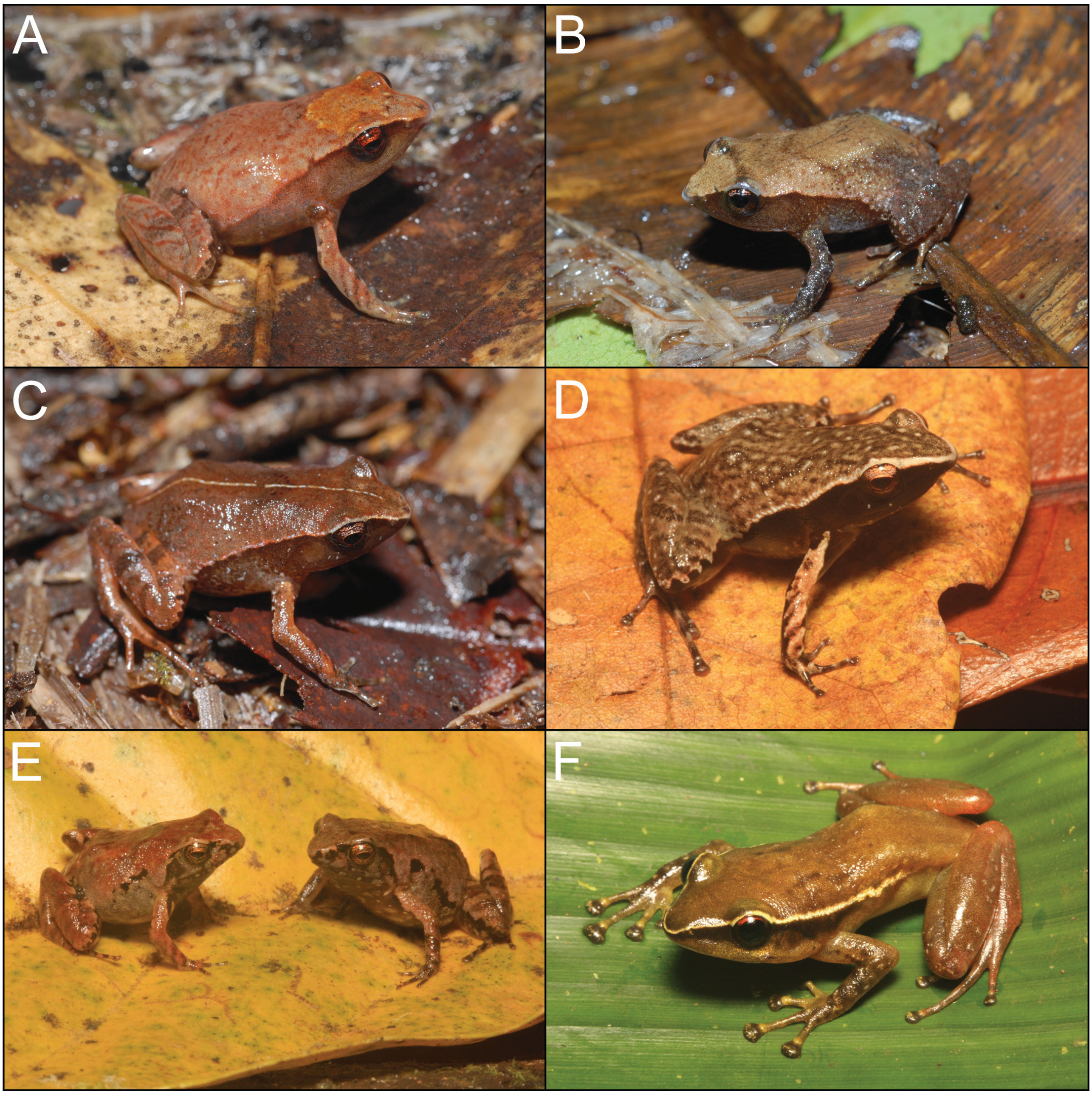

FIGURE 2. Photographs in life of the holotype (A: SAMA R64760) and paratypes (B: SAMA R64764; C: SAMA R64763) of *Cornufer* (*Batrachylodes*) *exedrus*, as well as other representatives of the subgenus *Batrachylodes* from the Solomon Archipelago (D: KU 341539, *Batrachylodes trossulus*, Choiseul Is., Solomon Islands; E: KU 341494–5, *Batrachylodes minutus*, Choiseul Is., Solomon Islands; F: KU 341497, *Batrachylodes wolfi*, Shortland Is., Solomon Islands).

Diagnosis. The new species is a member of the genus *Cornufer* based on molecular phylogenetic evidence. There are currently no morphological synapomorphies known for the genus *Cornufer*, however, based on the updated taxonomic arrangement of this clade (Brown *et al.* 2015) into several morpholgically diagnosible subgenera the new species can be assigned to the subgenus *Batrachylodes*, as defined by Brown *et al.* (2015), on the basis of its small, triangular shaped body, pointed snout, absence of interdigital webbing, absence of vomerine teeth, presence of a darkened loreal stripe extending diagonally across the flanks, and molecular phylogenetic placement (Brown *et al.* 2015:fig. 2). *Cornufer exedrus* is distinguished from congeners by a combination of (1) adult body size small (SVL 17.6–18.8 mm for six adult males, mean = 18.3 mm; SVL 18.3 mm for one adult female), (2) body shape triangular with a small, pointed head, (3) terminal disks of the fingers and toes narrowly expanded (among adults: Fin3DW 0.3–0.6 mm, mean = 0.5 mm; Toe4DW 0.4–0.7 mm, mean = 0.6 mm) (Figs. 2, 4, 5), (4) vomerine teeth absent, (5) digits lacking all vestiges of lateral flange and interdigital webbing, (6) dorsal skin smooth to finely granular, lacking prominent dermal tubercles or ridges, (7) subarticular tubercles of fingers, toes, hands and feet uniformly low and flattened, (8) dark band extending along the canthus rostralis and onto the flank with a smooth dorsal margin demarcating lighter dorsal and darker lateral colors, and (9) unique advertisement call consisting of a series of brief, high-frequency atonal notes.

Comparisons with other species. Among members of the subgenus *Batrachylodes*, *Cornufer exedrus* can be easily distinguished from *C. elegans*, *C. gigas*, *C. montanus*, *C. vertebralis*, and *C. wolfi* by the narrowly expanded (versus widely expanded) terminal finger disks except for the first finger (Fin3DW/SVL = 0.02–0.03, Fin3DW/Fin3L = 0.1–0.2, and Fin3DW/TD = 0.2–0.3 in *C. exedrus* versus Fin3DW/SVL > 0.03, Fin3DW/Fin3L > 0.2, and Fin3DW/TD > 0.3 in the aforementioned species) and smaller adult body size (SVL 17.6–18.8 mm in *C. exedrus* versus SVL > 20.0 mm in the aforementioned species) (Table 2). Of the *Batrachylodes* that lack prominently dilated finger disks, *Cornufer exedrus* differs from *C. mediodiscus* in having a smaller adult body size (SVL 17.6–18.8 mm in *C. exedrus* versus 20.2–26.0 mm in *C. mediodiscus*), slightly smaller third finger disk width (reflected in the Fin3DW/SVL, Fin3DW/Fin3L, and Fin3DW/TD ratios, Table 2), and lacking raised dorsal skin ridges (Brown & Parker 1970). *Cornufer exedrus* differs from *C. minutus* by its slightly larger body size (SVL 17.6–18.8 mm in *C. exedrus* versus 15.2–17.3 mm in *C. minutus*) and by differences in the proportions related to hind limb length (reflected in the HW/TBL, TBL/SVL, and PL/SVL ratios, Table 2). *Cornufer minutus* also differs in color pattern, with the dark band along the canthus rostralis more poorly defined, often broken or with an irregular dorsal margin, than in *Cornufer exedrus*. The new species differs from *C. trossulus* by its slightly smaller body size (SVL 17.6–18.8 mm in *C. exedrus* versus 18.9–24.3 mm in *C. trossulus*) and by differences in the proportions related to hind limb length (reflected in the HW/TBL, TBL/SVL, and PL/SVL ratios, Table 2).

On New Britain Island, *C. exedrus* can be differentiated from most congeners by its smaller adult body size (<25 mm), narrowly expanded finger disks, and/or absence of pedal webbing. Of the small-bodied *Cornufer* species on New Britain (<25 mm), *C. exedrus* can be further distinguished from *C. caesiops* (and the morphologically similar *C. browni*, on nearby New Ireland Island; Allison & Kraus 2001; Kraus & Allison 2009) in having narrowly expanded finger disks (versus widely expanded in *C. caesiops* and *C. browni*); from *C. akarithymus*, *C. bufonulus*, and *C. sulcatus* in having a smooth dorsal surface (versus tuberculate or with dorsal ridges in *C. akarithymus*, *C. bufonulus*, and *C. sulcatus*); and from *C. boulengeri* (males and juveniles previously assigned to *C. rhipiphalcus;* Kraus 2008), by the lack of a fanlike array of dorsal ridges in the scapular region and a less prominent dark face mask, which does not extend onto the flanks in *C. boulengeri*.

Description of holotype. Adult male, in good condition, preserved with mouth open, incision in left thigh where SAMA tag was threaded; habitus moderately robust; head not distinct, slightly narrower in dorsal aspect than body, length 41% of SVL; head length 120% of head width; snout short, tip acuminate in lateral aspect, rounded dorsal aspect, protruding prominently beyond lower jaw, unpigmented at tip; lower jaw notched at tip; eyes protrude only slightly beyond silhouette of head in both dorsal and lateral aspects; labial region rounded and smooth, lips not swollen, not extending past eyes when viewed in dorsal aspect; interorbital region slightly convex; eye diameter 90% of interorbital distance; pupil horizontally ovoid; canthus rostralis medially bowed; loreal region slightly concave; eye diameter 55% of snout length; nostrils slightly laterally protuberant; eye-narial distance 1.25 times the distance from nostril to snout tip; internarial region flat; tympanum distinct, its diameter 89% of eye diameter; slight supratympanic fold present, extending from posterior edge of eye, over dorsal edge of tympanum, and terminating at supra-axillary (post-rictal) region; tongue ovoid, with a slightly narrower anterior attachment; choanae round, minute, at anterolateral edge of palate, separated by a distance five to seven times greater than their diameter, obscured in ventral aspect by palatal shelf; vomerine teeth absent; openings to vocal sac minute slits, at level of the angle of jaw.

Dorsal skin of body, head, and limbs generally smooth, lacking dermal folds, tubercles, or ridges; ventral surfaces of trunk, head, throat, and limbs smooth, with the exception of fanlike array of 12–14 small white tubercles on anterior margin of chin.

TABLE 2. Summary of morphometric variation and morphometric ratios among adult *Cornufer* (subgenus *Batraychylodes*) specimens measured in this study (morphometric trait/ratio means presented above and ranges presented below in parentheses).

	C. exedrus **sp. nov.**		*C. trossulus*	*C. minutus*	*C. mediodiscus*	*C. wolfi*	*C. vertebralis*	*C. elegans*	*C. montanus*	*C. gigas*
	male (n = 6)	female (n = 1)	male (n = 16)	male (n = 6)	male (n = 17)	male (n = 15)	male (n = 9)	male (n = 15)	male (n = 1)	female (n = 1)
SVL	18.3 (17.6–18.8)	18.3	21.0 (18.9–24.3)	16.6 (15.2–17.3)	23.1 (20.2–26.0)	27.7 (23.5–30.0)	21.9 (20.2–25.0)	28.8 (24.2–33.4)	33.5 (26.7–35.4*)	43.1 (42.7–46.0*)
HL	7.3 (6.9–7.8)	7.5	7.7 (6.6–8.9)	6.2 (5.0–7.1)	8.9 (7.6–10.0)	10.8 (9.6–11.7)	10.0 (9.3–10.6)	11.6 (8.9–14.3)	12.6	16.5
SNL	3.4 (3.2–3.6)	3.0	3.5 (3.1–4.3)	2.6 (2.2–2.9)	3.9 (3.3–4.6)	4.6 (3.3–5.4)	3.8 (3.4–4.2)	4.9 (4.2–5.8)	5.5	6.8
IOD	1.9 (1.7–2.1)	2.0	2.8 (2.2–3.2)	2.0 (1.3–2.8)	2.7 (1.9–3.7)	3.2 (2.3–4.2)	2.8 (2.4–3.2)	3.6 (3.0–4.5)	2.9	5.0
ED	2.0 (1.8–2.2)	2.1	2.7 (2.4–3.1)	2.2 (1.5–2.7)	2.6 (1.8–3.5)	3.0 (2.4–3.8)	2.7 (2.2–3.3)	3.3 (2.6–3.9)	3.4	4.9
TD	1.8 (1.6–1.9)	1.6	2.0 (1.6–2.6)	1.6 (1.1–2.0)	2.3 (1.8–2.7)	1.9 (1.6–2.3)	1.8 (1.5–2.2)	2.1 (1.7–2.5)	2.1	2.5
HW	6.7 (6.2–7.2)	7.0	6.9 (5.6–8.3)	5.9 (5.4–6.5)	8.3 (6.9–9)	10.1 (8.9–10.9)	8.0 (7.6–8.9)	10.0 (7.7–12.2)	10.3	16.6
FL	8.1 (7.9–8.3)	9.3	10.0 (9.0–10.9)	8.0 (7.3–8.6)	10.9 (9–12.8)	11.9 (10.5–13.0)	10.0 (9.5–11.2)	12.1 (9.7–15.3)	13.4	19.1
TBL	7.8 (7.5–8.1)	8.5	10.5 (9.6–11.2)	8.2 (7.8–8.7)	11.2 (10.4–12.2)	12.9 (11.7–13.9)	10.5 (9.6–12.7)	14.3 (12.6–16)	14.6	20.4
TSL	4.9 (4.5–5.4)	5.3	6.3 (5.5–7.0)	4.9 (4.5–5.4)	6.5 (5.5–7.4)	7.8 (6.7–8.4)	6.7 (5.6–8.1)	8.6 (7.2–9.7)	15.2	11.5
PL	7.2 (6.7–7.7)	7.0	10.3 (9.1–11.5)	7.9 (6.8–8.7)	10.8 (8.5–12.1)	12.3 (11.2–13.2)	9.8 (8.1–11.9)	13.0 (11.1–15.1)	15.2	20.2
ML	3.9 (3.6–4.3)	4.1	4.9 (4.2–5.7)	3.7 (3.3–4.3)	5.5 (4.3–6.2)	7.3 (6.2–8.0)	5.8 (4.9–7.7)	7.7 (5.8–9.5)	8.7	10.3
FA	3.8 (3.5–4.2)	4.1	4.2 (3.6–4.9)	3.6 (3.4–4.1)	4.7 (3.4–5.5)	5.8 (4.3–7.2)	4.8 (4.2–5.9)	6.8 (4.8–8.9)	7.4	9.0
Toe4L	4.8 (4.1–5.6)	5.0	6.0 (5.3–6.9)	4.4 (3.5–4.8)	6.8 (5.9–8.1)	6.8 (5.9–7.8)	5.4 (4.7–6.1)	7.3 (5.8–8.3)	8.4	12.1
Fin1L	1.2 (1.1–1.4)	1.2	1.8 (1.2–2.3)	1.5 (1.0–1.8)	1.7 (1.1–2.4)	2.2 (1.9–2.4)	1.7 (1.4–2.1)	2.2 (1.4–2.6)	2.8	3.8
Fin3L	2.5 (2.1–2.9)	2.2	3.1 (2.6–4.2)	2.5 (1.8–3.7)	3.7 (3.2–4.5)	4.5 (2.9–5.2)	3.4 (2.9–3.7)	4.5 (2.6–5.6)	5.5	7.1
Fin1DW	0.4 (0.3–0.4)	0.4	0.5 (0.3–0.7)	0.6 (0.2–1.1)	0.6 (0.4–0.8)	0.8 (0.6–1.1)	0.7 (0.6–0.8)	0.7 (0.6–0.9)	1.1	1.3
Fin3DW	0.5 (0.3–0.6)	0.5	0.6 (0.4–0.9)	0.5 (0.3–0.6)	1.0 (0.7–1.4)	1.7 (1.2–2.1)	1.2 (0.7–1.5)	1.7 (1.4–2.0)	2.0	2.6
Toe4DW	0.6 (0.4–0.7)	0.6	0.8 (0.5–1.1)	0.5 (0.4–0.6)	0.9 (0.7–1.2)	1.2 (0.9–1.4)	0.9 (0.7–1.1)	1.2 (0.8–1.5)	1.0	1.8

......continued on the next page

TABLE 2. (Continued)

	C. exedrus **sp. nov.**		*C. trossulus*	*C. minutus*	*C. mediodiscus*	*C. wolfi*	*C. vertebralis*	*C. elegans*	*C. montanus*	*C. gigas*
	male (n = 6)	female (n = 1)	male (n = 16)	male (n = 6)	male (n = 17)	male (n = 15)	male (n = 9)	male (n = 15)	male (n = 1)	female (n = 1)
PpFin3	0.3 (0.2–0.4)	0.3	0.4 (0.3–0.6)	0.3 (0.3–0.4)	0.6 (0.4–0.8)	0.6 (0.3–1.0)	0.6 (0.5–0.7)	0.8 (0.7–0.8)	1.0	0.8
PpToe4	0.4 (0.3–0.5)	0.4	0.4 (0.3–0.5)	0.3 (0.2–0.4)	0.5 (0.3–0.7)	0.6 (0.5–0.7)	0.5 (0.5–0.6)	0.7 (0.6–0.8)	0.7	0.8
Fin3DW/ Fin3L	0.2 (0.1–0.2)	0.2	0.2 (0.1–0.3)	0.2 (0.2–0.3)	0.28 (0.21–0.41)	0.38 (0.28–0.48)	0.36 (0.22–0.45)	0.38 (0.29–0.54)	0.36	0.37
Fin3DW/ SVL	0.03 (0.02–0.03)	0.03	0.03 (0.02–0.04)	0.03 (0.02–0.04)	0.044 (0.032–0.060)	0.062 (0.043–0.077)	0.055 (0.033–0.064)	0.059 (0.050–0.066)	0.060	0.060
Fin3DW/ TD	0.3 (0.2–0.3)	0.3	0.3 (0.2–0.4)	0.3 (0.3–0.3)	0.45 (0.33–0.78)	0.93 (0.57–1.25)	0.68 (0.39–0.87)	0.82 (0.64–1.00)	0.95	1.04
Fin3DW/ PpFin3	1.6 (1.3–2.0)	1.7	1.5 (1.0–2.0)	1.4 (1.0–1.7)	1.8 (1.2–2.4)	3.0 (1.7–5.0)	2.0 (1.4–2.5)	2.2 (1.8–2.5)	2.0	3.3
Fin3DW/ Toe4DW	0.8 (0.7–1.2)	0.8	0.8 (0.4–1.8)	1.0 (0.6–1.3)	1.1 (1.0–1.3)	1.5 (1.1–2.0)	1.3 (1.0–2.1)	1.4 (1.1–2.1)	2.0	1.4
HW/ TBL	0.86 (0.80–0.95)	0.82	0.65 (0.55–0.77)	0.71 (0.66–0.76)	0.74 (0.66–0.83)	0.78 (0.70–0.86)	0.77 (0.70–0.86)	0.70 (0.60–0.80)	0.71	0.81
TBL/ SVL	0.43 (0.41–0.46)	0.46	0.50 (0.46–0.58)	0.50 (0.48–0.54)	0.49 (0.40–0.54)	0.47 (0.42–0.51)	0.48 (0.43–0.51)	0.50 (0.47–0.54)	0.44	0.47
PL/ SVL	0.40 (0.36–0.41)	0.38	0.49 (0.45–0.53)	0.47 (0.44–0.52)	0.47 (0.37–0.56)	0.45 (0.42–0.48)	0.45 (0.39–0.49)	0.45 (0.39–0.51)	0.45	0.47
Fin3L/ HW	0.37 (0.30–0.45)	0.31	0.46 (0.33–0.64)	0.43 (0.31–0.65)	0.44 (0.36–0.54)	0.45 (0.31–0.50)	0.42 (0.35–0.49)	0.45 (0.34–0.57)	0.53	0.43
Fin3DW/ IOD	0.3 (0.2–0.4)	0.3	0.2 (0.1–0.3)	0.3 (0.2–0.4)	0.39 (0.16–0.39)	0.56 (0.36–0.81)	0.44 (0.24–0.54)	0.47 (0.39–0.53)	0.69	0.52
IOD / Fin3L	0.80 (0.59–0.91)	0.91	0.91 (0.62–1.19)	0.81 (0.59–1.06)	0.73 (0.53–0.95)	0.70 (0.50–0.86)	0.82 (0.69–0.091)	0.82 (0.65–1.23)	0.53	0.70
IOD / Fin1L	1.63 (1.21–1.91)	1.67	1.56 (1.09–2.07)	1.36 (1.06–1.75)	1.66 (1.21–2.18)	1.43 (1.10–1.86)	1.66 (1.24–2.07)	1.68 (1.39–2.14)	1.04	1.32
ED / HW	0.29 (0.27–0.34)	0.30	0.40 (0.33–0.46)	0.38 (0.28–0.47)	0.32 (0.22–0.41)	0.30 (0.23–0.40)	0.34 (0.26–0.41)	0.33 (0.27–0.38)	0.33	0.30
Fin3DW/ Fin1L	0.4 (0.3–0.5)	0.4	0.3 (0.2–0.6)	0.3 (0.2–0.5)	0.64 (0.35–0.86)	0.79 (0.52–0.96)	0.72 (0.50–0.93)	0.78 (0.62–1.00)	0.71	0.68
Fin1DW/ Fin3DW	0.8 (0.6–1.0)	0.8	0.9 (0.6–1.2)	1.2 (0.7–1.8)	0.7 (0.4–1.0)	0.5 (0.3–0.7)	0.6 (0.4–1.0)	0.4 (0.3–0.5)	0.55	0.50
Fin3L/ HL	0.34 (0.29–0.41)	0.29	0.41 (0.29–0.52)	0.41 (0.32–0.52)	0.41 (0.34–0.51)	0.42 (0.30–0.49)	0.34 (0.28–0.39)	0.39 (0.29–0.49)	0.44	0.43
HW/ SVL	0.37 (0.34–0.40)	0.38	0.33 (0.26–0.39)	0.35 (0.34–0.38)	0.36 (0.32–0.41)	0.37 (0.34–0.39)	0.37 (0.34–0.42)	0.35 (0.32–0.40)	0.31	0.39

[*] From Brown & Parker 1970 (*C. montanus* n = 8 males and *C. gigas* n = 3 females)

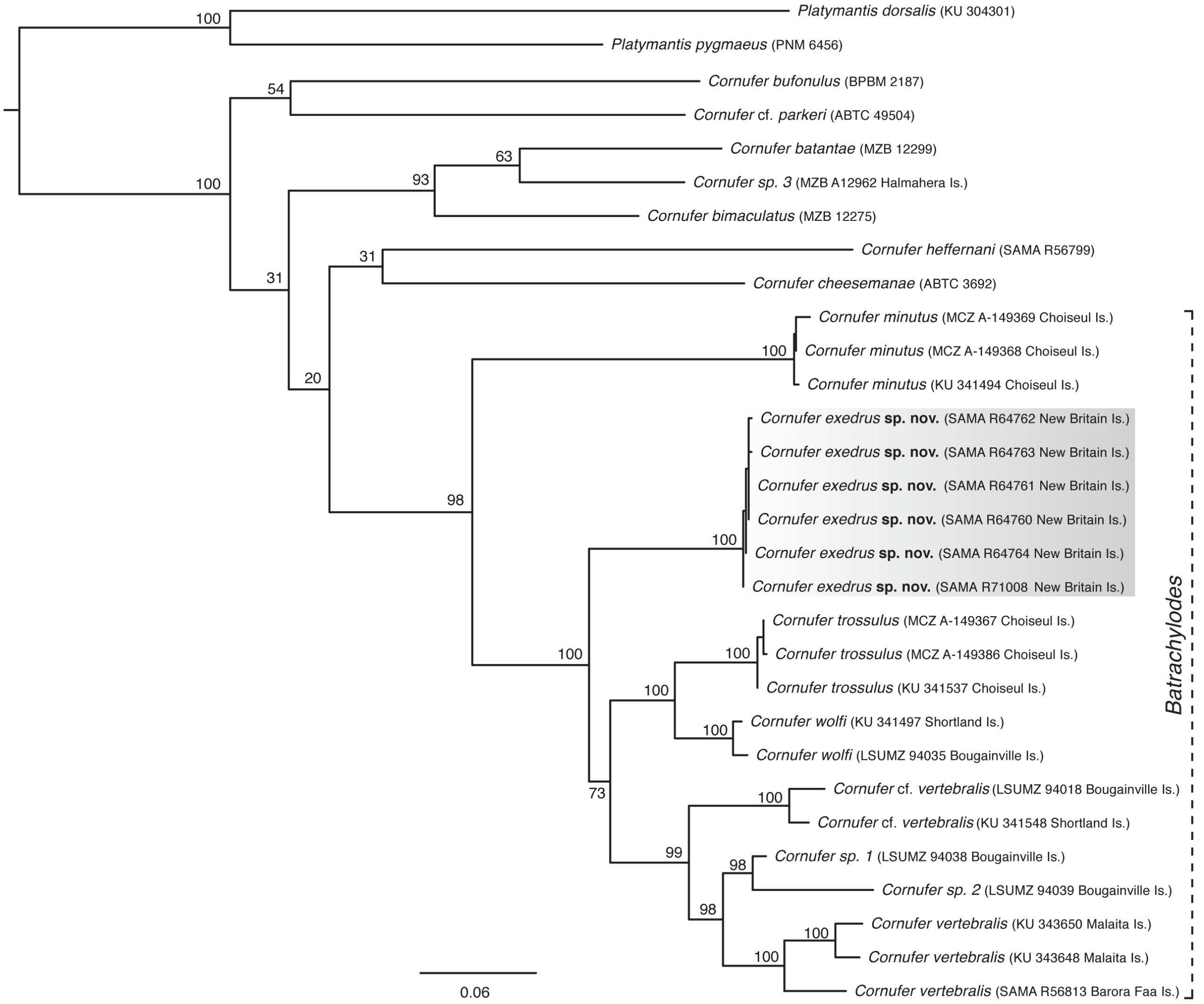

FIGURE 3. Maximum likelihood phylogeny of *Cornufer* focusing on the subgenus *Batrachylodes*, with the position of *C. exedrus* highlighted. Implemented in RAxML based on a fragment (~875-bp) of the mitochondrial 16S rRNA marker.

Manus length 50% of foot length; digits of manus narrow (Figs. 4–5), ovoid in cross-section; dermal flanges absent on lateral edges of digits; terminal finger disks barely expanded (< 2 times width of penultimate phalanges in Fingers I–IV), with short circum-marginal folds on distal tips of digits; minute supra-articular flaps present above penultimate-ultimate phalangeal articulation; fingers unwebbed; decreasing finger length III, IV, I, II; subarticular, supernumerary, and metacarpal tubercles poorly developed and unpointed; subarticular tubercles not prominent, low and rounded on ventral surfaces; one subarticular tubercle on Fingers I–II, two tubercles under Fingers III–IV; supernumerary tubercles indistinct, most distinguishable at base of Finger III; palmar surfaces basal to supernumary tubercles smooth, with slightly convex round tubercule between the supernumerary tubercle at base of Finger III and the medial palmar tubercle; thenar (inner metacarpal), medial palmar and outer metacarpal tubercles indistinct, flat, with poorly defined edges and distinguishable only by the lack of pigment; thenal tubercle elongate, along the medial edge of Finger I; medial palmar tubercle ovoid and larger than elongate, outer metacarpal; medial and outer metacarpal tubercles not separated at base; nuptial pads absent, forearm musculature not hypertrophied.

Hindlimbs short; tibia length 41% of snout-vent length, pes length 99% of tibia length; tarsus smooth, lacking folds, flaps, or tubercles; terminal disks of toes slightly expanded and ovoid (< 2 times width of penultimate phalanges in Toes I–V); disk width of Toe IV 130% of disk width of Finger III; lateral dermal flanges absent along distal phalanges; circum-marginal grooves on distal ends of digits; supra-articular cutaneous folds slight; plantar surfaces of pes smooth (Figs. 4–5), lacking supernumerary tubercles or texture on plantar surfaces, but with moderately developed, rounded (not pointed) subarticular tubercles, numbering one under Toes I–II and two under

Toes III–V; decreasing toe length IV, III, V, II, I; outer metatarsal tubercle small, low, and rounded; inner metatarsal tubercle moderate, low, flat, and oblong; toes without interdigital webbing. Cloacal region lacking tubercles, but with small supracloacal dermal flap.

Measurements of holotype. SVL 18.1; ED 1.8; TD 1.6; HL 7.4; SNL 3.3; IOD 2.0; HW 6.2; FL 8.1; TBL 7.5; TSL 4.5; PL 7.4; ML 3.7; FA 3.7; Toe4L 4.1; Fin1L 1.1; Fin3L 2.2; Fin1DW 0.3; Fin3DW 0.3; PpFin3 0.2; Toe4DW 0.4; PpToe4 0.3.

Color of holotype in preservative. Dorsal surfaces of body and head exhibit nearly homogeneous light brown coloration; under magnification, background color of dorsal surfaces is pale cream and unpigmented with dense and nearly uniform speckling of brown chromatophores; less brown pigmentation present in interorbital region, extending posteriorly in a U-shaped pattern to a midpoint between the scapulae, giving slightly paler appearance to region along top of head than rest of body; two small, dark brown interorbital spots between anterior margin of eyes; tip of snout unpigmented; dorsal surface of limbs similar in background coloration to rest of body, but with darker brown transverse bars (three on forearm, three on femur, three on tibia, one on tarsus, two on metatarsus) with irregular margins and poorly defined; dorsal surfaces of hands, feet, and digits similarly colored as rest of the body and limbs with irregular dark spots and bars; the lateral surfaces of the head and body have a distinct dark brown band (darker than dorsal coloration) covering entire loreal and supralabial region, extending posteriorly along flanks diagonally (anteriodorsally to posteroventrally) towards inguinal region; this lateral band is darkest and near uniformly shaded along head (although tympanum is slightly lighter) becoming lighter and more diffusely speckled posterior to the humerus, into light tan irregular blotching in the inguinal region; the dorsal margin of this lateral band is nearly smooth and darkest brown in coloration (with respect to the rest of band), forming a clear dark line demarcating lighter dorsal and darker lateral colors extending from snout tip (although absent from unpigmented snout tip) along the canthus rostralis (above nostril) and upper eyelid, and posterior onto flanks slightly above tympanum; dark dorsolateral line fades in the inguinal region becoming prominent again on hindlimbs (although with more irregular margin) particularly on anterior edge of thigh and knee, fading into diffuse irregular tan blotching on tibia; underside of throat dark brown with lighter unpigmented mottling throughout; brown ventral coloration of throat fades posterior to the pectoral region becoming diffuse irregular tan blotching on pale cream midventer; ventral surfaces of forearms tan, darker brown towards outer edge of forearms; inner forearm with unpigmented band extending to underside of humerous; underside of hindlimbs similar in coloration to midventer, pale cream with brown irregular mottling; when viewed in posterior aspect cloacal region nearly uniform dark brown with smooth, dark dorsal margin above cloaca extending along the posterior of thighs clearly demarcating it from lighter dorsum; when in a seated position, this dark cloacal-femoral band grades into similarly colored dark band along outer edge of tarsus; small dark brown blotch just above cloaca; ventral surfaces of hands and feet dark brown with pale subarticular banding.

Variation. Compared to the holotype (SAMA R64760), dorsal coloration of the head and body of the paratypes ranges from a darker brown (SAMA R64763, SAMA R64764, SAMA R71008, SJR 10843) to a lighter cream (SAMA R64761, SAMA R64762, SAMA R71007) background coloration, and whereas the holotype has a nearly uniform dorsal coloration, all of the paratypes exhibit some degree of dorsal markings. SAMA R71008, SAMA R64763, and SJR 10843 possess a faint, thin and lighter vertebral stripe. Four of the paratypes (SAMA R71007, SAMA R71008, SAMA R64762, SAMA R64761) possess a pair of discrete darker brown to black dorsal spots that are posteroventrally located just behind the projection of the sacrum. Several paratypes also have irregular darker paravertebral spots between the scapulae, which are similar in size to the posterior dorsal spots in some (SAMA R64761, SAMA R64762) or a faint speckling in others (SJR 10843, SAMA R64763). SAMA R64761 exhibits more extensive irregular dark flecking and blotching along the dorsum. Three paratypes (SAMA R64764, SAMA R64761, SAMA R71007) possess a faint, thin and darker interorbital bar. Several paratypes also exhibit faint darker banding extending from behind eyes and/or the sacral region intersecting at the midscapular region, leaving a faint x or v-shaped pattern along the dorsum. All of the paratypes possess the transverse bars on the limbs as described in the holotype.

There is variation in breadth and extent of the dark lateral band that extends from the loreal region onto the flanks. In some individuals, the lateral band is darker and more filled in throughout the snout and flank region, giving appearance of dark face mask which remains solid (not fading) along the flanks. However, in others the lateral band is limited to more of a dark stripe from the tip of the snout, along the canthus rostralis, and posterior towards the inguinal region, which quickly fades ventrally into a light-brown coloration similar to the color of the dorsum. In two individuals (SAMA R64761, SAMA R71007), the lateral band is almost entirely limited to the snout along the canthus rostralis and quickly broken and fading posteriorly behind the eye, and in these individuals there is almost no darker shading below the band in the loreal and supralabial region of the snout or along the flanks. Ventral coloration of several of the paratypes is similar to that of the holotype, with a darker brown chin and throat region fading into a lighter cream midventral region and the underside of the hindlimbs with diffuse brown speckling. However, in one individual (SAMA R64762) the entire vertrum is similar in coloration to the brown throat, and in three individuals (SAMA R64761, SAMA R71007, SJR 10843) the brown pigmentation has faded, leaving the entire ventrum pale cream in coloration.

In most of the paratypes the skin texture is smooth, similar to that of the holotype, however several specimens exhibit finely granular skin along the dorsum, and one indiviudal (SAMA R64761) possesses small raised dorsal ridges and minute tubercles associated with the darker brown spots and flecks along the dorsal surface of the body. The small unpigmented tubercles on the chin and throat of the holotype are also present on most of the paratypes (although varying in number and extend along the throat); however, they are absent on the juvenile (SJR 10843) and female (SAMA R64763) specimens, suggesting that it may be a sexually dimorphic character. Additionally, the unpigmented projection of the snout on the holotype is prominent on most of the paratypes except the aforementioned juvenile and female paratypes, suggesting it may also be a sexually dimorphic character. Mensural variation is presented in Table 2. All mensural ratios for the single female paratype are within the ranges found in males, possibly indicating little sexual dimorphism in morphometric characters.

Color in life. Based on color images of the holotype (SAMA R64760, Figs. 2–3) and two paratypes (SAMA R64763 and SAMA R64764, Fig. 2) in life taken during the daytime, prior to preservation: Dorsal ground coloration of body and limbs of the holotype (SAMA R64760) a pale pinkish-salmon that is overlain with small darker pinkish-orange spots or streaking (streaks most prominent on the tibia) with some small irregular whitish spotting throughout; thicker (but faint) darker brown transverse bars extending across the hindlimbs and three thin (broken) darker brown transverse bars on the forearm; dorsal coloration of the head orangish, giving the appearance of a head cap (from just behind the unpigmented snout projection extending in a U-shaped pattern posterior to the eyes to the mid-scapular region); three small whitish and two small dark brown interorbital spots between the anterior margins of the eyes; margin of the upper eyelid with a thin light whitish band speckled with diffuse brown flecking. Dorsal coloration of the two paratypes different than that of the holotype. One paratype (SAMA R64763) has a more solid and uniformly darker brown coloration across the head, body, and limbs flecked with minute irregular dark brown, whitish, and reddish spots; limbs also with some suffused lighter orangish-brown highlights; a thin and slightly broken vertebral stripe is present, and a cluster of small dark-brown paravertebral spots in the midscapular region; faint darker brown transverse bars present on the limbs. The other paratype (SAMA R64764) possesses lighter tan dorsal coloration on the head and body, fading to darker brownish-gray hindlimbs (forearms of similar color as hindlimbs), leaving the transverse bars on the hindlimbs poorly diagnosable; faint minute irregular dark-brown, whitish, and reddish spots or blotching on the dorsal surfaces of the body and limbs; light yellow-gold pigment faintly dusting the forelimbs and hands; two darker brown dorsal bands also apparent, one interorbital band between the midpoints of the orbits and upper eyelids, and one extending as a forward-facing V-shape connecting at the midscapular region and extending posteroventrally to the mid-dorsum.

The shading of the dark-brown lateral band (from the snout tip to the flanks) also varies slightly. In all three specimens the dorsal margin of the lateral band is the darkest brown, particularly in the loreal region along the canthus rostralis; in SAMA R64763 the dorsal margin of this lateral band is edged by a thin (slightly broken) white line that extends from the inguinal region diagonally (posteroventrally to anteriodorsally) across the distal margin of the upper eyelid, along the canthus rostralis, over the nostril, and around the tip of the snout (which lacks the unpigmented protrusion), and there is also some reddish-orange coloration associated with this white line along the flanks; this thin white line is absent in SAMA R64760 and SAMA R64764, which only have a lighter whitish distal margin along the upper eyelid; in SAMA R64763 and SAMA R64764 the shading of the dark brown lateral band is nearly homogeneous throughout the loreal and labial region and posteriorly onto the flanks (only becoming slightly paler on the tympanum and flanks, with scattered white flecks on the flanks), whereas in the holotype (SAMA R64760) the dark brown rapidly fades to a lighter brown ventrally towards the labial region and on the flanks posterior to the tympanum (where the background coloration is more pinkish-salmon, similar to the dorsum); in all three specimens (SAMA R64760, SAMA R64763, and SAMA R64764) this dark lateral band transitions onto the inner thigh out to the knee, although its dorsal margin is irregular.

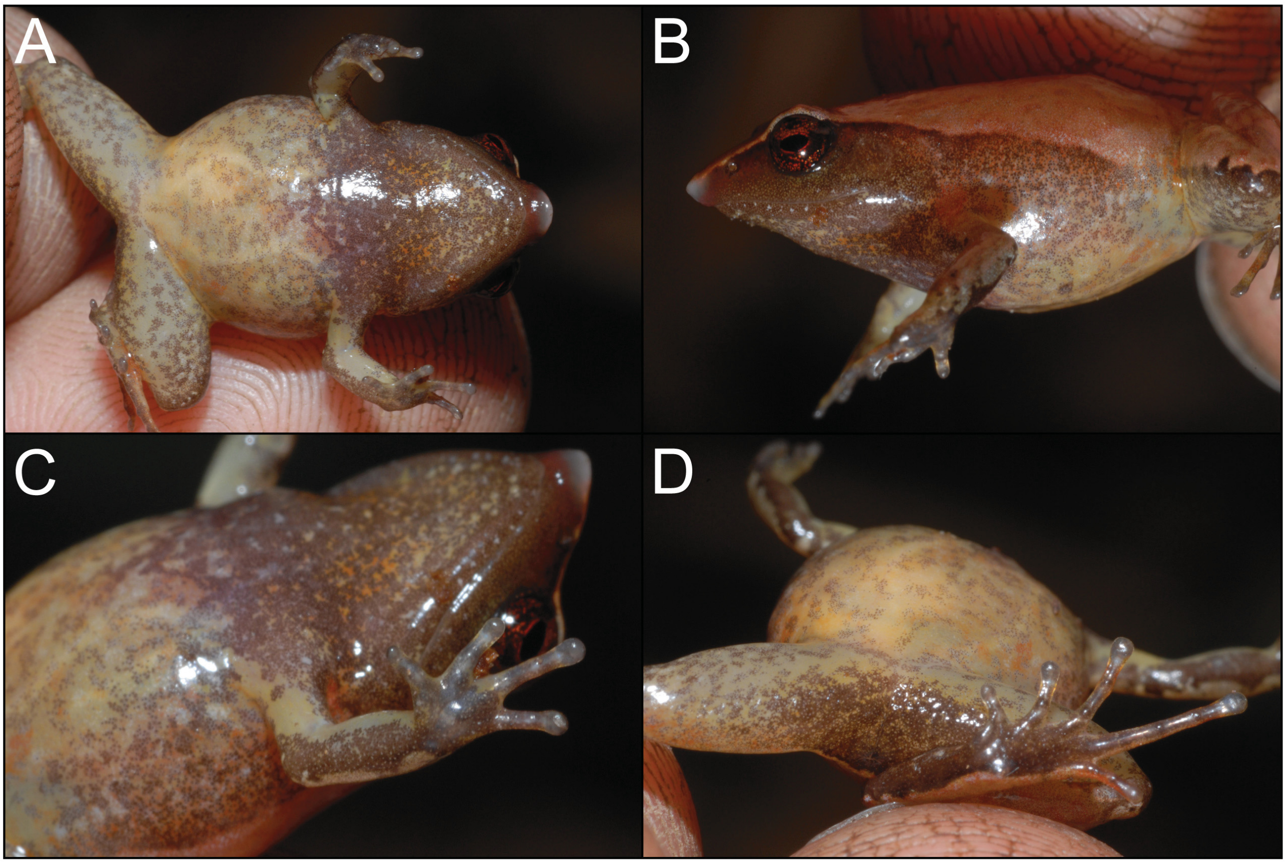

FIGURE 4. Close-up images of the holotype of *C. exedrus* (SAMA R64760) in life showing ventral (A), lateral (B), palmar (C), and plantar and cloacal (D) regions.

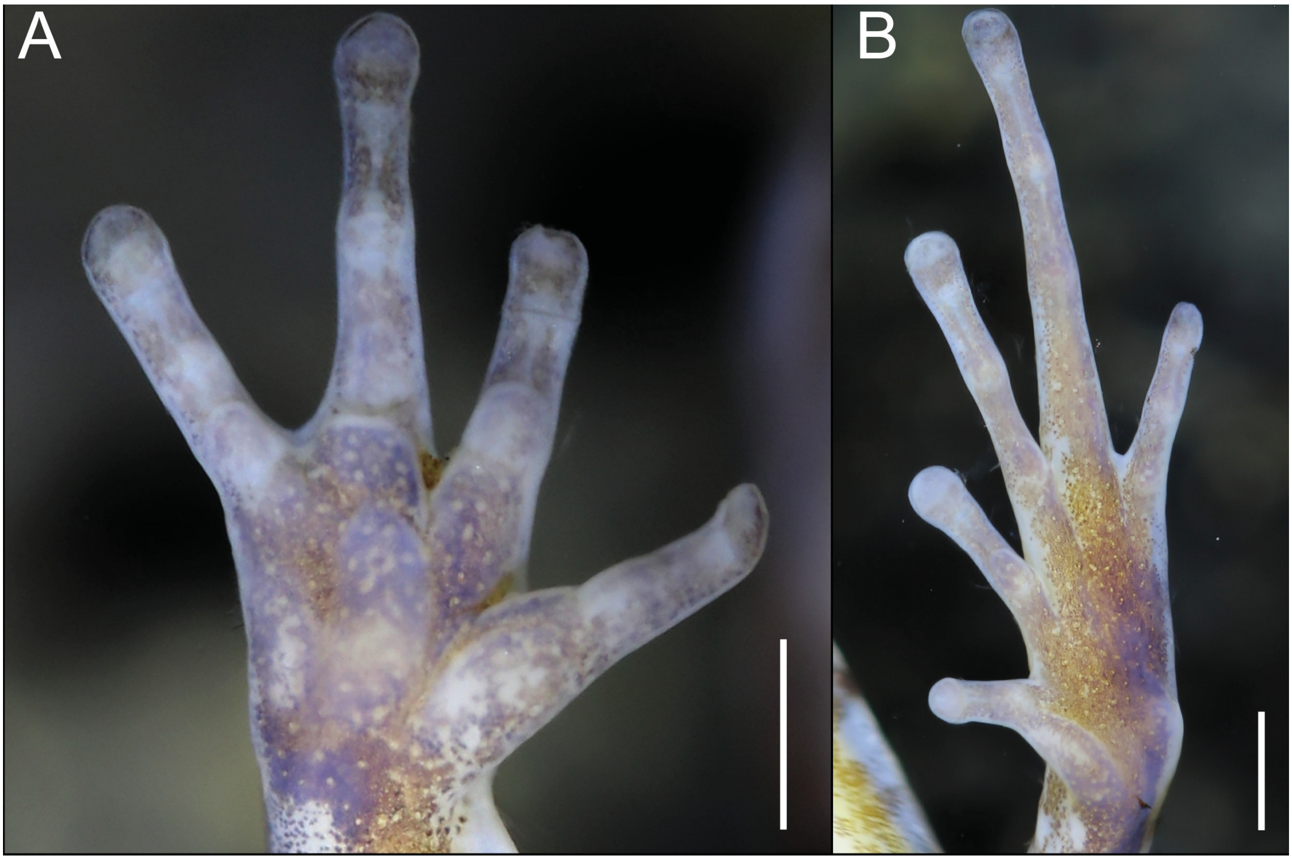

FIGURE 5. Close-up images of the ventral surfaces of the right hand (A) and left foot (B) of the holotype of *C. exedrus* (SAMA R64760) in preservative (scale bar = 1 mm).

Background ventral coloration of the holotype a light yellowish-straw overlaid with brown flecks that are suffused throughout the chin, throat, and pectoral region and fading posteriorly to faint brown blotches, giving the venter and overall dark (anterior) to light (posterior) appearance. Orange pigmentation in the form of blotching is also diffusely scattered throughout the ventral surfaces and most concentrated on the throat. The ventral surfaces of the hands and feet are mostly brown, which extends as an irregular dark band on the underside of the forearm and tarsus. Iris reddish with black streaking above and below the pupil.

Advertisement call. We quantified both temporal properties (calling rate, call duration, intercall interval, note repetition rate, internote interval), structure (number of notes), spectral characters (dominant frequency, other frequency components, harmonics), and variation in peak amplitude across distinct frequency components of the call. Our description of the advertisement call of male *C. exedrus* is based on recording segments (10 complete calls; 2 per subject, separated by a single intercall interval per male) from five individual males, one of which was captured and preserved (SAMA R64762). The other four calls corresponded to males that eluded capture. Because the majority of recorded males escaped, we report only ambient temperatures, which ranged only from 18.2–19.2°C. Typical calling behavior in focal males was initiated by stimulation by other, nearby calling individuals; the majority of our recordings (4/5) contain calls of other individual males, precisely alternating notes, in the background of the focal subject (Fig. 6).

The call of *C. exedrus* is a series of brief, high-frequency atonal notes, delivered in a slow train of variable duration, numbers of notes, and note repetition rates. We define the call as distinct group of atonal notes clustered temporally, and corresponding to times when calling males' posture was upright, and when vocal sac inflation cycles and lateral body wall (flank) compressions were observed during sound production. Discrete calling efforts were unambiguously offset from periods of silence before and after sound production, corresponding to periods when the individual's posture was less erect, and no vocal sac inflation, nor flank compression was observed. The typical call of *C. exedrus* begins with a series of slow, low-amplitude notes in the form of a quiet "tink….tink…tink," which gradually increases in note repetition rate and amplitude, until a near constant rate and amplitude are achieved (Fig. 6). Other than this initial "warm-up" period, rates and amplitudes of notes remain remarkably constant across the call of the new species.

Across all recording segments (n = 5 males), calling rate varied from 0.007 to 0.014 (mean = 0.011 ± 0.03 SD; n = 4) calls/s, and average call duration ranged from 16.0 to 93.9 (mean = 54.3 ± 30.1 SD; n = 5) s, with 17–75 (mean = 47.6 ± 24.4) notes/call. Intercall interval per male varied from 24.5 to 66 (mean = 39.5 ± 19 SD; n = 4) s. Within calls, internote intervals ranged from 0.80 to 0.95 (mean = 0.90 ± 0.06 SD) s, and note repetition rate varied from 0.79 to 1.1 (mean = 0.90 ± 0.11; n = 5) notes/s.

The spectral structure of calls of the new species are remarkably stereotyped (Fig. 6). Individual notes contain discrete frequency components that are invariant across the call and apparently fixed within individuals. No frequency modulation or shifts in emphasis of individual frequency components were observed in any of the calls studied here (n = 5). Calls consist of internally identical notes (no switching of dominant and fundamental frequency observed), each containing a fundamental (lowest; mean = 2.2 ± 0.1 SD; range 2.0–2.3 kHz; n=5) frequency, differing discretely from the dominant (= emphasized; mean = 4.3 ± 0.2 SD; range = 4.1–4.7 kHz; n = 5) frequency. Calls possess 2–5 additional frequency components at means of 6.7 (± 0.3 SD; range = 6.3–7.2; n = 5), 8.6 (± 0.4 SD; range = 8.3–9.2; n = 5), 11.4 (± 0.4 SD; range = 10.9–11.7; n= 3), and approximately 13 and 15 (n = 2 each) kHz, respectively. Relative amplitude of the fundamental frequency ranged from 0.88–0.96 (mean = 0.91 ± 0.04; n = 5).

The call of the new species is similar to *C. vertebralis* (the only other *Cornufer* [subgenus *Batrachylodes*] with recorded calls available for comparison) in overall structure: a series of slow, high-frequency notes. However the call of *C.* (*B.*) *vertebralis* is more rapid (calling rate mean = 0.019 ± 0.05 SD; range = 0.014–0.023; n = 3) calls/s, generally consists of fewer (11–39; mean = 21.3 ± 15.4; n= 3) notes/call, which are delivered at a more rapid rate, and pulse repetition rate varied from 0.96 to 1.6 (mean = 1.3 ± 0.33; n = 3). *Cornufer* (*Batrachylodes*) *vertebralis* calls also have distinct intranote structure, whereas *C. exedrus* calls contain only simple, unstructured atonal notes, entirely lacking within-note structure or variable amplitude modulation.

Ecology, Distribution, and Natural History. *Cornufer exedrus* is known only from elevations of 1500–1700 m above sea level, based on our surveys in the vicinity of the type locality, Tompoi Camp, in the Nakanai Mountains of East New Britain Province in the Bismarck Archipelago. (Fig. 1). The camp was located in a patch of mossy montane forest surrounded by dense, near-impenetrable thickets of thin, scrambling *Nastus* bamboo. During the survey period (19–25 April, 2009), this site was extremely wet from the frequent rain and dense fog that shrouded the forest on most days. Males called from hidden positions in wet litter on the forest floor, and densities were highest where the forest had not been invaded by dense bamboo thickets. The species appears to be crepuscular (calling activity peaked at dawn and dusk) but many non-calling individuals were active in wet litter during the day, particularly after rain. In contrast, calling activity was greatly reduced at night, and few animals were observed to be active on the forest floor after dusk. Sympatric species included *Cornufer adiastolus*, *C. citrinospilus*, *C. mamusiorum*, *C. nakanaiorum, C.* cf. *sulcatus*, and *Oreophryne brachypus*.

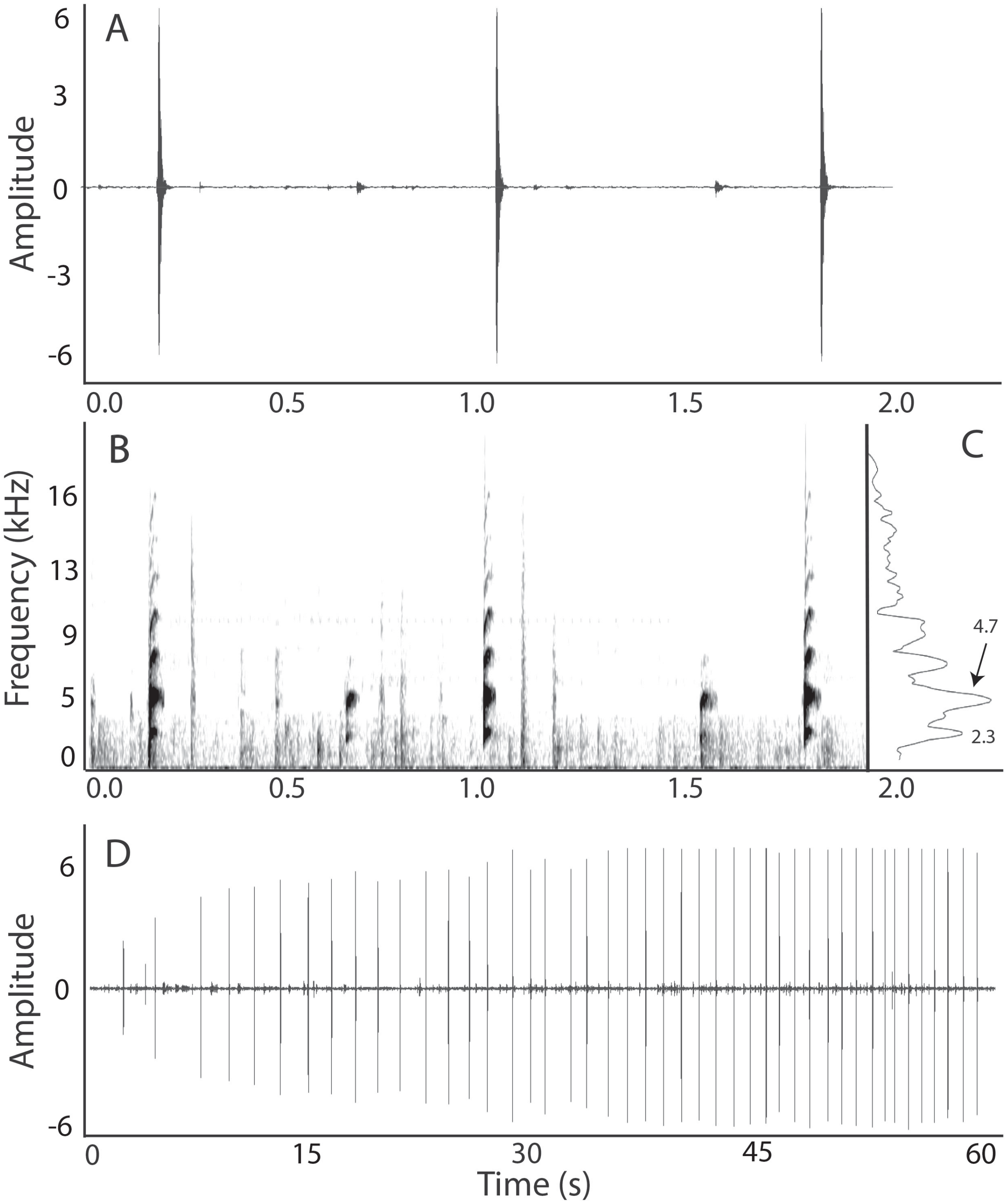

FIGURE 6. The advertisement call of a male *C. exedrus* paratype (SAMA R64762) recorded at ambient temperature of 18.4°C on 21 April 2009 (1830 hr, by SJR): (A) oscillogram (relative amplitude vs. time in s) of three typical notes and (B) a 2 s audiospectrogram (frequency in kHz vs. time in s) from the middle of a 60 s, 44-pulsed call (D, relative amplitude vs. time in s). Note (C) the corresponding power spectrum (Fast Fourier Transformation; relative amplitude vs. frequency in kHz) of a single note, depicting a fundamental (lowest) frequency of 2.3 kHz and the dominant (emphasized) frequency of 4.7 kHz.

Discussion

Although the overwater distance between the closest major islands in the Solomon and Bismarck Archipelagos (Buka and New Ireland respectively) is less than 200 km, there is little overlap in the anuran communities between these two regions (Menzies 2006; Pikacha *et al.* 2008). Thus, the discovery of a new biogeographically disjunct member of the diminutive *Batrachylodes* clade in the highlands of New Britain is a surprising and unexpected finding. Among ceratobatrachids, which comprise most of the frog diversity in these Eastern Melanesian archipelagos, only one species (*Cornufer guppyi*) occurs in both island groups, and these two populations exhibit high genetic divergence, likely representing distinct species (Brown *et al.* 2015). The number of older biogeographic transitions of *Cornufer* between these two regions also appears to be limited (Brown *et al.* 2015); however, additional work is needed to resolve the deeper relationships within this clade for accurate inferences into the biogeographic history of *Cornufer*. This lack of overlap between the Solomon and Bismarck *Cornufer* communities suggests that historical and recent anuran exchange between these two archipelagos has been limited. However, enigmatic new discoveries such as *Cornufer exedrus* and others (e.g., Oliver *et al.* 2016), coupled with molecular phylogenetic analyses, will continue to improve our understanding of the biogeography of these Melanesian island arcs.

Knowledge of the endemic frog communities of New Britain and the rest of the Bismarck Archipelago has increased dramatically over the past two decades (Allison & Kraus 2001; Foufopoulos & Brown 2004; Brown *et al.* 2006a,b, 2013; Kraus & Allison 2007, 2009; Richards *et al.* 2007, 2014). However, levels of *Cornufer* diversity are still underestimated here (Richards & Aplin 2015). The description of *C. exedrus* brings the number of New Britain *Cornufer* species to 17, and this island has quickly become recognized as a hotspot of *Cornufer* diversity with an ecologically diverse assemblage of species, many of which can occur in sympatry (Kraus & Allison 2007; Foufopoulos & Richards 2007; Brown *et al.* 2013, 2015). However, additional species are still likely to be discovered as the remote highland regions of this island become more thoroughly surveyed.

In the Solomon Archipelago, the radiation of *Batrachylodes* remains a taxonomically confusing group that has received little attention since the revision by Brown & Parker (1970). Their small size, conserved morphology, and often highly variable color patterns make them extraordinarily difficult to assign to species. Even other diminutive *Cornufer* taxa that are not part of this subgenus can be mistakenly identified as a *Batrachylodes*. For example, we recently collected a new population of *Batrachylodes* from Choiseul that is morphologically diagnosable as *C. minutus* (previously only known from Bougainville). Here, we include genetic data for this population along with the "*C. minutus*" (ABTC 49504) individual included in the phylogenetic work by Brown *et al.* (2015). This was the only *Batrachylodes* species in their analyses that potentially rendered the subgenus paraphyletic (Brown *et al.* 2015:figs. 2–3), and they suggested *C. minutus* be excluded from the subgenus. Our analyses here recovered no close relationship between these two lineages: the former falls out within the *Batrachylodes* clade with strong support while the latter does not (labeled as *Cornufer* cf. *parkeri* in Fig. 3). We suspect that ABTC 49504 may represent *Cornufer parkeri*, another miniature terrestrial *Cornufer* from Bougainville that could be mistaken for *Cornufer minutus* (Brown 1965), and we recommend the inclusion of *C. minutus* within the subgenus *Batrachylodes*.

The tendency of some *Batrachylodes* species to occupy limited geographical ranges, restricted solely to high-elevation rainforests, while others can be found in a variety of low-elevation habitats and even coastal areas on several islands, poses an intriguing challenge for future research as species boundaries and taxonomic diversity in this clade remain poorly understood. As originally noted (Brown & Parker 1970), many of the characters that diagnose these diminutive taxa broadly overlap, and some species are diagnosable primarily by their call characteristics (which were never described) or coloration in life (which have faded in collections) (unpublished data). To address this taxonomic confusion, we have begun to target this frog group during recent surveys throughout the Solomons to collect the bioacoustic, morphological, ecological, and genetic data that will be necessary to sort out species boundaries in this clade (Travers *et al.* unpublished data).

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APPENDIX I. Specimens examined. Collection acronyms: AMNH, American Museum of Natural History; BMNH, British Museum of Natural History; BPBM, Bernice P. Bishop Museum; CAS, California Academy of Sciences; CAS-SU, California Academy of Sciences, Stanford University Collection; KU, University of Kansas Biodiversity Institute; MCZ, Museum of Comparative Zoology, Harvard University; MZB, Museum Zoologicum Bogoriense, Indonesia; PNGNM, Papua New Guinea National Museum; SAMA, South Australia Museum; SJR, Stephen J. Richards field series; TNHC, Texas Memorial Museum, University of Texas at Austin; USNM, National Museum of Natural History, Washington D.C., USA; UWZM, Zoology Museum, University of Wisconsin, Madison.

Subgenus *Aenigmanura*:

Cornufer adiastolus (14 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, East New Britain Province, Wanui River Valley, Wanui Village: SAMA R61906 (holotype), 57014–15, R60257–59, R61907–09, PNGNM 8874–76 (paratypes); Vouvou Camp: SAMA R64704, 64797.

Cornufer admiraltiensis (16 specimens): Papua New Guinea, Admiralty Archipelago, Manus Province, Manus Island Chachuau Camp, near Tulu 1 Village: SAMA R62799 (holotype), PNGNM 10049, SAMA R62800–01, PNGNM 10050, SAMA R62802–03; Lorengau: SAMA R62804–05; Tulu 1 Village: SAMA R62808–10; Tingau Village: SAMA R62806; Natnewai Camp: SAMA R62811–16; Los Negros Island, Salami Village: SAMA R62807 (paratypes).

Cornufer akarithymus (8 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, S coast, ca 14 km NW Pomugu, Kandrian: CAS-SU 22875 (paratype); Moramora, 3 km N, 7 km E Hoskins: MCZ-A 88823; Pomugu, SAMA R7073 (holotype), SAMA R6982 (paratype); East New Britain, Malasait (04.464°S, 151.889°E), SAMA R7066, R7082; SAMA 57020–21; Camp: SAMA R64679, 64680.

Cornufer boulengeri (5 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, ca 40 km S of Talasea, San Remo Plantation on Willaumez Peninsula: CAS-SU 22876; "New Britain Archipelago": MCZ-A 1729, 9372; Moramora, 3 km N, 7 km E Hoskins: MCZ-A 92711; CAS-SU 22873 (paratype of *P. rhipiphalcus*), SAMA R7078 (paratype paratype of *P. rhipiphalcus*); Pomugu: SAMA R7071 (holotype of *P. rhipiphalcus*); East New Britain Province, Vouvou Camp: SAMA R64798.

Cornufer citrinospilus (4) Papua New Guinea, New Britain Island, East New Britain Province, Nakanai Mountain Range, Tompoi Camp, 1590–1700 m elevation: SAMA R64758 (holotype), R64756, R64757, PNGNM 24042 (paratypes).

Cornufer desticans (4 specimens): Solomon Islands, Isabel Province, Barora Faa Island, (off the western tip of Isabel Island): SAMA R56849 (holotype), and SAMA R56850–52 (paratypes).

Cornufer gillardi (17 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, S coast, ca 7 mi NW Pomugu, Kandrian: CAS-SU 22877–78; northern Nakanai Mountains, ridge between the Ivule and Sigole rivers on the northern edge of the Nakanai Plateau: UWZM 23787–96, 23799–800; East New Britain Province, Vouvou Camp: SAMA R64801–02.

Cornufer hedigeri (formerly *Platymantis guppyi*; Brown *et al.* 2015; 59 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Camp Torokina: USNM 120852–53; Kunua: MCZ-A 38628, 38632–33, 38635, 38638–39, 38664–666, 38668, 38674, KU 93736–40, 98159–65, 98468; Melilup: MCZ-A 38629, 38659–60, 38667, 38669–72, 59498–501; Mutahi: CAS 106553–106565; Solomon Islands, Barora Faa Island (near Isabel Island): SAMA R56839, 56840; Guadalcanal Island, Tadai District, Mt. Austen, Barana Village: KU 307359, 307375–76, 307381, 307384–86.

Cornufer latro (18 specimens): Papua New Guinea, Admiralty Archipelago, Manus Island, Manus Province: KU 93750–54; Chachuau Camp near Tulu 1 Village: SAMA R62819 (holotype), PNGNM 10051, SAMA R62820; Natnewai Camp: SAMA R62826; Lorengau: PNGNM 10052–54, SAMA R62821–23; Rambutyo Island, Penchal Village: SAMA R62827; Los Negros Island, Salami Village: SAMA R62828–29 (paratypes).

Cornufer macrosceles (4 specimens): Papua New Guinea, Bismarck Archipelago, West New Britain Province, Ti, Nakanai Mountains (central New Britain): BPBM 1005 (holotype); Nakanai Mountains, ridge between the Ivule and Sigole Rivers: UWZM 23721, PNGNM 10007; East New Britain Province, Vouvou Camp: SAMA R64815.

Cornufer magnus (4 specimens): Papua New Guinea, Admiralty Archipelago, New Ireland Island, New Ireland Province, W. Coast, approx. 88 km S Kavieng ("Madina High School area"): CAS 143640, (holotype); CAS 143639 (paratype); Utu, 1 km S, 5 km E Kavieng: MCZ-A 92671–72 (paratypes).

Cornufer mamusiorum (2 specimens): Papua New Guinea, Bismarck Archipelago, West New Britain Province, northern Nakanai Mountains, ridge between the Ivule and Sigole rivers on the northern edge of the Nakanai Plateau (05° 33.112'S, 151° 04.269'E): UWZM 23720 (holotype), UWZM 23719, 23722, PNGNM 9992 (Paratypes); Papua New Guinea, East New Britain Province, Vouvou Camp: SAMA R64713–14.

Cornufer manus (2 specimens): Papua New Guinea, Admiralty Archipelago, Manus Island Manus Province, Lorengau, MCZ-A 87512 (holotype), 87513 (paratopotype)

Cornufer nakanaiorum (8 specimens): Papua New Guinea, Bismarck Archipelago, West New Britain Province, northern Nakanai Mountains, northern edge of the Nakanai plateau, on a ridge between the Ivule and Sigole rivers 1640 m elevation; UWZM 23897–98, PNGNM 10010–11 (holotype and three paratypes); Papua New Guinea, Bismarck Archipelago, New Britain Island, East New Britain Province, Vouvou Camp: SAMA R64806–09, SJR 10733.

Cornufer neckeri (47 specimens): Papua New Guinea, Bougainville Island, Bougainville Province: MCZ-A 30145–46 (paratypes); Kunua: USNM 217441; Melilup: MCZ-A 66853–56, 66849, 66849, 66851–53; Mutahi: MCZ-A 66877–78, 66881–82, 66885–90, 66893; 66926–38; CAS 106451–106458; Solomon Islands, Barora Faa island (near Isabel Island): SAMA R56792–93, 56841–42.

Cornufer nexipus (17 specimens): Papua New Guinea, Bismarck Archipelago, West New Britain Province, New Britain Island, Nakanai Mountains, ridge between the Ivule and Sigole Rivers, 900–1200 m above sea level: PNGNM 10007–09, UWZM 23893, 23895–23896; East New Britain Province, Wanui Camp, Wanui River Valley (near Wide Bay), 310 m above sea level (05° 21.638'S, 152° 05.266'E): SAMA 56783–84; Gazelle Peninsula, Baining Mountains, St. Paul's, 100–400 m above sea level, BPBM 1009 (holotype); Vouvou Camp: SAMA R64690–91, 64806–09, SJR 10733.

Cornufer occidentalis (22 specimens): Indonesia, Raja Ampat Islands, Batanta Island, Warinkabom: MZB 12060, 12065; Waire Camp: MZB 12063; Wailebet Village: MZB 12062; Salawati Island, Weybya Camp: MZB 12059; Papua mainland, Manokwari, Gunung Meja: MZB 12296; Indonesia, Sulawesi Tengah Province, Kabupaten Banggai, Kecamatan Tinangkung, Peleng Island, Desa Saiyang, 3 km S of Saiyang on road to Ambelang: TNHC 59673–88.

Cornufer papuensis (12 specimens): Indonesia, Papua Province, 'Hollandia"' CAS-SU: 8790–91; Lake Sentani: CAS-SU 9709–12; Papua New Guinea, Madang, Naru Village: TNHC 51544–46; Indonesia, Papua Province, Madang, Baiteta cave: TNHC 51541, 51978, 51980.

Cornufer parilis (4 specimens): Solomon Islands, Isabel Island, northwestern Isabel Island, Kolopakisa Village: SAMA R56911 (holotype), SAMA R56908–10 (paratypes).

Cornufer schmidti (41 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, East New Britain Province, Karat, Cherub Plantation: CAS 139651–52; Baining Mountain Range, Gazelle Peninsula: CAS-SU 22880–91 (paratypes); Talasea Plantation, Willaumez Peninsula: SAMA R6762, 6764, 6784, 6786, 6791, 6795, 6813, 7093, 7097 (paratypes), 7618 (holotype); San Remo, Willaumez Peninsula: 6858, 6862, 6912, 6923 (paratypes); L.A.E.S., Karavat, Gazella Penninsula (near Rabaul): SAMA R7147, 7099 (paratypes); Wanui, Wanui River Valley (near Wide Bay), 310 m above sea level (05° 21.638'S, 152° 05.266'E), SAMA R57014–16, 57040–43; West New Britain Province, northern Nakanai Mountains, ridge between the Ivule and Sigole rivers on the northern edge of the Nakanai Plateau: UWZM 23775–78; 23782, 23890.

Cornufer solomonis (29 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Topanas: CAS 109817; Mutahi: CAS 109825–26; 109829–30, 109840; Solomon Islands, Barora Faa Island (near Isabel Island): SAMA R56843–44; Kunua: KU 93762–63; 98477; Solomon Islands, Western Province, Lola Island: KU 307144–25, 307136; Guadalcanal Province, Guadalcanal Island, Metapono District, Keamami Village: KU 307311; Tadai District, Mt. Austen, Barana Village: KU 307357, 307377, 307382, 307389, 307393, 307411, 307428.

Cornufer sulcatus (2 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, East New Britain Province, Nakanai Mountains, Vouvou Camp (859 masl): East New Britain Province, Vouvou Camp: SAMA R64818–19.

Cornufer weberi (29 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Mutahi: CAS 106567–72, 108313–19, 110918–19; MCZ-A 64586–87, 64589–90; Kunua: KU 98478; Solomon Islands, Guadalcanal Island, Tadai District, Mt. Austen, Barana Village: KU 30744, 307350, 307430, 307358, 307367, 307373–74, 307378, 307410; Barora Faa Island (near Isabel Island): SAMA R56853–54, 56856; Isabel Island, Kolopakisa Village: SAMA R56916.

Subgenus *Batrachylodes*:

Cornufer elegans (15 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Mutahi: KU 145096–102, 145104–05, 145107, 145110, 145112–13, 145118, 145136 (paratypes).

Cornufer exedrus **sp. nov.** (8 specimens): See holotype and paratype sections.

Cornufer gigas (1 specimen): Papua New Guinea, Bougainville Island, Bougainville Province, Lake Loloru: CAS 117442 (paratype).

Cornufer mediodiscus (17 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Mutahi: CAS 203526–39; Pipekei: CAS-SU 21815 (paratype); Kunua area: CAS-SU 21811; Aresi area: CAS-SU 21813.

Cornufer minutus (6 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Mutahi area: CAS-SU 23991–92 (paratypes); southern end Ororoi area: CAS-SU 23989 (paratype); Aresi: CAS 101781 (paratype); Solomon Islands, Choiseul Province, Choiseul Island, Sarelata Camp (7.07126°S, 157.0127°E): KU 341494–95.

Cornufer montanus (1 specimen): Papua New Guinea, Bougainville Island, Bougainville Province, Melilup: CAS 117443 (paratype).

Cornufer trossulus (16 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Pipekei area: CAS-SU 21853–21855; Mutahi area, northwest sector: CAS-SU 23967, 23969–76; Solomon Islands, Choiseul Province, Choiseul Island, Sarelata Camp (7.07126°S, 157.0127°E): KU 341536–38; Western Province, Shortland Island, Koliai Village, Taloven camp (7.04175°S, 155.8479°E): KU 341539.

Cornufer vertebralis (10 specimens): Solomon Islands, Western Province, Faro Island BMNH 1947.2.29.96 (holotype); Guadalcanal Province, Guadalcanal Island, Tadai District, Mt. Austen, Barana Village: KU 307405–09, KU 307431–32; Papua New Guinea, Bougainville Island, Bougainville Province, Kunua lowlands: KU 98463–64.

Cornufer wolfi (15 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: CAS 101791, KU 98465–66; Mutahi area, northwest sector: CAS-SU 23980–88; southern end Ororoi area: CAS-SU 23977–79.

Subgenus *Ceratobatrachus*:

Cornufer guentheri (11 specimens): Solomon Islands, Guadalcanal Province, Guadalcanal Island, Tadai District, Mt. Austen, Barana Village, Moka River: KU 307379, 307383, 307395, 307397, 307401–02, 307412, 307425–27; Papua New Guinea, Bougainville Island, Bougainville Province, Mutahi: KU 128662.

Subgenus *Cornufer*:

Cornufer vitianus (8 specimens): Fiji, Viti Levu Isls., Viwa Island, Viwa Village, SW side of island: CAS 172510–12; Ovalau Island, 0.5 mi N of Navuloa Village: CAS 172525–29.

Cornufer vitiensis (13 specimens): Fiji, Viti Levu Isls., Viti Levu Island, Savura Creek Rd., ca 1 km W of Savura Creek: CAS 172437, 172439–40, 172447, 172449–50, 172452–55, 172457; Ovalau Island, 10 km S, of Levuka, St. John's: CAS 172531–32.

Subgenus *Discodeles*:

Cornufer guppyi (3 specimens): Solomon Islands, Western Province, Shortland Island: BMNH 1947.2.1.87 (holotype); Guadalcanal Province, Guadalcanal Island: CAS 49964; Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: KU 98168–69.

Subgenus *Palmatorappia*:

Cornufer heffernani (9 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: KU 93747–48, 98473–74; Mutahi: 108734, 108743, 108745–47.

Subgenus *Potamorana*:

Cornufer bufoniformis (13 specimens): Solomon Islands, Western Province, Treasury Island: BMNH 1947.2.1.85 (holotype); Ranongga Island, Poroi Village: KU 307203, 307247–49, 307254–55, 307260–62, 307264–65, 307273–74.

Cornufer malukuna (4 specimens): Solomon Islands, Western Province, Kohingo Island, Iriri Pasapasa Village: KU 307163–64, 307179–80.

Cornufer opisthodon (1 specimen): Papua New Guinea, Bougainville Island, Bougainville Province: AMNH A-35355.

Subgenus unassigned:

Cornufer acrochordus (17 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: MCZ-A 38196 (paratype); Asesi, S. of Kunua MCZ-A 41871–72, 44256–67 (paratypes); Solomon Islands, Isabel Island, Kolopakisa Village: SAMA R56300; Posarae, Choiseul Island, SAMA R56932.

Cornufer aculeodactylus (7 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: MCZ-A 36961–64; KU 98475; Solomon Islands, Choiseul Island, Posarae: SAMA R56991; Barora Faa Island (near Isabel Island): SAMA R56838.

Cornufer batantae (5 specimens): Indonesia, Raja Ampat Islands, Batanta Island, Warinkabom: MZB 12256; Waire Camp: MZB 12258; Yakut Camp: MZB 12268; Waigeo Island, Camp near Urbinasopen: MZB 12276; Papua, Manokwari, Gunung Meja: MZB 12299.

Cornufer bimaculatus (4 specimens): Indonesia, Raja Ampat Islands, Waigeo: MZB 12267, 12272, 12275, 12279.

Cornufer browni (10 specimens): Papua New Guinea, Admiralty Archipelago, New Ireland Island, Weitin River Valley, 8 km N, 7 km W of river mouth, "River Camp," 150 m elevation: BPBM 12090, 12099, 12102, 12104, 12106l, 12109, 12113, 12115, 12188, 12191 (paratypes).

Cornufer bufonulus (1 specimen): Papua New Guinea, New Britain Island, East New Britain Province, Vouvou Camp: SAMA R64805.

Cornufer caesiops (2 specimens): Papua New Guinea, New Britain Island, East New Britain Province, Vouvou Camp: SAMA R10730, 10732.

Cornufer cheesemanae (3 specimens) Indonesia, Cyclops Mountains, Wambena Camp: SJR 6212, 6201, 6204.

Cornufer macrops (4 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: MCZ-A 38195–96 (paratypes); Aresi, S. of Kunua: MCZ-A 41864 (holotype); Matsiogu: MCZ-A 78820.

Cornufer mimicus (6 specimens): Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, ca 18 mi S of Talasea, Numundo Plantation on Willaumez Peninsula: CAS–SU 22874 (paratype), SAMA R6868 (holotype), R7064 (paratype); Kandrian: SAMA R 7069 (paratype); Moramora, 3 km N, 7 km E Hoskins: MCZ-A 88826, 89053.

Cornufer myersi (7 specimens): Solomon Islands, Guadalcanal Island, river E Popomaneseu track: MCZ-A 79068–72; Papua New Guinea, Bougainville Island, Torokina: USNM 119584; Papua New Guinea, Bougainville Island, Kunua, AMNH 70066 (paratype).

Cornufer parkeri (10 specimens): Papua New Guinea, Bougainville Island, Bougainville Province, Kunua: MCZ-A 36914–22 (paratypes), 36923 (holotype).

Cornufer punctatus (4 specimens): Indonesia, Raja Ampat Islands, Batanta Island, Waire Camp, near Urbinasopen: MZB 12047, 12051, 12054, 12055.

APPENDIX II. List of species identifications, catalog numbers, GenBank accession numbers, and locality data for taxa sampled in molecular analyses. Museum and field number acronyms: ABTC, Australian Biological Tissue Collection, South Australia Museum; BPBM, Bernice P. Bishop Museum; KU, University of Kansas Biodiversity Institute; LSUMZ, Louisiana State University, Museum of Natural Science; MCZ, Museum of Comparative Zoology, Harvard University; MZB, Museum Zoologicum Bogoriense, Indonesia; PNM, National Museum of the Philippines; SAMA, South Australia Museum; ACD, Arvin C. Deismos field series; CCA, Chris C. Austin field series; CDS, Cameron D. Siler field series; BJE, Ben J. Evans field series; FK, Fred Kraus field series; SJR, Stephen J. Richards field series; SLT, Scott L. Travers field series.

Genus	Subgenus	Species	Field #	Catalog #	16S GenBank	Locality
Cornufer	*Batrachylodes*	cf. *vertebralis*	CCA 2581	LSUMZ 94018	KP298018	Papua New Guinea, Bougainville, Togarau Two Village, SE Slope of Mt. Balbi
Cornufer	*Batrachylodes*	cf. *vertebralis*	SLT 317	KU 341548	MG434566	Solomon Islands, Shortland, Koliai Village, Taloven Camp
Cornufer	*Batrachylodes*	*exedrus* **sp. nov.**	SJR 10784	SAMA R64760	MG434556	Papua New Guinea, New Britain, Tompoi Camp
Cornufer	*Batrachylodes*	*exedrus* **sp. nov.**	SJR 10798	SAMA R64761	MG434557	Papua New Guinea, New Britain, Tompoi Camp
Cornufer	*Batrachylodes*	*exedrus* **sp. nov.**	SJR 10815	SAMA R64762	MG434558	Papua New Guinea, New Britain, Tompoi Camp
Cornufer	*Batrachylodes*	*exedrus* **sp. nov.**	SJR 10819	SAMA R64763	MG434559	Papua New Guinea, New Britain, Tompoi Camp
Cornufer	*Batrachylodes*	*exedrus* **sp. nov.**	SJR 10820	SAMA R64764	MG434560	Papua New Guinea, New Britain, Tompoi Camp
Cornufer	*Batrachylodes*	*exedrus* **sp. nov.**	SJR 10821	SAMA R71008	MG434561	Papua New Guinea, New Britain, Tompoi Camp
Cornufer	*Batrachylodes*	*minutus*	SLT 201	KU 341494	MG434554	Solomon Islands, Choiseul, Sarelata Camp, E Slope of Mt. Maetambe
Cornufer	*Batrachylodes*	*minutus*	SLT 210	MCZ A-149368	MG434555	Solomon Islands, Choiseul, Sarelata Camp, E Slope of Mt. Maetambe
Cornufer	*Batrachylodes*	*minutus*	SLT 211	MCZ A-149369	MG434553	Solomon Islands, Choiseul, Sarelata Camp, E Slope of Mt. Maetambe
Cornufer	*Batrachylodes*	sp. 1	CCA 2619	LSUMZ 94038	KP298015	Papua New Guinea, Bougainville, Togarau Two Village, SE Slope of Mt. Balbi
Cornufer	*Batrachylodes*	sp. 2	CCA 2622	LSUMZ 94039	KP298019	Papua New Guinea, Bougainville, Togarau Two Village, SE Slope of Mt. Balbi
Cornufer	*Batrachylodes*	*trossulus*	SLT 204	MCZ A-149367	MG434563	Solomon Islands, Choiseul, Trail from Ghargara Village to Sarelata Camp
Cornufer	*Batrachylodes*	*trossulus*	SLT 261	KU 341537	MG434562	Solomon Islands, Choiseul, Sarelata Camp, E Slope of Mt. Maetambe
Cornufer	*Batrachylodes*	*trossulus*	SLT 264	MCZ A-149386	MG434564	Solomon Islands, Choiseul, Sarelata Camp, E Slope of Mt. Maetambe
Cornufer	*Batrachylodes*	*vertebralis*	SJR 5324	SAMA R56813	KP298033	Solomon Islands, Barora Faa Is. off western tip of Isabel Is.

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APPENDIX 2. (Continued)

Genus	Subgenus	Species	Field #	Catalog #	16S GenBank	Locality
Cornufer	*Batrachylodes*	*vertebralis*	SLT 596	KU 343648	MG434567	Solomon Islands, Malaita, Hahorarumu Uru Tribal Land, West 'Are'are Region
Cornufer	*Batrachylodes*	*vertebralis*	SLT 646	KU 343650	MG434568	Solomon Islands, Malaita, Gofou Tribal Land, West Kwaio Region
Cornufer	*Batrachylodes*	*wolfi*	CCA 2606	LSUMZ 94035	KP298017	Papua New Guinea, Bougainville, Togarau Two Village, SE Slope of Mt. Balbi
Cornufer	*Batrachylodes*	*wolfi*	SLT 315	KU 341497	MG434565	Solomon Islands, Shortland, Koliai Village, Taloven Camp
Cornufer	not assigned	cf. *parkeri*	ABTC 49504	ABTC 49504	KP298016	Papua New Guinea, Bougainville, Central Bougainville
Cornufer	not assigned	*bimaculatus*	SJR 7600	MZB 12275	KP298092	Indonesia, New Guinea
Cornufer	not assigned	*cheesemanae*	ABTC 3692	ABTC 3692	KP298096	Papua New Guinea, New Guinea, Utai, Northern New Guinea
Cornufer	not assigned	sp. 3	BJE 1606	MZB Amph. 12962	KP298140	Indonesia, Halmahera, Jailolo
Cornufer	not assigned	*batantae*	SJR 7812	MZB 12299	KP298090	Indonesia, New Guinea, Manokwari, Gunung Meja
Cornufer	not assigned	*bufonulus*	FK 10918	BPBM 22187	KP298082	Papua New Guinea, New Britain, 11.8 km NNW of Marmar (Point 14)
Cornufer	*Palmatorappia*	*heffernani*	SJR 5303	SAMA R56799	KP298042	Solomon Islands, Barora Faa Is. off western tip of Isabel Is.
Platymantis	*Lahatnanguri*	*pygmaeus*	ACD 2067	PNM 6456	KP298130	Philippines, Luzon, Municipality of Palanan, Barangay Didian
Platymantis	*Lupacolus*	*dorsalis*	CDS 1708	KU 304301	KP298099	Philippines, Catanduanes, Municipality of San Miguel, Barangay San Roque