

**Synopsis of the Amphibians of Equatorial Guinea
based upon the Authors' Field Work and
Spanish Natural History Collections**

**Alberto Sánchez-Vialas¹, Marta Calvo-Revuelta¹,
Santiago Castroviejo-Fisher², and Ignacio De la Riva^{1,*}**

¹ *Museo Nacional de Ciencias Naturales (MNCN-CSIC), C/ José Gutiérrez Abascal, 2. 28006, Madrid, Spain;* ² *Laboratorio de Sistemática de Vertebrados, Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Av/ Ipiranga, 6681, Prédio 40, sala 110, 90619-900, Porto Alegre, Brazil;*

* *Corresponding author: IDIR (iriva@mncn.csic.es)*

TABLE OF CONTENTS

(Abstract)	138
(Introduction)	138
Material and Methods	139
Study area	141
Results and Discussion	144
Synopsis of the Amphibians of Equatorial Guinea	146
Order Anura	146
Family Arthroleptidae	146
Subfamily Arthroleptinae	146
Genus <i>Arthroleptis</i>	146
Genus <i>Cardioglossa</i>	148
Subfamily Astylosterninae	150
Genus <i>Astylosternus</i>	150
Genus <i>Leptodactylodon</i>	150
Genus <i>Nyctibates</i>	150
Genus <i>Scotobleps</i>	151
Genus <i>Trichobatrachus</i>	151
Subfamily Leptopelinae	151
Genus <i>Leptopelis</i>	151
Family Bufonidae	154
Genus <i>Didynamipus</i>	154
Genus <i>Nectophryne</i>	154
Genus <i>Sclerophrys</i>	155
Genus <i>Werneria</i>	157
Genus <i>Wolterstorffina</i>	158
Family Conrauidae	158
Genus <i>Conraua</i>	158
Family Hyperoliidae	159
Genus <i>Acanthixalus</i>	159
Genus <i>Afrixalus</i>	159
Genus <i>Alexteroon</i>	161
Genus <i>Arlequinus</i>	161
Genus <i>Cryptothylax</i>	161
Genus <i>Hyperolius</i>	161
Genus <i>Opisthothylax</i>	163

Genus <i>Phlyctimantis</i>	164
Family Petropedetidae	164
Genus <i>Petropedetes</i>	164
Family Phrynobatrachidae	165
Genus <i>Phrynobatrachus</i>	165
Family Pipidae	167
Genus <i>Hymenochirus</i>	167
Genus <i>Xenopus</i>	168
Family Ptychadenidae	169
Genus <i>Ptychadena</i>	169
Family Pyxicephalidae	170
Genus <i>Aubria</i>	170
Family Ranidae	170
Genus <i>Amnirana</i>	170
Family Rhacophoridae	171
Genus <i>Chiromantis</i>	171
Order Gymnophiona	172
Family Dermophiidae	172
Genus <i>Geotrypetes</i>	172
Family Herpelidae	172
Genus <i>Herpele</i>	172
Acknowledgments	173
Bibliography	173
Photographs	179
Distribution Maps	203

Equatorial Guinea is a small west-central African tropical country situated in the Gulf of Guinea. It has a main insular area comprising the volcanic land-bridge island Bioko, the oceanic island Annobón, and a continental part known as Río Muni, which accounts for most of the country's land area and borders on Cameroon to the north and Gabon to the east and south. Only a few and mostly old publications have dealt specifically with the amphibians of Equatorial Guinea, and an accurate and updated catalogue is lacking. Based on fieldwork, a compilation of literature, and the examination of two important Spanish scientific collections, we present a comprehensive catalogue of the amphibian fauna for Equatorial Guinea. We report 80 species belonging to 32 genera, 13 families and two orders. Of these 80 species, 14 are present only on Bioko, 36 are known only in Río Muni, and 30 occur in both regions. No amphibians are currently known from Annobón. There is a very low level of endemism, with only one species endemic to Bioko. This may be due to the country's small size, to the relatively uniform landscape (lowland rainforest) of Río Muni, and to the recent connections between Bioko and the continent. Our work revealed several new species and country records and highlighted problems in the taxonomic status of many amphibian populations that need to be addressed. As further field and taxonomic work is carried out, we expect new species records for the country that will assuredly enrich this catalog.

The diversity and distribution of African amphibians are, in general, still poorly known (Poyn-ton et al. 2007; Blackburn 2008; Menegon et al. 2008). During the last decade, amphibians of Central Africa, especially those from countries bordering the Gulf of Guinea, have been the subject of several studies within a systematic or biogeographic framework (e.g., Blackburn 2010; Barej et al. 2014; Bell et al. 2015, 2017; Evans et al. 2015; Charles et al. 2018; Sánchez-Vialas et

al. 2018). Most of the published herpetofaunal surveys in this region have been conducted in particular countries such as Cameroon (Perret 1966; Zimkus 2009; Amiet 2012; Portik et al. 2016) and Gabon (Frétey and Blanc 2001; Burger et al. 2006; Pauwels and Rödel 2007; Frétey et al. 2011; Carlino and Pauwels 2015; Jongtsma et al. 2017; Dewynter et al. 2018), whereas others, like Equatorial Guinea, remain largely unexplored (De la Riva 1994; Lasso et al. 2002; Blackburn 2010).

In spite of the geographic and biological interest in the Gulf of Guinea region, several basic aspects of the amphibian fauna of Equatorial Guinea remain mostly unknown (see, for example, Rödel et al. 2004), and only a handful of old publications deal specifically with the amphibians of this country. For example, Boulenger (1899a, 1899b, 1900, 1903, 1906a, 1906b) provided records and described several new species of amphibians collected in the continental part —Río Muni—, and Mertens (1965) presented a synthesis of the amphibians of Bioko (at that time known as Fernando Poo). It was not until 1994, with a study on the amphibians of Monte Alén National Park, in Río Muni, that the amphibians of Equatorial Guinea again attracted attention (De la Riva 1994). In De la Riva's study, 41 species were recorded from the park, 24 of them representing first records for Río Muni. Later, Frétey and Blanc (2000) carried out a literature-based synthesis of the amphibian species from seven countries of central Africa, including Equatorial Guinea, for which they reported 74 species. Lasso et al. (2002) provided an updated checklist and several notes on natural history of amphibians and reptiles of Monte Alén National Park (including four additional new records of amphibian species for Río Muni), and Gonwouo and Nsang (2005) focused on the herpetofauna of Monte Mitra, also part of the Monte Alén National Park. Blackburn (2010) described a new species of *Arthroleptis* from Bioko and commented about the diversity of the island's amphibians. Recently, Ceriaco et al. (2018) published a checklist of the herpetofauna of São Tomé, Príncipe, and Annobon islands, the latter belonging to Equatorial Guinea, stating that no record exists for any species of amphibian in Annobon. Despite the existence of several molecular studies including samples of amphibians from Equatorial Guinea (mostly from Bioko) (Blackburn 2008; Barej et al. 2014; Liedtke et al. 2016; Bell et al. 2017; Charles et al. 2018; Jongtsma et al. 2018); Bell et al. 2019; Leaché et al. 2019), a comprehensive regional synthesis of the amphibians of Equatorial Guinea has yet to be carried out.

One of the main problems that governments must face when developing environmental policies is the lack of basic faunal information. Despite its small size, Equatorial Guinea remains a poorly known country from a biological standpoint, specifically its biodiversity. And as already noted above, to date no comprehensive catalogue of the amphibians of the whole country with accurate information has been published. With this contribution, in addition to encouraging further research, it is our aim to make available a basic tool to be used by both scientists and environmental agencies when dealing with the faunistic diversity of Equatorial Guinea and the ways to preserve it.

In summary, the main goals of this work are to: 1) provide an updated list of the amphibians of Equatorial Guinea with data on their distribution; 2) comment on some particular problems concerning the taxonomic status and/or distribution of several species; and 3) provide a comprehensive list of the pertinent literature relating to the amphibians from this country.

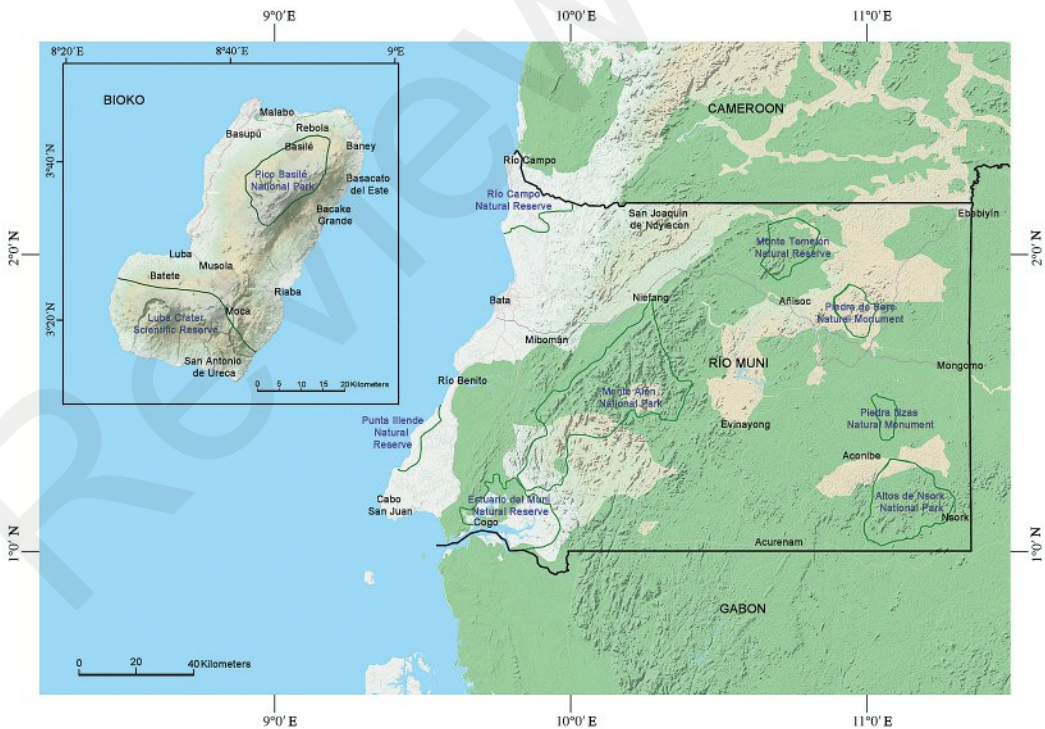
MATERIAL AND METHODS

The information presented herein comes mainly from four different sources: 1) the personal field experience of the authors, IDIR, mostly at Monte Alén National Park (Río Muni) from May to December 1993 (De la Riva 1994), and of SC-F along southern Bioko in November and December 2003. Both field campaigns yielded valuable material and biological data; 2) the specimens held in the collections of the Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain (MNCN)

and the Estación Biológica de Doñana-CSIC, Sevilla, Spain (EBD); 3) the databases of the California Academy of Sciences (CAS) and the Museum of Comparative Zoology-Harvard University; and 4) the literature. We have not examined the specimens of amphibians of Equatorial Guinea in other collections or reported in online databases (e.g., GBIF [Global Biodiversity Information Facility]: Muséum National d'Histoire Naturelle, France [reportedly holding 332 specimens], Senckenberg Museum [113 specimens], Natural History Museum in London [80 specimens], North Carolina Museum of Natural Sciences [236 specimens], Cornell University [221 specimens], Peabody Museum, Yale University [128 specimens], Field Museum of Natural History, Chicago [35 specimens], and Royal Museum for Central Africa, Belgium [number unknown]). We are aware that, most likely, some additional species and, for sure, new distribution data, do exist in these and maybe other collections, but we did not rely on databases mainly because locality data and/or taxonomic identifications are usually in need of confirmation via direct examination of specimens.

A total of 685 specimens of 54 species of amphibians held at the EBD and MNCN collections were examined. Most of the specimens held at EBD were collected during the 1980s and early 90s by the researchers J. Juste and R. Castelo, with minor older contributions by J.A. Valverde, whereas the MNCN collection conserves both old specimens (collected by M. M. Escalera during 1901 and by F. Bonet and Gil Collado during 1933) and recently collected specimens (by Santiago Castroviejo-Fisher during 2003 and Ignacio Martín during 2005 and 2007). Also, the MNCN herpetological collection conserves the holotype of *Schistometopum garzonheydti* Taylor and Salvador, 1978 [synonym of *Geotrypetes seraphini* (Duméril, 1859)] and the neotype of *Petropedetes newtonii* (Bocage, 1895), recently designated (Sánchez-Vialas et al. 2018).

Specimens were fixed in the field with 10% formalin and then preserved in 70% ethanol. In



MAP 1. Map of Equatorial Guinea showing Bioko and Río Muni with their respective natural protected areas.

the catalog text that follows, each species entry generally consists of the species name, the type locality, distribution, comments, and a list of material examined. Nomenclature and general distribution information used herein mostly follow Frost (2020). Distribution maps were made at the Laboratorio de Biogeografía Informática, Museo Nacional de Ciencias Naturales.

ADDENDUM: When this work was almost totally edited and formatted, it came to our attention that three species, the arthroleptid *Cardioglossa nigromaculata* Nieden, 1908, and the hyperoliids *Arlequinus krebsi* (Mertens, 1938) and *Hyperolius kuligae* Mertens, 1940, were reported for Bioko by Channing & Röddel (2019) (and already updated by Frost [2020]) in their recent field guide of African amphibians. The picture of *C. nigromaculata* in this book's page 245 corresponds to an individual from southern Cameroon, being the record from Bioko based on three specimens deposited in the North Carolina Museum of Natural Sciences; these specimens have an unusual coloration (Patrick McLaughlin, pers. comm.). The picture of *A. krebsi* in Channing & Röddel's field guide (page 167) was taken by Jessica Weinberg of an individual from Bioko. We contacted Jessica Weinberg and she called our attention to an additional new species record for the island, the bufonid *Wolterstorffina parvipalmata* (Werner, 1898), which confirms the already suspected presence of this species in Equatorial Guinea. Likewise, she loaned us photos of *A. krebsi* (including an individual distinct from that portrayed by Channing & Röddel) and *W. parvipalmata*; additional photos of the latter species were kindly provided by P. McLaughlin as well. For editorial reasons, instead of being in their proper taxonomic and alphabetical order, these photos and the distribution maps for *A. krebsi*, *H. kuligae* and *W. parvipalmata* are placed at the end of their respective groups (Figure 25 and Map 27)]. The four species mentioned were found during surveys made under the Bioko Biodiversity Protection Program (BBPP) of the Drexel University in Philadelphia; Dr. Mary Gonder, BBPP's director, kindly allowed us to include these records here.

STUDY AREA

Equatorial Guinea is a small country located in the vicinity of the Gulf of Guinea, Central West Africa (Map 1), formed by a mainland part, Río Muni, and five islands in the Gulf of Guinea (Bioko, Annobon, Elobey Grande, Elobey Chico and Corisco). The largest island is Bioko (on whose northern coast lies Malabo, the capital of the country), which has an area of 2017 km² and is 32 km distant from the nearest mainland (Cameroon). Bioko is located in the northern hemisphere, between 03°12'N and 03°48'N, whereas the small island of Annobon (or Pagalu; 17 km²) is in the southern hemisphere, between 01°24'S and 01°28'S. Bioko and Annobon are 565 km apart, and between them there is another insular country, São Tomé and Príncipe. Finally, the smaller islands of Corisco and the two Elobeyes are located off the coast of Río Muni, the continental part of the country. Río Muni, with an area of 26,000 km², which accounts for about 90% of the land area of Equatorial Guinea, lies between 01°01'N and 02°21'N, and it borders with Cameroon to the north, and Gabon to the east and the south, and is part of an ancient granitic plateau with a maximum altitude of 1250 m (Fa 1991).

Equatorial Guinea has a tropical climate, hot and humid year-round. The continental Río Muni has an annual mean temperature of 25°C with oscillations rarely exceeding more than 5°C, and with annual precipitation that ranges from 1800 to 3800 mm, most of which occurring between September and December; there are two dry seasons, one between December and February, which is influenced by the dry Harmattan season and is less severe, not reaching the southern part of the region, and the second one during June and August (Fa 1991).

The climate of Bioko is more heterogeneous than that of Río Muni, being mainly affected by the continental proximity, latitudinal location, oceanic currents, and the island's mountainous topography, which is of volcanic origin. It is characterized by two seasons; the dry season extends

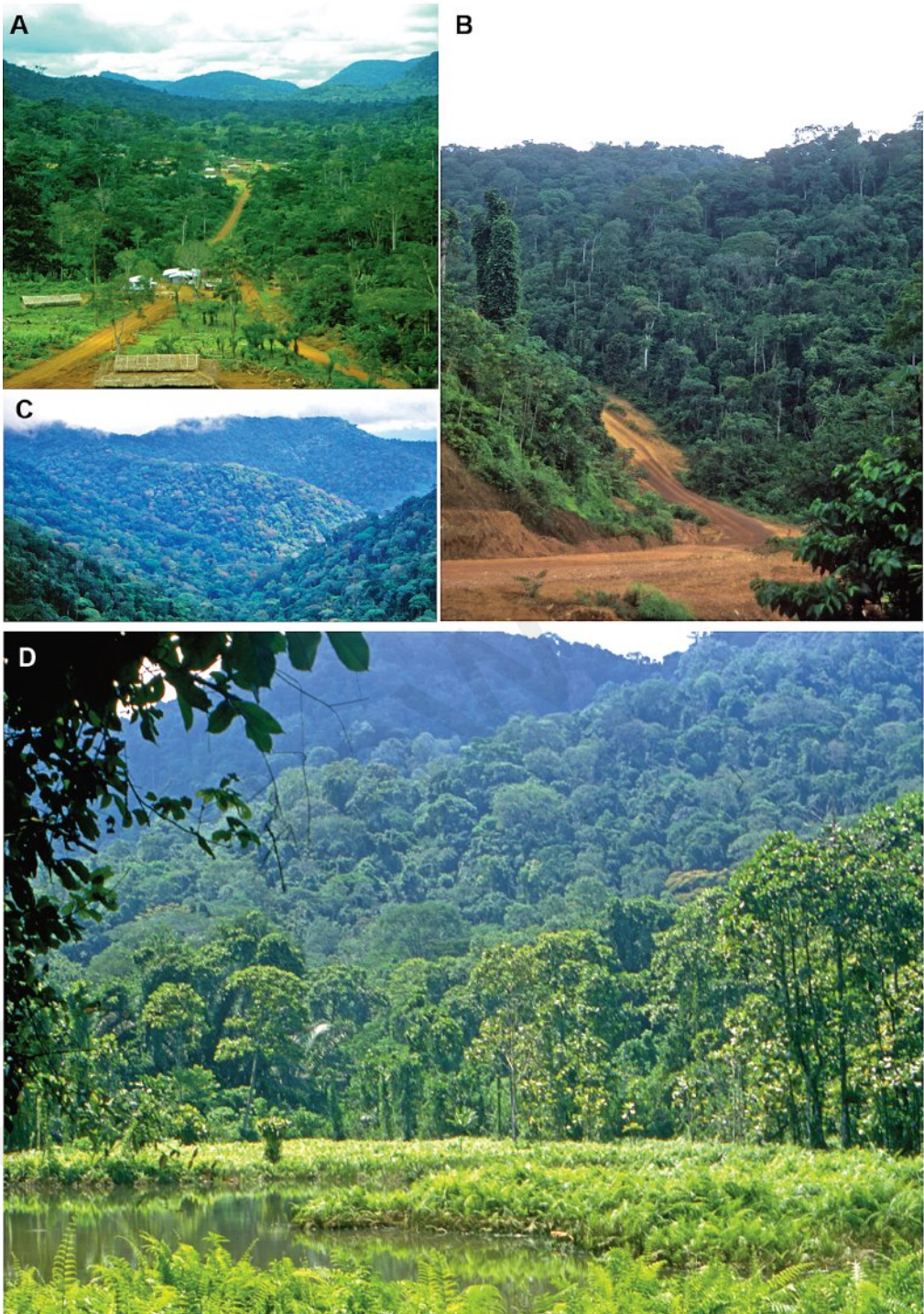


FIGURE 1. A. Moka, Monte Alén National Park, Río Muni. Photo IDIR; B. Los Altos de Nsork, Río Muni. Photo TL; C. Monte Alén National Park, Río Muni. Photo IDIR; D. Atoc Lake, Monte Alén National Park, Río Muni. Photo IDIR.



FIGURE 2. A. Asia Rapids, Midyobo, Río Muni. Photo IDIR.; B. Laña River, Río Muni. Photo IDIR.

from November to March (Fa 1991; Galán Cela et al. 2018) and is followed by a variable and often wet period from April through October. There are three volcanic calderas on Bioko: Pico Basilé, located in the north, with 3011 m in elevation, and Pico Biao and Caldera de Luba in the southern region, with elevations of 2009 m and 2261 m respectively. Annual mean temperature is about 25°C in Malabo with maximum of 26.2°C in February and minimum of 24°C in September. Bioko exhibits marked differences in rainfall between its northern and southern blocks. The northern block of Bioko receives an annual mean precipitation of 1930 mm, while the southern block, which experiences a monsoon season, reaches an annual mean of 10900 mm, with a record of 14451 mm in Ureca (one of the highest precipitations recorded in the world) (Fa 1991).

Overall, the vegetation of Equatorial Guinea is quite uniform, due to the homogeneous topography, geology, and climate, and to the small area covered by the country. The Lower Guinean forest ecosystem covers most of the country (Bell et al. 2017) (Figs. 1 and 2), and it is formed by 70–80 tree species in Río Muni (Fa 1991). Only Bioko is characterized by different vegetation communities, as a result of the altitudinal gradients and the marked precipitation differences between the northern and southern blocks. The highlands of Bioko are dominated by montane forest (800–1400 m), *Schefflera* forest/Mossy forest (1400–2600 m) and heath and grass/shrubs (2600–3000 m) (Butynski and Koster 1994; Juste and Pérez del Val 1995). This island forms part of the Cameroon Volcanic Line, which is considered a biodiversity hotspot (Myers et al. 2000). A synthesis of vegetation types and most common species plants of Equatorial Guinea was presented by Fa (1991).

RESULTS AND DISCUSSION

Our study recovered 80 species of described amphibians present in Equatorial Guinea, 14 of them only present on Bioko, 36 only in Río Muni, and 30 known from both regions. Overall, our list differs quantitatively from Frétey and Blanc's (2000) by adding seven more species, but the geographic allocation differs as well, since they report only eight species exclusively from Bioko and, in contrast, as many as 44 from Río Muni, and only 22 from both regions. There are also qualitative differences, as they report species now referred to the synonymy of other species or subjected to taxonomic or other nominal changes. Besides their 74 "confirmed" species, they suggested as possible the presence in the country of five species (*Hoplobatrachus occipitalis*, *Hyperolius marmoratus*, *Phrynobatrachus hylaios*, *Sclerophrys regularis*—also cited with no data by Dewynter and Frétey [2019]—, and *Xenopus andrei*), none of which are listed in our catalog.

Several new undescribed species are known to occur within Equatorial Guinea (De la Riva 1994; Jongsma et al. 2018). Thus, an increase in the number of described species is to be expected in the near future. Also, the taxonomic status of several species recorded in Equatorial Guinea remains uncertain (*Hymenochirus boettgeri*, *Arthroleptis* aff. *poecilnotus*, *Phlyctimantis* cf. *leonardi*, *Leptodactylodon* cf. *stevarti*, *Sclerophrys funerea*, and *Werneria* cf. *mertensiana*; see each account). Furthermore, some species names cited in the literature likely represent misidentifications and are not included in this checklist; these include: *Arthroleptis taeniatus*, recorded by Dewynter and Frétey (2019) and previously by Mertens (1965) (as *A. bivittatus*), and considered herein as *A. sylvaticus*; *Astylosternus diadematus*, a Cameroonian species recorded by Gonwouo and Nsang (2005) (misspelled as "*Astylosternus diadematis*") who did not provide either data or comments on this record; *Leptopelis viridis*, a savannah-living species mostly distributed in West Africa (Schlötter 1999), listed by Frétey and Blanc (2000), excluded herein until further evidence on its presence in the country is obtained; *Sclerophrys maculatus*, recorded by Gonwouo and Nsang (2005), considered herein as *S. latifrons*; *Sclerophrys pusilla*, cited by Dewynter & Frétey (2019) without data, excluded herein from the checklist until further evidence on its presence in the country is obtained; *Hyperolius concolor*, recorded by Mertens (1965), considered herein as *H. tuber-*

culatus; *Hyperolius fusciventris*, another West African species (Schjötz 1999) listed by Frétey and Blanc (2000), excluded herein from the checklist until further evidence on its presence in the country is obtained; *Hyperolius mosaicus*, considered of likely presence in the country by Frost (2020) and cited with no data by Dewynter & Frétey (2019), excluded herein from the checklist until further evidence on its presence is obtained; and *Ptychadena mascareniensis*, recorded by Boulenger (1903) and Gonwouo and Nsang (2005), considered herein as *P. aequiplicata*. We report *Afrixalus osorioi*, *Nectophryne batesii*, and *Wolterstorffina parvipalmata* (but see comment under species account) for the first time in Equatorial Guinea, *Cardioglossa leucomystax* and *Opisthothylax immaculatus* (but see comment under species account) for the first time on Bioko, and *Arthroleptis sylvaticus* for Río Muni; we also provide several additional records for most of the species both on Bioko and in Río Muni, emphasizing the importance of scientific collections.

Most species from Río Muni are widely distributed across the Central African region; however, some species seem to be geographically located within a restricted area, such as for example *Werneria* cf. *mertensiana*, and *Leptodactylodon* cf. *stevarti*, which have only been found in Monte Alén National Park (De la Riva 1994), and it has been suggested that these populations could belong to undescribed species (Rödel and Pauwels 2003; Rödel et al. 2004). One of the localities where *Afrixalus osorioi* has been found lies in southeastern Río Muni, an overlooked region from a biological standpoint. Many species remain poorly known as only one or two records exist, mainly due to lack of fieldwork in Río Muni and, possibly, the elusive nature of some taxa. This could be the case of *Acanthixalus spinosus*, *Alexteroon obstetricans*, *Cardioglossa escalerae*, *C. gracilis*, *Hyperolius olivaceus*, *H. pardalis*, *H. phantasticus*, *H. platyceps*, *Leptodactylodon* cf. *stevarti*, *Opisthothylax immaculatus*, *Phrynobatrachus sandersoni*, and *Werneria* cf. *mertensiana*. Currently, no endemic formally described species are known from Río Muni. Likewise, despite being an island, Bioko presents low levels of endemism, and relatively close phylogenetic relationships among species populations from Bioko and Cameroon have been reported (Jones 1994; Blackburn 2010; Barej et al. 2014; Bell et al. 2017, 2019; Charles et al. 2018; Leaché et al. 2019), mainly due to the cycles of rising and retreating sea levels that resulted in repeated periods of isolation and connection between Bioko and the continental mainland (Jones 1994; Bell et al. 2017). The authors' unpublished molecular data (12S partial gene) from taxa such as *Phrynobatrachus cornutus* and *Cardioglossa leucomystax* support this hypothesis; however, in contrast, some phylogeographic structure is revealed by the existence of distinct allopatric lineages of *Leptopelis modestus* (Portillo et al. 2015) and *L. calcaratus* (unpublished data) from Bioko and Cameroon, suggesting a more complex pattern of diversification for several taxa on Bioko. Future research should focus on the integration of additional sources of evidence to determine whether the mentioned lineages of *Leptopelis* fall within the intraspecific variation of formerly described species or they represent distinctive, new taxonomic units. Most of the efforts for studying amphibians in Equatorial Guinea have focused on Bioko and on the western half of Río Muni, specially Monte Alén National Park, whereas no published work deals with the eastern part of Río Muni, where some interesting and putatively protected natural areas also exist (e.g., Monte Temelón Natural Reserve, Altos de Nsork National Park, Piedra Bere Natural monument, and Piedra Nzás Natural monument). In the same way, within the western part of Río Muni, the amphibian diversity of other natural protected areas is mostly unknown (e.g., Río Campo Natural Reserve, Punta Llendi Natural Reserve, Estuario del Muni Natural Reserve). The revision of the amphibians collected from southeastern Río Muni has revealed new populations of *Afrixalus osorioi*, more than 360 km northward from the closest recorded populations of southern Gabon (Dewynter et al. 2018). This suggest that future field work along most regions of Río Muni, including the natural protected areas, should be carried out for a better understanding of the biodiversity of these overlooked areas.

Some of the candidate species suggested by De la Riva (1994) to be found during future field work at Monte Alén National Park have not been yet reported in Equatorial Guinea and they might be discovered in the future; these are: *Leptopelis aubryioides* (Anderson, 1907), *Hyperolius koehleri* Mertens, 1940, and *Ptychadena perreti* Guibé and Lamotte, 1958. Likewise, *Afrivalus equatorialis* (Laurent, 1941), *Alexeroon hypsiphonus* Amiet, 2000, *Hyperolius adpersus* Peters, 1877, *H. dartavellei* Laurent, 1943, *H. guttulatus* Günther, 1858, *H. kuligae* Mertens, 1940, *H. mosaicus* Perret, 1959, *Arthroleptis taeniatus* Boulenger, 1906, *A. tuberosus* Andersson, 1905, *Phrynobatrachus mayokoensis* Rödel, Burger, Zassi-Boulou, Emmrich, Penner, and Barej, 2015 and *Wolterstorffina parvipalmata* could be found in Río Muni. Overall, we assume that the diversity of amphibians of Equatorial Guinea, as currently known, is underestimated.

SYNOPSIS OF THE AMPHIBIANS OF EQUATORIAL GUINEA

Order Anura

Arthroleptidae Mivart, 1869

Arthroleptinae Mivart, 1869

Arthroleptis Smith, 1849

Arthroleptis adelphus Perret, 1966

Photo figures 3A–C

TYPE LOCALITY.—“Foulassi”, near Sangmelima, Cameroon.

DISTRIBUTION.— This species ranges over the forests of the Gulf of Guinea region, from southern Cameroon to Gabon. In Equatorial Guinea, *A. adelphus* has been recorded in Río Muni, at Monte Alén National Park (De la Riva 1994), and on Bioko at Pico Basilé (Blackburn 2008) (Map 2A).

COMMENTS.— Our identifications of the preserved *A. adelphus* are confirmed by molecular data (authors' unpublished data). Two preserved specimens (MNCN 48825–48826) from Batete, Bioko, have a striped pattern. The external morphology of this species is similar to that of members of the *A. poecilonotus* species complex (see entry for *A. aff. poecilonotus*), and a close relationship has been evidenced by molecular data (Blackburn 2008). However, in life, *A. adelphus* can be diagnosable by the presence of marked and larger skin granules over the dorsal and lateral parts of the body, whereas in *A. poecilonotus* the dorsal surface of the skin is smoother and homogeneously granulated. Additional subtle differences such as the metatarsal tubercle and the subarticular tubercle of Finger I seem to be diagnostic (Dewynter et al. 2018).

SPECIMENS EXAMINED.— Nine specimens. Illadji River, Bioko, 03°19'46.04"N, 08°40'26.13"E, 14 November 2003 (MNCN 48833); surroundings of BBPP camp, Caldera de Luba, Bioko, 03°20'47.32"N, 08°29'48.44"E, 26 November 2003 (MNCN 48827–48828, MNCN 48830, 48832), 27 November 2003 (MNCN 48829, 48831); path behind church in Bakelele forest, Batete, Bioko, 03°26'37.34"N, 08°30'24.76"E; 02 November 2003 (MNCN 48825–48826).

Arthroleptis bioko Blackburn, 2010

TYPE LOCALITY.—“Republic of Equatorial Guinea, Bioko Norte Province, along Pico Basilé road, northeast slope of Pico Basilé, 03°37'42.4"N, 08°48'11"E, ca. 1820 m elevation”.

DISTRIBUTION.— This species was known only from some localities of the Pico Basilé region (Blackburn 2010), from where it was presumably endemic, but we record an additional population from Bioko Sur province, close to Caldera de Luba surroundings (Map 2B).

COMMENTS.— This species is currently the only known endemic amphibian of Equatorial

Guinea. The additional record provided herein represents the southernmost known locality for this species. The identity of the single examined specimen, a female, was also confirmed by molecular analyses (authors unpublished data).

SPECIMENS EXAMINED.— One specimen. Narciso's farm, Moka, Bioko, 03°20'53.57"N, 08°39'49.91"E, 12 November 2003 (MNCN 48835).

Arthroleptis* aff. *poecilnotus

Photo figures 3D–E

TYPE LOCALITY.— Unknown taxonomic identity (see comments).

DISTRIBUTION.— Members of the *Arthroleptis poecilnotus* species complex are widely distributed, ranging from Guinea-Bissau to Uganda, and southwards to Gabon, Congo and Central African Republic. In Equatorial Guinea, it has been recorded both in Río Muni at Cabo San Juan (Boulenger 1900, 1903), Monte Alén (De la Riva 1994) and in several localities on Bioko (Mertens 1965; Hydeman et al. 2017) (Map 2C).

COMMENTS.— See comments on *A. adelphus*.

Phylogenetic evidence suggests that under the name *A. poecilnotus* Peters, 1863 there is a species complex comprising multiple allopatric species from (1) Western Ghana and Sierra Leone, (2) Togo Hills of Eastern Ghana, (3) Cameroon, and (4) Bioko (Blackburn 2008). The lineage identified from Bioko by Blackburn (2008) was formally described as *A. bioko* (Blackburn 2010). *Arthroleptis poecilnotus* has two available synonyms, *A. macrodactylus* Boulenger, 1882 described from Gabon and *A. inguinalis* Boulenger, 1900 described from Benito River (Equatorial Guinea). As the type locality of *A. poecilnotus* is in Ghana (Holländischen Besitzungen (Boutry) [Ghana] an der Küste von Guinea), the different lineage from Cameroon, and also, the unstudied populations from Gabon and Equatorial Guinea deserve other nomenclatural denominations once an exhaustive taxonomic revision is made.

SPECIMENS EXAMINED.— 26 specimens. Patio Alosa (Niefang), 14 August 1985 (EBD 21033); Cabo San Juan, Río Muni, 21 August 1901 (MNCN 3921–3942); Río Muni, 21 August 1901 (MNCN 3958); Río Muni, Cabo San Juan, 25 May 1901 (MNCN 3997–3998).

***Arthroleptis sylvaticus* (Laurent, 1954)**

Photo figure 3F

TYPE LOCALITY.— “Buta”, Uele, Dem. Rep. Congo.

DISTRIBUTION.— *Arthroleptis sylvaticus* (sensu lato) ranges from southern Cameroon and Gabon to Republic of Congo, Democratic Republic of Congo and Central African Republic. In Equatorial Guinea, this species is known from Bioko, where it has been recorded near Moka (Blackburn 2008; Hydeman et al. 2017) (Map 3A). It is present in Monte Alén, Río Muni (IDIR, Fig. 3F).

COMMENTS.— This taxon may comprise several undescribed cryptic species (Blackburn 2008). Frost et al. (2006) included in their study a specimen (CAS 207926) from Moka, Bioko, identified as *Schoutedenella taeniata*, which was previously assigned to *A. sylvaticus* by Blackburn (2008), and briefly described as a juvenile with a pair of light dorsolateral lines. This striped phenotype exhibited by some specimens of *A. sylvaticus* could have led Mertens (1965) to misidentify his specimens of *Arthroleptis* from Moka as *A. bivittatus* Müller, 1885. At that time, Mertens (1965) considered *A. bivittatus* as a senior synonym of *A. taeniatus* Boulenger, 1906 (another taxon in which the dorsal pattern can be formed by light dorsolateral lines). However, both taxa (*A. bivittatus* and *A. taeniatus*) are currently recognized as different species (Perret 1991); while *A. bivittatus* is restricted to its type locality (Tumbo-Insel [Tumbo Island, Sierra Leone]), *A. taeniatus* is widespread along the Gulf of Guinea mainland. Mertens (1965) compared the specimen from Moka with specimens of *A. taeniatus* from Cameroon, noting morphological similarity. The

conservative morphological evolution undergone by some species groups of the genus *Arthroleptis*, sometimes only revealed by molecular data, suggests that at the times of Mertens' work, the limitations for studying the diversity of this group of frogs were considerable, and consequently, yielded misidentifications, especially for the smallest species of *Arthroleptis*, such as the Mertens' specimens. Thus, based on current evidences, it is likely that the specimen from Moka recorded by Mertens (1965) is neither *A. bivittatus* nor *A. taeniatus*; despite further sampling efforts carried out at Moka surroundings, no specimens of *A. taeniatus* have been recorded, but some other congeneric species such as *A. poecilnotus*, *A. variabilis*, and *A. sylvaticus* are commonly found. Consequently, we consider that the identity of Mertens' (1965) specimen from Moka corresponds to *A. sylvaticus*, a taxon that can also exhibit the dorsolateral light stripes shown by the sequenced specimen (CAS 207926) from the same locality (Blackburn 2008). Therefore, we exclude the taxon *A. taeniatus* (or *A. bivittatus* sensu Mertens [1965]) from the checklist of amphibians of Equatorial Guinea. However, *A. taeniatus* could be found during future field work in Río Muni.

SPECIMENS EXAMINED.— Seven specimens. Moka, Bioko Sur, 23 July 1984 (EBD 18612–18614); Belebu to Ureca, along the path, Bioko, 03°24'25.81"N, 08°33'03.23"E, 19 November 2003 (MNCN 48884); Illadji River, Bioko, 03°19'46.04"N, 08°40'26.13"E, 14 November 2003 (MNCN 48883); surroundings of BBPP camp, Caldera de Luba, Bioko, 03°20'47.32"N, 08°29'48.44"E, 27 November 2003 (MNCN 48834); Caldera de Luba, Bioko, 03°21'17.59"N, 08°31'42.35"E, 14 March 2007 (MNCN 46705).

***Arthroleptis variabilis* Matschie, 1893**

Photo figures 3G–H; 4A–E

TYPE LOCALITY.— “Buea, Barombie, Kamerun”, Cameroon.

DISTRIBUTION.— This species inhabits the lowland rainforest over the Gulf of Guinea region, extending from Nigeria to Gabon, and inward reaching Central African Republic and Democratic Republic of Congo. In Equatorial Guinea, it occurs both in Río Muni and Bioko. Within Río Muni, *Arthroleptis variabilis* had only been recorded in Monte Alén (De la Riva 1994), while on Bioko it is known from several localities over most part of the island (Bocage 1895a; Boulenger 1900, 1906a; Mertens 1965; Hydeman et al. 2017) (Map 3B).

COMMENTS.— This species has been redescribed by Blackburn et al. (2009). Old highland records from Basilé (2000 m a.s.l) (Bocage 1895a) need confirmation since a newly described congeneric taxon (*A. bioko*) inhabits the same region at high altitudes. Mraz et al. (2018) reported a case of predation of *A. variabilis* by an unidentified shrew within a human-mediated trap.

SPECIMENS EXAMINED.— 24 specimens. Ayene, Wele Nzaz, 9 September 1985 (EBD 21041); [Batonós, Guinea Ec] (not found), January 1933 (MNCN 3943); Monte Alén lake, 22 August 2001 (MNCN 46336); Caldera de Luba, Bioko, 03°20'46.54"N, 08°29'48.20"E, 12 March 2007 (MNCN 46702, MNCN 46707); Forest close to Illadji River, Bioko, 03°19'46.04"N, 08°40'26.13"E, 14 November 2003 (MNCN 48836–48839); Río San Nicolás, Belebu to Ureka along the path, Bioko, 03°24'25.81"N, 08°33'03.23"E, 20 November 2003 (MNCN 48840); descending into Caldera de Luba, Bioko, 03°20'05.02"N, 08°29'14.33"E, 26 November 2003 (MNCN 48841); surroundings of BBPP camp, Caldera de Luba, Bioko, 03°20'47.32"N, 08°29'48.44"E, 26 November 2003 (MNCN 48842–48851), 27 November 2003 (MNCN 48852–48853); Batete, path behind church, Bakelele forest, 03°26'37.34"N, 08°30'24.76"E, 02 December 2003 (MNCN 48854).

***Cardioglossa* Boulenger, 1900**

***Cardioglossa elegans* Boulenger, 1906**

Photo figures 5A–B

TYPE LOCALITY.— “Efulen”, Cameroon.

DISTRIBUTION.— From Cameroon to Gabon, in lowland rainforest. In Equatorial Guinea, it is recorded from Monte Alén (De la Riva 1994) (Map 3C).

COMMENTS.— This is a poorly known species. Amiet and Goutte (2017) provided an account including the call spectrum.

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Cardioglossa escalerae* Boulenger, 1903**

TYPE LOCALITY.— “Cap Saint Jean, Guinée espagnole” (Cabo San Juan, Río Muni, Equatorial Guinea).

DISTRIBUTION.— This species occurs in lowland rainforests from Cameroon and Equatorial Guinea to Central African Republic and Democratic Republic of Congo. In Equatorial Guinea, it has been recorded at the type locality, and at Monte Alén by Lasso et al. (2002) (Map 4A).

COMMENTS.— This is a poorly known species. Amiet and Goutte (2017) provided an account including the call spectrum.

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Cardioglossa gracilis* Boulenger, 1900**

Photo figure 5C

TYPE LOCALITY.— “Benito River”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— This species is distributed over southeastern Nigeria, Cameroon, continental Equatorial Guinea, Gabon and Democratic Republic of Congo. In Equatorial Guinea, it was only known from the type locality, at Río Muni (Boulenger 1900), from Cabo San Juan (Boulenger 1903), and from Monte Alén National Park (De la Riva 1994); the specimen examined provides an additional record (Map 4B).

COMMENTS.— This is a poorly known species. Amiet and Goutte (2017) provided an account including the call spectrum.

SPECIMENS EXAMINED.— One specimen. Noayong (Evinayong-Aconibe), 16 March 1987 (EBD 25045).

***Cardioglossa gratiosa* Amiet, 1972**

TYPE LOCALITY.— “Ongot, env. 750 m, Cameroon”.

DISTRIBUTION.— This species ranges from Cameroon to Gabon and Democratic Republic of Congo. In Equatorial Guinea is listed for Río Muni by Frétey and Blanc (2000), but no particular locality was provided (Map 4C).

COMMENTS.— It is expected to be found in Monte Alén (De la Riva 1994).

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Cardioglossa leucomystax* (Boulenger, 1903)**

Photo figures 5D–E

TYPE LOCALITY.— “Cap Saint Jean, Guinée espagnole”, Cabo San Juan, Río Muni, Equatorial Guinea.

DISTRIBUTION.— This species has the largest geographic range in the genus, occurring from Nigeria to Gabon, and throughout Central African Republic, Democratic Republic of Congo and Republic of Congo. Within Equatorial Guinea, it has been recorded from Río Muni only, in Cabo San Juan (Boulenger 1903) and in Monte Alén National Park (De la Riva 1994). Here we present the first records of *C. leucomystax* for Bioko, and also an additional locality for Río Muni (Map 5A).

COMMENTS.— The newly recorded populations from Bioko are closely related to the ones from Cameroon (authors' unpublished data).

SPECIMENS EXAMINED.— Seven specimens. Niefang, Alosa, 14 August 1985 (EBD 34220); River mouth of Moaba, Bioko, 03°14'01.41"N, 08°37'19.64"E, 21 November 2003 (MNCN 48923–48925); Río Ole, on the way to Caldera de Luba, Bioko, 03°15'55.40"N, 08°28'31.64"E, 26 November 2003 (MNCN 48926–48927); between Río Ole and Casa Moraca, Bioko, 03°15'33.05"N, 08°29'11.18"E, 29 November 2003 (MNCN 48928).

***Cardioglossa nigromaculata* Nieden, 1908**

TYPE LOCALITY.— “Johann-Albrechtshöhe [=Kumbaj]”, Cameroon.

DISTRIBUTION.— This species ranges from southeastern Nigeria to southwestern Cameroon, and it is also present on Bioko (Channing & Rödel 2019) (Map 5B).

COMMENTS.— This species was found for the first time in Equatorial Guinea by the BBPP in Caldera de Luba, Bioko, during November 2015. Recorded specimens are held at the North Carolina Museum of Natural Sciences. Channing & Rödel (2019) published the presence of this species on Bioko (without specific locality) based on these specimens. See addendum in Material and Methods.

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

Astylosterninae Noble, 1927

***Astylosternus* Werner, 1898**

***Astylosternus batesi* (Boulenger, 1900)**

Photo figures 6A–B

TYPE LOCALITY.— “Benito River, Equatorial Guinea”.

DISTRIBUTION.— This species ranges from southern Cameroon to Gabon, western Democratic Republic of Congo and southwestern Central African Republic. In Equatorial Guinea, it has been reported from three localities of Río Muni (Boulenger 1900, 1903; De la Riva 1994) (Map 5C).

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Leptodactylodon* Anderson, 1903**

***Leptodactylodon* cf. *stevarti* Rödel and Pauwels, 2003**

Photo figures 6C–E

TYPE LOCALITY.— “Forest stream, 550 m a.s.l., 0°37'301"N, 10°24'402"E, near Tchimbélé dam, Haut-Komo Department, Woleu-Ntem Province, Gabon”.

DISTRIBUTION.— Currently, *L. stevarti* is only known from the type locality. See comments below regarding the Equatorial Guinea population (Map 6A).

COMMENTS.— Rödel and Pauwels (2003) suggested that the population of Monte Alén recorded as *L. albiventris* (Boulenger, 1905) by De la Riva (1994) could represent an undescribed species or an additional population of *L. stevarti*, conclusion also followed by Dewynter and Frétey (2019). De la Riva et al. (2001) described the calls for Río Muni populations.

SPECIMENS EXAMINED.— No specimens were found in the collections we have examined.

***Nyctibates* Boulenger, 1904**

***Nyctibates corrugatus* Boulenger, 1904**

Photo figures 7A–B

TYPE LOCALITY.— “Efulen, Bulu Country, Southern Cameroon”.

DISTRIBUTION.— It is distributed from Nigeria to Gabon in lowland rainforest. In Equatorial Guinea, *N. corrugatus* has been recorded from Río Muni at Monte Alén (De la Riva 1994) (Map 6B).

COMMENTS.— De la Riva et al. (2001) described the calls for Río Muni populations.

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Scotobleps* Boulenger, 1900**

***Scotobleps gabonicus* Boulenger, 1900**

Photo figure 7C

TYPE LOCALITY.— “Benito River”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— It is distributed across the Gulf of Guinea region, from eastern Nigeria to Gabon and Democratic Republic of Congo. In Equatorial Guinea, it has been reported in Río Muni, at the type locality, at Cabo San Juan (Boulenger 1903), and in Monte Alén (De la Riva 1994). Our results provide several additional records, suggesting that this is a widespread species within continental Equatorial Guinea (Map 6C).

COMMENTS.— De la Riva et al. (2001) described the calls for Río Muni populations.

SPECIMENS EXAMINED.— Twenty-six specimens. Miboman, Litoral Bata, 01 September 1984 (EBD 18282), April 1988 and December 1977 (EBD 28046, 28059, 28062–28065, 28067, 28069, 28070, 28071), April 1988 (EBD 28075, 28081, 28079, 28084, 28073, 28088), December 1987 (EBD 28080); Miboman, Km 27 Bata–Niefang, October 1987 (EBD 28068, EBD 28077); San Joaquín de Ndyiacom, December 1987 (EBD 28060, 28061); Ayamiken (EBD 27498); Nvom-Noayong, (Evinayong-Aconibe), 16 April 1987 (EBD 25044); without data (two specimens from EBD labeled B9120, B9119).

***Trichobatrachus* Boulenger, 1900**

***Trichobatrachus robustus* Boulenger, 1900**

Photo figures 7D–E

TYPE LOCALITY.— “Benito River”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— It ranges over the Gulf of Guinea, from Nigeria to Gabon and Democratic Republic of Congo and, more recently, was also recorded from Angola (Ernst et al. 2014:298). In Equatorial Guinea, it is only known from Río Muni, where the type locality is (Boulenger 1900). It has been also found in Monte Alén (Río Bilene, close to lake Atoc [De la Riva 1994] and Río Lobo [Lasso et al. 2002]) and in Monte Mitra (Gonwouo and Nsang 2005) (Map 7A).

SPECIMENS EXAMINED.— Three specimens. Mirador de Moka, Río Lobo, Evinayong, 21 May 1986 (EBD 21019); Miboman (Bata), August 87 (EBD 27496); Río Muni, Equatorial Guinea (EBD 23072).

Leptopelinae Laurent, 1972

***Leptopelis* Günther, 1859**

***Leptopelis aubryi* (Duméril, 1856)**

Photo figures 8A–B

Type locality.— Gabon.

DISTRIBUTION.— It is distributed from southern Nigeria to Democratic Republic of Congo and Central African Republic, including Gabon, Cameroon and Equatorial Guinea, where it has been recorded in Río Muni at Cabo San Juan (Boulenger 1903) and Monte Alén (De la Riva 1994), and on Bioko at Moka (Hydeman et al. 2017); more recently, it was also reported from Angola (Marques et al. 2018). Our revision provides additional records from Río Muni (Map 7B). Descriptions of the advertisement calls from Monte Alén were provided by Bosch et al. (2000).

SPECIMENS EXAMINED.— Twelve specimens. Miboman, Movo, Bata, Litoral, Río Muni, 08 September 1984 (EBD 18251), 24 August 1987 (EBD 27501–27505); Miboman, Bata, April 1988 (EBD 27836, 27838), December 1988 (EBD 27838); Akurenam Centro Sur, 27 August 1984 (EBD

18426); Cabo San Juan, Río Muni, 08 September 1901 (MNCN 3999), 25 August 1901 (MNCN 4004).

***Leptopelis boulengeri* (Werner, 1898)**

Photo figure 8C

TYPE LOCALITY.—“Victoria Kamerun”, [Limbé, Cameroon]

DISTRIBUTION.— This species is widespread over the Gulf of Guinea region, from southeastern Nigeria to Gabon and Democratic Republic of Congo. In Equatorial Guinea, it has been recorded from Bioko (Boulenger 1906a; Ahl 1929; Bell et al. 2019) and Río Muni (Ahl 1929; De la Riva 1994). Our revision provides additional records from Río Muni (Map 7C).

COMMENTS.— Some records of this species are located in Equatorial Guinea under the synonym of *Leptopelis poensis* Ahl, 1929 for Bioko populations (Type locality: Fernando Poo [=Bioko]), and *Leptopelis violescens* Ahl, 1929 for Río Muni populations (Type locality: Makomo, Spanish-Guinea).

SPECIMENS EXAMINED.— Nineteen specimens. Miboman km 27 Ctra Bata-Movo, 1984 (EBD 19633), April 1988 (EBD 27824); Ayebe (Akurene), cerca de la cascada de Nguelensok, 15 June 1986 (EBD 21012, EBD 21020); Cabo San Juan, 19 August 1901 (MNCN 4000–4001), 21 August 1901 (MNCN 4002–4003, MNCN 4038–4041), August 1901 (MNCN 4042–4048).

***Leptopelis brevirostris* (Werner, 1898)**

Photo figure 8D

TYPE LOCALITY.—“Kamerun (ein Exemplar aus Victoria, ...)”.

DISTRIBUTION.— This species is widespread over the rainforests of the Gulf of Guinea region, from southern Nigeria to Gabon and Democratic Republic of Congo. In Equatorial Guinea, it has been recorded from Bioko (Boulenger 1906a; Mertens 1965; Hydeman et al. 2017; Bell et al. 2019) and Río Muni (Boulenger 1900; De la Riva 1994), where our revision adds a new record (Map 8A).

COMMENTS.— The taxonomic identity of *L. brevipes* (Boulenger, 1906) (only known from its type locality at Musola, Bioko) has been problematic (Mertens 1965; Lötters et al. 2005; Channing & Rödel 2019). This taxon has been recently synonymized with *L. brevirostris* based on morphological and molecular evidences (Bell et al. 2019).

SPECIMENS EXAMINED.— 1 specimen. Besabeba (02°10'N 10°12'E), orilla del río Campo en la confluencia, centro sur, Kie-Ntem, 24 September 1985 (EBD 21011).

***Leptopelis calcaratus* (Boulenger, 1906)**

Photo figure 8E

TYPE LOCALITY.—“Efulen”, Cameroon, and “Cape St. John and the Rio Benito District” (Cabo San Juan and Benito River, Equatorial Guinea).

DISTRIBUTION.— *Leptopelis calcaratus* inhabits the rainforests of the Gulf of Guinea region, from southeastern Nigeria to Gabon and eastern Democratic Republic of Congo. In Equatorial Guinea, it is present on Bioko (Mertens 1965; Hydeman et al. 2017) and Río Muni (Boulenger 1906a; De la Riva 1994) (Map 8B).

COMMENTS.— Populations from Bioko represent an independent lineage from those from mainland Cameroon (authors' unpublished data). However, an integrative approach is necessary to test if this insular lineage is part of the geographically structured intraspecific variability or a distinctive species.

SPECIMENS EXAMINED.— Illadji River, Bioko, 03°19'46.04"N, 08°40'26.13"E, 13 November 2003 (MNCN 48862–48868).

***Leptopelis millsoni* (Boulenger, 1895)**

TYPE LOCALITY.—“Mouths of the Niger”, Nigeria.

DISTRIBUTION.— This species occurs over the rainforests of the Gulf of Guinea region, from southern Nigeria to Gabon and eastern Democratic Republic of Congo. *Leptopelis millsoni* has been only recorded in Equatorial Guinea at Río Muni (Ahl 1929; see comments) (Map 8C).

COMMENTS.— Ahl (1929) recorded this species in Río Muni under the synonym *L. guineensis* Ahl, 1929 (Type locality: Makomo, Río Muni). Our results provide a new record, confirming the presence of this species in Río Muni, where it had not been recorded since Ahl (1929).

SPECIMENS EXAMINED.— One specimen. Wele-Nzas, Ayene, 09 September 1985 (EBD 21016).

***Leptopelis modestus* (Werner, 1898)**

TYPE LOCALITY.— “Kamerun”; restricted to “Buéa, Cameroon” by lectotype designation.

DISTRIBUTION.— This species inhabits the forests of southern Nigeria and Cameroon. In Equatorial Guinea, it is only recorded from Bioko (Hydeman et al. 2017) (Map 9A).

COMMENTS.— Populations from Bioko represent an independent lineage from those in mainland Cameroon (authors’ unpublished data). However, an integrative approach is necessary to test if this insular lineage is part of the geographically structured intraspecific variability or a different species.

SPECIMENS EXAMINED.— One specimen. Moka, Bioko, 03°20'23.47"N, 08°40'6.20"E, 15 November 2003 (MNCN 50377).

***Leptopelis notatus* (Peters, 1875)**

TYPE LOCALITY.— “Cameruns”, Douala, Cameroon (see Frétey et al. 2014).

DISTRIBUTION.— The distribution of *L. notatus* encompasses the rainforests of the Gulf of Guinea region, extending from south-eastern Nigeria through Cameroon to northern Angola. In Equatorial Guinea, it has been recorded from Bioko (Nieden 1908) and Río Muni (Nieden 1909; Lasso et al. 2002) (Map 9B).

COMMENTS.— Nieden (1909) recorded this species in Río Muni under the synonym *L. tessmanni* Nieden, 1909 (Type locality: Makomo, Río Muni). Our revision provides two additional records for Río Muni.

SPECIMENS EXAMINED.— Five specimens. Nvom Aconibe-Asoc, 08 April 1987 (EBD 25047); Engong Aconibe-Asoc, 01 April 1987 (EBD 25067–25070).

***Leptopelis ocellatus* (Mocquard, 1902)**

Photo figure 8F

TYPE LOCALITY.— “Gabon ... à environ 50 kilomètres au Sud-Ouest de Lambaréné”.

DISTRIBUTION.— It occurs in the rainforests from southern Cameroon through Equatorial Guinea and Gabon to Republic Democratic of Congo and Republic of Congo. In Equatorial Guinea, it has been recorded only in Río Muni (Lake Atoc, Monte Alén National Park) by De la Riva (1994) (Map 9C).

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

***Leptopelis rufus* Reichenow, 1874**

Photo figures 8G–H

TYPE LOCALITY.— “Walde bei Victoria, am Fusse der Camerunberge”, Limbé, Cameroon.

DISTRIBUTION.— It occurs throughout the rainforests of the Gulf of Guinea region, from south-eastern Nigeria through Cameroon to northern Angola, although Marques et al. (2018) did not include it in the Angolan amphibian fauna. In Equatorial Guinea, it has been recorded from Bioko (Boulenger 1900; Boulenger 1906a) and Río Muni (Boulenger 1903; De la Riva 1994) (Map 10A).

COMMENTS.— We provide additional records from both Bioko and Río Muni.

SPECIMENS EXAMINED.— Five specimens. Moka, Bioko, 03 March 1933 (MNCN 3739); Miboman, Bata, December 1987 (EBD 27837); Yengue, Litoral (Bata), 22 February 1988 (EBD 27826); Miboman, Km 27 Ctra Bata–Niefang, Guinea, October 1987 (EBD 27825); Ayamiken (San Joaquin de Ndyiacom), 1990 (without EBD number, labeled B8972).

Family Bufonidae Gray, 1825

Didynamipus Andersson, 1903

Didynamipus sjostedti Andersson, 1903

TYPE LOCALITY.— “Kamerun”, Cameroon.

DISTRIBUTION.— This species occurs both in continental Africa, where it extends from Cameroon (see Gonwouo et al. 2013) to Nigeria (Onadeko et al. 2010), and on Bioko, where it was reported from Basilé by Boulenger (1906a). Since then, no additional records have been published for this country. We found an additional population from south Bioko province, located in the surroundings of Caldera de Luba (Map 10B).

COMMENTS.— The distribution of this poorly known species has been recently revised by Gonwouo et al. (2013), who also provided insights on its natural history, stating that its reproductive mode is direct development. Our record from southern Bioko expands the distribution range of this species southwards.

No phylogeographic studies have been performed including this monotypic taxon. The synonym *Atelophryne minutus* Boulenger, 1906, described from Bioko, represents an available name if future work confirms the specific distinctiveness of insular populations.

SPECIMENS EXAMINED.— Nine specimens. From Belebu to Ureca, 3°24'25.81"N, 8°33'3.23"E, 19 November 2003 (MNCN 48947–48954, 46872).

Nectophryne Buchholz and Peters, 1875

Nectophryne afra Buchholz and Peters, 1875

Photo figure 9A

TYPE LOCALITY.— “Cameruns”, restricted to Douala by Frétey et al. (2014).

DISTRIBUTION.— *Nectophryne afra* occurs throughout West Africa including Nigeria, Cameroon, Equatorial Guinea, Gabon and Democratic Republic of Congo. In Equatorial Guinea, *N. afra* has been recorded from mainland at Cabo San Juan (Boulenger 1903), Benito River (Boulenger 1900), and Monte Alén (Lasso et al. 2002), and on Bioko at Basilé, Bahía de San Carlos, Musola (Boulenger 1906a), Río Iladyi (Mertens 1965) and along the road to Pico Basilé (Hydeman et al. 2017) (Map 10C).

COMMENTS.— *Nectophryne afra* was the only species of the genus present in Equatorial Guinea until this work (see *N. batesii* section). Juveniles of *Nectophryne afra* are characterized by a dorsal pattern based on thin whitish lines that form rings or loops over the nostril and mid-body region respectively, together with additional transversal stripes over a blackish surface (Scheel 1970).

SPECIMENS EXAMINED.— Thirteen specimens. Cabo San Juan, Río Muni, 15 October 1901 (MNCN 3152–3161, 3163); path behind church in Bakelele forest, Batete, Bioko, 03°26'37.34"N, 8°30'24.76"E, 02 December 2003 (MNCN 48824); north of Caldera de Luba, 3°21'28.73"N, 8°31'55.01"E, 13 March 2007 (MNCN 46704).

Nectophryne batesii Boulenger, 1913

Photo figures 9B–C

TYPE LOCALITY.— “Neighbourhood of Bitey, on the Ja River (Congo System)”, Cameroon.

DISTRIBUTION.— *Netophryne batesii* is known from Nigeria, Cameroon, Gabon, and Demo-

cratic Republic of Congo. In Equatorial Guinea, it has been found both at Río Muni and Bioko (Map 11A).

COMMENTS.— The presence of *N. batesii* in Río Muni and Bioko had gone unnoticed until this work. The distribution of the species needs to be revised and, following the work of Blackburn and Droissart (2008), we suggest that the records of *N. afra* from Fernand-Vaz (Gabon) provided by Boulenger (1906a) and from Ijebu Oru (Nigeria) by Onadeko and Rödel (2009), correspond to *N. batesii*, as both records were based on juveniles showing the typical pattern of this species (Blackburn and Droissart 2008). The phenotype of juveniles of *N. batesii* is formed by four solid and wide transversal whitish stripes located at roughly equal intervals over a black dorsal surface, lacking the loops and ring pattern present in the juveniles of *N. afra* (Blackburn and Droissart 2008). The specimen from north of Bioko (Rebola) presents osteological singularities when compared with other specimens (author's unpublished data) suggesting that more field work should be carried out at this region for the study of additional individuals throughout integrative approaches including molecular analyses and detailed morphological and ecological studies.

We herein provide the first records of *N. batesii* for Río Muni and Bioko.

SPECIMENS EXAMINED.— Eight specimens. Cabo San Juan, Río Muni, 15 October 1901 (MNCN 3162); north of Campamento Hormiga, Caldera de Luba, 03°18'27.34"N 08°28'15.68"E, 08 March 2007 (MNCN 46715–46716); Campamento UPM-Campamento Hormiga, Caldera de Luba, 3°20'46.54"N 8°29'48.20"E, 08 March 2007 (MNCN 46717); River Osa, creek Chopepe, San Antonio de Ureca, 03°14'52.19"N, 08°32'23.77"E, 22 November 2003 (MNCN 48823); BBPP Camp, Caldera de Luba, 03°20'47.32"N, 08°29'48.44"E, 26 November 2003 (MNCN 48822); San Joaquín de Ndyiacom (EBD 31487); Rebola, Bioko, January 1933 (MNCN 3151).

Sclerophrys Tschudi, 1838

Sclerophrys camerunensis (Parker, 1936)

Photo figures 9D; 10A–D

TYPE LOCALITY.— “Oban, Calabar”, Nigeria.

DISTRIBUTION.— This species is widely distributed across the Guinean forest in West Africa, extending from Guinea to East Africa, across Central African Republic and Tanzania. In Equatorial Guinea, it has been recorded both from Río Muni, at Monte Alén (De la Riva 1994), and Bioko (Mertens 1965; Hydeman et al. 2017) (Map 11B).

COMMENTS.— Our revision provides several new records from Río Muni and Bioko.

In their molecular phylogeny, Liedtke et al. (2016) included samples from Bioko, which seem to be closely related to the Cameroonian ones. Márquez et al. (2000) described the calls for Río Muni populations.

SPECIMENS EXAMINED.— Thirtytwo specimens. Bata, Río Muni, 1965 (EBD 2714); Niefang, 13 July 1984 (EBD 18602); Oveng-Akurenám, 27 August 1984 (EBD 18406–18407); Bioko Sur (Luba), 08 June 1984 (EBD 18660); Oveng-Akurenám, 23 August 1984 (EBD 18432); Bata, Río Bizingui, 30 August 1986 (EBD 25024); Nvom (Aconibe-Asoc), 8 May 1987 (EBD 25025); Miboman, 01 September 1984 (EBD 18286); Anisoc (orillas del río Nobo), 17 September 1987 (EBD 27499); Akoaseng (Evinayong-Mongomo), 09 July 1987 (EBD 27500); San Joaquín de Ndyiacom (EBD 31489, B9242); San Joaquín de Ndyiacom (6 specimens with number EBD 31519); Moka, Bioko (MNCN 3085); Caldera de Luba, Bioko, 03°21'34.88"N 08°31'55.50"E, 09 December 2005 (MNCN 46713–46714); Ureca camp, Caldera de Luba, Bioko, 03°21'12.59"N 08°30'47.36"E, 18 March 2007 (MNCN 46718); Ureca camp, Caldera de Luba, Bioko, 03°21'12.59"N, 08°30'47.36"E, 10 March 2007 (MNCN 46723–46724); Biao Lake, Moka, Bioko, 3°21'14.97"N 8°37'25.64"E, 10 November 2003 (MNCN 48876–48881); Mariluz's farm, Moka, Bioko, 03°20'23.47"N, 8°40'6.20"E, 12 November 2003 (MNCN 48882).

***Sclerophrys funerea* (Bocage, 1866)**

TYPE LOCALITY.—“Duque de Bragança”, Calandula, Angola.

DISTRIBUTION.— This species has a wide range extending across the rainforests throughout west-central Africa, from Gabon to Uganda, and southwards to Angola. In Equatorial Guinea, it has been reported only from Bioko by Boulenger (1882) as *Bufo benguelensis* Boulenger, 1882 (Map 11C).

COMMENTS.— This species was described from a juvenile specimen collected in Calandula, Angola “Duque de Bragança”. In Equatorial Guinea, Boulenger (1882) reported this species, as *Bufo benguelensis*, on Bioko (then known as Fernando Poo) and “Benguela”; this taxon was synonymized with *B. funereus* by Bocage (1895b). However, the taxonomic status and, consequently, the distribution of *S. funerea* is not clear (Marques et al. 2018), and its presence in Equatorial Guinea is doubtful.

SPECIMENS EXAMINED.— We did not find any specimen of this taxon in the collections examined in this study.

Sclerophrys gracilipes* (Boulenger, 1899)*Photo figure 10E**

TYPE LOCALITY.—“Benito River, French (Congo) (sic)”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— *Sclerophrys gracilipes* is known from West-Central Africa extending from Nigeria to Democratic Republic of Congo and Republic of Congo. Within Equatorial Guinea it has been recorded in Río Muni by Boulenger (1899a) (Type locality: “Benito River”) and De la Riva (1994), and on Bioko by Mertens (1965) (as *Bufo funereus gracilipes*) and Hydeman et al. (2017) (Map 12A).

COMMENTS.— The molecular phylogeny provided by Liedtke et al. (2016) suggests that this taxon is not monophyletic; thus, a taxonomic revision is in order. As the type locality is in mainland Equatorial Guinea, the specific epithet would be retained for the populations of the clade inhabiting the region of Río Muni and surroundings. On the other hand, populations from Bioko seem to represent a distinct undescribed taxonomic unit (Liedtke et al. 2016).

SPECIMENS EXAMINED.— Fourteen specimens. Ctra. airport Malabo-Luba (10 km from Malabo), 02 June 1984 (EBD 18658); Bata: Río Bizingui, 30 August 1986 (EBD 25038); Miboman, 01 September 1984 (EBD18285); Miboman, April 1988 (EBD 28090); San Joaquín de Ndyia-comm (B8438, B8541–B8544); Equatorial Guinea, without precise locality (5 specimens, one of them with the label EBD 27840).

Sclerophrys latifrons* (Boulenger, 1900)*Photo figure 10F**

TYPE LOCALITY.—“Benito River”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— It inhabits dense and high tropical forests over the Gulf of Guinea region from Cameroon to Gabon and Congo, extending to the Democratic Republic of Congo. In Equatorial Guinea *S. latifrons* has been recorded in Río Muni (where the type locality is: “Benito River”) (Boulenger 1900; De la Riva 1994) and on Bioko (Boulenger 1906a) (Map 12B).

COMMENTS.— The record of Bioko is doubtful. Despite the efforts to sample amphibians from Bioko, *S. latifrons* has not been recorded from the island since Boulenger (1906a). This species has been included in a recent molecular phylogeny (Liedtke et al. 2016). However, the phylogeographic structure across most of its range, including the Equatorial Guinean populations, remains unknown. The record identified as “*Bufo maculatus*” from Monte Mitra at Monte Alén National Park (Gonwouo and Nsang 2005) likely belongs to *S. latifrons*.

SPECIMENS EXAMINED.— Eight specimens. Miboman, Bata-Movo (Km 27), 24 June 1984 (EBD 18601); Miboman-Movo-Bata (Km 27), 05 October 1984 (EBD 18253); Guinea Ecuatorial,

without precise locality (four specimens, three of them with the label EBD 27844, 27839, 27846); Miboman, 01 September 1984 (EBD 18283–18284).

***Sclerophrys superciliaris* (Boulenger, 1888)**

Photo figures 11A–B

TYPE LOCALITY.— “Rio del Rey, Cameroons”.

DISTRIBUTION.— The nominal subspecies (see comments) is known from Nigeria, Cameroon, Gabon, Equatorial Guinea and, tentatively, Central African Republic. In Equatorial Guinea, *S. superciliaris superciliaris* has been recorded from Río Muni (Boulenger 1900; De la Riva 1994) (Map 12C).

COMMENTS.— Barej et al. (2011) revealed the existence of three distinct taxa within the formerly known *S. superciliaris* sensu lato. One of them is represented by *S. superciliaris superciliaris*, which is distributed from eastern Nigeria, Cameroon, Gabon and Equatorial Guinea; a second taxon, *S. superciliaris chevalieri*, is distributed from Sierra Leone, Guinea, Liberia, Ivory Coast and Ghana; the third taxon is located over the eastern Democratic Republic of Congo and was described as a distinct species, *Amietophrynus channingi* Barej, Schmitz, Menegon, Hillers, Hinkel, Böhme, and Rödel, 2011 (currently *S. channingi*).

SPECIMENS EXAMINED.— No specimens of this species were found in the collections examined by us in this study.

***Sclerophrys tuberosa* (Günther, 1858)**

Photo figures 11C–E

TYPE LOCALITY.— “Fernando Po”, Bioko, Equatorial Guinea.

DISTRIBUTION.— It occupies the tropical forest of the Gulf of Guinea region from Cameroon to Gabon, Congo and Democratic Republic of Congo. In Equatorial Guinea, this species occurs both on Bioko and in Río Muni. Within Bioko it has been recorded from several localities (Mertens 1965; Boulenger 1900), while it is only known from two localities in the continental region of Río Muni (Boulenger 1903; De la Riva 1994) (Map 13A).

COMMENTS.— Populations from Río Muni appear morphologically different from those on Bioko and in Cameroon. Phylogenetic relationships within the genus were studied by Liedtke et al. (2016) based on molecular data.

SPECIMENS EXAMINED.— Twelve specimens. Nvom (Aconibe-Asoc), 08 May 1987 (EBD 25026); Acocnseng (Km 10 Aconibe-Asoc), 30 May 1987 (EBD 25027); UPM camp-Riaco river, Caldera de Luba, Bioko, 03°20'46.54"N, 08°29'48.20"E, 14 December 2005 (MNCN 46709–46710, 46712), 13 December 2005 (MNCN 46711); Moaba, Bioko, 03°14'01.41"N, 08°37'19.64"E, 21 November 2003 (MNCN 48870); top of trail into Caldera de Luba, Bioko, 3°20'5.02"N, 8°29'14.33"E, 26 November 2003 (MNCN 48871–48873); surroundings of BBPP camp, 03°20'47.32"N, 08°29'48.44"E, 26 and 27 November 2003 (MNCN 48874–48875, respectively).

***Werneria* Poche, 1903**

***Werneria* cf. *mertensiana* Amiet, 1976**

Photo figures 12A–B

TYPE LOCALITY.— “Mt. Nlonako, env. de N’Kongsamba, 1.000 m”, Cameroon.

DISTRIBUTION.— In Equatorial Guinea it is only known from Monte Alén National Park, Río Muni (De la Riva 1994) (Map 13B).

COMMENTS.— This genus was originally reported in Equatorial Guinea by De la Riva (1994) at Monte Alén National Park based on a single specimen, which was regarded as *W. mertensiana* Amiet, 1976. However, Rödel et al. (2004) suggested that the taxonomic status of the *Werneria* species from Equatorial Guinea needs to be revised, as no morphological characters concordant with those of other congeneric species, including *W. mertensiana* from Cameroon, were detected.

Thus, the population from Río Muni could represent an undescribed species (Rödel et al. 2004), but more data are necessary to test this hypothesis.

SPECIMENS EXAMINED.— No specimens of *Werneria* from Equatorial Guinea were found in the collections examined by us in this study.

***Wolterstorffina* Mertens, 1939**

***Wolterstorffina parvipalmata* (Werner, 1898)**

Photo figures 25A–D

TYPE LOCALITY.— “Kamerun?”, Cameroon.

DISTRIBUTION.— It is distributed from eastern Nigeria to Cameroon. There is a single published record of this species in Equatorial Guinea (see supplementary material in Liedke et al. [2016]), where it has been found on Bioko (Map 27A).

COMMENTS.— This species was found for the first time in the country by the Bioko Biodiversity Protection Program at the surroundings of Moka cascades viewing site (along Illadji River, Bioko). See addendum in Material and Methods. Liedke et al. (2016) sequenced a specimen collected on Bioko in 2015 by R.C. Bell and deposited in the CUMV (Cornell University Museum of Vertebrates) collections.

SPECIMENS EXAMINED.— We did not find any specimen of this taxon in the collections examined by us in this study.

Conrauidae Dubois, 1992

***Conraua* Nieden, 1908**

***Conraua crassipes* (Buchholz and Peters, 1875)**

Photo figure 13A

TYPE LOCALITY.— “Abo”, Nigeria.

DISTRIBUTION.— This species ranges from Nigeria to Democratic Republic of Congo. In Equatorial Guinea, it has been recorded both on Bioko (Bocage 1985b; Mertens 1968) and in Río Muni (Boulenger 1900, 1903; De la Riva 1994) (Map 13C).

SPECIMENS EXAMINED.— Forty-three specimens. Miboman, Bata-Movo (Km 27), 11 August 1984 (EBD 18710); Miboman, Litoral, Bata, (EBD 18623), December 1987 (EBD 28100), April 1988 (EBD 28092–28093, 28095–28096, 28099, 28102–28104, 28106–28110, 28112–28113, 28089); Kie Temp, Miboman (close to Asonga) (EBD 18279–18281); Ctra Mbini-Bata, Litoral Carut, 29 November 1985 (EBD 21022); Nsork, January 1986 (EBD 25042); Km 30 Ctra Bata-Niefang, December 1987 (EBD 28101, 28105, 28094), October 1987 (EBD 28097–28098); San Joaquín de Ndyiacom, April 1988 (EBD 28091); Santa Isabel, Malabo, Bioko Norte, 09 January 1933 (MNCN 3877), 01 February 1933 (MNCN 3883); Cabo San Juan, 15/19 September 1901 (MNCN 3884–3892); Nvom (Aconibe-Asoc), 6 May 1987 (EBD 25050); Poblado de Muga, Moka, Monte Alén, 22 August 2001 (MNCN 46338).

***Conraua goliath* (Boulenger, 1906)**

Photo figure 13B

TYPE LOCALITY.— “Efulen”, South Cameroon.

DISTRIBUTION.— *Conraua goliath* is distributed over south-western Cameroon (Nkongsamba region) and mainland Equatorial Guinea. In Equatorial Guinea, it has been recorded in several localities in Río Muni (Sabater Pi 1985; De la Riva 1994) (Map 14A).

COMMENTS.— This is the largest living frog in the world. The holotype measured 25 cm of snout-vent length (Boulenger 1906b), and the largest specimen recorded weighted 3.3 kg (Sabater Pi 1985). Adults live in the fast-flowing rivers in lowland rainforest, below 1000 m a.s.l., where they rest over the rocks, emerging from rapids during the day, while they move along the river margins during the night (Sabater Pi 1985). Some aspects of their reproductive behaviour, such as nest construction for spawning, have been recently described (Schäfer et al. 2019).

SPECIMENS EXAMINED.— Twenty specimens. [Río Muni] (MNCN 4050). Niefang, Sense (1°33'N, 09°48'W) June/July 1964 (EBD 2699–2701, EBD 2754–2756, EBD 20842–20854); San Joaquín de Ndyiacom (EBD 31507).

Hyperoliidae Laurent, 1943

***Acanthixalus* Laurent, 1944**

***Acanthixalus spinosus* (Buchholz and Peters, 1875)**

TYPE LOCALITY.— “Cameruns”, restricted to Douala by Frétey et al. (2014).

DISTRIBUTION.— *Acanthixalus spinosus* ranges across the rainforests of Nigeria, Cameroon and Democratic Republic of Congo, as well as Equatorial Guinea, where it has been recorded in Río Muni at Cabo San Juan (Boulenger 1903) (Map 14B).

COMMENTS.— No more specimens have been observed in Equatorial Guinea since Boulenger (1903).

SPECIMENS EXAMINED.— No specimens were found at the collections examined by us in this study.

***Afrixalus* Laurent, 1944**

***Afrixalus dorsalis* (Peters, 1875)**

TYPE LOCALITY.— “Boutry” mouth of River Butre, Ghana, and “Victoria in einem Wassertümpel”, Cameroon. Meterns (1938) restricted the type locality to “Boutry”.

DISTRIBUTION.— From eastern Sierra Leone to Cameroon, southwards to Angola. There are general references to the presence of this species in mainland Equatorial Guinea (Schlötter 1999; Frétey and Blanc (2000) (Map 14C).

COMMENTS.— We provide the first accurate record of *A. dorsalis* for Equatorial Guinea, confirming its presence in Río Muni. The coloration pattern of the specimen examined here corresponds to the taxon *A. d. regularis* Laurent, 1951 (see Amiet 2012).

SPECIMENS REVISED.— One specimen. Río Muni: Asonga, Bata, 14 October 1985 (EBD 21025).

***Afrixalus fulvovittatus* (Cope, 1861)**

Photo figure 14A

TYPE LOCALITY.— “Liberia”.

DISTRIBUTION.— This species extends over a vast area ranging from Guinea to Cameroon, including Equatorial Guinea, where it has been recorded from Monte Alén (De la Riva 1994). There are no records from Bioko (Map 15A).

COMMENTS.— We provide an additional record of the species in Río Muni.

Currently, the populations of Equatorial Guinea are ascribed to the subspecies *A. f. brevipalmatus* (Amiet 2012). Descriptions of the advertisement calls from Monte Alén were provided by Bosch et al. (2000) (as *A. brevipalmatus* [Ahl, 1931]).

SPECIMENS EXAMINED.— Fifteen specimens. Engong (Aconibe-Asoc), 01 May 1987 (EBD 25102–25116).

***Afrixalus laevis* (Ahl, 1930)**

TYPE LOCALITY.— “Kamerun”.

DISTRIBUTION.— This species ranges from southern Cameroon to Gabon and Republic of Congo, extending eastwards to Uganda. *Afrixalus laevis* has been recently reported in Equatorial Guinea at Bioko, by Hydeman et al. (2017) (Map 15B).

COMMENTS.— This species is likely to occur in Río Muni.

SPECIMENS EXAMINED.— No specimens of *A. laevis* were found in the collections examined by us in this study.

Afrixalus osorioi* (Ferreira, 1906)*Photo figures 14B–C**

TYPE LOCALITY.—“Quilombo”, northern Angola.

DISTRIBUTION.—*Afrixalus osorioi* occurs from northern Angola and Gabon to Kenya and Uganda throughout Democratic Republic of Congo. There are no previous published records of this species in Equatorial Guinea (Map 15C).COMMENTS.— We report for the first time the presence of *A. osorioi* in Equatorial Guinea. Specimens were found in southeastern Río Muni (see list of specimens examined) and in Monte Alén (IDIR photographic records: Fig. 14B–C). We tentatively assign the examined specimens to this taxon based on external morphological characters. However, these specimens differ slightly from the species' typical pattern (Schjötz 1999; Amiet 2012). Recently, Jongsma et al. (2017) discovered this species in Gabon, providing three photographs: the figured specimen GFMJ1356 shows the typical pattern (see also Schjötz 1999), whereas the other two figured specimens, CAS 258270 and CAS 258161, present a more uniform dorsal pattern where the dark dorsal rectangle is absent. Jongsma et al. (2017) stated that their specimen's identifications were confirmed by molecular data. Later, Dewynter et al. (2018) provided an additional record for Gabon, and some specimens were figured, showing a pattern similar to the ones observed by us from Equatorial Guinea. This suggest that the typical pattern of *A. osorioi* (a well-defined dark rectangular mark on dorsum) in Gabon and Equatorial Guinea might be uncommon or absent. Instead, these populations have irregular and smaller spots, often arranged in two areas: between the eyes and over the neck region (see Fig. 14B–C and pictures in Dewynter et al. 2018). However, a closely related species and morphologically similar, *A. equatorialis* (Laurent, 1941), is distributed in Cameroon and Democratic Republic of Congo (Amiet 2012; Portik et al. 2019). The dorsal pattern of *A. osorioi* is sometimes very similar to that of *A. equatorialis* from Cameroon. Although Jongsma et al. (2017) stated that the identification was confirmed by comparing DNA sequence data of the specimens from Gabon to another previously identified sample from Uganda, additional phylogenetic studies including samples from the type localities of each species will be necessary for resolving the taxonomy and distributional limits of the species in this group.

SPECIMENS EXAMINED.— Eight specimens. Engong (Aconibe-Asoc), 01 May 1987 (EBD 25094–25101).

Afrixalus paradorsalis* Perret, 1960*Photo figures 14D–E**

TYPE LOCALITY.—“Foulassi, Cameroun”.

DISTRIBUTION.— This species ranges from southeastern Nigeria to Cameroon, Gabon and Republic of Congo. In Equatorial Guinea, *A. paradorsalis* has been recorded both on Bioko (Boulenger 1906a [as *Megalixalus fornasinii*]; Mertens 1965 [as *Afrixalus dorsalis*]; Hydeman et al. 2017; Charles et al. 2018) and in Río Muni (De la Riva 1994) (Map 16A).

COMMENTS.— Distinct allopatric lineages were detected over most of the species range; two of them are present in Equatorial Guinea: the first one is insular, belonging to the populations from Bioko, which are closely related to another lineage distributed over the Cameroonian Volcanic Line; the second lineage ranges from southern Cameroon to Gabon and Republic of Congo (Charles et al. 2018). Although no samples from Río Muni were included by Charles et al. (2018), it is highly likely that Río Muni populations fit within this latter lineage. Descriptions of the advertisement calls from Monte Alén were provided by Bosch et al. (2000).

SPECIMENS EXAMINED.— Twelve specimens. BBPP camp, Caldera de Luba, Bioko, 03°20'47.32"N, 08°29'48.44"E, 28 November 2003 (MNCN 48855, MNCN 48860); Red swamp, Caldera de Luba, Bioko 03°21'27.99"N, 08°30'52.11"E, 27 November 2003 (MNCN 48856–

48859); path behind church, Bakelele forest, Batete, Bioko, 03°26'37.34"N, 8°30'24.76"E, 02 December 2003 (MNCN 48861).

Alexeroon Perret, 1988

Alexeroon obstetricans (Ahl, 1931)

Photo figures 15A–C

TYPE LOCALITY.— neotype from “Foulassi, rivière Lobô”; lost holotype from “Bipindi, Kamerun” Cameroon.

DISTRIBUTION.— It occurs from Cameroon to Gabon. In Equatorial Guinea, *A. obstetricans* has been recorded from Monte Alén, Río Muni (De la Riva 1994) (Map 16B).

COMMENTS.— Descriptions of the advertisement calls from Monte Alén were provided by Bosch et al. (2000).

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

Arlequinus Perret, 1988

Arlequinus krebsi (Mertens, 1938)

Photo figures 25E–F

TYPE LOCALITY.— “Mubengue”, Cameroon.

DISTRIBUTION.— This species ranges from southwestern Cameroon to Bioko (Map 27B).

COMMENTS.— The presence of *Arlequinus* on Bioko was expected by Mertens (1938). This species was only known from a set of localities in southwestern Cameroon until the recently discovered population in Equatorial Guinea during the field surveys of the BBPP at the surroundings of Pico Basilé, Bioko. This Bioko population was reported by Channing & Rödel (2019) (without specific locality). See addendum in Material and Methods.

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

Cryptothylax Laurent and Combaz, 1950

Cryptothylax greshoffii (Schilthuis, 1889)

Photo figures 15D–E

TYPE LOCALITY.— “Boma (Congo, W. Africa)”, Democratic Republic of Congo.

DISTRIBUTION.— This species has been reported from Cameroon, Equatorial Guinea, Democratic Republic of Congo, Angola and Central African Republic. In Equatorial Guinea, it has been only found in Monte Alén, Río Muni (De la Riva 1994) (Map 16C).

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

Hyperolius Rapp, 1842

Hyperolius kuligae Mertens, 1940

TYPE LOCALITY.— “Camp II: 920 m über Mubenge, Kamerun-Berg”, Cameroon.

DISTRIBUTION.— This species has been recorded from Cameroon, Gabon, Democratic Republic of Congo and Equatorial Guinea (Map 27C). There are also dubious records of this species in Uganda (Schjötz 1999). In Equatorial Guinea, it has been recently recorded on Bioko (Channing & Rödel 2019) although new material, said to be identical to that recorded by Channing & Rödel, was collected on Bioko and identified as *H. endjami* (Portik et al. 2019, Supplemental Table 1 [said to be accessible online but not verified by us {IDLR}]).

COMMENTS.— Channing & Rödel (2019) mentioned the presence of this species on Bioko (without specific locality), possibly based on specimens collected from the surroundings of Biao Lake and held at the collection of the Cornell University (not examined by us). See addendum in Material and Methods.

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

Hyperolius ocellatus* (Günther, 1858)*Photo figures 16A–E**

TYPE LOCALITY.—“Fernando Po”, Bioko, Equatorial Guinea and “Angola”. Perret (1975) restricted the type locality to “Fernando Po” by lectotype designation.

DISTRIBUTION.— This species ranges over a vast area, from south-eastern Nigeria to Democratic Republic of Congo and southwards to Gabon and Republic of Congo. In Equatorial Guinea, it has been recorded both in Río Muni (De la Riva 1994; Bell et al. 2017) and Bioko (Boulenger 1900, 1906a; Mertens 1941, 1965; Hydeman et al. 2017; Bell et al. 2017) (Map 17A).

COMMENTS.— *Hyperolius ocellatus* sensu lato shows a complex phylogeographic structure formed by several lineages (Bell et al. 2017), which need taxonomic revision. Currently, there is one mitochondrial lineage on Bioko, whereas Río Muni could lie in a contact zone between two mainland mitochondrial lineages (Bell et al. 2017). Descriptions of the advertisement calls from Monte Alén were provided by Bosch et al. (2000).

SPECIMENS EXAMINED.— Twenty-nine specimens. Bioko Sur (Luba), Moka, (3°19'N, 8°40'E), 25 July 1984 (14 specimens with the voucher number EBD 18606); Ayamiken (San Joaquín de Ndyiacom) (4 specimens without individual voucher number, EBD 31516), 1990; Caldera de Luba, Campamento Ureca, 11 March 2007 (MNCN 46720); Río San Antonio, Caldera de Luba, 13 March 2007 (MNCN 46725); northeast of Caldera de Luba, 12 March 2007 (MNCN 46726); BBPP camp, Caldera de Luba, Bioko, 03°20'47.32"N, 08°29'48.44"E, 28 November 2003 (MNCN 48945–48946); Río Iladyi, Bioko, 03°19'46.04"N, 08°40'26.13"E, 13 November 2003 (MNCN 48939–48944).

Hyperolius olivaceus* Peters, 1876*Photo figure 17A**

TYPE LOCALITY.—“Limbareni am Ogowe”, Lambaréné, Gabon.

DISTRIBUTION.— This species ranges from the coastal region of Gabon and Republic of Congo to southwestern Equatorial Guinea, where it has been recorded in Río Muni, at lake Atoc, Monte Alén (De la Riva 1994). There are no records of this species from Bioko (Map 17B).

COMMENTS.— *Hyperolius olivaceus* (formerly considered as a subspecies of *H. cinnamomeoventris* Bocage, 1886) forms part of the *H. cinnamomeoventris* species complex. Bell et al. (2015) identified distinct evolutionary lineages within this complex across most part of its distribution and revealed that *H. cinnamomeoventris* represents a paraphyletic taxon. Subsequently, in order to resolve the taxonomy of the group, Bell et al. (2017) elevated the subspecies *H. cinnamomeoventris olivaceus* to full species status for the lineages inhabiting the Gabon region and south of the Congo River, which likely includes Río Muni populations (as considered herein). *Hyperolius olivaceus* is the sister species to a clade formed by the insular *Hyperolius thomensis* Bocage, 1886, *H. mollerii* (Bedriaga, 1892) and *H. drewesi* Bell, 2016 (Bell et al. 2017).

SPECIMENS EXAMINED.— Nine specimens. Engong (Aconibe-Asoc), 01 May 1987 (EBD 25089–25093, EBD 25071, 25073–25075).

Hyperolius pardalis* Laurent, 1948*Photo figures 17B–D**

TYPE LOCALITY.—“Bitye, S. Cameroons”.

DISTRIBUTION.— This species ranges over the forests from southern Cameroon to southwestern Central African Republic and northwestern Republic of Congo, Gabon, and Equatorial Guinea, where there it has been recorded from Monte Alén only (De la Riva 1994) (Map 17C).

SPECIMENS EXAMINED.— Equatorial Guinea, Río Muni, no precise locality available, 1989 (EBD 32033).

***Hyperolius phantasticus* (Boulenger 1899)**

TYPE LOCALITY.—“Benito River, French Congo”, currently Río Muni, Equatorial Guinea.

DISTRIBUTION.— This species ranges from southwestern Cameroon and Gabon to Democratic Republic of Congo and Republic of Congo. In Equatorial Guinea, it was recorded from Río Muni by Boulenger (1899a) (Map 18A).

COMMENTS.— Since Boulenger (1899a, 1900) no specimens of this species have been recorded.

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

***Hyperolius platyceps* (Boulenger, 1900)**

TYPE LOCALITY.— “Benito River, north of the Gaboon River between 20 and 30 miles inland from the coast, Gaboon”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— It ranges from southern Cameroon to Angola, Republic of Congo and Democratic Republic of Congo, including Central African Republic. In Equatorial Guinea, it has been recorded from Río Muni (Boulenger 1900) (Map 18B).

COMMENTS.— Since Boulenger (1900) no specimens of this species have been recorded.

SPECIMENS EXAMINED.— No specimens of this taxon were found in the collections examined by us in this study.

***Hyperolius tuberculatus* (Mocquard, 1897)**

Photo figures 17E–G

TYPE LOCALITY.— “Lambaréné”, Gabon.

DISTRIBUTION.— This species extends over rainforests from southeastern Nigeria to western Central African Republic, and southwards to Republic of Congo and Democratic Republic of Congo. In Equatorial Guinea, it has been recorded from both Río Muni (De la Riva 1994; Bell et al. 2017) and Bioko (Bell et al. 2017) (Map 18C).

COMMENTS.— Mertens (1965) cited *Hyperolius concolor* (Hallowell, 1844) on Bioko (Moca lake surroundings) but this record likely represents a misidentification with *H. tuberculatus*, which has a similar dorsal pattern at juvenile stages, and it is a very common species around that locality (surprisingly, no records of *H. tuberculatus* were provided by Mertens [1965]). Thus, we exclude *H. concolor*—a species distributed from Sierra Leona to western Cameroon—from the amphibian list of Equatorial Guinea. Phylogeographic patterns of this species were studied by Bell et al. (2017). Descriptions of the advertisement calls from Monte Alén were provided by Bosch et al. (2000).

SPECIMENS EXAMINED.— Twenty-two specimens. Asonga (Bata-Niefang), 12 October 1984 (EBD 18256–18260), 09 October 1984 (EBD 18261–18263), 24 April 1985 (EBD: 21006–21007); Engong (Aconibe-Asoc), 01 May 1987 (EBD 25072); Ayamiken, San Joaquín de Ndyiacom, 1990 (11 specimens, without individual voucher numbers, EBD 31516).

***Opisthoxylax* Perret, 1966**

***Opisthoxylax immaculatus* (Boulenger, 1903)**

TYPE LOCALITY.— “Cap Saint-Jean”, Cabo San Juan, Río Muni, Equatorial Guinea.

DISTRIBUTION.— This species ranges from Nigeria to Gabon, Democratic Republic of Congo and Republic of Congo. In Equatorial Guinea, it was recorded in Río Muni by Boulenger (1903), at the type locality (Map 19A).

COMMENTS.— We provide the first record of the genus *Opisthoxylax* on Bioko although Portik et al. (2019) sequenced a specimen they listed as coming from Bioko in their online Supplemental Table 1 to their paper (said to be accessible but not verified by us [IDLR]).

SPECIMENS EXAMINED.— Pico Basilé, Bioko, 01 February 1933 (MNCN 3915).

Phlyctimantis* Laurent and Combaz, 1950**Phlyctimantis* cf. *leonardi* (Boulenger, 1906)****Photo figures 18A–B**

TYPE LOCALITY.—“Punta Frailes, Fernando Po”, Bioko, Equatorial Guinea and “N’Djolè, French Congo” Ndjolé, Gabon. Capocaccia (1957) restricted the type locality by lectotype designation to “N’Djolè”, Gabon.

DISTRIBUTION.— This species is distributed from Cameroon to Gabon, Republic of Congo and Democratic Republic of Congo. In Equatorial Guinea, it has been cited in Río Muni, over the coast of Bome, and Monte Alén (De la Riva 1994), and on Bioko at Punta Europa (= Punta Frailes) (Boulenger 1906a) (Map 19B).

COMMENTS.— There is a second described species of *Phlyctimantis* inhabiting west-central Africa, namely *Phlyctimantis boulengeri* Perret, 1986 (Type locality: “Fainchang, région de Mamfe, Cameroon occidental”), considered as a subspecies of *P. leonardi* by some authors (Amiet 2012; Amiet and Goutte 2017). The identity of several populations from west and central-western Africa remains problematic (Amiet 2007; Köhler et al. 2005). Although there are records identified as *P. leonardi* from Bioko and Río Muni, the taxonomic allocation of both mainland and insular populations needs to be revised. Köhler et al. (2005) suggested that several populations from Cameroon, Gabon, Equatorial Guinea and Democratic Republic of Congo probably belong to *P. boulengeri*. Bosch et al. (2000) provided a call spectrogram of putative *Phlyctimantis leonardi* from Bome, Río Muni, which are highly similar to those of *P. boulengeri* from Barrage de Tchimbélé, Gabon (Köhler et al. 2005). However, both species names (*P. boulengeri* and *P. leonardi*) are likely representing still more undescribed species (Köhler et al. 2005; Amiet 2007; Onadeko and Rödel 2009). The specimen in the EBD collection came from Bata region, Río Muni, and morphologically resembles *P. leonardi*. Thus, we tentatively keep the populations from Equatorial Guinea as *P. cf. leonardi* until more studies help to clarify these questions.

SPECIMENS EXAMINED.— Asonga, Bata, 1984 (EBD 18254).

Petropedetidae Noble, 1931***Petropedetes* Reichenow, 1874*****Petropedetes cameronensis* Reichenow, 1874**

TYPE LOCALITY.— “Gebirgsbach bei Bimbia, in den Vorbergen des Camerun”, Limbé, Cameroon.

DISTRIBUTION.— It ranges from southeastern Nigeria to southwestern Cameroon, including Bioko, the only place in Equatorial Guinea where it has been recorded, at Musola (Boulenger 1906a) (Map 19C).

SPECIMENS EXAMINED.— No specimens were found at the collections examined by us in this study.

Petropedetes newtonii* (Bocage, 1895)*Photo figures 19A–B**

TYPE LOCALITY.— Restricted by Neotype designation at “Chopepe creek at its confluence with Río Osa (03°14'52.19"N, 08°32'23.77"E, 27 m a.s.l.), Bioko, Equatorial Guinea” (Sánchez-Vialas et al. 2018). Lost holotype from “L’île de Fernão do Po dans le golfe de Guiné” (Bocage, 1895c).

DISTRIBUTION.— This species occurs in both provinces of Bioko (Bioko Norte and Bioko Sur) and in the southern coast of Cameroon (Bakingili and Mt. Etinde region) (Sánchez-Vialas et al. 2018) (Map 20A).

COMMENTS.— The taxonomical problems relating to the identity of this taxon were discussed by Sánchez-Vialas et al. (2018).

SPECIMENS EXAMINED.— Twelve specimens. Campamento Smith, Río Tudela, close to Caldera de Luba, Bioko, 07 March 2007 (MNCN 46703); Campamento UPM-Río Riaco, Caldera de Luba, Bioko, 10 March 2007 (MNCN 46708); Río Riaco, Caldera de Luba, Bioko, 15 March 2007 (MNCN 46719); Cho pepe creek on its confluence with Río Osa, Bioko, 3°14'52.19"N, 8°32'23.77"E, 22 November 2003 (MNCN 48728); Río Sibatá, Bococo Avendaño, Bioko, 3°26'46.04"N, 8°26'52.39"E (MNCN 48729); Afluent of Río Olé, on track to Caldera de Luba, Bioko, 3°18'27.08"N 8°28'24.36"E, 25 November 2003 (MNCN 48730); Río Olé, on the way to Caldera de Luba, Bioko, 3°18'27.08"N 8°28'24.36"E, 25 November 2003 (MNCN 48955); Cho pepe creek on its confluence with Río Osa, Bioko, 3°14'52.19"N, 8°32'23.77"E, 25 November 2003 (MNCN 48956); Río Sibatá, Bococo Avendaño, Bioko, 3°26'46.04"N, 8°26'52.39"E, 03 December 2003 (MNCN 48957); Cho pepe creek on its confluence with Río Osa, Bioko, 3°14'52.19"N, 8°32'23.77"E, 22 November 2003 (MNCN 48958–48959); BBPP camp, Caldera de Luba, Bioko, 3°20'47.32"N, 8°29'48.44"E, 26 November 2003 (MNCN 48960).

***Petropedetes palmipes* Boulenger, 1905**

Photo figures 19C–F

TYPE LOCALITY.— “Efulen, South Cameroon”.

DISTRIBUTION.— This species ranges from Cameroon to northwestern Gabon. In Equatorial Guinea, it has been recorded from Monte Alén, along the Laña and Bilene rivers (De la Riva 1994) (Map 20B).

SPECIMENS EXAMINED.— No specimens of this species were found in the collections examined by us in this study.

***Petropedetes parkeri* Amiet, 1983**

Photo figures 20A–C

TYPE LOCALITY.— “Atolo (region de Mamfe)”, Cameroon.

DISTRIBUTION.— It ranges from eastern Nigeria to Equatorial Guinea, where it has been recorded by De la Riva (1994) in Engong, Monte Alén, Río Muni. There are no records from Bioko (Map 20C).

SPECIMENS EXAMINED.— One specimen. Evinayong, Río Muni (EBD 18252).

***Petropedetes vulpiae* Barej, Rödel, Gonwouo, Pauwels, Böhme, and Schmitz, 2010**

Photo figures 20D–E

TYPE LOCALITY.— “Cameroon, Mt. Nlonako, Ekomtolo, 4°51'N, 9°54'E, app. 450 m a.s.l.”

DISTRIBUTION.— This species ranges from eastern Nigeria to Southern Gabon. In Equatorial Guinea, *P. vulpiae* has been recorded (considered as *P. newtonii*) in two localities from Monte Alén (De la Riva 1994) (Map 21A).

COMMENTS.— Taxonomical problems relating to this and other taxa such as *P. johnstoni* and *P. newtonii* were discussed by Barej et al. (2010; 2014) and Sánchez-Vialas et al. (2018).

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us.

Phrynobatrachidae Laurent, 1941

***Phrynobatrachus* Günther, 1862**

***Phrynobatrachus africanus* (Hallowell, 1858)**

Photo figures 21A–C

TYPE LOCALITY.— “Gaboon”.

DISTRIBUTION.— *Phrynobatrachus africanus* ranges from Cameroon to southern Gabon and eastwards to Central African Republic, Republic of Congo and Democratic Republic of Congo. In Equatorial Guinea, this species is found both on Bioko (Böhme 1994; Zimkus 2009) and in Río Muni (Boulenger 1900, 1903; De la Riva 1994) (Map 21B).

COMMENTS.— This species was previously considered under the nominotypic genus *Dimorphognathus*, currently a synonym of *Phrynobatrachus* (Scott 2005). Márquez et al. (2000) described the calls for Río Muni populations.

SPECIMENS EXAMINED.— Ten specimens. Centro-Sur, Patio Alosa, Niefang, 1985 (EBD 21024, EBD 21035, EBD 21045); Miboman, Bata, Litoral, April 1988 (EBD 28086); Ayamiken (San Joaquín de Ndyiacom) (B9806–9808, B9810); San Joaquín de Ndyiacomm (B9809); Cabo San Juan, Río Muni, 18 September 1901 (MNCN 3993).

***Phrynobatrachus auritus* Boulenger, 1900**

Photo figures 21D–G

TYPE LOCALITY.— “Benito River”, Río Muni, Equatorial Guinea.

DISTRIBUTION.— This species is distributed from Nigeria and Cameroon to Gabon, and eastwards to Rwanda and western Uganda. In Equatorial Guinea, it has been recorded both from Río Muni (Boulenger 1900; De la Riva 1994) and Bioko (Bocage 1895a; Boulenger 1903, 1906a; Mertens 1941, 1965; Zimkus 2009; Zimkus et al. 2010; Taboue and Fokam 2016; Hydeman et al. 2017) (Map 21C).

COMMENTS.— This species seems to be abundant throughout Equatorial Guinea. Populations from Bioko are placed within the same clade of Cameroonian populations (Zimkus et al. 2010). The taxonomic status of *P. auritus* has been problematic (see Lamotte and Xavier 1966) due to Boulenger’s (1903) synonymization of it with *P. plicatus* (Günther, 1858), which is its vicariant sister species from West Africa. The identity of *P. auritus* as a full species and its relationships with *P. plicatus* have been studied using molecular data by Zimkus et al (2010). Márquez et al. (2000) described the calls for Río Muni populations.

SPECIMENS EXAMINED.— Eighty-three specimens. Miboman, Km 27 Bata-Movo (EBD 18294–18315); Noayong (Evinayong-Aconibe), 16 April 1987 (EBD 25043); Alosa, Niefang (EBD 21032, 21042, 21036–21037, EBD 21028, 21009, 21010, 21013); Ctra Bata-Movo, Km 27, 1984 (EBD 18629). Rebola, Bioko, 13 January 1933 (MNCN 3899); Cabo San Juan, Río Muni, 21 August (MNCN 3951–3992); Caldera de Luba, Bioko, 13 March 2007 (MNCN 46706, 46721); BBPP camp, Caldera de Luba, Bioko, 03°20′47.32″N, 08°29′48.44″E, 26 November 2003 (MNCN 48891–48894); Red swamp, Caldera de Luba, Bioko, 03°21′27.99″N, 08°30′52.11″E, 27 November 2003 (MNCN 48895–48899).

***Phrynobatrachus batesii* (Boulenger, 1906)**

TYPE LOCALITY.— “Efulen and ...Zima” Sangmelima, Cameroon.

DISTRIBUTION.— Recorded from Ghana, Nigeria, Gabon and Cameroon. In Equatorial Guinea, there is a doubtful record from Monte Mitra (Map 22A).

COMMENTS.— Gonwouo and Nsang (2005) provided the first record of this species for Equatorial Guinea, misspelled as “*Phrynobatrachus batesii*”. Surprisingly, there are no additional comments about the relevance of this record in their work, and we recommend that it be considered with caution until more evidence is provided. Dewynter and Frétey (2019) also include Equatorial Guinea in the distribution of the species, without more information.

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Phrynobatrachus calcaratus* (Peters, 1863)**

TYPE LOCALITY.— “Boutry”, Ghana.

DISTRIBUTION.— This species ranges from Senegal and Guinea to Cameroon, and eastward to Central African Republic. In Equatorial Guinea, this species was recorded on Bioko at Punta Frailes (= Punta Europa) by Boulenger (1906a) (Map 22B).

COMMENTS.— There are no additional records of this species from Bioko since Boulenger's (1906a) citation. This taxon represents a species complex (Zimkus et al. 2010).

SPECIMENS EXAMINED.— No specimens were found in the collections examined by us in this study.

***Phrynobatrachus cornutus* (Boulenger, 1906)**

TYPE LOCALITY.— “Zima” (= Sangmelima), Cameroon.

DISTRIBUTION.— *Phrynobatrachus cornutus* is distributed from Cameroon to western Republic of Congo, Gabon and Central African Republic. In Equatorial Guinea, it has been recorded from Río Muni at Monte Alén (as *Phrynobatrachus* sp. of the *P. cornutus* group; De la Riva 1994) and from Bioko at several localities (Mertens 1965; Zimkus 2009; Hydeman et al. 2017) (Map 22C).

COMMENTS.— There is no deep phylogeographic structure between Bioko and Cameroonian populations, which are part of the same lineage (authors' unpublished data). The populations reported from Río Muni are morphologically similar to *P. mayokoensis* (authors' pers. obs.), but additional studies are needed to confirm its systematic relationships and taxonomic identity.

SPECIMENS EXAMINED.— Six specimens. Forest close to Illadji River, Bioko, 03°19'46.04"N, 08°40'26.13"E, 14 November 2003 (MNCN 48885–48887); Rio Lukuele, on the way from Belebu to Ureka, Bioko, 03°24'25.81"N, 08°33'3.23"E, 20 November 2003 (MNCN 48888); casa Moraka, 9 km west of Ureka, Bioko, 03°15'33.05"N, 08°29'11.18"E, 24 November 2003 (MNCN 48889); path behind church, Bakelele forest, Batete, Bioko, 03°26'37.34"N, 08°30'24.76"E, 02 December 2003 (MNCN 48890).

***Phrynobatrachus sandersoni* (Parker, 1935)**

Photo figure 21H

TYPE LOCALITY.— “5 miles inland from Kribi, S. Cameroon”.

DISTRIBUTION.— This species is present in southwestern Cameroon and in Equatorial Guinea, where it has been recorded at Monte Alén by De la Riva (1994) (as *Phrynodon sandersoni*). There are no records of this species from Bioko (Map 23A).

COMMENTS.— This species was erroneously cited by Mertens (1968) from Bioko based on four specimens misidentified as *P. africanus* and subsequently deleted from the faunal list of Bioko by Böhme (1994).

SPECIMENS EXAMINED.— No specimens of this species were found in the collections examined by us in this study.

Pipidae Gray, 1825

***Hymenochirus* Boulenger, 1896**

***Hymenochirus boettgeri* (Tornier, 1886)**

Hymenochirus boettgeri camerunensis Perret and Mertens, 1957

TYPE LOCALITY.— “Foulassi”, 6 km northwest of Sangmelima, Cameroon.

DISTRIBUTION.— This species is known from southern Cameroon at Foulassi, Bibundi, Nkongsamba (Perret and Mertens 1957) and Kribi (Noble 1924), Republic Democratic of Congo at Bonguma (Perret 1966) and Equatorial Guinea, where it has been recorded in Benito (= Uoro) River (Boulenger 1899b) and in Monte Alén (Lasso et al. 2002) (Map 23B).

COMMENTS.— In spite of the low current taxonomic diversity of the genus, formed by only four species, the phylogenetic relationships between them remain unknown. A comprehensive systematic and taxonomic work on this genus is needed and should incorporate molecular data, including samples from the type locality of each species. Currently, there are two subspecies of *H. boettgeri*: *H. b. boettgeri*, widespread from north-central and eastern Cameroon to northeastern

Republic Democratic of Congo, and *H. b. camerunensis* Perret and Mertens, 1957, that occurs from southern Cameroon to the lowlands of the Congo Basin.

SPECIMENS EXAMINED.— Six specimens. Miboman, Bata, 01 September 1984 (EBD 18325, 18335); Río Bizingui, 1986 (EBD 25039); Miboman, Bata, Movo (EBD 18305); Arroyo Lobo, Poblado de Muga, Mirador de Moka, Monte Alén, 20 August 2001 (MNCN 46335); Poblado de Muga, Mirador de Moka, Monte Alén, 22 August 2001 (MNCN 46339).

***Xenopus* Wagler, 1827**

***Xenopus allofraseri* Evans, Carter, Greenbaum, Gvoždík, Kelley, McLaughlin, Pauwels, Portik, Stanley, Tinsley, Tobias, and Blackburn, 2015**

TYPE LOCALITY.— “Republic of Equatorial Guinea, Bioko Island, Bioko Sur Province, Arena Blanca road, N 3.5275°, E 8.5793°, ~30 m”.

DISTRIBUTION.— This species is known from Bioko (Arena Blanca and Comedor), coastal Cameroon and the Democratic Republic of Congo (Evans et al. 2015). The record of Boulenger (1906a) from “Punta Frailes, Musola” is herein considered *X. allofraseri* (Map 23C).

COMMENTS.— This species belongs to the subgenus *Xenopus*. Parker (1936) had allocated Boulenger’s (1906a) specimen to the taxon *X. fraseri*, whereas we refer it to *X. allofraseri*.

SPECIMENS EXAMINED.— Eight specimens. In a pond along the path from Belebu to Ureka, Bioko, 03°24′25.81″N, 08°33′3.23″E, 19 November 2003 (MNCN 48900–48907).

***Xenopus calcaratus* Peters, 1875**

TYPE LOCALITY.— “Cameruns (Victoria)”, Limbe, Southwest Province, Republic of Cameroon.

DISTRIBUTION.— *Xenopus calcaratus* is distributed in the lowlands of Bioko and in the coastal region of Limbe, Cameroon. In Equatorial Guinea, this species is only present on Bioko, where it inhabits the low elevations at Punta Europa (Boulenger 1906a), Basupú and Arena Blanca (Evans et al. 2015) (Map 24A).

COMMENTS.— This species belongs to the subgenus *Silurana*. The record of *X. calcaratus* provided by Boulenger (1900) from “Benito River”, Río Muni, is herein allocated in the taxon *X. (Silurana) mellotropicalis* (see the respective comments in its species account) and, in a similar way, the record of Boulenger (1903) of *X. calcaratus* of “Cap Saint-Jean” (=Cabo San Juan), Río Muni, is herein considered as *X. parafraseri*, based on the description of the coloration pattern of the examined specimens (Boulenger 1903) and in the extended revision of the genus by Evans et al. (2015).

SPECIMENS EXAMINED.— No specimens of the subgenus *Silurana* from Equatorial Guinea were found in the collections examined by us in this study.

***Xenopus mellotropicalis* Evans, Carter, Greenbaum, Gvoždík, Kelley, McLaughlin, Pauwels, Portik, Stanley, Tinsley, Tobias, and Blackburn, 2015**

TYPE LOCALITY.— “Gabonese Republic, Estuaire Province, Monts de Cristal National Park, Kinguele, N 0.4536°, E 10.2781°, 75 m”.

DISTRIBUTION.— *Xenopus mellotropicalis* occurs in disturbed and forested areas from Cameroon to Gabon, Republic of Congo and Democratic Republic of Congo. In Equatorial Guinea, this species has been cited in Río Muni by Boulenger (1900) as *X. calcaratus* (see comments below) (Map 24B).

COMMENTS.— This species belongs to the subgenus *Silurana*. Boulenger (1900) cited *X. calcaratus* based on a specimen (prepared as a skeleton) from Río Muni (Benito River), in which he

noted the fusion of the two first presacral vertebrae, a diagnostic character of the subgenus *Silurana* (see Evans et al. 2015). However, *Xenopus (Silurana) calcaratus* is only known from Bioko and the coastal region of Limbe, Cameroon, and does not reach the coastal area between southern Cameroon and Gabon. Based on its distribution and the revision provided by Evans et al. (2015), Boulenger's specimen is herein regarded as *X. (Silurana) mellotropicalis*.

SPECIMENS EXAMINED.— No specimens of the subgenus *Silurana* from Equatorial Guinea were found in the collections examined by us in this study.

***Xenopus parafraseri* Evans, Carter, Greenbaum, Gvoždík, Kelley, McLaughlin, Pauwels, Portik, Stanley, Tinsley, Tobias, and Blackburn, 2015** **Photo figures 22A–B**

TYPE LOCALITY.— “Republic of Cameroon, Centre Region, Mfoundi Department, Old Douala Road, N 3.7931°, E 11.4170°, 715 m”.

DISTRIBUTION.— This species is found in Southern Cameroon, central and eastern Gabon, and north-western Republic of Congo, where it inhabits pools in agricultural landscapes and pristine forest. In Equatorial Guinea, it has been recorded as *Xenopus calcaratus* from Cabo San Juan (Boulenger 1903) and as *X. fraseri* for specimens from Monte Alén (De la Riva 1994; Lasso et al. 2002) (Map 24C).

COMMENTS.— This species belongs to the subgenus *Xenopus*. We adscribe the records of *Xenopus* of Equatorial Guinea provided by Boulenger (1903), De la Riva (1994) and Lasso et al. (2002) to this recently described taxon, *X. parafraseri*. The records provided herein, based on collection specimens, suggest that it is widespread within Río Muni.

SPECIMENS EXAMINED.— Twentyseven specimens. Nsork, Wele-Nzas, January 1986 (EBD 25041); Añisoc, Bata, 1986 (EBD 24984–24986); Miboman, 1984 (EBD 18272, 18275, 18278); Miboman, Bata (EBD 18711); Oveng-Akurenam (EBD 18453–18458); Akurenam (5 specimens with a single label: EBD 27833); San Joaquín de Ndyiacom (4 specimens with a single label EBD 31490); Asonga, Bata (EBD 18255).

Ptychadenidae Dubois, 1987

***Ptychadena* Boulenger, 1917**

***Ptychadena aequiplicata* (Werner, 1898)** **Photo figures 22C–D**

TYPE LOCALITY.— “Kamerun (Victoria und Buca)” Limbé and Buea, Cameroon.

DISTRIBUTION.— This species occurs across the rainforests of southern Guinea, Ivory Coast, eastern Liberia, and southwards to Central African Republic and western Democratic Republic of Congo. In Equatorial Guinea, it has been recorded both in Río Muni, at Cabo San Juan (Boulenger 1903), Benito River (Boulenger 1900), Monte Alén region (De la Riva 1994) and Bioko, at Basupú (Bocage 1895a) (Map 25A).

COMMENTS.— Two records of *Ptychadena mascareniensis* (Duméril and Bibron, 1841) deserve some comments. The first one, from Cabo San Juan (Río Muni) was provided by Boulenger (1903), and the second one (misspelled as “*P. mascaraniensis*”) by Gonwouo and Nsang (2005) for the region of Monte Mitra, in Monte Alén National Park. However, due to the lack of reliable records and the morphological similarity with *P. aequiplicata* (a very common species in Cabo San Juan and in Monte Alén National Park), we herein consider these records as *P. aequiplicata*.

SPECIMENS EXAMINED.— Eighty-five specimens. Bata (N°02681); Miboman (EBD 18277–18278); Miboman, Km 27 Ctra Bata-Niefang, December 1987 (EBD 27881), April 1988 (EBD 27882–27890, EBD 27892–27894, EBD 27896), October 1987 (EBD 27891, EBD 27895, EBD

27897, EBD 27865–27872, 27874–27879), April 1988 (EBD 27873, EBD 27880); Noayong (Evinayong-Aconibe), 19 April 1987 (EBD 25046); Asonga-Bata, 24 July 1984 (EBD 18615); Akurenam, 24/27/28/29 August 1984 (EBD 18395–18405, EBD 18433–18436, EBD 18438–18439, EBD 18463), 24 August 1984 (EBD 18446); Río Muni (17 specimens with a single label EBD 20995); San Joaquín de Ndyiacom (7 specimens with a single label EBD 31517); Evinayong, Bata (EBD 18265–18271); Cabo San Juan, Río Muni, August/September 1901 (MNCN 3865–3871); Cabo San Juan, Río Muni, 15 September 1901 (MNCN 3876); Lago de Monte Alén, 22 August 2001 (MNCN 46337).

Pyxicephalidae Bonaparte, 1850

Aubria Boulenger, 1917

Aubria subsigillata (Duméril, 1856)

TYPE LOCALITY.— Gabon.

DISTRIBUTION.— This species is distributed in rainforests from southern Guinea and northern Liberia to Gabon. In Equatorial Guinea, it has been recorded from Río Muni at Cabo San Juan (Boulenger 1903) and Benito River (Boulenger 1900). There is also a record of this species from Bioko based on the specimen CAS 207956, tentatively identified by Drewes et al. (1999) (Map 25B).

COMMENTS.— The specimens examined from Equatorial Guinea correspond to the long-legged form with the femoral glands half-way between knee and vent. These features correspond to *A. subsigillata* as stated by Ohler (1996), who also proved that *A. occidentalis* Perret, 1964, is a junior synonym and that the short-legged form with femoral glands closer to knees should be considered as *A. masako* Ohler and Kazadi, 1990. Rödel et al. (2005) provided a summary of the taxonomic history of *A. masako* and *A. subsigillata*, and suggested that the later might comprise more than one species. Members of this genus (currently comprising two morphologically distinct species, *A. subsigillata* and *A. masako*) present a remarkable sexual dimorphism in which the secondary sexual characters characterize females (see Perret 1994): femoral glands are best developed in females, while they are smaller or absent in males. Drewes et al. (1999) suggest the possible presence of this species on Bioko based on a tentative identification of a single specimen, that is yet unconfirmed.

SPECIMENS EXAMINED.— Six specimens. Bata, Río Muni, 1966 (N° 2694–2697); without data (B8715); Cabo San Juan, Río Muni (MNCN 3872).

Ranidae Batsch, 1796

Amnirana Dubois, 1992

Amnirana albolabris (Hallowell, 1856)

Photo figure 23A

TYPE LOCALITY.— “West Africa”. Perret (1977) restricted the type locality to “Gabon” and Jongsma et al. (2018) deduced that it is “north of the Ogooué River in Gabon”.

DISTRIBUTION.— This species is widespread across lowland rainforests of Gabon, Equatorial Guinea, Cameroon, Democratic Republic of Congo, Republic of Congo, Central African Republic and Uganda, also reaching northern Angola (*vide* Marques et al. 2018). In Equatorial Guinea, it occurs in Río Muni, where it has been recorded from Cabo San Juan and Monte Alén (Boulenger 1903; De la Riva 1994). Published records from Bioko are at Musola, San Carlos de Luba region, Ureca, and Basupu (Boulenger 1900, 1906a; Mertens 1965; Hydeman et al. 2017) (Map 25C).

COMMENTS.— *Amnirana albolabris* is a polyphyletic taxon that contains several undescribed species (Jongsma et al. 2018). Populations from Bioko form part of an undescribed species close-

ly related to the nominotypic *A. albolabris*, which is present in Río Muni (Jongsma et al. 2018). The undescribed species from Bioko is also recorded from the coast of Cameroon (Jongsma et al. 2018); a similar distribution pattern is shown by *Petropedetes newtonii* (Sánchez-Vialas et al. 2018).

SPECIMENS EXAMINED.—Ninety specimens. Ayamiken (San Joaquín de Ndyiacom), Litoral, 1990 (EBD 31488); Bata, Litoral, 22 July 1987 (EBD 25040); Mbini-Bata, Carut, Litoral 21 October 1986 (EBD 21014, 21027); Miboman, Bata, Litoral, December 1987 (EBD 28111, EBD 28082–28083), (EBD 18290, EBD 18292–18293); Miboman, Km 27 Bata – Movo (EBD 18707–18709); Ela Nguema, Bioko Norte, 20 September 1984 (EBD 18661); Bolondo, 21 June 1984 (EBD 18624–18625, EBD 18627–18628, EBD 18630–18632); Centro Sur (Evinayong), Akurenan, 24 August 1984 (EBD 18450–18452, EBD 18456–18462, EBD 18440–18445, EBD 18447–18449, EBD 18411–18431, EBD 18402); Ayamiken (San Joaquín de Ndyiacom), December 1987 (EBD 28085), without date (EBD 23078, EBD 31518); [Río Muni] (EBD 27850, 27852, 27853, 27854, 27855, 27856, 27857, 27859, 27860, 27862, 27863, 27864); Aconibe, 1 May 1987 (EBD, no label found); Basilé, Bioko, 01 February 1933 (MNCN 3916–3917); Concepción (=Riaba), Bioko Sur, 21 February 1933 (MNCN 4073–4075); Sosolo pond, Bioko, 03°14'44.83"N, 08°34'54.67"E 21 November 2003 (MNCN 48912–48913); River mouth of Baka, Bioko, 03°14'44.83"N, 08°34'54.67"E, 21 November 2003 (MNCN 48914–48919); River mouth of Fola, Bioko, 03°14'44.13"N, 08°34'41.58"E, 21 November 2003 (MNCN 48920); Río Osa, Bioko, 03°14'52.19"N, 08°32'23.77"E, 22 November 2003 (MNCN 48921); Río Rocrim Bococo Aven-daño, Bioko, 03°26'46.04"N, 08°26'52.39"E, 03 December 2003 (MNCN 48922).

***Amnirana amnicola* (Perret, 1977)**

Photo figure 23B

TYPE LOCALITY.—“Ilanga, Eséka, Cameroun meridional”

DISTRIBUTION.—This species ranges from Cameroon to Republic of Congo. In Equatorial Guinea, it has been cited from Monte Alén, Río Muni (De la Riva 1994). An additional record is herein provided from Río Muni (Miboman) (Map 26A).

SPECIMENS EXAMINED.—Four specimens. Miboman, Litoral, 01 September 1984 (EBD 18287); Miboman, Litoral, Bata, April 1988 (EBD 28076, EBD 28074); Equatorial Guinea, without data (B9126).

***Amnirana lepus* (Andersson, 1903)**

Photo figure 23C

TYPE LOCALITY.—“Kamerun”.

DISTRIBUTION.—*Amnirana lepus* is distributed from Cameroon through Gabon to western of Democratic Republic of Congo and northwestern Angola. In Equatorial Guinea, there are records from Monte Alén, Río Muni (De la Riva 1994) (Map 26B).

SPECIMENS EXAMINED.—Eight specimens. Etom, Evinayong-Mongomo (EBD 27497); Miboman, Km 27 Ctra Bata-Movo, 02 June 1985 (EBD 21000); Miboman, Km 27, Ctra Bata-Niefang, October 1987 (EBD 28087); Ayene-Akuvene. Cercanías de la cascada Nguelenso, 13 July 1985 (EBD 21001); Equatorial Guinea, without data (B8429–8430); Noayong, Evinayong, Aconibe, 1987 (EBD 25048–25049).

Rhacophoridae Hoffman, 1932 (1958)

***Chiromantis* Peters, 1854**

***Chiromantis rufescens* (Günther, 1869)**

Photo figures 24A–B

TYPE LOCALITY.—“West Africa”.

DISTRIBUTION.— This species presents a wide distribution from Sierra Leone and Liberia to Uganda, and southwards to Democratic Republic of Congo. In Equatorial Guinea, it is known from Río Muni at Monte Alén (De la Riva 1994) and Bioko at Luba (Boulenger 1906a). We provide additional records from Río Muni and Bioko (Map 26C).

COMMENTS.— Márquez et al. (2000) described the calls for Río Muni populations, whereas Leaché et al. (2019) studied the phylogenetic diversification of this widely distributed rain forest species.

SPECIMENS EXAMINED.— Five specimens. Miboman, Litoral, 01 September 1984 (EBD 18288), April 1988 (EBD 27827–27830); BBPP camp, Caldera de Luba, Bioko, 03°20'47.32"N, 08°29'48.44"E, 28 November 2003 (MNCN 48908); path behind church, Bakelele forest, Batete, Bioko, 03°26'37.34"N, 08°30'24.76"E, 02 December 2003 (MNCN 48909–48911).

Order Gymnophiona Dermophiidae Taylor, 1969

Geotrypetes Peters, 1880

Geotrypetes seraphini (Duméril, 1859)

TYPE LOCALITY.— “Gabon”.

DISTRIBUTION.— This species ranges over Sierra Leone, Liberia, Guinea, and Ivory Coast to Ghana, Nigeria and Cameroon, expanding southwards to Gabon, Republic of Congo and Democratic Republic of Congo. In Equatorial Guinea, it has been recorded from Río Muni at Monte Alén National Park (Lasso et al. 2002). There is a dubious record from Bioko (see comments) (Map 28A).

COMMENTS.— The reliability of some records of caecilians from Equatorial Guinea has been highly problematic (Nussbaum and Pfrender 1998). The record of *G. seraphini* from Bioko is based on a single specimen, the holotype of *Schistometopum garzonheydti* Taylor and Salvador, 1978. This taxon was synonymized with *G. seraphini* by Nussbaum and Pfrender (1998), who suggested that the presence of this species on Bioko is dubious as the locality may be in error. Thus, these authors suggest removing the taxon *Geotripetes seraphini* from the faunal list of Bioko until additional specimens are found. We follow the suggestion provided by Nussbaum and Pfrender (1998) of not considering the species as part of the fauna of the island.

SPECIMENS EXAMINED.— One specimen [the following locality of the label may be in error]: Fernando Poo (=Bioko), <1885 (MNCN 1239); holotype of *Schistometopum garzonheydti* Taylor and Salvador, 1978 (synonym of *Geotrypetes seraphini*).

Herpelidae Laurent, 1984

Herpele Peters, 1880

Herpele squalostoma (Stutchbury, 1836)

TYPE LOCALITY.— “Gaboos, Africa”.

DISTRIBUTION.— This species is distributed from Nigeria to eastern of Central African Republic and southwards to Democratic Republic of Congo. In Equatorial Guinea, it has been recorded from Bioko (Martínez and Sáez 1886; Mertens 1941, 1965), and Río Muni (Nussbaum and Pfrender 1998; Lasso et al. 2002) (Map 28B). Furthermore, Taylor and Salvador (1978) mentioned the species on Elobey Island.

COMMENTS.— In a similar way to the argument presented about the reliability of the *Geotrypetes seraphini* record from Bioko, Nussbaum and Pfrender (1998) raised the question of

whether the locality of the specimen MNCN 1232 (collected from Bioko by Amado Osorio in 1865; see Bueno and Blanco 2002) is reliable. Even if the locality of this specimen represents a cataloguing error, there is another record of this species from the island between Musola and San Carlos (Mertens 1941, 1965). Wilkinson et al. (2003) provided a revision of the genus.

SPECIMENS EXAMINED.— Three specimens. Equatorial Guinea, Fernando Poo (=Bioko), <1885 (MNCN 1232); Equatorial Guinea, Río Muni <1885 (MNCN 1238); Bata, Litoral, <1885 (MNCN 1741).

ACKNOWLEDGMENTS

We are indebted to Victoria González Cascón, of Laboratorio de Biogeografía Informática of the Museo Nacional de Ciencias Naturales, who made the species distribution maps. We give thanks to María Tirante, who kindly made available the vertebrate collection facilities of Estación Biológica de Doñana, Sevilla. We are also grateful to Ignacio Martín and Twan Leenders, for kindly providing some pictures of amphibians from Equatorial Guinea. Mary Gonder, Patrick McLaughlin, and Jessica Weinberg, from the Bioko Biodiversity Protection Program; Rayna Bell, from the California Academy of Sciences; and Bryan Stuart, from the North Carolina Museum of Natural Sciences, helped us with information on new records and photographs. This paper was partially funded by projects CGL2014-56160-P and PGC2018-097421-B-100 of the Spanish Government (PI: I. De la Riva). The authors wish to express their appreciation to Dr. Aaron Bauer, who reviewed the paper and offered many suggestions and grammatical edits for its improvement, as did Dr. Rayna Bell, and to Dr. Alan Leviton for his invaluable editorial advice.

BIBLIOGRAPHY

- AHL, E. 1929. Zur Kenntnis der afrikanischen Baumfrosch-Gattung *Leptopelis*. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 1929:185–222.
- AMIET, J.L. 2007. Les *Phlyctimantis* et *Kassina* du Cameroun (Amphibia, Anura, Hyperoliidae). *Revue Suisse de Zoologie* 114:87–126.
- AMIET, J.L. 2012. *Les Rainettes du Cameroun (Amphibiens Anoures)*. Saint-Nazaire, France, La Nef des Livres. 591 pp.
- AMIET, J.L., AND S. GOUTTE. 2017. *Chants d'Amphibiens du Cameroun*. J.L. Amiet and éditions Petit Genie. 280 pp + 4 CD. Saint-Nazaire, France.
- BAREJ, M.F., M.-O. RÖDEL, L.N. GONWOUO, O.S.G. PAUWELS, W. BÖHME, AND A. SCHMITZ. 2010. Review of the genus *Petropedetes* Reichenow, 1874 in Central Africa with the description of three new species (Amphibia: Anura: Petropedetidae). *Zootaxa* 2340:1–49.
- BAREJ, M.F., A. SCHMITZ, M. MENEGON, A. HILLERS, H. HINKEL, W. BÖHME, AND M.-O. RÖDEL. 2011. Dusted off—the African *Amietophrynus superciliaris*-species complex of giant toads. *Zootaxa* 2722:1–32.
- BAREJ, M.F., M.-O. RÖDEL, S.P. LOADER, M. MENEGON, N.L. GONWOUO, J. PENNER, G. GVOŽDÍK, R. GÜNTHER, R.C. BELL, P. NAGEL, AND A. SCHMITZ. 2014. Light shines through the spindrift – phylogeny of African torrent frogs (Amphibia, Anura, Petropedetidae). *Molecular Phylogenetics and Evolution* 71:261–273.
- BELL, R.C., R.C. DREWES, A. CHANNING, V. GVOZDIK, J. KIELGAST, S. LÖTTERS, B.L. STUART, AND K.R. ZAMUDIO. 2015. Overseas dispersal of *Hyperolius* reed frogs from Central Africa to the oceanic islands of São Tome and Principe. *Journal of Biogeography* 42:65–75.
- BELL, R.C., J.L. PARRA, G. BADJEDJEA, M.F. BAREJ, D.C. BLACKBURN, M. BURGER, A. CHANNING, J.M. DEHLING, E. GREENBAUM, V. GVOŽDÍK, J. KIELGAST, C. KASUMBA, S. LÖTTERS, P.J. McLAUGHLIN, Z.T. NAGY, M.-O. RÖDEL, D.M. PORTIK, B.L. STUART, J. VANDERWAL, A.G. ZASSI-BOULOU, AND K.R. ZAMUDIO. 2017. Idiosyncratic responses to climate-driven forest fragmentation and marine incursions in reed frogs from Central Africa and the Gulf of Guinea Islands. *Molecular Ecology* 26:5223–5244.
- BELL, R.C., P.J. McLAUGHLIN, G.F.M. JONGSMA, D.C. BLACKBURN, AND B.L. STUART. 2019. Morphological and genetic variation of *Leptopelis brevirostris* encompasses the little-known treefrogs *Leptopelis*

- crystallinorum* from Gabon and *Leptopelis brevipes* from Bioko Island, Equatorial Guinea. *African Journal of Herpetology* 68(2):91–117.
- BLACKBURN, D.C. 2008. Biogeography and evolution of body size and life history of African frogs: phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. *Molecular Phylogenetics and Evolution* 49(3):806–826.
- BLACKBURN, D.C. 2010. A new squeaker frog (Arthroleptidae: *Arthroleptis*) from Bioko Island, Equatorial Guinea. *Herpetologica* 66(3):320–334.
- BLACKBURN, D.C., AND V. DROISSART. 2008. *Nectophryne batesii*: juvenile coloration. *Herpetological Review* 39:208–209.
- BLACKBURN, D.C., L.N. GONWOUO, R. ERNST, AND M.-O. RÖDEL. 2009. A new squeaker frog (Arthroleptidae: *Arthroleptis*) from the Cameroon Volcanic Line with redescription of *Arthroleptis adolfriederici* Nieden, 1911 “1910” and *A. variabilis* Matschie, 1893. *Breviora* 515:1–22.
- BOCAGE, J.V.B. 1895a. Reptiles et Batraciens nouveaux ou peu connus de Fernão do Pó. *Jornal de Ciências Matemáticas, Físicas e Naturais, Academia das Ciências de Lisboa*, ser 2, 4:16–20.
- BOCAGE, J.V.B. 1895b. Herpétologie de l’Angola et du Congo. Lisbonne: Ministère de la Marine et des Colonies.
- BOCAGE, J.V.B. 1895c. Sur un batracien nouveau de Fernão do Pó. *Jornal de Ciências Matemáticas, Físicas e Naturais, Academia das Ciências de Lisboa*, ser. 2, 3:270–272.
- BÖHME, W. 1994. A record of *Dimorphognathus africanus* from Bioko, Equatorial Guinea, and deletion of *Phrynodon sandersoni* from the faunal list of this island (Anura: Ranidae: Petropedetinae). *Bonner zoologische Beiträge* 45:125–128.
- BOSCH, J., I. DE LA RIVA, AND R. MÁRQUEZ. 2000. Advertisement calls of seven species of hyperoliid frogs, from Equatorial Guinea. *Amphibia-Reptilia* 21(2):246–255.
- BOULENGER, G.A. 1882. Catalogue of the Batrachia Saliéntia s. Ecaudata in the Collection of the British Museum. Second Edition. London: Taylor and Francis.
- BOULENGER, G.A. 1899a. Descriptions of new batrachians in the collection of the British Museum (Natural History). *Annals and Magazine of Natural History*, ser.7, 3:273–277.
- BOULENGER, G.A. 1899b. XI. On *Hymenochirus*, a new type of aglossal Batrachians. *Journal of Natural History*, 4(20):122–125.
- BOULENGER, G.A. 1900. A list of the batrachians and reptiles of the Gaboon (French Congo), with descriptions of new genera and species. *Proceedings of the Zoological Society of London* 1900:433–456.
- BOULENGER, G.A. 1903. Batraciens de la Guinée espagnole. *Memorias de la Real Sociedad Española de Historia Natural*, Madrid 1:61–64.
- BOULENGER, G.A. 1906a. Report on the reptiles collected by the late L. Fea in West Africa. *Annali del Museo Civico di Storia Naturale di Genova* 3(2):157–172.
- BOULENGER, G.A. 1906b. Descriptions of new batrachians discovered by Mr. G.L. Bates in South Cameroon. *Annals and Magazine of Natural History* 17(7):317–323.
- BUENO, A.G., AND A.G. BLANCO 2002. Los naturalistas españoles en el África hispana (1860–1936). Organismo Autónomo Parques Nacionales. Madrid.
- BURGER, M., O.S.G. PAUWELS, W.R. BRANCH, E. TOBI, AND J. YOGA. 2006. An assessment of the amphibian fauna of the Gamba Complex of Protected Areas, Gabon. *Bulletin of the Biological Society of Washington* 12:297–307.
- BUTYNSKI, T.M., AND S.H. KOSTER. 1994. Distribution and conservation status of primates in Bioko Island, Equatorial Guinea. *Biodiversity & Conservation* 3(9):893–909.
- CAPOCACCIA, L. 1957. Catalogo dei tipi di anfibi del Museo Civico di Storia Naturale di Genova. *Annali del Museo Civico di Storia Naturale di Genova* 69(3):208–222.
- CARLINO, P., AND O.S.G. PAUWELS. 2015. An updated reptile list of Ivindo National Park, the herpetofaunal hotspot of Gabon. *Bulletin of the Chicago Herpetological Society*, 503:25–39.
- CERIACO, L.M., M.P. MARQUES, AND A.M. BAUER. 2018. Miscellanea Herpetologica Sanctithomae, with a provisional checklist of the terrestrial herpetofauna of São Tomé, Príncipe and Annobon islands. *Zootaxa* 4387(1):91–108.
- CHARLES, K.L., R.C. BELL, D.C. BLACKBURN, M. BURGER, M.K. FUJITA, V. GVOŽDÍK, G.F.M. JONGSMA, M.T.

- KOUETE, A.D. LEACHÉ, AND D.M. PORTIK. 2018. Sky, sea, and forest islands: diversification in the African leaf-folding frog *Afraxalus paradorsalis* (Anura: Hyperoliidae) of the lower Guineo-Congolian rain forest. *Journal of Biogeography* 45:1781–1794.
- CHANNING, A., AND M.-O. RÖDEL. 2019. Field Guide to the Frogs & Other Amphibians of Africa. Cape Town, South Africa: Struik Nature. 408 pp.
- DE LA RIVA, I. 1994. Anfíbios anuros del Parque Nacional de Monte Alén, Río Muni, Guinea Ecuatorial. *Revista Española de Herpetología* 8:123–139.
- DE LA RIVA, I., J. BOSCH, AND R. MÁRQUEZ. 2001. Calls of three species of arthroleptid frogs from Río Muni, Equatorial Guinea. *African Zoology* 36(1):107–110.
- DEWYNTER, M., T. FRÉTEY, G.F.M. JONGSMA, A. BAMBA-KAYA, AND O.S.G. PAUWELS. 2018. L'herpétofaune du site Ramsar des Monts Birougou (Gabon): catalogue illustré des espèces. *Les cahiers de la fondation Biotope*, 18:1–50.
- DEWYNTER, M., AND T. FRÉTEY. 2019. Liste taxonomique commentée et catalogue illustré des Amphibiens du Gabon. *Les cahiers de la fondation Biotope* 27:1–84.
- DREWES, R.C., J.V. VINDUM, AND L. HENWOOD. 1999. Preliminary report on a survey of the herpetofauna of Bioko; Equatorial Guinea. Chapter 2, part II, pp. 58–61 in: B. Larison, T. B. Smith, D. Girman, D. Stauffer, B. Milá, R. C. Drewes, C. E. Griswold, J. V. Vindum, D. Ubick, K. O'Keefe, J. Nguema and L. Henwood, eds., *Biotic surveys of Bioko and Río Muni, Equatorial Guinea*. Technical Report submitted to Biodiversity Support Program.
- EVANS B.J., T.F. CARTER, E. GREENBAUM, V. GVOŽDÍK, D.B. KELLEY, P.J. MCLAUGHLIN, O.S. PAUWELS, D.M. PORTIK, E.L. STANLEY, R.C. TINSLEY, M.L. TOBIAS, AND D.C. BLACKBURN. 2015. Genetics, morphology, advertisement calls, and historical records distinguish six new polyploid species of African clawed frog (*Xenopus*, Pipidae) from West and Central Africa. *PLoS ONE* 10(12):e0142823:1–51.
- FA, J.E. 1991. *Conservación de los ecosistemas forestales de Guinea Ecuatorial*. International Union for Conservation of Nature, Gland, Switzerland. 105 pp.
- FRÉTEY, T., AND C.P. BLANC. 2000. Liste des Amphibiens d'Afrique Centrale. Cameroun, Congo, Gabon, Guinée-Equatoriale, République Centrafricaine, République Démocratique du Congo, São Tomé et Príncipe. *Les dossiers de l'ADIE, Série Biodiversité*, 2:1–39.
- FRÉTEY, T., AND C.P. BLANC. 2001. Inventaire systématique des amphibiens anoures du centre du Gabon. *Bulletin de la Société Zoologique de France* 126:375–390.
- FRÉTEY, T., M. DEWYNTER, AND C.P. BLANC. 2011. Amphibiens d'Afrique centrale et d'Angola: Clé de détermination illustrée des amphibiens du Gabon et du Mbini. *Biotope, Mèze (Collection Parthénope) & Muséum National d'Histoire Naturelle*, Paris, France.
- FRÉTEY, T., A. DUBOIS, AND A. OHLER. 2014. The status of the nomen *Hyperolius guttatus* Peters, 1875 (Amphibia, Anura) and allied nomina. *Alytes* 30:11–26.
- FROST, D.R. 2020. Amphibian Species of the World: An Online Reference. Version 6.0 (20 January 2020). Electronic Database accessible at <<http://research.amnh.org/herpetology/amphibia/index.html>>. American Museum of Natural History, New York, New York, USA.
- FROST, D.R., T. GRANT, J. FAIVOVICH, R.H. BAIN, A. HAAS, C.F.B. HADDAD, R.O. DE SÁ, A. CHANNING, M. WILKINSON, S.C. DONNELLAN, C.J. RAXWORTHY, J.A. CAMPBELL, B.L. BLOTTO, P.E. MOLER, R.C. DREWES, R.A. NUSSBAUM, J.D. LYNCH, D.M. GREEN, AND W.C. WHEELER. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297:1–370.
- GALÁN CELA, P., R. GAMARRA, AND R. ORTÚÑEZ, E. 2018. Catálogo de la familia Orchidaceae en Guinea Ecuatorial. *Collectanea Botanica* 37: e003.
- GONWOUO, N.L., AND A. NSANG. 2005. An assessment of the reptiles and amphibians of the Monte Mitra forest, Monte Alen National Park. Pages 32–49 in T.C.H. Sunderland, ed., *A Biodiversity Assessment of the Monte Mitra Forest, Monte Alen National Park, Equatorial Guinea*. Smithsonian Institution, Washington, DC, USA.
- GONWOUO, N.L., A.D. NDEH, W.P. TAPONDJOU, AND B.P. NOONAN. 2013. Amphibia, Bufonidae, *Didynamipus sjostedti* Anderson, 1903: new records and a review of geographic distribution. *Check List* 9(4):780–782.
- HYDEMAN, M.E., A.V. LONGO, G. VELO-ANTÓN, D. RODRÍGUEZ, K.R. ZAMUDIO, AND R.C. BELL. 2017. Prevalence and genetic diversity of *Batrachochytrium dendrobatidis* in Central African islands and continen-

- tal amphibian communities. *Ecology and Evolution* 7(19):7729–7738.
- JONES, P.J. 1994. Biodiversity in the Gulf of Guinea: an overview. *Biodiversity and Conservation* 3(9): 772–784.
- JONGSMA G.F.M., E. TOBI, G.P. DIXON-MAC CALLUM, A. BAMBA-KAYA, J.A. YOGA, J.D. MBEGA, J. MVE BEH, A.M. EMRICH, AND D.C. BLACKBURN. 2017. Amphibians of Haut-Ogooué Province, southeastern Gabon. *Amphibian & Reptile Conservation* 11(1):1–23.
- JONGSMA, G.F.M., M.F. BAREJ, C.D. BARRATT, M. BURGER, W. CONRADIE, R. ERNST, E. GREENBAUM, M. HIRSCHFELD, A.D. LEACHÉ, J. PENNER, D.M. PORTIK, A.G. ZASSI-BOULOU, M.-O. RÖDEL, AND D.C. BLACKBURN. 2018. Diversity and biogeography of frogs in the genus *Amnirana* (Anura: Ranidae) across sub-Saharan Africa. *Molecular Phylogenetics and Evolution* 120:274–285.
- JUSTE, J., AND J. PÉREZ DEL VAL. 1995. Altitudinal variation in the subcanopy fruit bat guild in Bioko Island, Equatorial Guinea, Central Africa. *Journal of Tropical Ecology* 11:141–146.
- KÖHLER, J., K. SCHEELKE, S. SCHICK, M. VEITH, AND S. LÖTTERS. 2005. Contribution to the taxonomy of hyperoliid frogs (Amphibia: Anura: Hyperoliidae): advertisement calls of twelve species from East and Central Africa. *African Zoology*, 40(1):127–142.
- LAMOTTE, M., AND F. XAVIER. 1966. Étude comparée de deux espèces de *Phrynobatrachus* souvent confondues: *Phr. plicatus* Günther et *Phr. auritus* Boulenger. *Bulletin de l'Institut Fondamental d'Afrique Noire, Série A, Sciences Naturelles* 28:1605–1619.
- LASSO, C.A., A.I. RIAL, J. CASTROVIEJO, AND I. DE LA RIVA. 2002. Herpetofauna del Parque Nacional de Monte Alén (Río Muni, Guinea Ecuatorial). *Graellsia* 58:21–34.
- LEACHÉ, A.D., D.M. PORTIK, D. RIVERA, M.-O. RÖDEL, J.PENNER,| V. GVOŽDÍK, E. GREENBAUM, G.F.M. JONGSMA, C. OFORI-BOATENG, M. BURGER, E.A. ENIANG, R.C. BELL, AND M;K. FUJITA. 2019. Exploring rain forest diversification using demographic model testing in the African foam-nest treefrog *Chiromantis rufescens*. *Journal of Biogeography* 2019;00:1–16.
- LIEDTKE H.C., H. MÜLLER, M.-O. RÖDEL, M. MENEGON, L.N. GONWUO, M.F. BAREJ, V. GVOŽDÍK, A. SCHMITZ, A. CHANNING, P. NAGEL, AND S.P. LOADER. 2016. No ecological opportunity on a continental scale? Diversification and life-history evolution of African true toads (Bufonidae: Anura). *Evolution* 70:1717–1733.
- LÖTTERS, S., M.-O. RÖDEL, AND M. BURGER. 2005. A new large tree frog from north-western Gabon (Hyperoliidae: *Leptopelis*). *Herpetological Journal* 15:149–152.
- MARQUES, M.P., L.M.P. CERÍACO, D.C. BLACKBURN, AND A.M. BAUER. 2018. Diversity and distribution of the amphibians and reptiles of Angola: an atlas of historical and bibliographical records (1840–2017). *Proceedings of the California Academy of Sciences*, ser. 4, 65:1–501.
- MÁRQUEZ, R., I. DE LA RIVA, AND J. BOSCH. 2000. Advertisement calls of *Bufo camerunensis*, *Chiromantis rufescens*, *Dimorphognathus africanus* and *Phrynobatrachus auritus*, from Equatorial Guinea (Central Africa). *Herpetological Journal* 10(1):41–44.
- MARTÍNEZ AND F. P. SÁEZ. 1886. Enumeración y estudio de las colecciones recogidas en su viaje por el Dr. Osorio. Vertebrados. *Anales de la Sociedad Española de Historia Natural*, 15:339.
- MENEGON, M., N.H. DOGGART, AND N. OWEN. 2008. The Nguru mountains of Tanzania, an outstanding hotspot of herpetofaunal diversity. *Acta Herpetologica*. 3:107–127.
- MERTENS, R. 1938. Herpetologische Ergebnisse einer Reise nach Kamerun. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 442:1–52.
- MERTENS, R. 1941. Zur Kenntnis der Herpetofauna von Fernando Poo. *Zoologischer Anzeiger* 135:275–281.
- MERTENS, R. 1965. Die Amphibien von Fernando Poo. *Bonner Zoologische Beiträge* 16:14–29.
- MERTENS, R. 1968. Zur Kenntnis der Herpetofauna von Kamerun und Fernando Poo. *Bonner Zoologische Beiträge* 19(2):69–84.
- MRAZ, A., M. WEIR, AND P. MCLAUGHLIN. 2018. Efficacy of anuran trapping and monitoring techniques in the tropical forests of Bioko Island, Equatorial Guinea. *Amphibia-Reptilia* 39(4): 435–444.
- MYERS, N., R. A MITTERMEIER, C.G. MITTERMEIER, G.A. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772):853–858.
- NIEDEN, F. 1908. Die Amphibienfauna von Kamerun. *Mitteilungen aus dem Zoologischen Museum in Berlin* 3:491–518.

- NIEDEN, F. 1909. Über westafrikanische *Hylambates*-Arten nebst Beschreibung einer neuen Art. *Archiv für Naturgeschichte* 75:361–366.
- NOBLE, G.K. 1924. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. *Bulletin of the American Museum of Natural History* 49:147–347.
- NUSSBAUM, R.A., AND M.E. PFRENDER. 1998. Revision of the African caecilian genus *Schistometopum* Parker (Amphibia: Gymnophiona: Caeciliidae). *Miscellaneous Publications, Museum of Zoology, University of Michigan* 187:1–32.
- OHLER, A. 1996. Systematics, morphometrics and biogeography of the genus *Aubria* (Ranidae, Pyxicephalinae). *Alytes* 13:141–166.
- ONADEKO, A.B., AND M.-O. RÖDEL. 2009. Anuran surveys in south-western Nigeria. *Salamandra* 45(1):1–14.
- ONADEKO A.B., M.-O. RÖDEL, R.I. EGONMWAN, AND J.K. SALIU. 2010. Herpetological surveys of south-western and south-eastern regions of Nigeria. *The Zoologist* 8:34–43.
- PAUWELS, O.S., AND M.-O. RÖDEL. 2007. Amphibians and national parks in Gabon, western Central Africa. *Herpetozoa* 19(3/4):135–148.
- PARKER, H.W. 1936. The amphibians of the Mamfe Division, Cameroon.—(1) Zoogeography and systematics. *Proceedings of the Zoological Society of London* 1936:135–163.
- PERRET, J.L. 1966. Les amphibiens du Cameroun. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie* 93:289–464.
- PERRET, J.L. 1975. Les sous-espèces d'*Hyperolius ocellatus* Günther (Amphibia, Salientia). *Annales de la Faculté des Sciences du Cameroun, Yaoundé* 20: 23–31.
- PERRET, J.L. 1977. Les *Hylarana* (Amphibiens, Ranidés) du Cameroun. *Revue Suisse de Zoologie* 84: 841–868.
- PERRET, J.L. 1991. Le statut d'*Arthrolepis bivittatus* F. Müller (Anura, Arthroleptidae). *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 114:71–76.
- PERRET, J.L. 1994. Revision of the genus *Aubria* Boulenger, 1917 (Amphibia, Ranidae) with the description of a new species. *Tropical Zoology* 7:255–269.
- PERRET, J.L., AND R. MERTENS. 1957. Étude d'une collection herpétologique faite au Cameroun de 1952 à 1955. *Bulletin de l'Institut Française d'Afrique Noire. Série A, Sciences Naturelles* 19:548–601.
- PORTIK, D.M., G.F.M. JONGSMA, M.T. KOUETE, L.A. SCHEINBERG, B. FREIERMUTH, W.P. TAPONDJOU, AND D.C. BLACKBURN. 2016. A survey of amphibians and reptiles in the foothills of Mount Kupe, Cameroon. *Amphibian & Reptile Conservation* 10(2):37–67.
- PORTIK, D.M., R.C. BELL, D.C. BLACKBURN, A.M. BAUER, C.D. BARRATT, W.R. BRANCH, M. BURGER, A. CHANNING, T.J. COLSTON, W. CONRADIE, J.M. DEHLING, R.C. DREWES, R. ERNST, E. GREENBAUM, V. GVOŽDÍK, J. HARVEY, A. HILLERS, A. HIRSCHFELD, G.F.M. JONGSMA, J. KIELGAST, M.T. KOUETE, L.P. LAWSON, A.D. LEACHÉ, S.P. LOADER, S. LÖTTERS, A. VAN DER MEIJDEN, M. MENEGON, S. MÜLLER, Z.T. NAGY, C. OFORI-BOATENG, A. OHLER, T.J. PAPANFUSS, D. RÖSSLER, U. SINSCH, M.-O. RÖDEL, M. VEITH, J. VINDUM, A.G. ZASSI-BOULOU, AND J.A. MCGUIRE. 2019. Sexual dichromatism drives diversification within a major radiation of African amphibians. *Systematic Biology* 68:859–875.
- PORTILLO, F., E. GREENBAUM, M. MENEGON, C. KUSAMBA, AND J.M. DEHLING. 2015. Phylogeography and species boundaries of *Leptopelis* (Anura: Arthroleptidae) from the Albertine Rift. *Molecular Phylogenetics and Evolution* 82:75–86.
- POYNTON, J.C., S.P. LOADER, E. SHERRATT, AND B.T. CLARKE. 2007. Amphibian diversity in East African biodiversity hotspots: altitudinal and latitudinal patterns. *Biodiversity and Conservation* 16(4):1103–1118.
- RÖDEL, M.-O., AND O.S. PAUWELS. 2003. A new *Leptodactylodon* species from Gabon (Amphibia: Anura: Astylosternidae). *Salamandra* 39:139–148.
- RÖDEL, M.-O., A. SCHMITZ, O.S. PAUWELS, AND W. BÖHME. 2004. Revision of the genus *Werneria* Poche, 1903, including the descriptions of two new species from Cameroon and Gabon (Amphibia: Anura: Bufonidae). *Zootaxa* 720(1):1–28.
- RÖDEL, M.-O., M. GIL, A.C. AGYEI, A.D. LEACHÉ, R.E. DÍAZ, M.K. FUJITA, AND R. ERNST. 2005. The amphibians of the forested parts of south-western Ghana. *Salamandra* 41:107–127.
- SABATER PI, J. 1985. Contributions to the biology of the giant frog (*Conraua goliath* Boulenger). *Amphibia-*

Reptilia 6(2):143–153.

- SÁNCHEZ-VIALAS, A., M. CALVO-REVUELTA, S. CASTROVIEJO-FISHER, AND I. DE LA RIVA. 2018. The taxonomic status of *Petropedetes newtonii* (Amphibia, Anura, Petropedetidae). *ZooKeys* 765:59–78.
- SCHÄFER, M., S.J. TSEKANÉ, F.A.M. TCHASSEM, S. DRAKULIĆ, M. KAMENI, N.L. GONWOUO, AND M.-O. RÖDEL. 2019. Goliath frogs build nests for spawning—the reason for their gigantism? *Journal of Natural History* 53(21-22):1263–1276.
- SCHEEL, J.J. 1970. Notes on the biology of the African tree-toad, *Nectophryne afra* Buchholz and Peters, 1875, (Bufonidae, Anura) from Fernando Po. *Revue de Zoologie et de Botanique Africaines* 81:225–236.
- SCHIÖTZ, A. 1999. *Treefrogs of Africa*. Editions Chimaira, Frankfurt am Main, Germany. 350 pp.
- SCOTT, E. 2005. A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. *Cladistics* 21(6):507–574.
- TABOUE, G.C.T., AND E.B. FOKAM. 2016. Life History of the Golden Puddle Frog, *Phrynobatrachus auritus* Boulenger, 1900 (Anura: Phrynobatrachidae). *International Journal of Biology* 8(3):77–83.
- TAYLOR, E.H., AND A. SALVADOR. 1978. Afrikanische Blindwühlen im Naturhistorischen Museum Madrid, nebst Beschreibung des *Schistometopum garzonheydti* n. sp. *Salamandra* 14:58–62.
- WILKINSON, M., H. MÜLLER, AND D.J. GOWER. 2003. On *Herpele multiplicata* (Amphibia: Gymnophiona: Caeciliidae). *African Journal of Herpetology* 52:119–122.
- ZIMKUS, B.M. 2009. Biogeographical analysis of Cameroonian puddle frogs and description of a new species of *Phrynobatrachus* (Anura: Phrynobatrachidae) endemic to Mount Oku, Cameroon. *Zoological Journal of the Linnean Society* 157(4):795–813.
- ZIMKUS, B.M., M.-O. RÖDEL, AND A. HILLERS. 2010. Complex patterns of continental speciation: Molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). *Molecular Phylogenetics and Evolution* 55:883–900.

Photographs

Photographers: Ignacio De la Riva (IDIR), Ignacio Martín (IM), Twan Leenders (TL), Rayna Bell (RB), Patrick McLaughlin (PM), and Jessica Weinberg (JW).



FIGURE 3. A. *Arthroleptis adelphus* (Caldera de Luba, Bioko Sur, Bioko). Photo IM.; B–C. *Arthroleptis adelphus* (Monte Alén National Park, Río Muni). Photos IDIR.; D. *Arthroleptis* aff. *poecilonotus*, female (Monte Alén National Park, Río Muni). Photo IDIR.; E. *Arthroleptis* aff. *poecilonotus*, male (Río Muni). Photo TL.; F. *Arthroleptis sylvaticus* (Monte Alén National Park, Río Muni). Photo IDIR.; G–H. *Arthroleptis variabilis* (Monte Alén National Park, Río Muni). Photos IDIR.

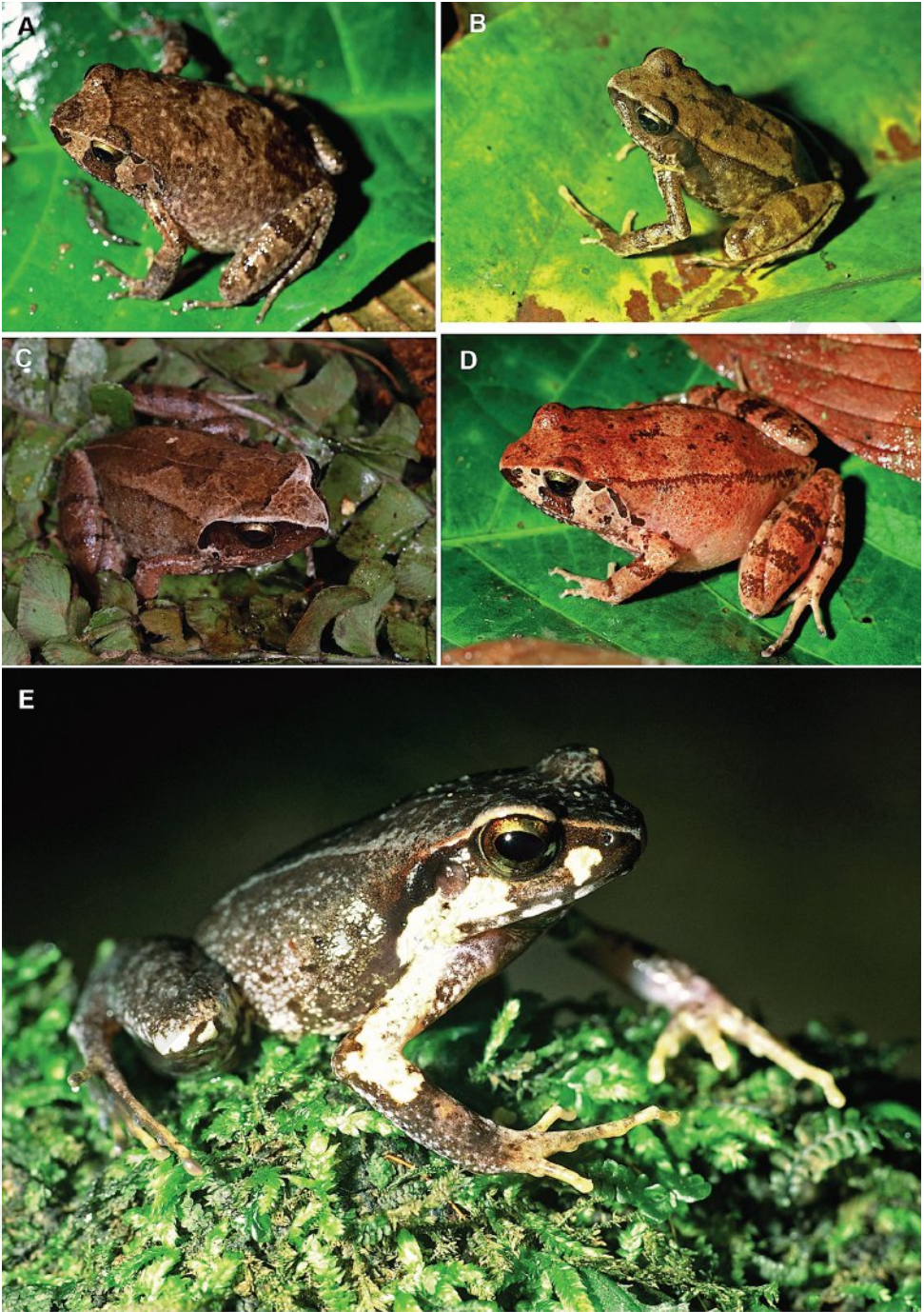


FIGURE 4. A–B, D–E. *Arthroleptis variabilis* (Monte Alén National Park, Río Muni). Photos IDIR.; C. *Arthroleptis variabilis* (Caldera de Luba, Bioko Sur, Bioko). Photo IM.

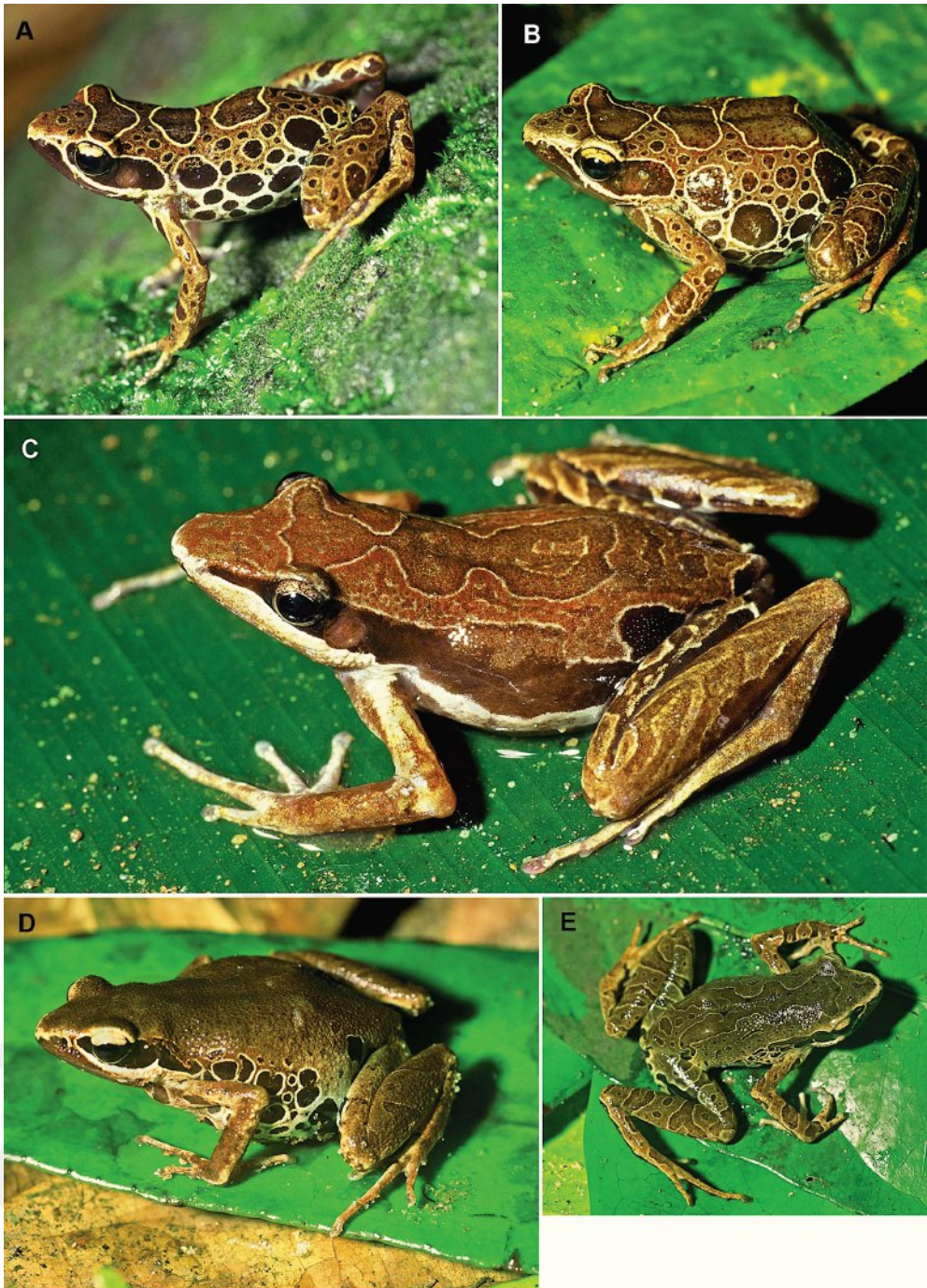


FIGURE 5. A–B. *Cardioglossa elegans* (Monte Alén National Park, Río Muni). Photos IDIR.; C. *Cardioglossa gracilis* (Monte Alén National Park, Río Muni). Photo IDIR.; D–E. *Cardioglossa leucomystax* (Monte Alén National Park, Río Muni). Photos IDIR.



FIGURE 6. A–B. *Astylosternus batesi* (Monte Alén National Park, Río Muni). Photos IDIR.; C–E. *Leptodactylodon* cf. *stevarti* (Monte Alén National Park, Río Muni). Photos IDIR.



FIGURE 7. A–B. *Nyctibates corrugatus* (Monte Alén National Park, Río Muni). Photos IDIR.; C. *Scotobleps gabonicus* (Monte Alén National Park, Río Muni). Photo IDIR.; D–E. *Trichobatrachus robustus* (Monte Alén National Park, Río Muni). Photos IDIR.



FIGURE 8. A–B. *Leptopelis aubryi* (Monte Alén National Park, Río Muni). Photos IDIR.; C. *Leptopelis boulengeri* (Monte Alén National Park, Río Muni). Photo IDIR.; D. *Leptopelis brevirostris* (Monte Alén National Park, Río Muni). Photo IDIR.; E. *Leptopelis calcaratus* (Monte Alén National Park, Río Muni). Photo IDIR.; F. *Leptopelis ocellatus* (Atoc Lake surrounding, Monte Alén National Park, Río Muni). Photo IDIR.; G–H. *Leptopelis rufus* (Monte Alén National Park, Río Muni). Photos IDIR.

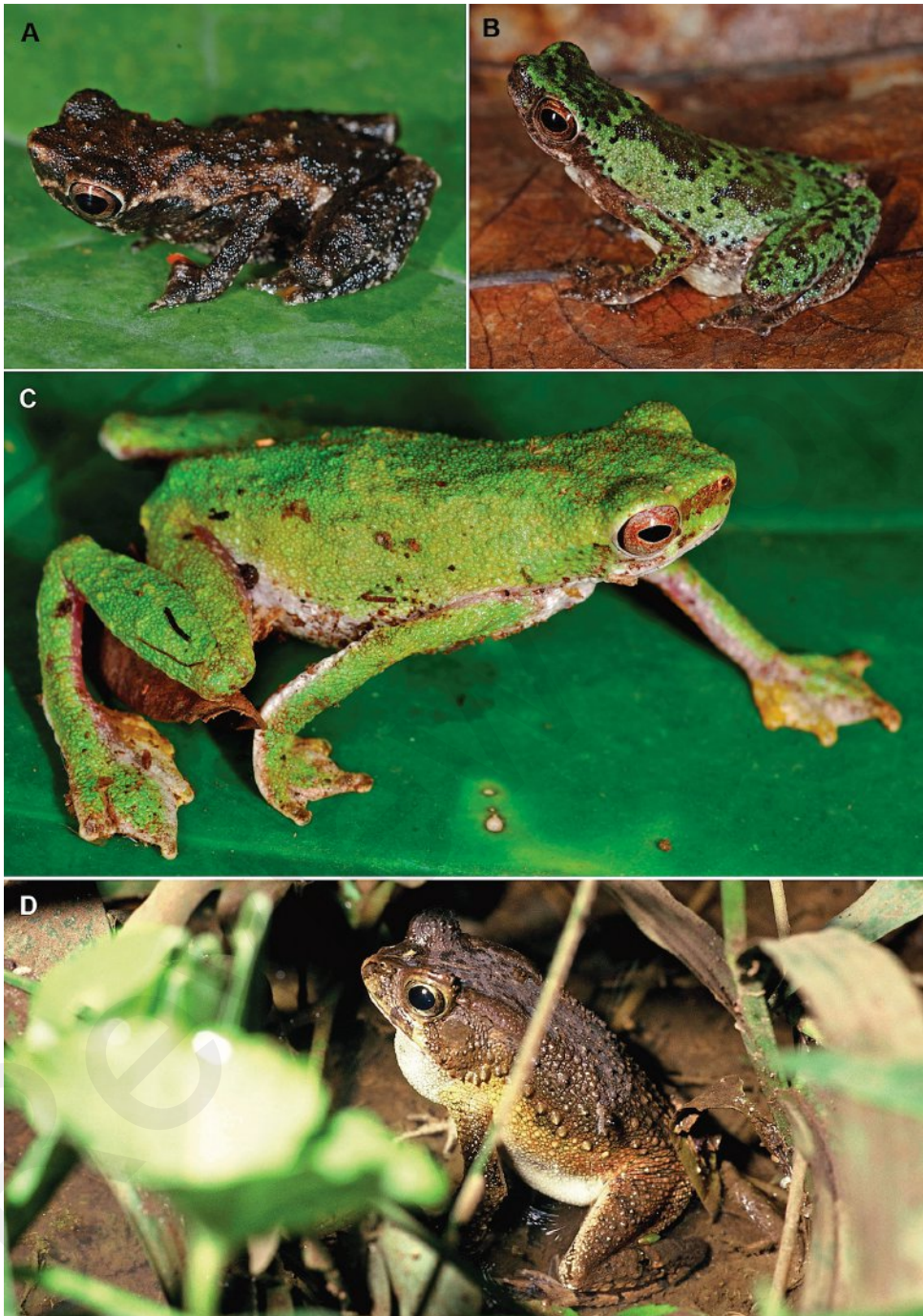


FIGURE 9. A. *Nectophryne afra* (North of Caldera de Luba, Bioko Sur, Bioko). Photo IM.; B–C. *Nectophryne batesii* (Caldera de Luba, Bioko Sur, Bioko). Photos IM.; D. *Sclerophrys camerunensis*, calling male (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 10. A, C–D. *Sclerophrys camerunensis* (Caldera de Luba, Bioko Sur, Bioko). Photos IM.; B. *Sclerophrys camerunensis* (Monte Alén National Park, Río Muni). Photo IDIR.; E. *Sclerophrys gracilipes* (Monte Alén National Park, Río Muni). Photo IDIR.; F. *Sclerophrys latifrons* (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 11. A–B. *Sclerophrys superciliaris* (Río Muni). Photos TL.; C–D. *Sclerophrys tuberosa* (Caldera de Luba, Bioko Sur, Bioko). Photos IM.; E. *Sclerophrys tuberosa*, amplexus (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 12. A–B. *Werneria cf. mertensiana* (Monte Alén National Park, Río Muni). Photos IDIR.

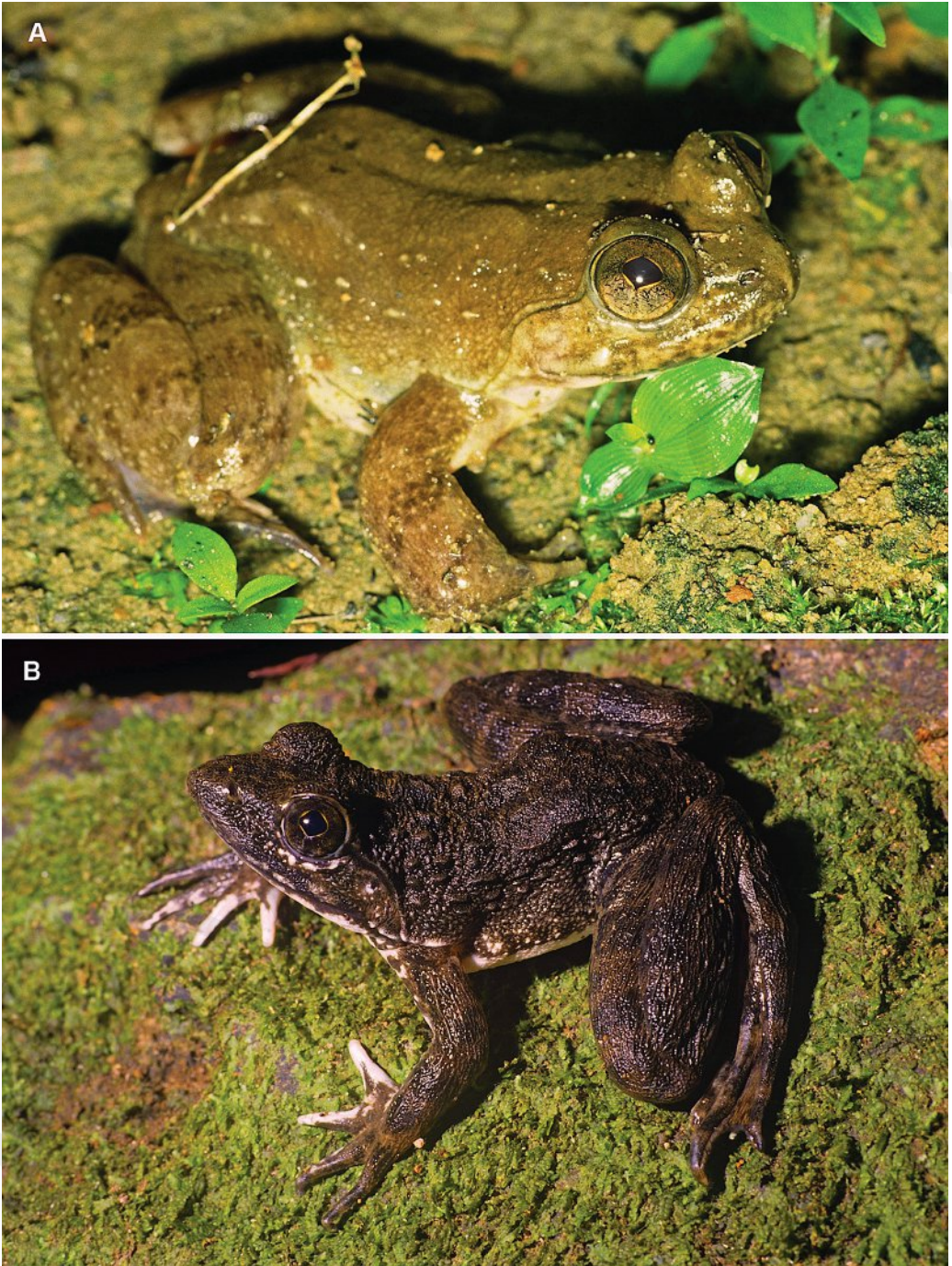


FIGURE 13. A. *Conraua crassipes* (Monte Alén National Park, Río Muni). Photo IDIR.; B. *Conraua goliath* (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 14. A. *Afrixalus fulvovittatus* (Monte Alén National Park, Río Muni). Photo IDIR.; B–C. *Afrixalus osorioi* (Monte Alén National Park, Río Muni). Photos IDIR.; D. *Afrixalus paradorsalis* (Caldera de Luba, Bioko Sur, Bioko). Photo IM.; E. *Afrixalus paradorsalis* (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 15. A–C. *Alexteroon obstetricans*, an egg clutch is showed in figure B (Monte Alén National Park, Río Muni). Photos IDIR.; D–E. *Cryptothylax greshoffii*, amplexus (E) (Monte Alén National Park, Río Muni). Photos IDIR.

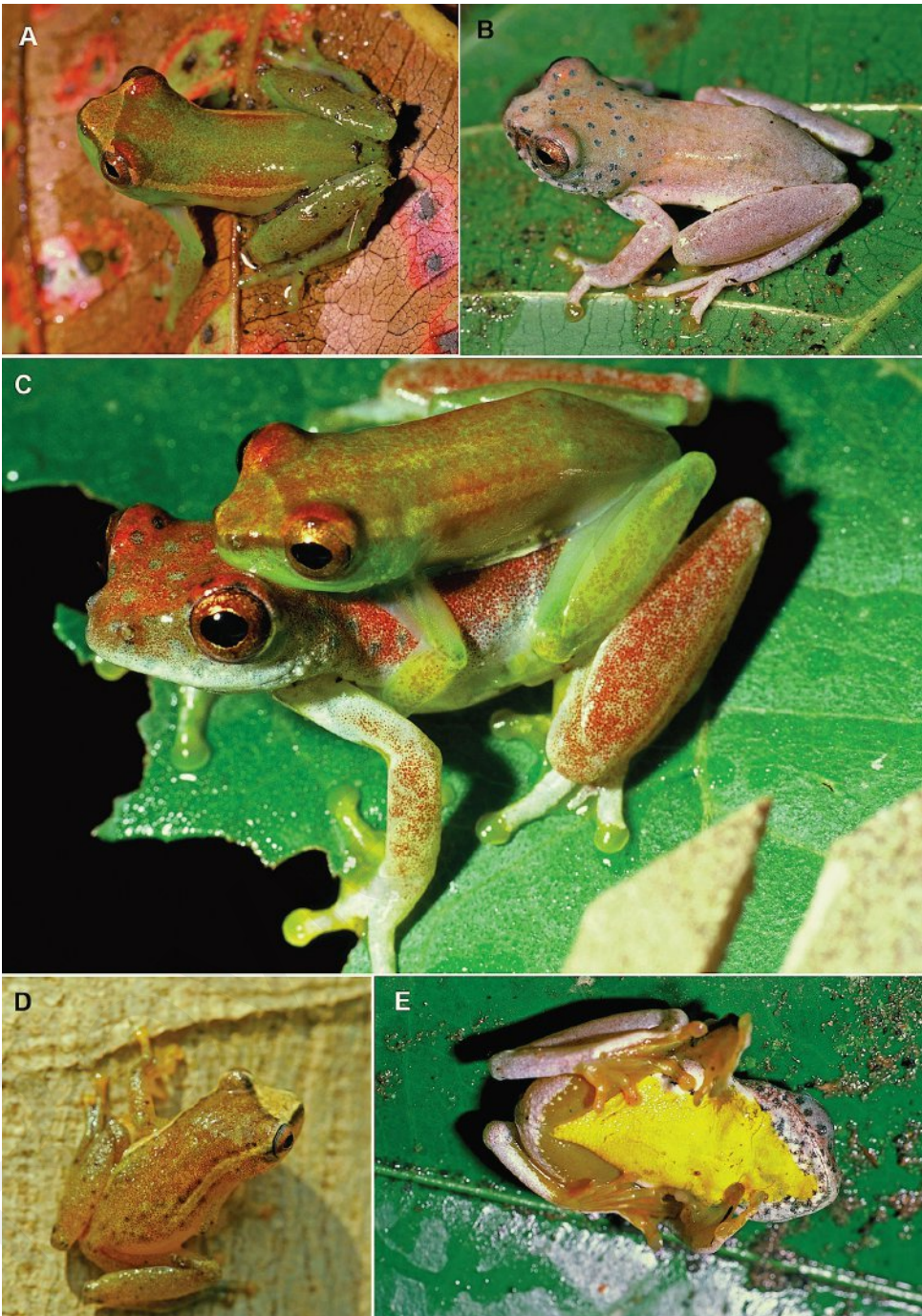


FIGURE 16. A. *Hyperolius ocellatus*, male (Monte Alén National Park, Río Muni). Photo IDIR.; B. *Hyperolius ocellatus*, female (Monte Alén National Park, Río Muni). Photo IDIR.; C. *Hyperolius ocellatus*, amplexus (Monte Alén National Park, Río Muni). Photo IDIR.; D. *Hyperolius ocellatus*, male (Caldera de Luba, Bioko Sur, Bioko). Photo IM.; E. *Hyperolius ocellatus*, ventral view, female (Monte Alén National Park, Río Muni). Photo IDIR.

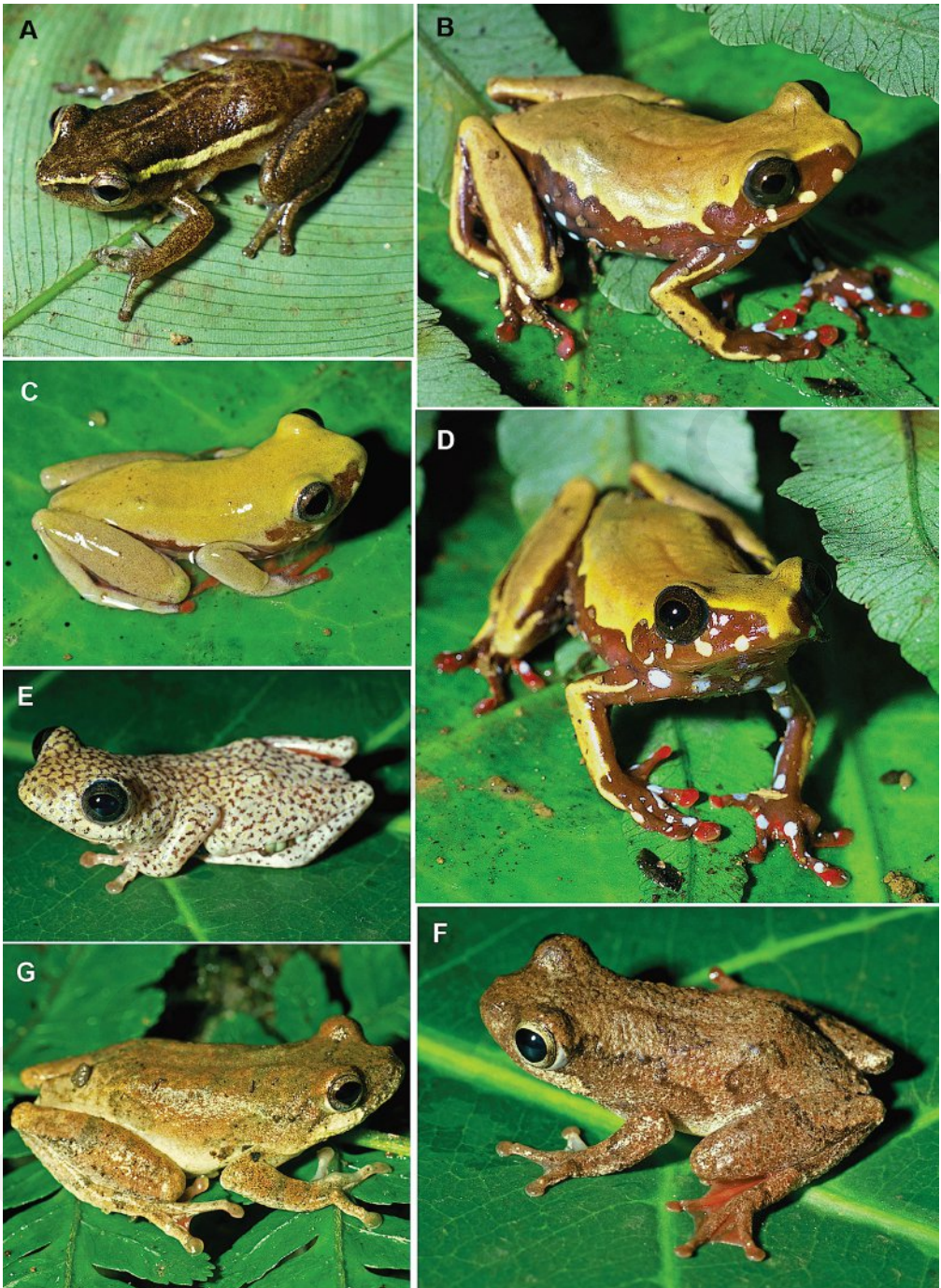


FIGURE 17. A. *Hyperolius olivaceus*, male (Monte Alén National Park, Río Muni). Photo IDIR.; B, D. *Hyperolius pardalis*, female (Monte Alén National Park, Río Muni). Photos IDIR.; C. *Hyperolius pardalis*, male (Monte Alén National Park, Río Muni). Photo IDIR.; E–F. *Hyperolius tuberculatus* (Bome, Río Muni). Photos IDIR.; G. *Hyperolius tuberculatus* (Monte Alén National Park, Río Muni). Photo IDIR.

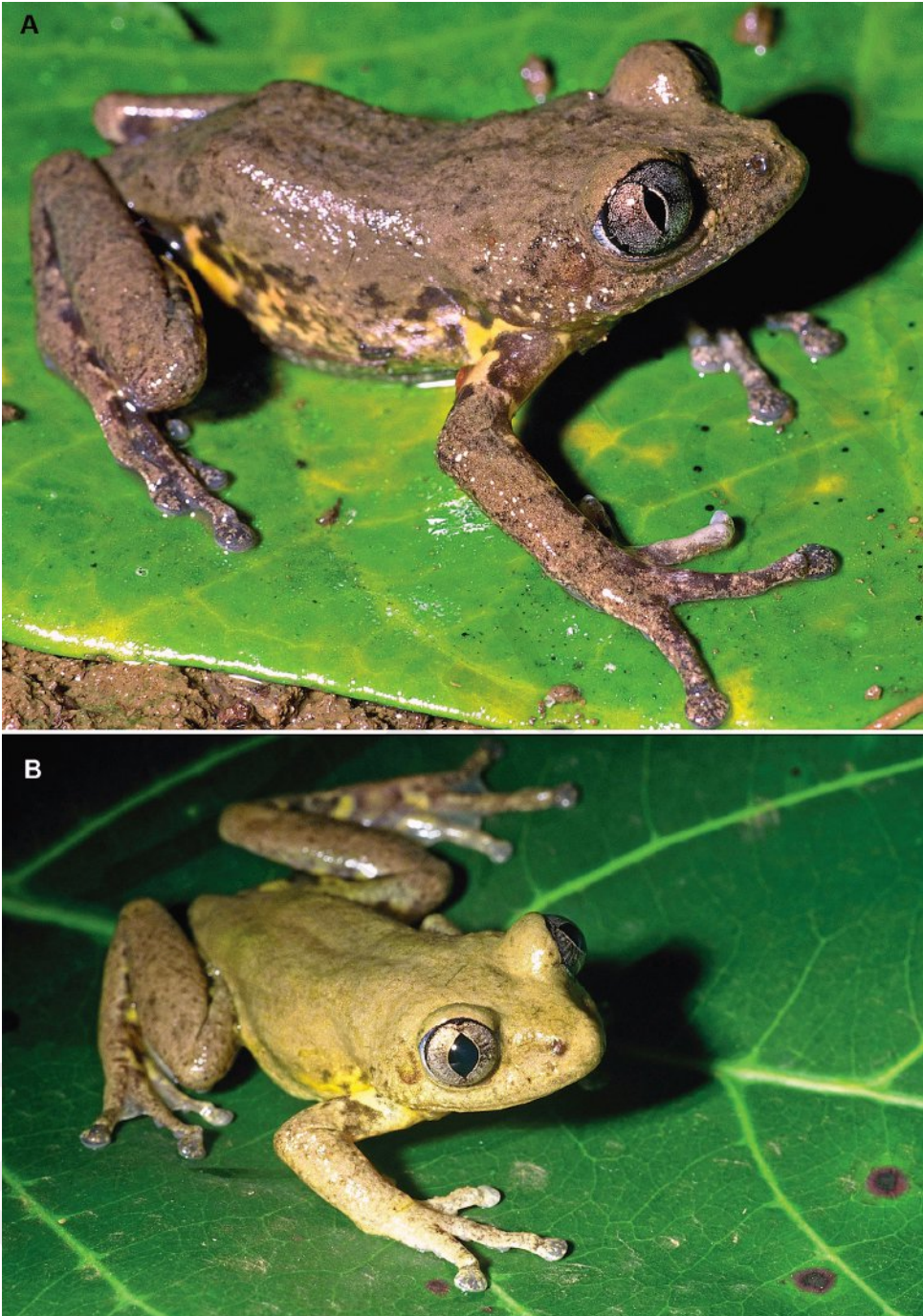


FIGURE 18. A. *Phlyctimantis* cf. *leonardi* (Monte Alén National Park, Río Muni). Photo IDIR.; B. *Phlyctimantis* cf. *leonardi* (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 19. A–B. *Petropedetes newtonii*, females (Caldera de Luba, Bioko Sur, Bioko). Photos IM.; C–D. *Petropedetes palmipes*, male (Monte Alén National Park, Río Muni). Photos IDIR.; E. *Petropedetes palmipes*, tadpoles and egg clutch (Monte Alén National Park, Río Muni). Photo IDIR.; F. *Petropedetes palmipes*, juvenile (Monte Alén National Park, Río Muni). Photo IDIR.

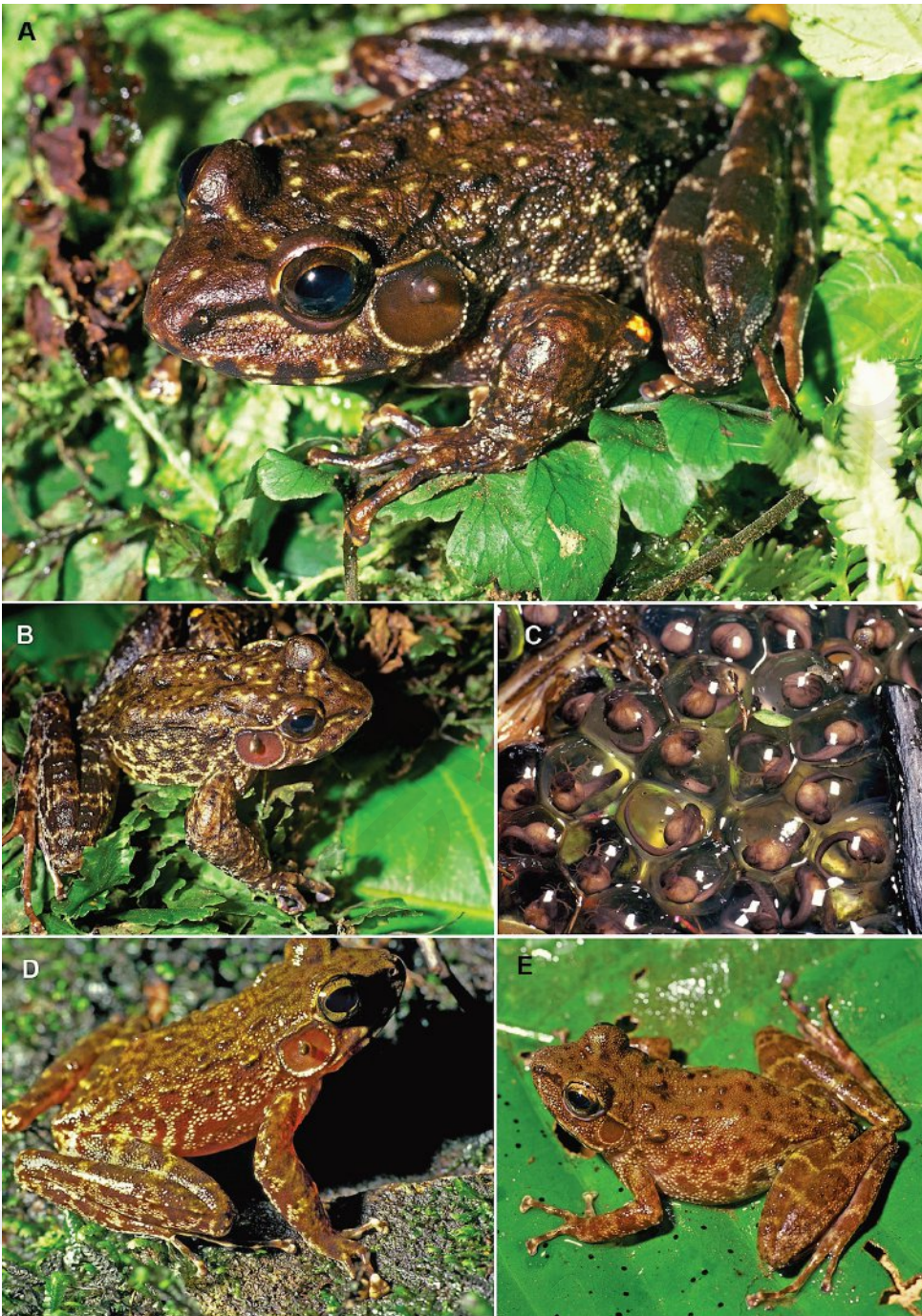


FIGURE 20. A–B. *Petropedetes parkeri*, male (Monte Alén National Park, Río Muni). Photos IDIR.; C. *Petropedetes parkeri* embryos in the egg clutch (Monte Alén National Park, Río Muni). Photo IDIR.; D. *Petropedetes vulpiae*, male (Monte Alén National Park, Río Muni). Photo IDIR.; E. *Petropedetes vulpiae*, female (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 21. A. *Phrynobatrachus africanus*, male (Monte Alén National Park, Río Muni). Photo IDIR.; B. *Phrynobatrachus africanus*, detail of the male hand showing the suprametacarpal gland (Monte Alén National Park, Río Muni). Photo IDIR.; C. Ventral view of *Phrynobatrachus africanus*, male (Monte Alén National Park, Río Muni). Photo IDIR.; D–G. Different coloration patterns of *Phrynobatrachus auritus* (Monte Alén National Park, Río Muni). Photos IDIR.; H. *Phrynobatrachus sandersoni* (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 22. A–B. *Xenopus parafraseri* (Monte Alén National Park, Río Muni). Photo IDIR.; C–D. *Ptychadena aequiplicata* (Monte Alén National Park, Río Muni). Photo IDIR.

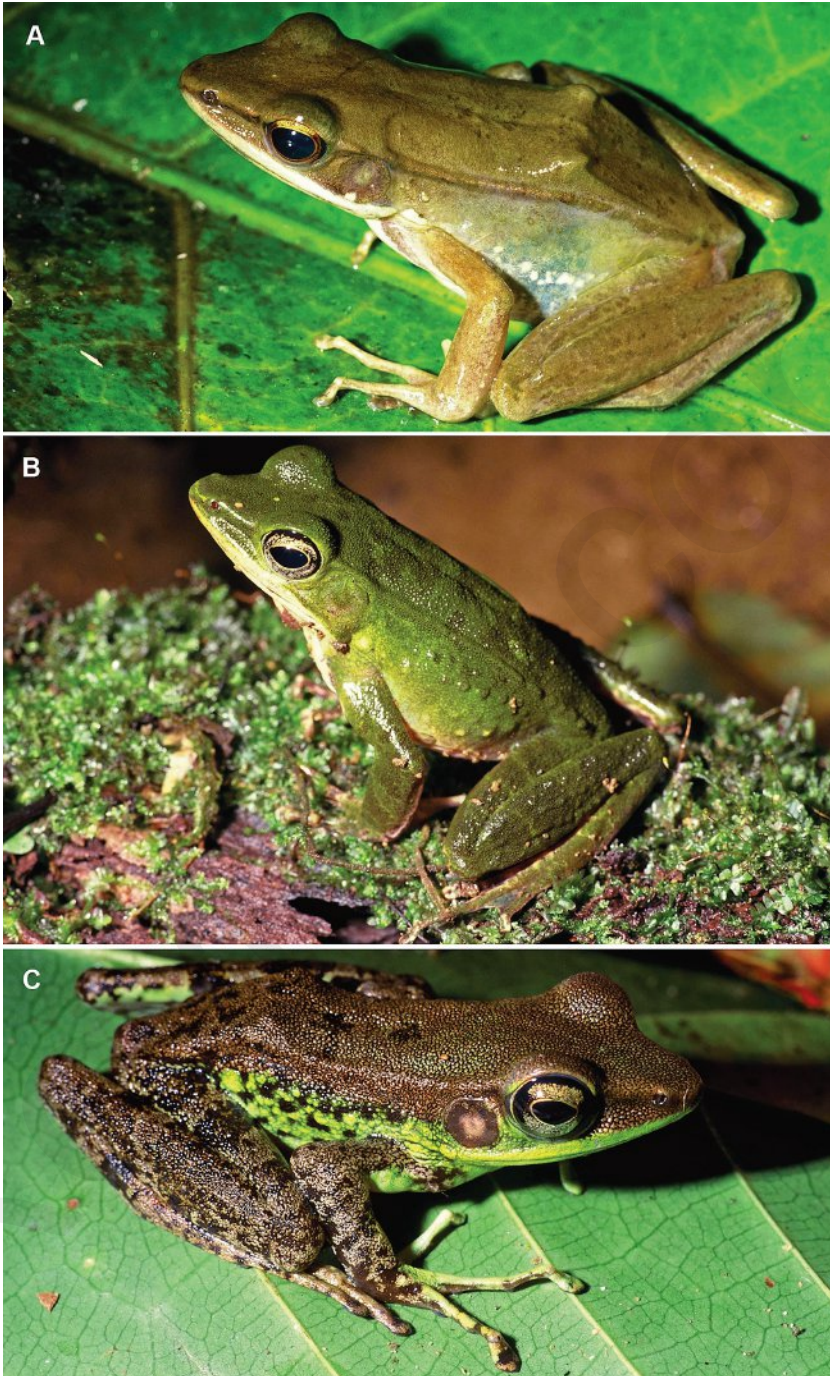


FIGURE 23. A. *Amnirana albolabris* (Monte Alén National Park, Río Muni). Photo IDIR.; B. *Amnirana amnicola* (Monte Alén National Park, Río Muni). Photo IDIR.; C. *Amnirana lepus* (Monte Alén National Park, Río Muni). Photo IDIR.



FIGURE 24. A. *Chiromantis rufescens* (Monte Alén National Park, Río Muni). Photo IDIR.; B. *Chiromantis rufescens*, foam nests (Monte Alén National Park, Río Muni). Photo IDIR.

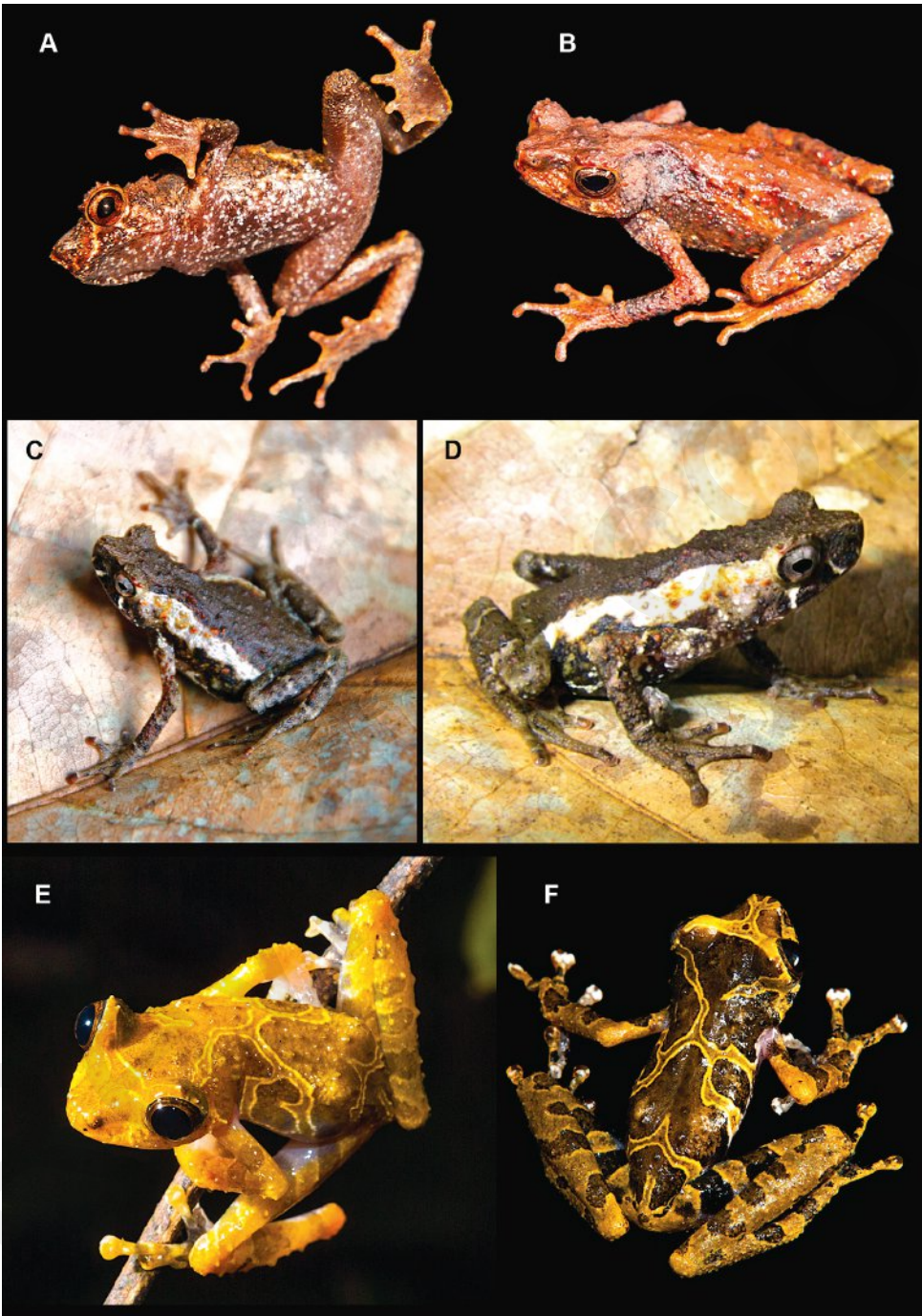
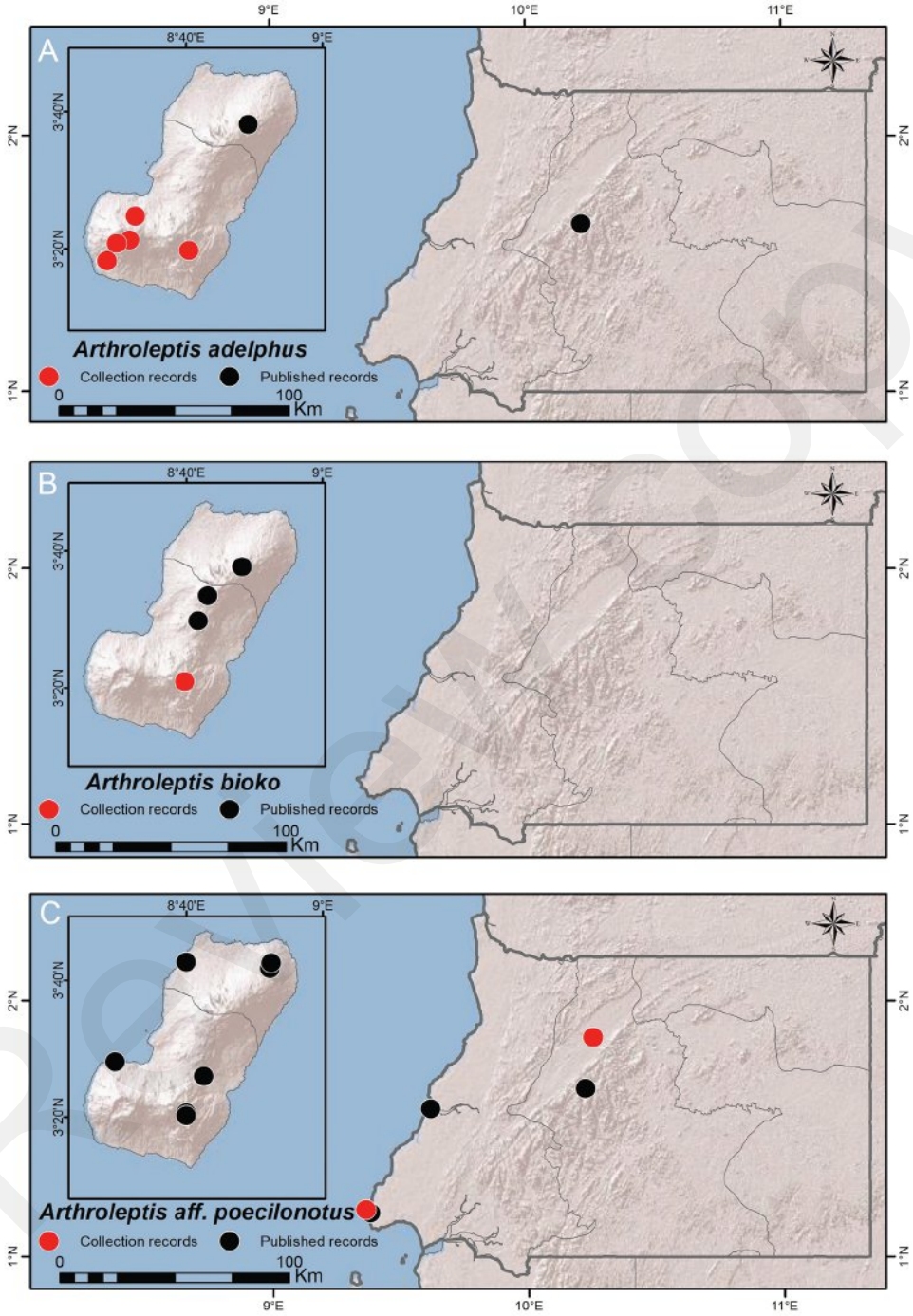


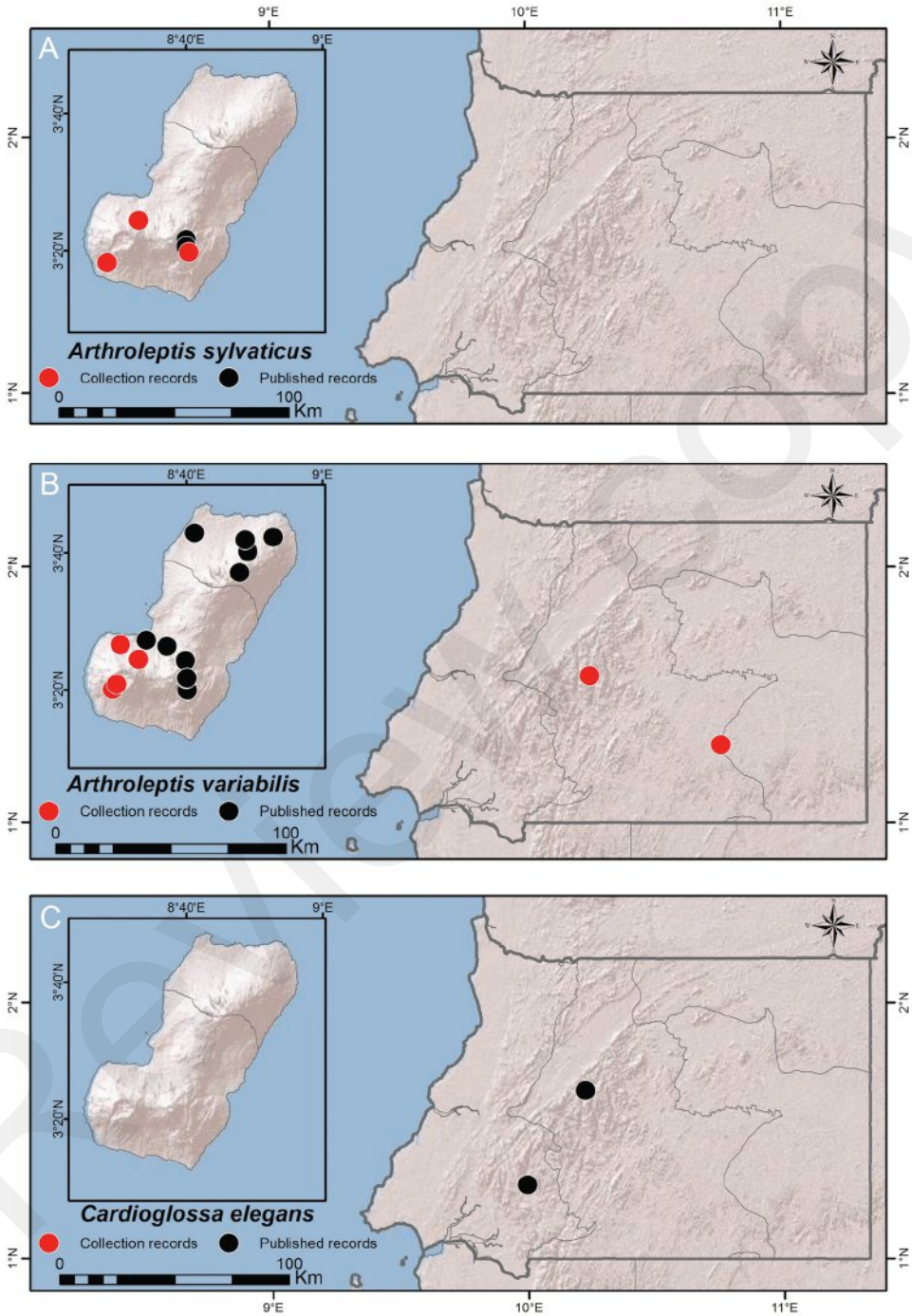
FIGURE 25. A. Ventral view of *Wolterstorffina parvipalmata* (surroundings of Moka, Bioko). Photo JW.; B. *Wolterstorffina parvipalmata*, same specimen as A (surroundings of Moka, Bioko). Photo JW.; C. *Wolterstorffina parvipalmata* (surroundings of Moka, Bioko). Photo PM.; D. *Wolterstorffina parvipalmata*, same specimen as C (surroundings of Moka, Bioko). Photo RB.; E–F. *Arlequinus krebsi* (surroundings of Pico Basilé, Bioko). Photos JW.

Distribution Maps

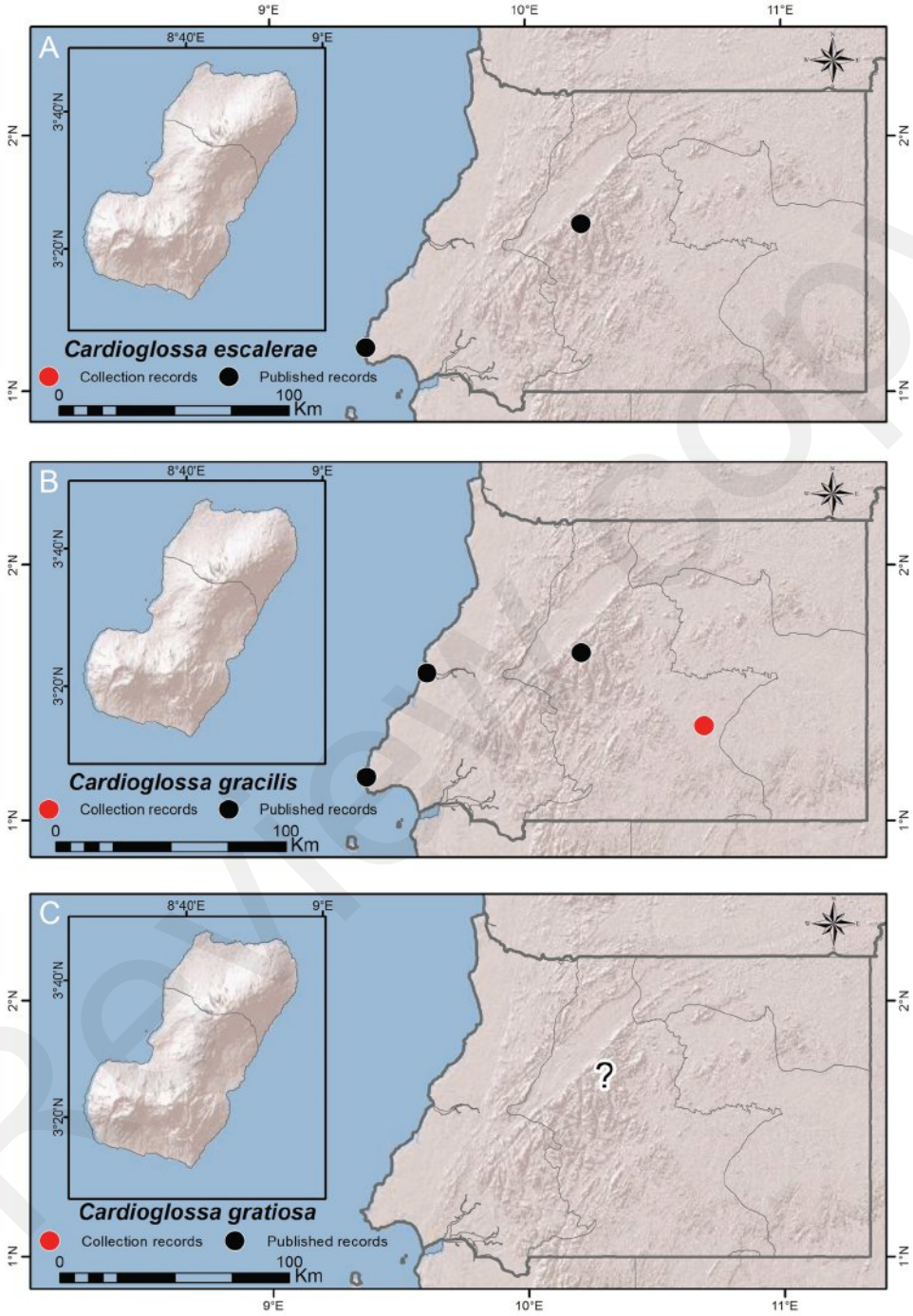
Review Copy



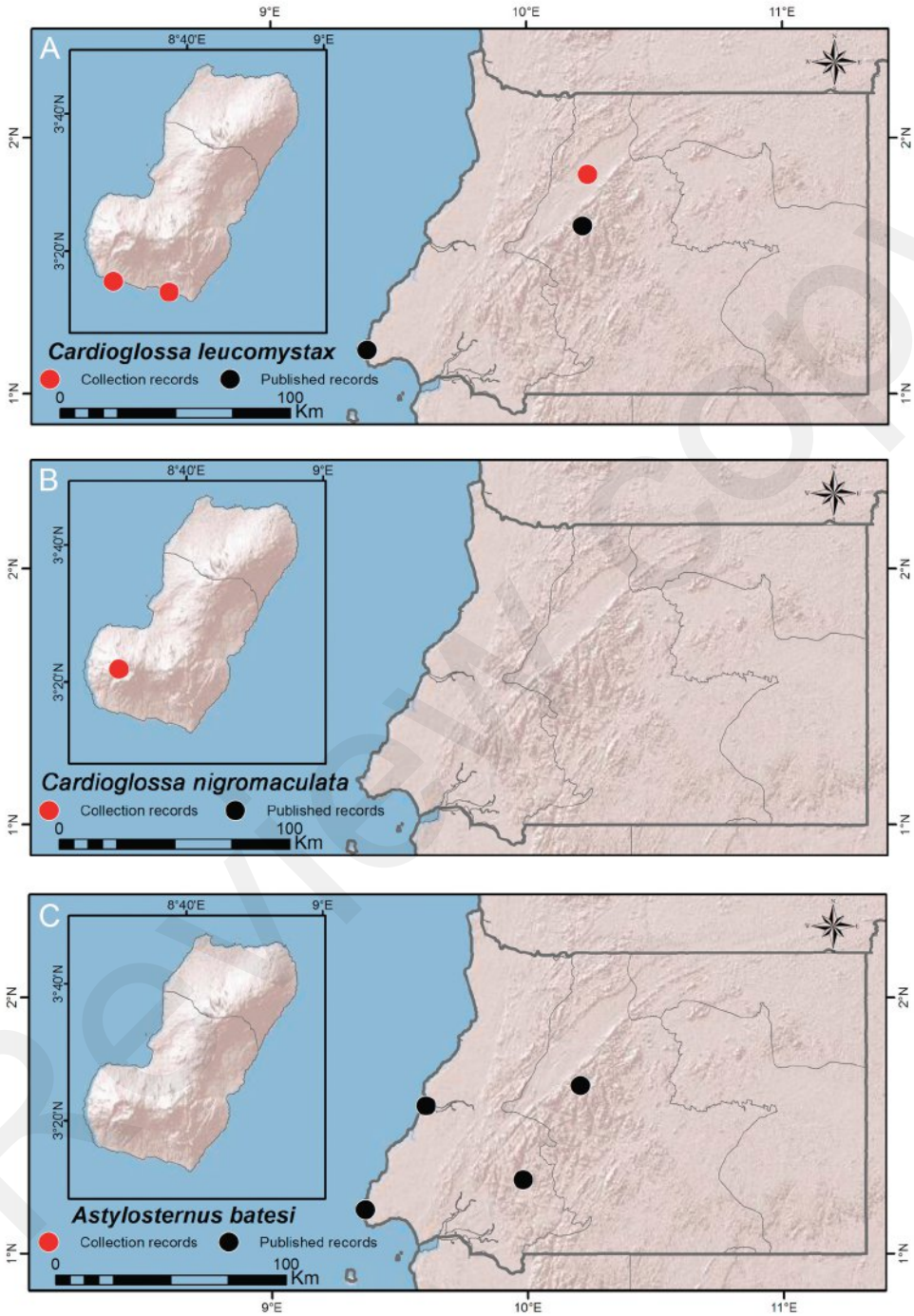
MAPS 2A–C. Distribution maps for Equatorial Guinean records of (A) *Arthroleptis adelphus*; (B) *Arthroleptis bioko*; (C) *Arthroleptis aff. poecilonotus*.



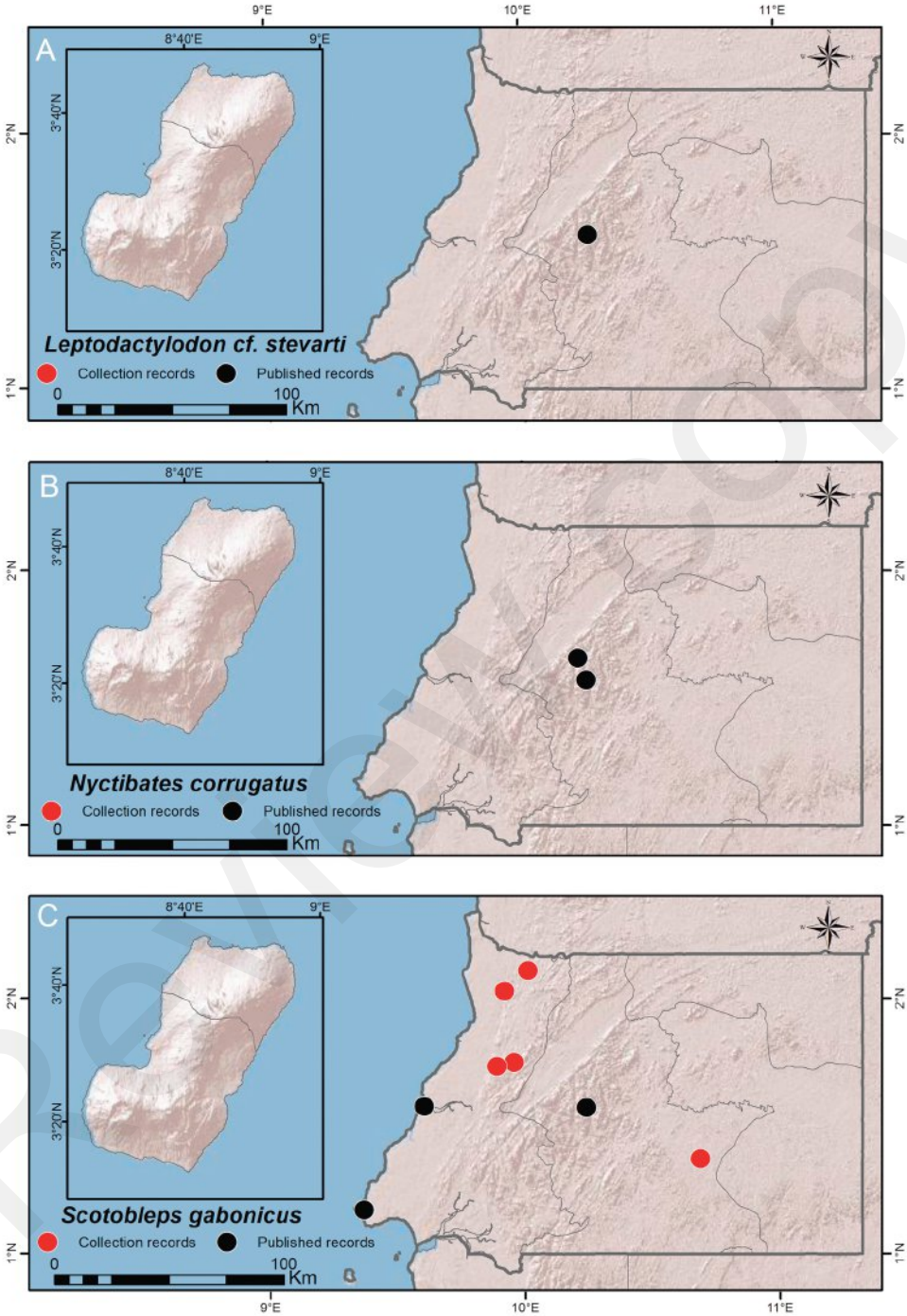
MAPS 3A–C. Distribution maps for Equatorial Guinean records of (A) *Arthroleptis sylvaticus*; (B) *Arthroleptis variabilis*; (C) *Cardioglossa elegans*.



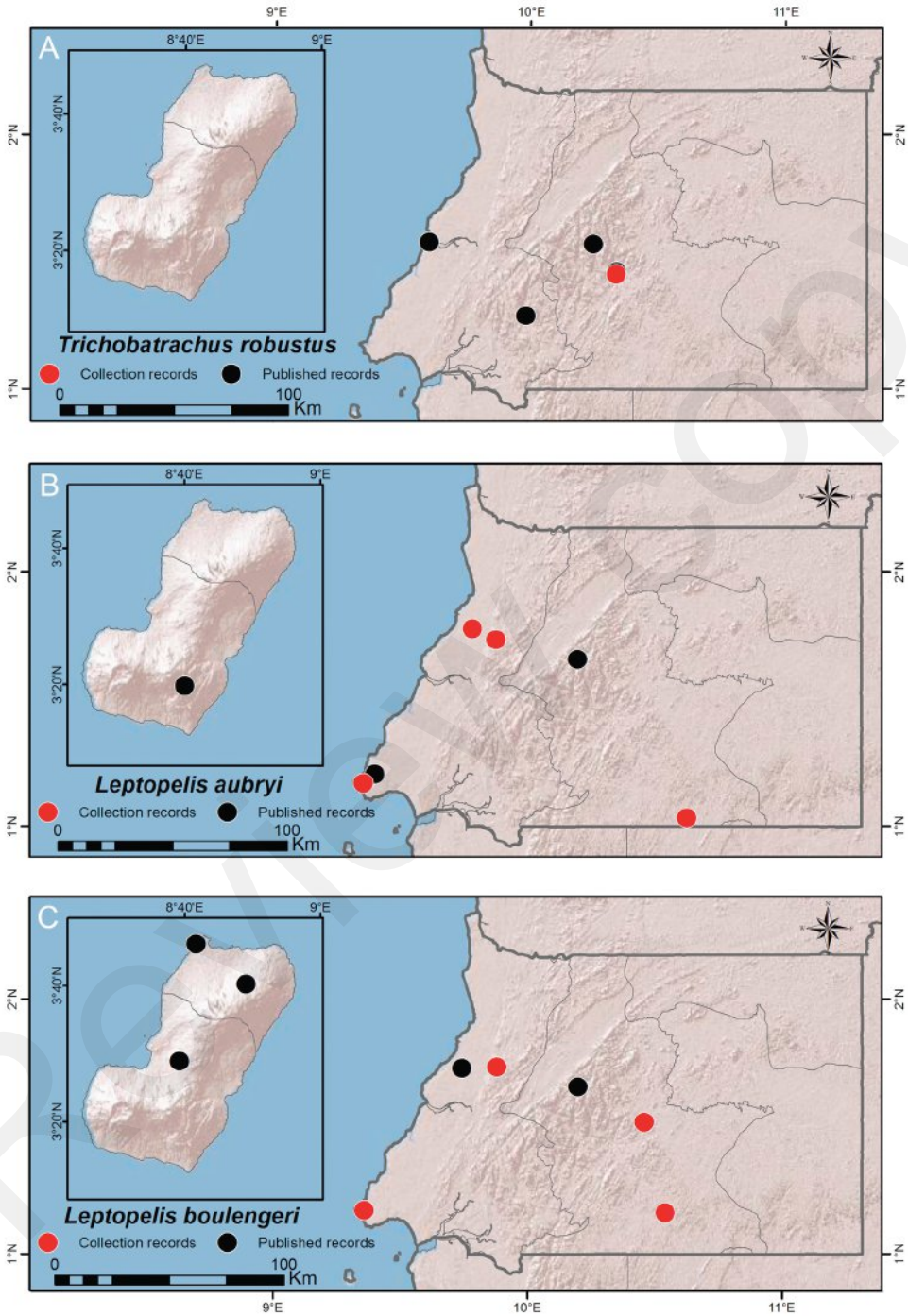
MAPS 4A–C. Distribution maps for Equatorial Guinean records of (A) *Cardioglossa escalerae*; (B) *Cardioglossa gracilis*; (C) *Cardioglossa gratiosa*.



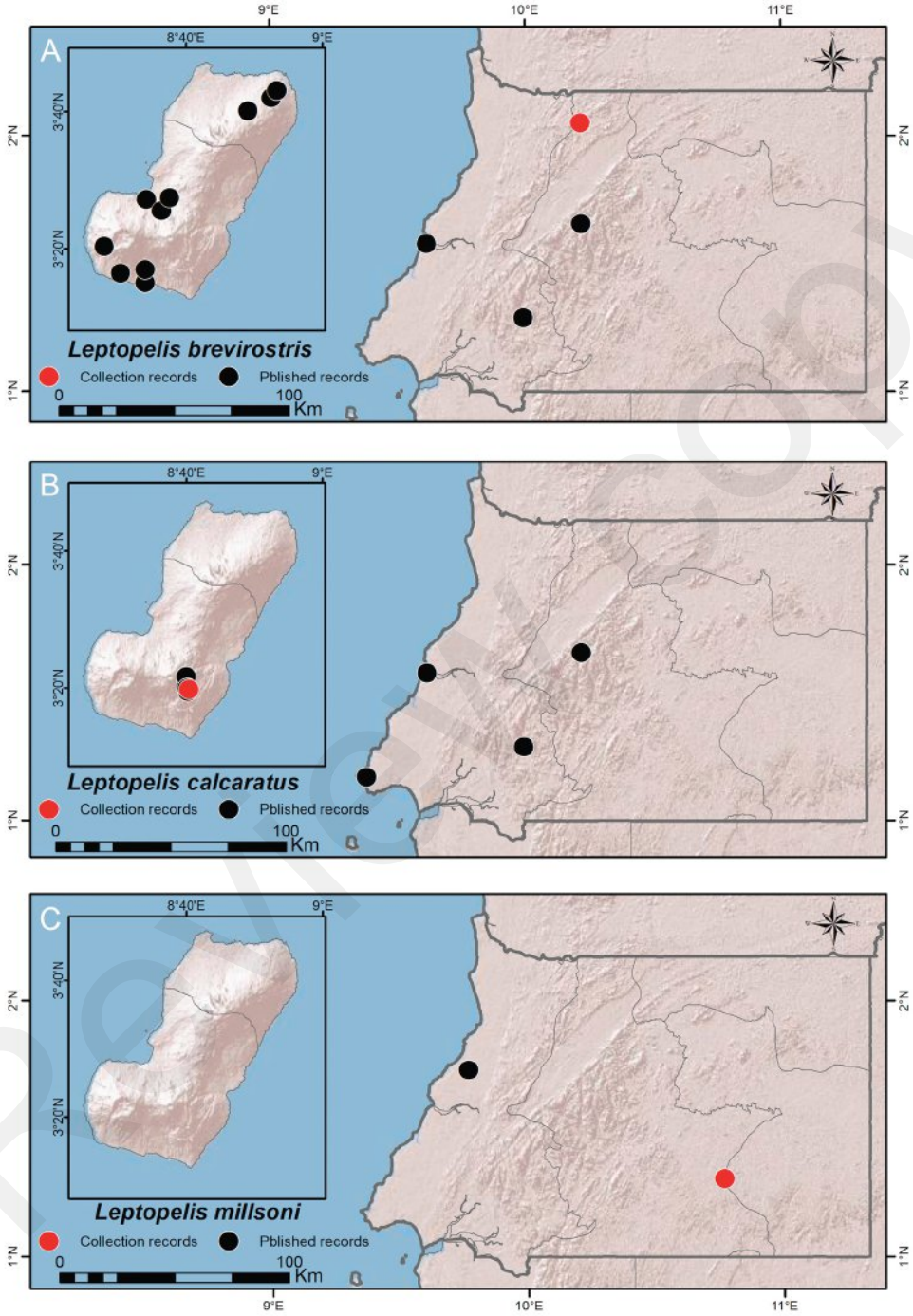
MAPS 5A–C. Distribution maps for Equatorial Guinean records of (A) *Cardioglossa leucomystax*; (B) *Cardioglossa nigromaculata*; (C) *Astylosternus batesi*.



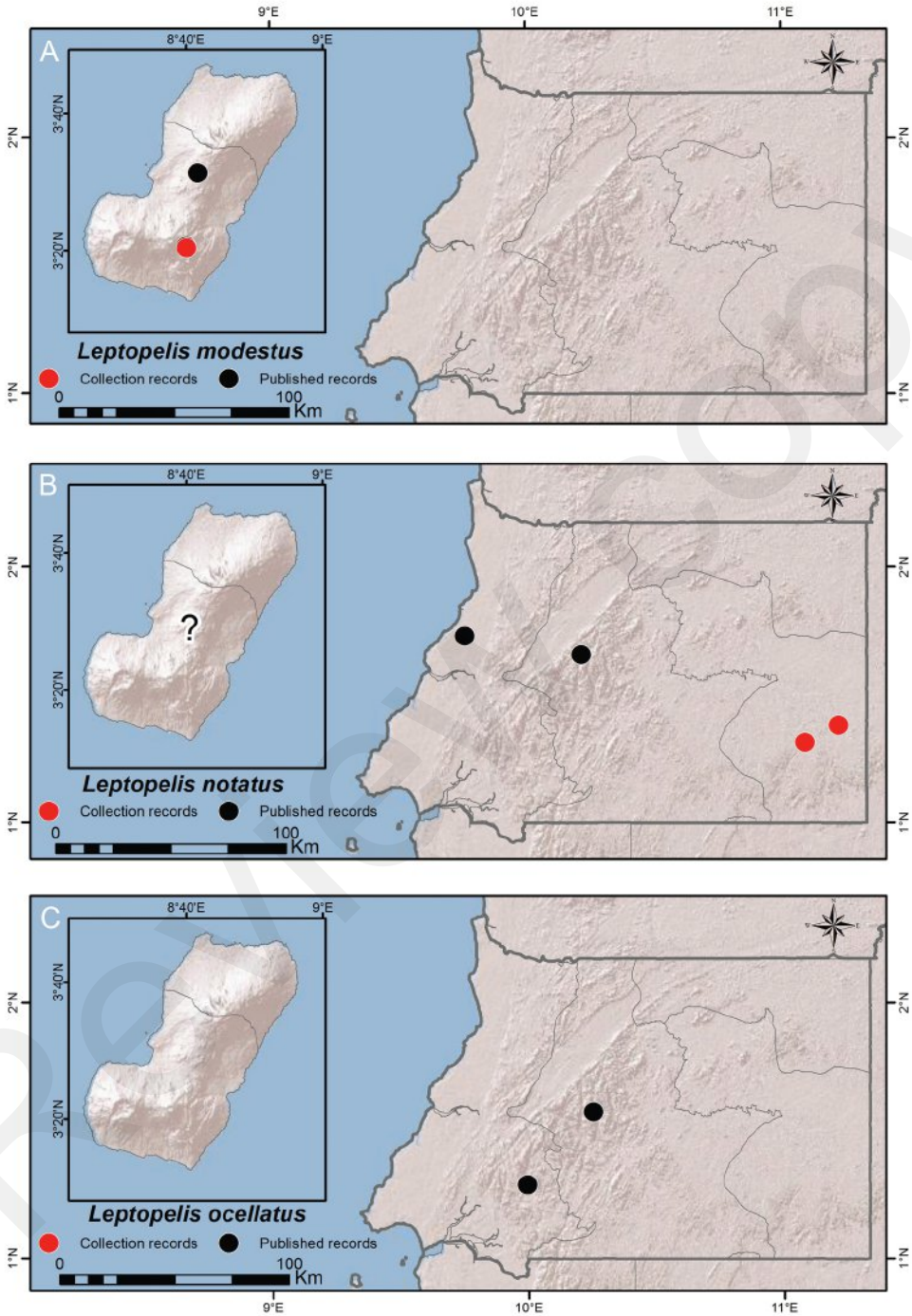
MAPS 6A–C. Distribution maps for Equatorial Guinean records of (A) *Leptodactylodon cf. stevarti*; (B) *Nyctibates corrugatus*; (C) *Scotobleps gabonicus*.



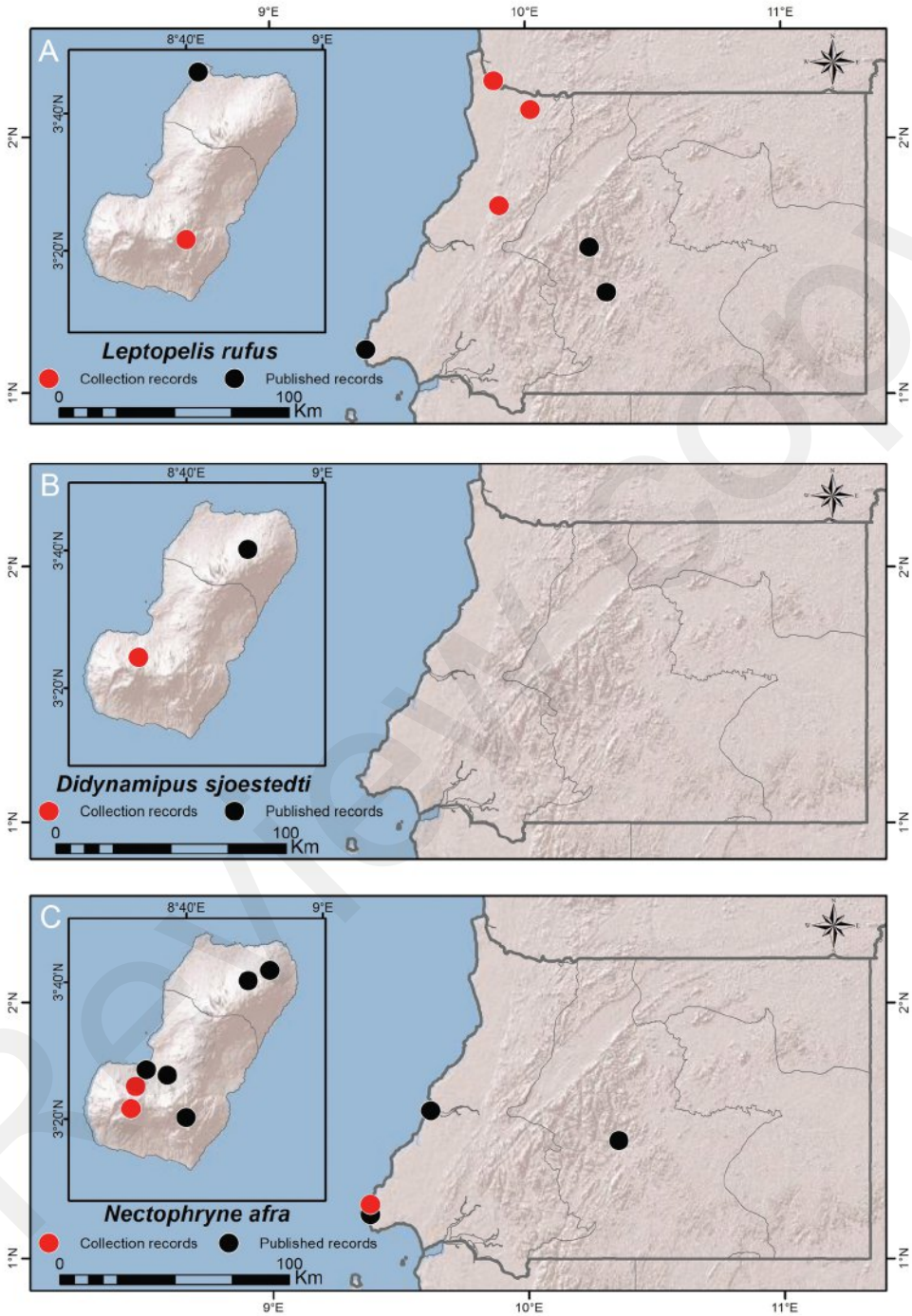
MAPS 7A–C. Distribution maps for Equatorial Guinean records of (A) *Trichobatrachus robustus*; (B) *Leptopelis aubryi*; (C) *Leptopelis boulengeri*.



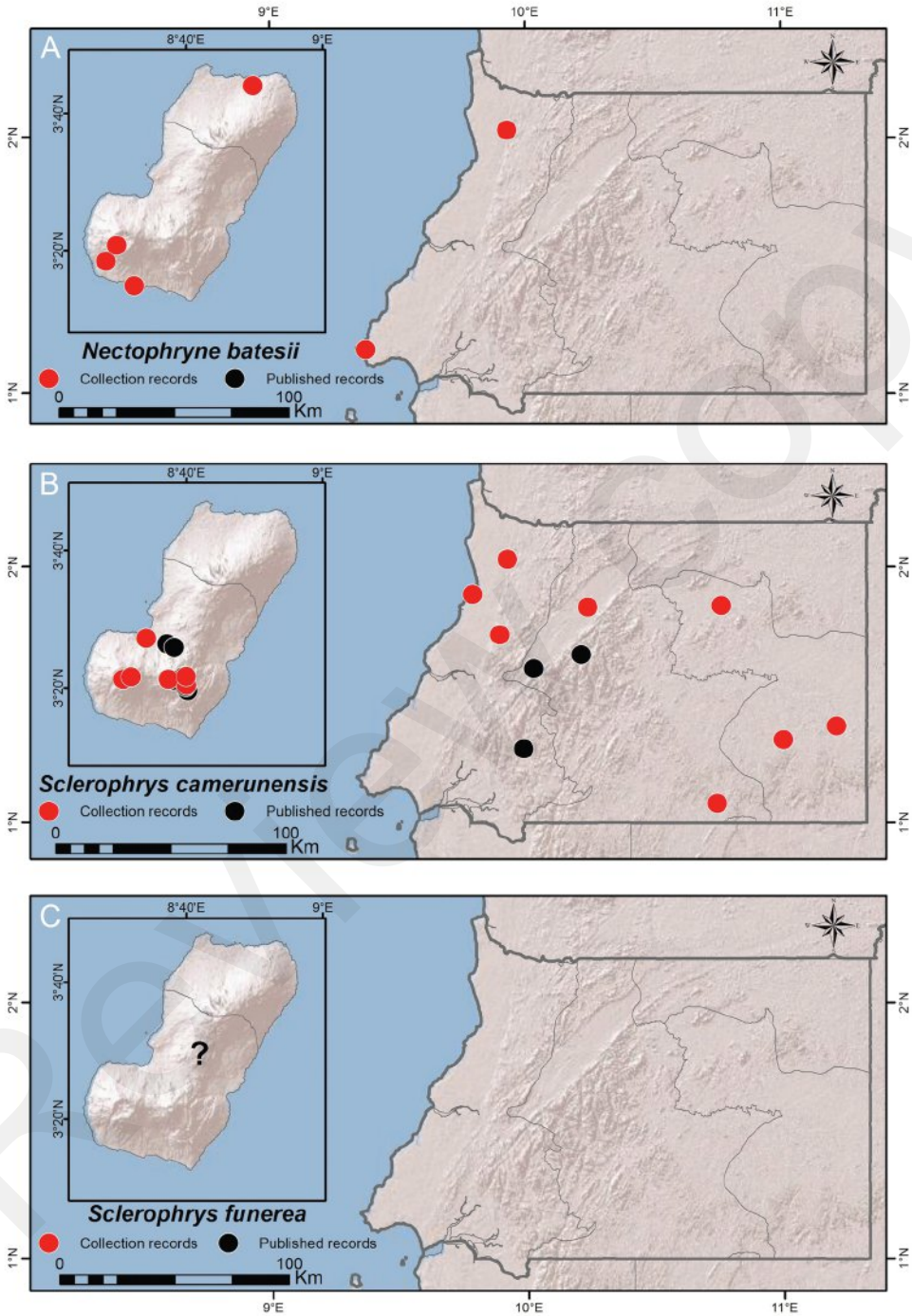
MAPS 8A–C. Distribution maps for Equatorial Guinean records of (A) *Leptopelis brevirostris*; (B) *Leptopelis calcaratus*; (C) *Leptopelis millsoni*.



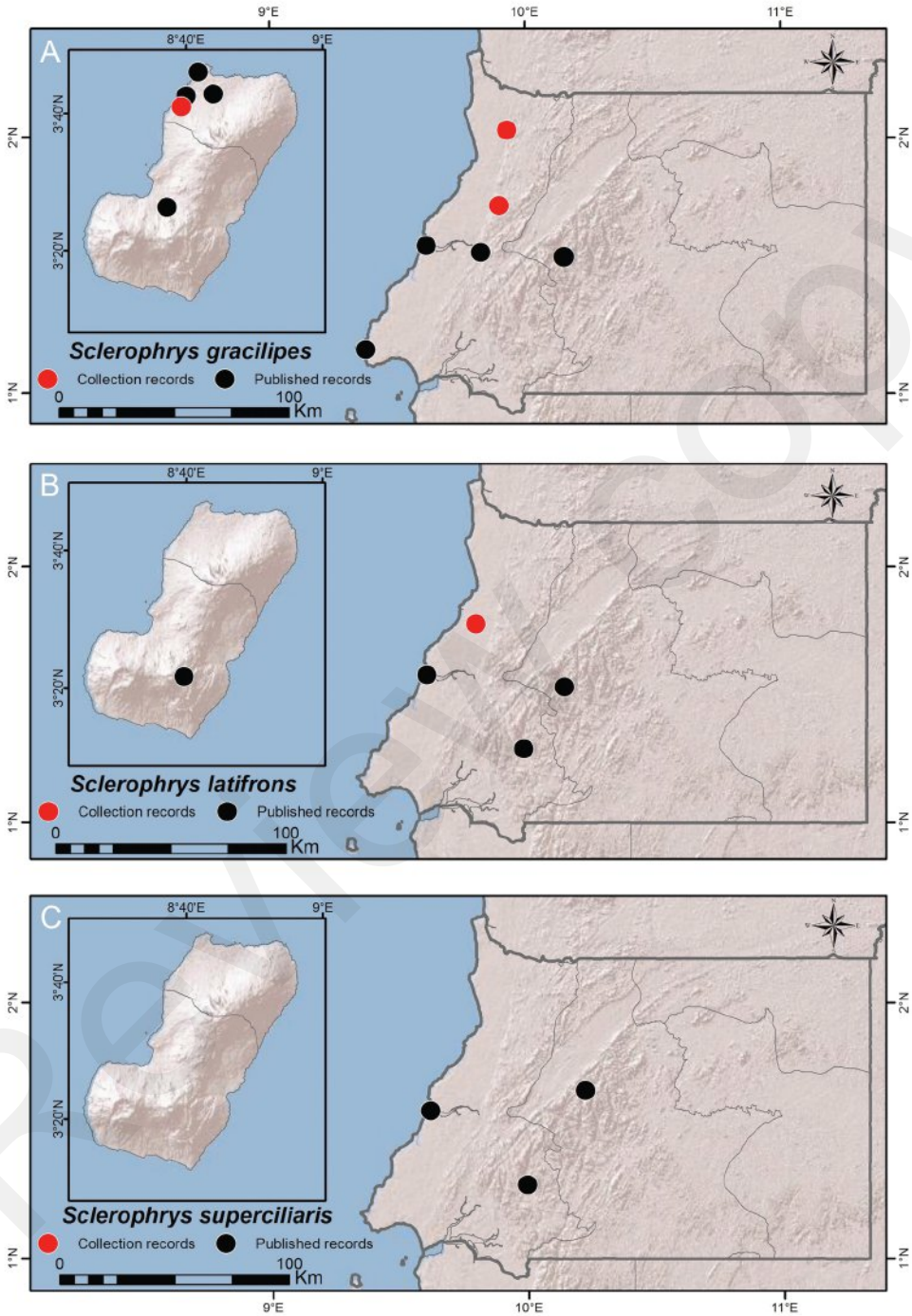
MAPS 9A–C. Distribution maps for Equatorial Guinean records of (A) *Leptopelis modestus*; (B) *Leptopelis notatus*; (C) *Leptopelis ocellatus*.



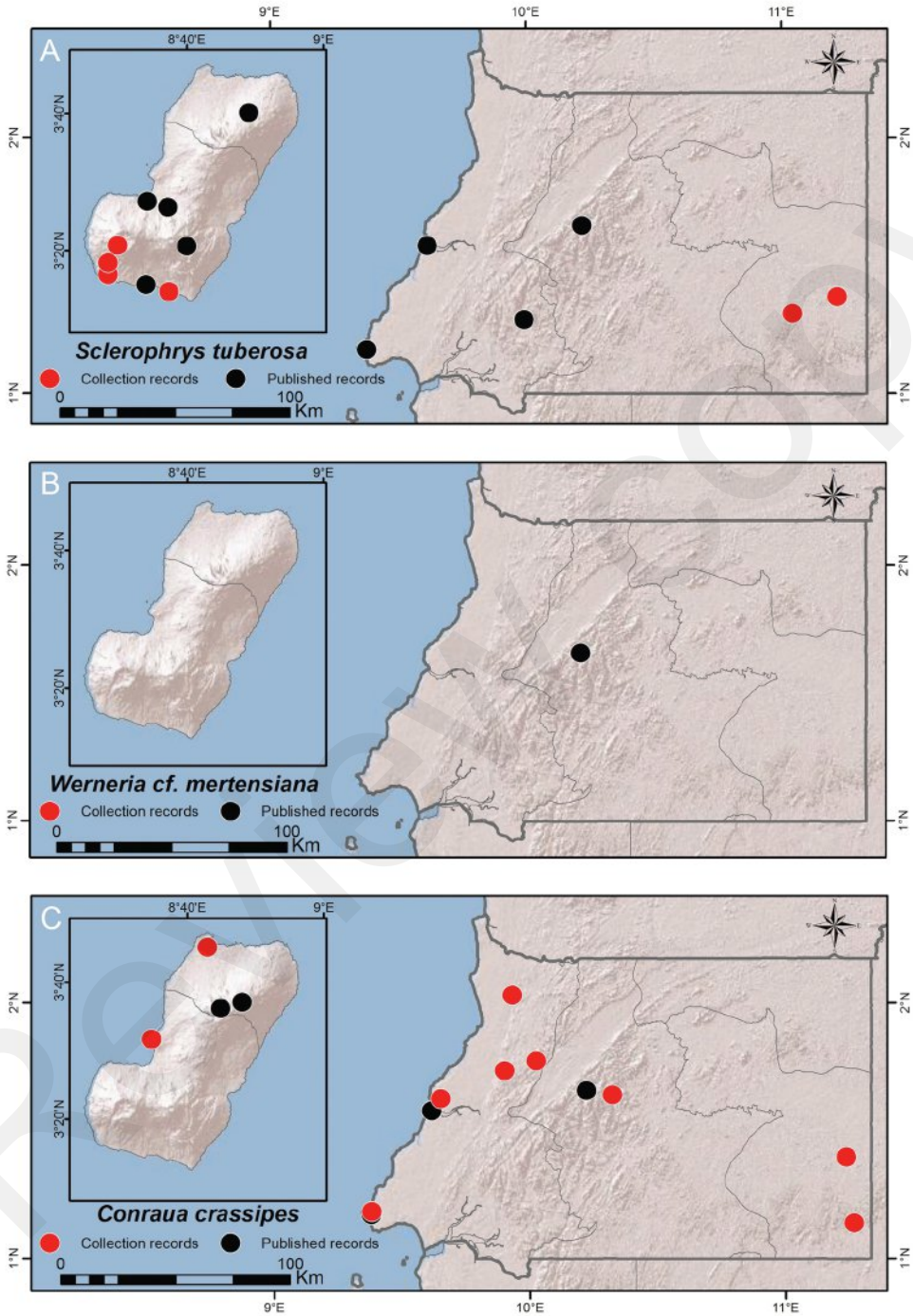
MAPS 10A–C. Distribution maps for Equatorial Guinean records of (A) *Leptopelis rufus*; (B) *Didynamis sjoestedti*; (C) *Nectophryne afra*.



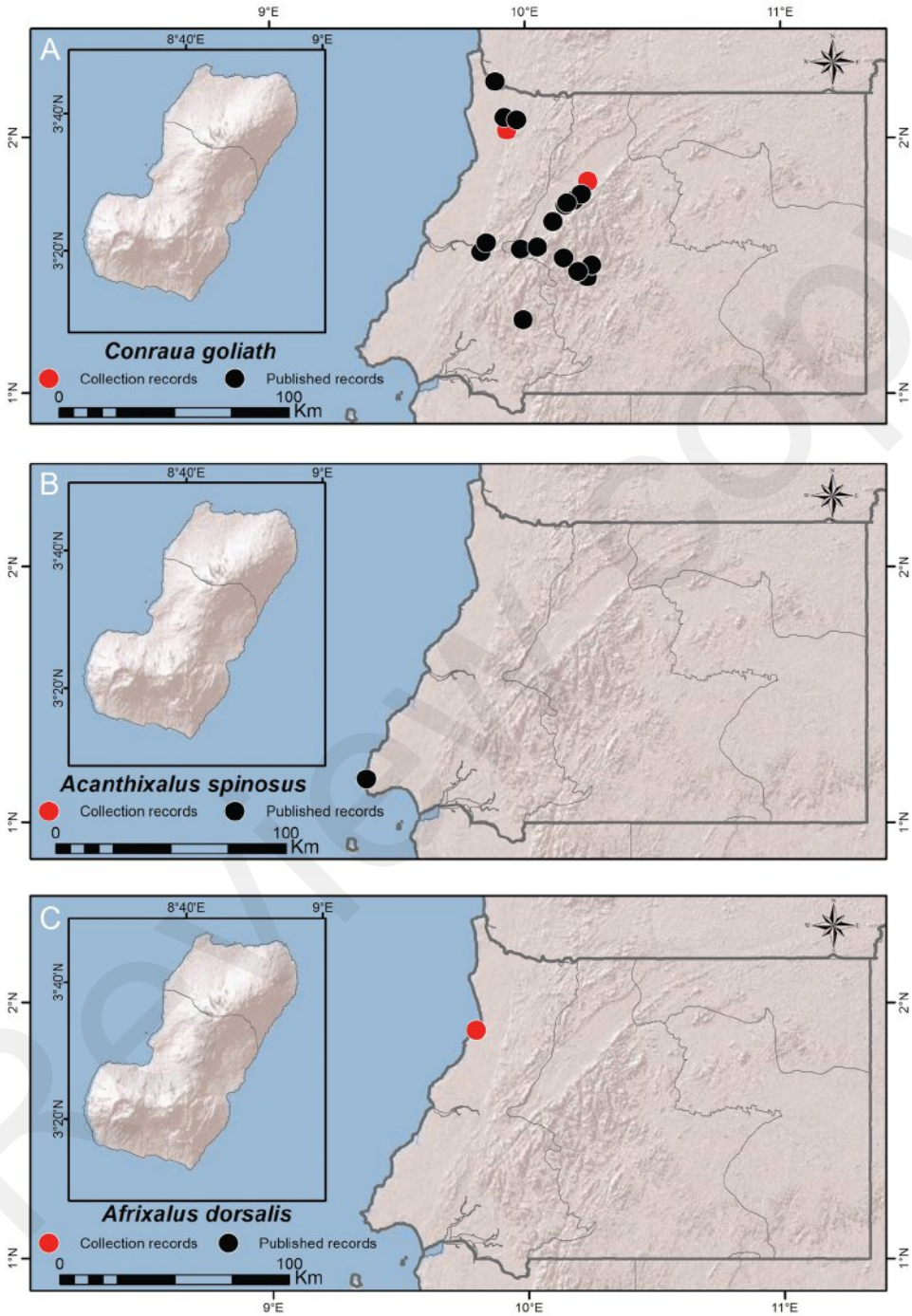
MAPS 11A–C. Distribution maps for Equatorial Guinean records of (A) *Nectophryne batesii*; (B) *Sclerophrys camerunensis*; (C) *Sclerophrys funerea*.



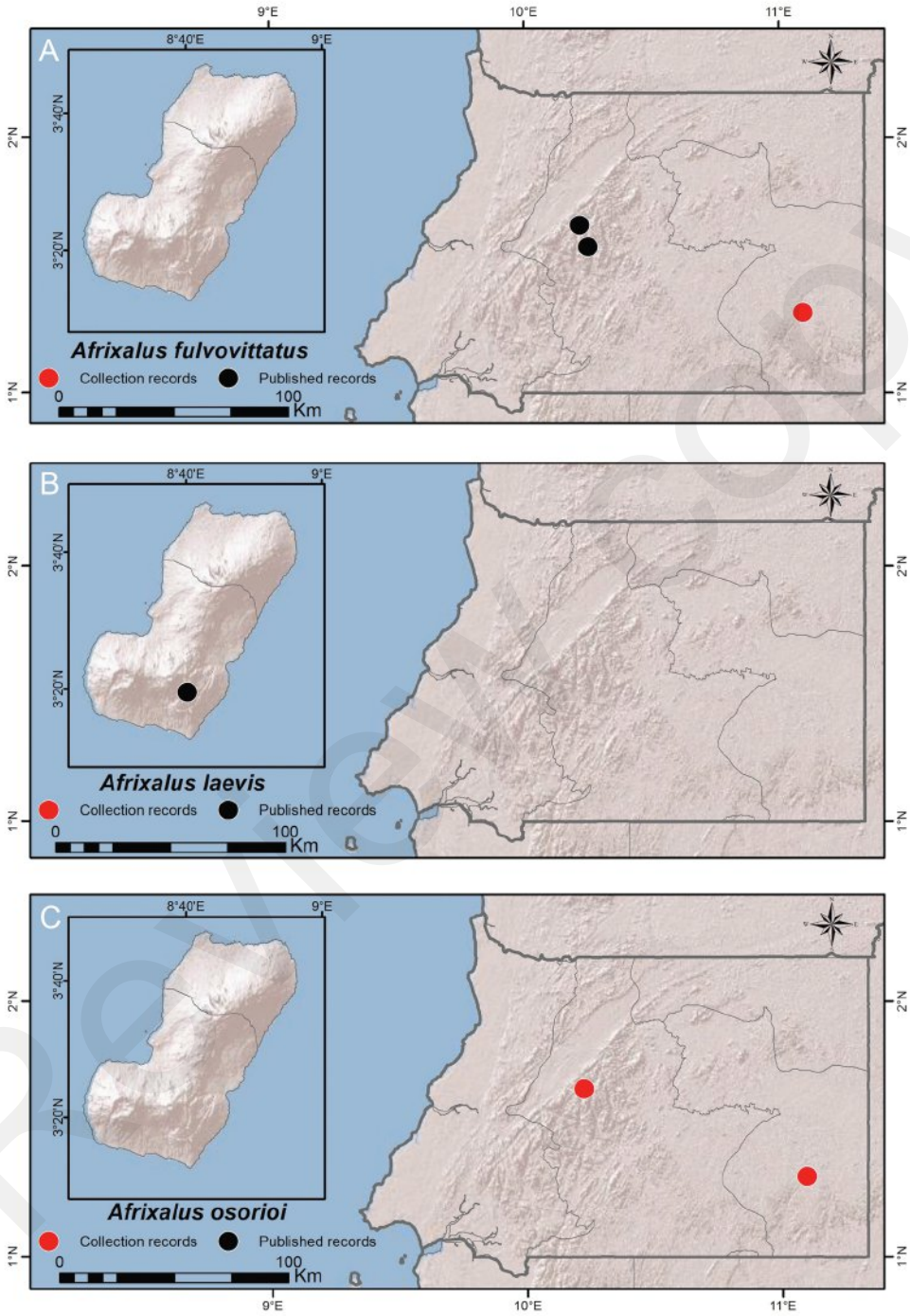
MAPS 12A–C. Distribution maps for Equatorial Guinean records of (A) *Sclerophrys gracilipes*; (B) *Sclerophrys latifrons*; (C) *Sclerophrys superciliaris*.



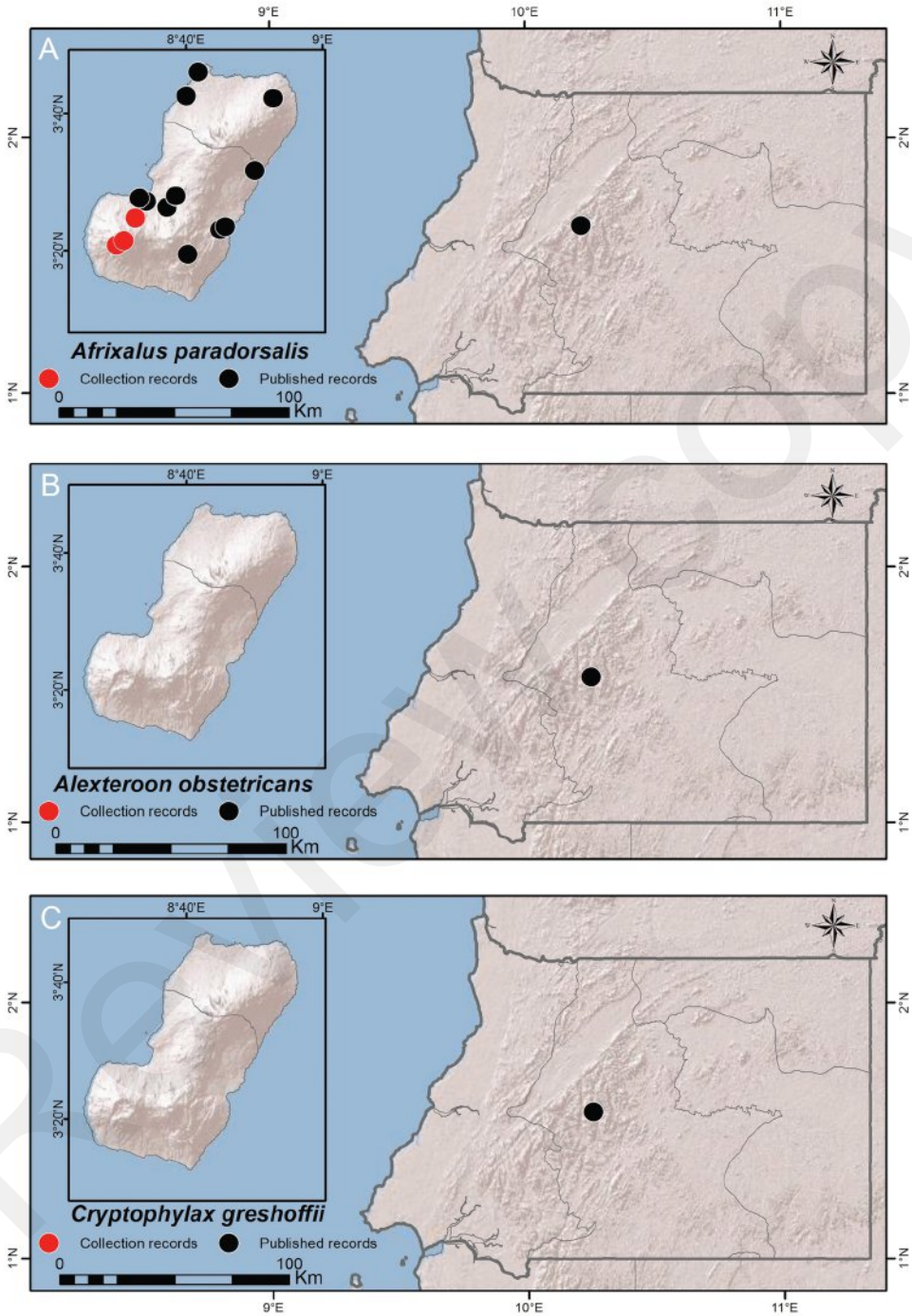
MAPS 13A–C. Distribution maps for Equatorial Guinean records of (A) *Sclerophrys tuberosa*; (B) *Werneria cf. mertensiana*; (C) *Conraua crassipes*.



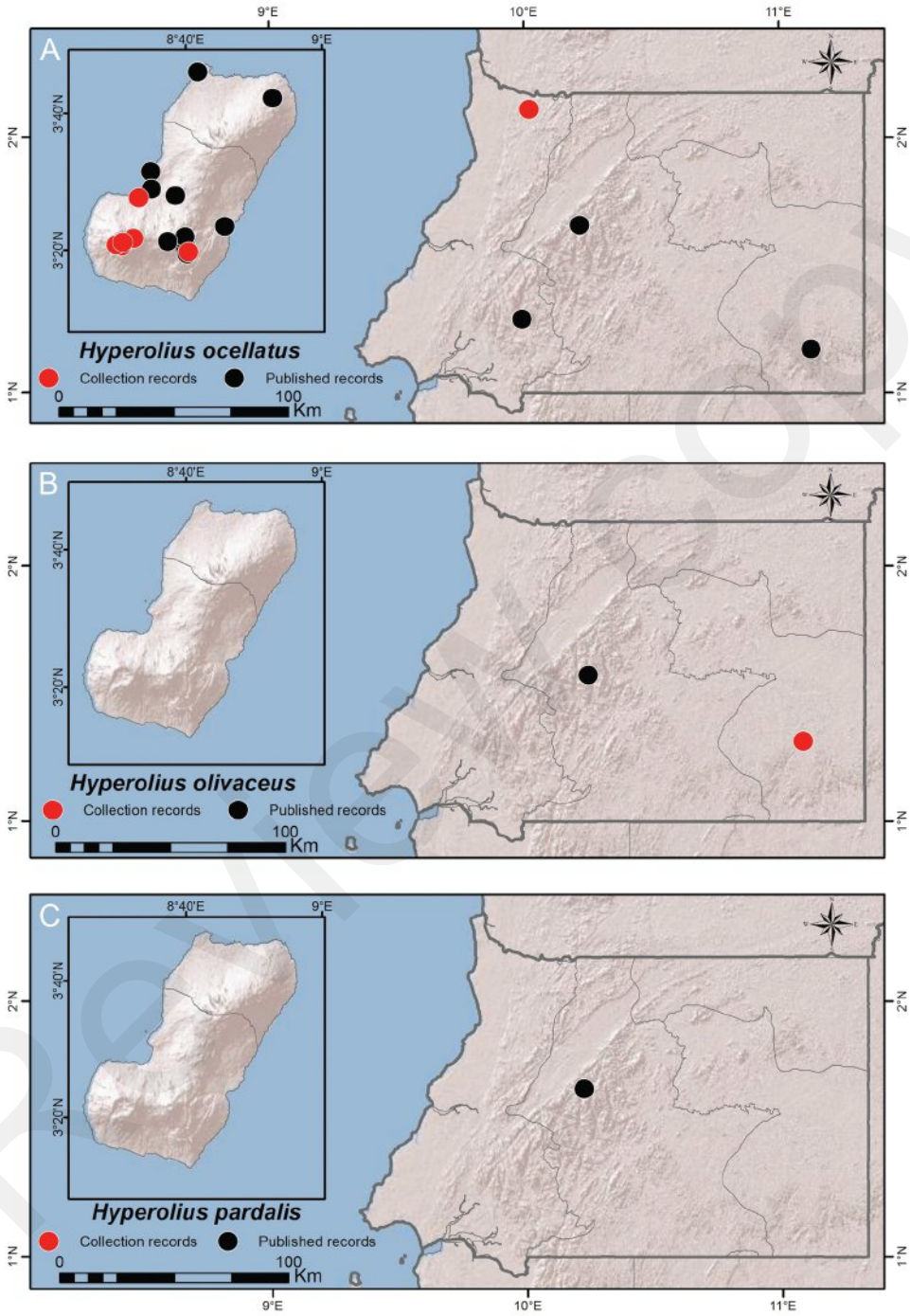
MAPS 14A–C. Distribution maps for Equatorial Guinean records of (A) *Conraua goliath*; (B) *Acanthixalus spinosus*; (C) *Afrixalus dorsalis*.



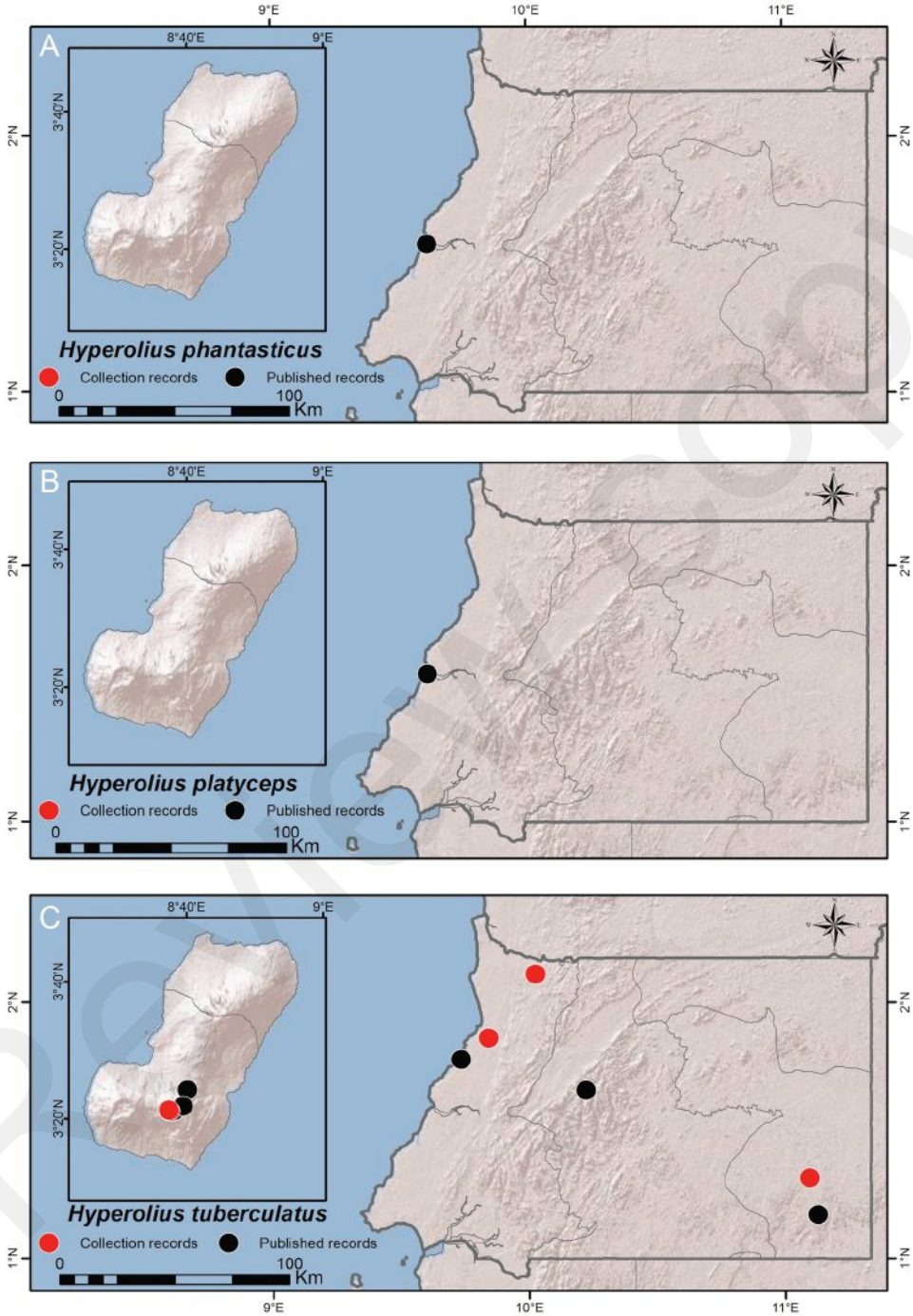
MAPS 15A–C. Distribution maps for Equatorial Guinean records of (A) *Afrixalus fulvovittatus*; (B) *Afrixalus laevis*; (C) *Afrixalus osorioi*.



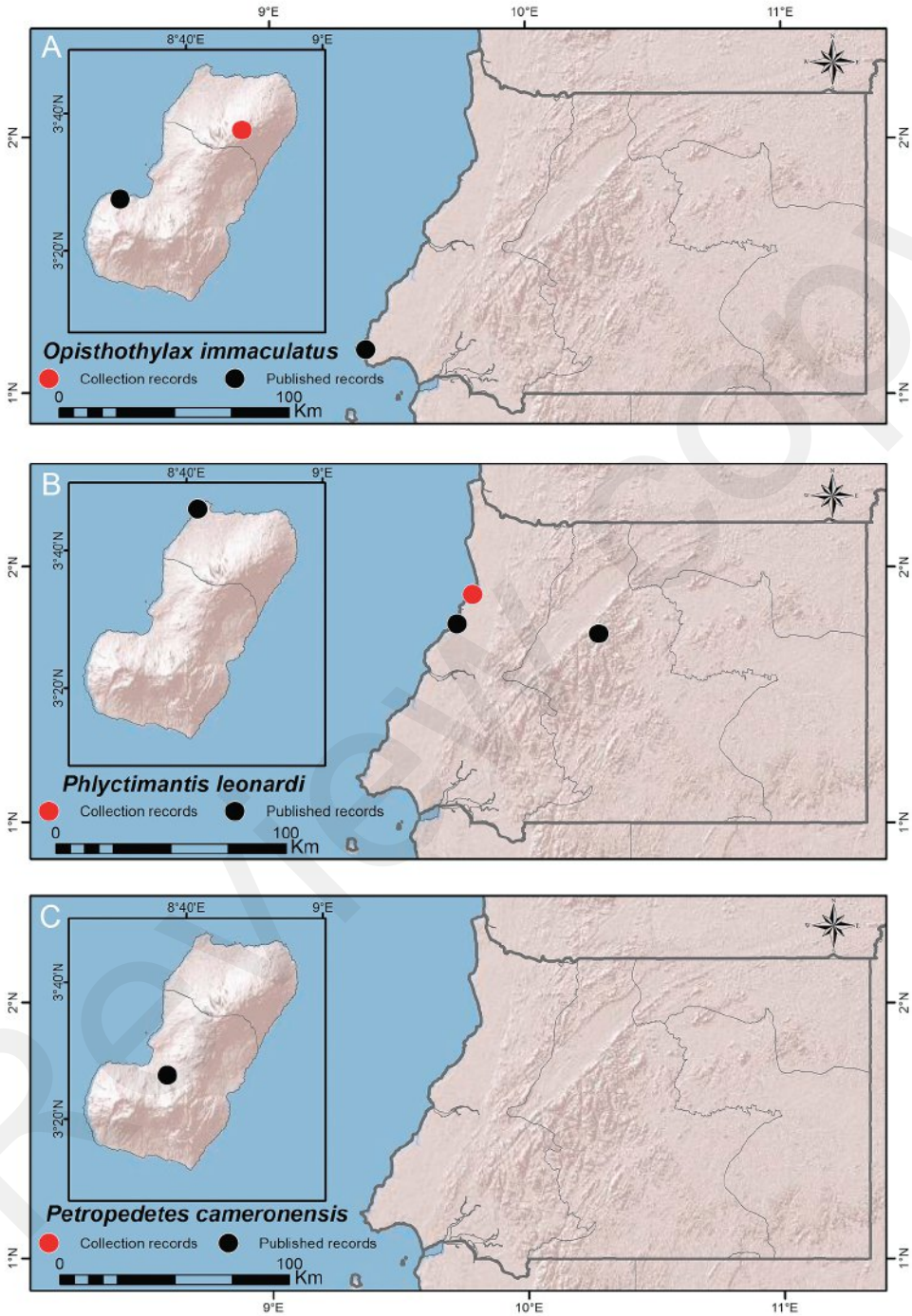
MAPS 16A–C. Distribution maps for Equatorial Guinean records of (A) *Afrixalus paradorsalis*; (B) *Alexteroon obstetricans*; (C) *Cryptophylax greshoffii*.



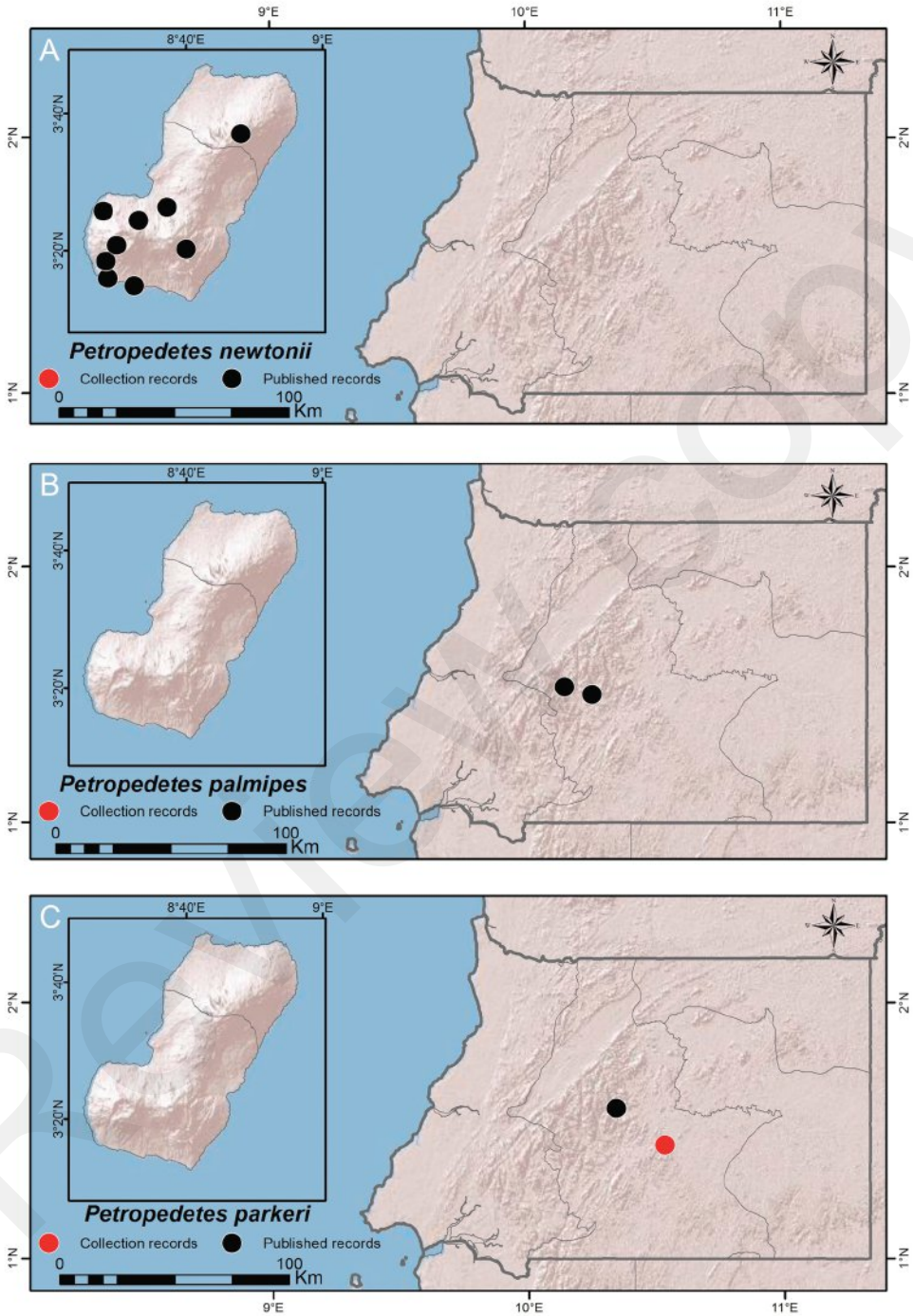
MAPS 17A–C. Distribution maps for Equatorial Guinean records of (A) *Hyperolius ocellatus*; (B) *Hyperolius olivaceus*; (C) *Hyperolius pardalis*.



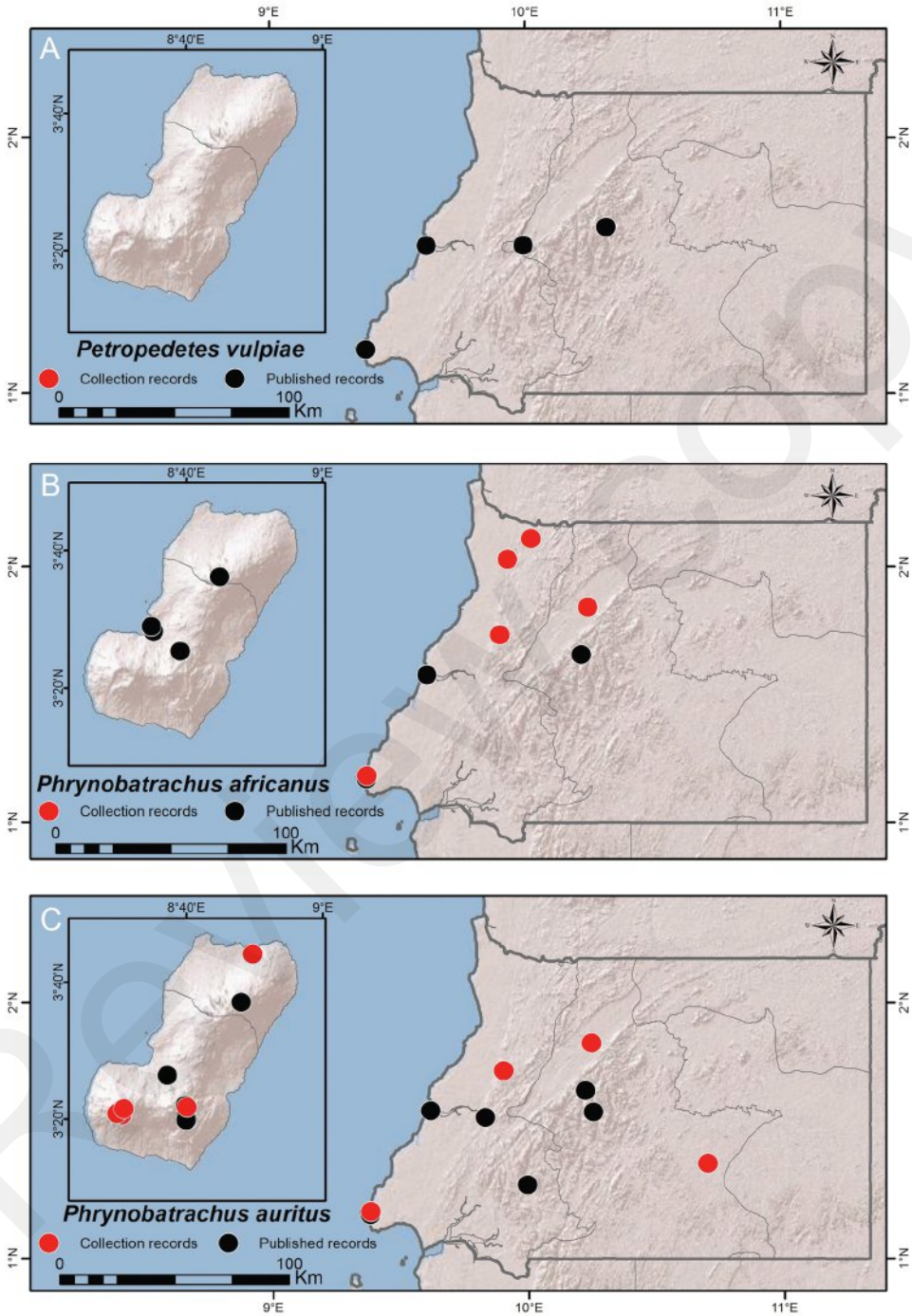
MAPS 18A–C. Distribution maps for Equatorial Guinean records of (A) *Hyperolius phantasticus*; (B) *Hyperolius platyceps*; (C) *Hyperolius tuberculatus*.



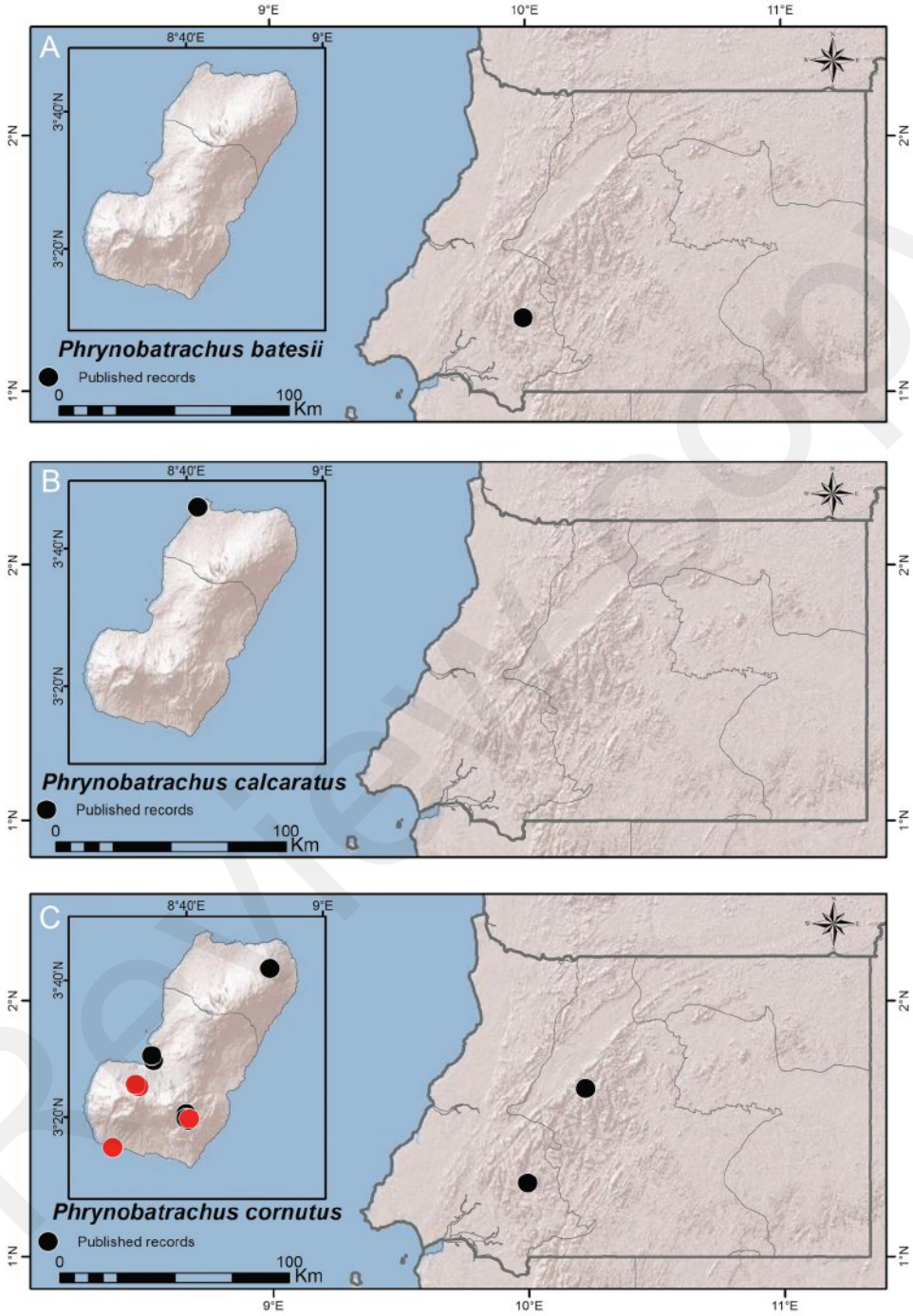
MAPS 19A–C. Distribution maps for Equatorial Guinean records of (A) *Opisthothylax immaculatus*; (B) *Phlyctimantis* cf. *leonardi*; (C) *Petropedetes cameronensis*.



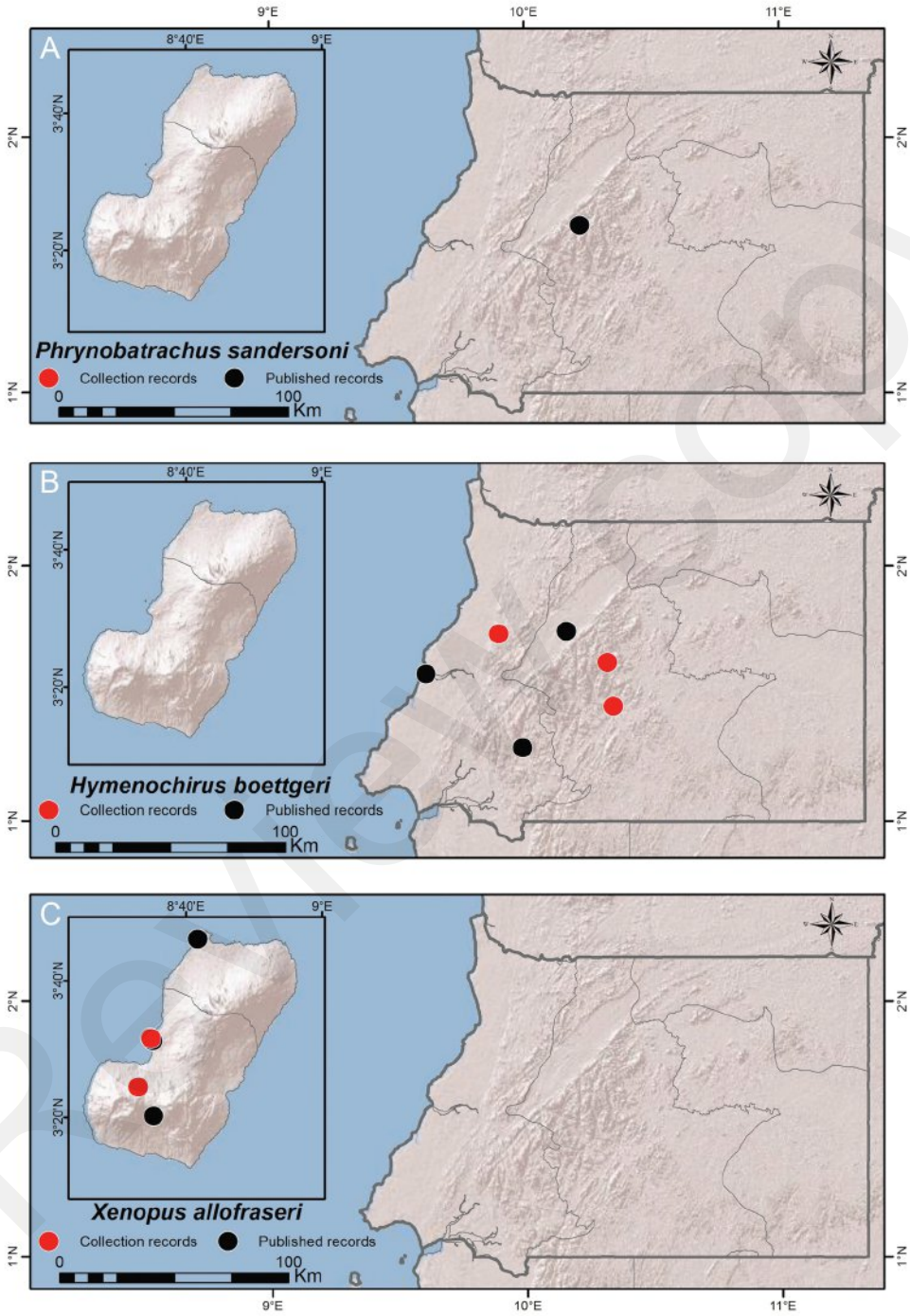
MAPS 20A–C. Distribution maps for Equatorial Guinean records of (A) *Petropedetes newtonii*; (B) *Petropedetes palmipes*; (C) *Petropedetes parkeri*.



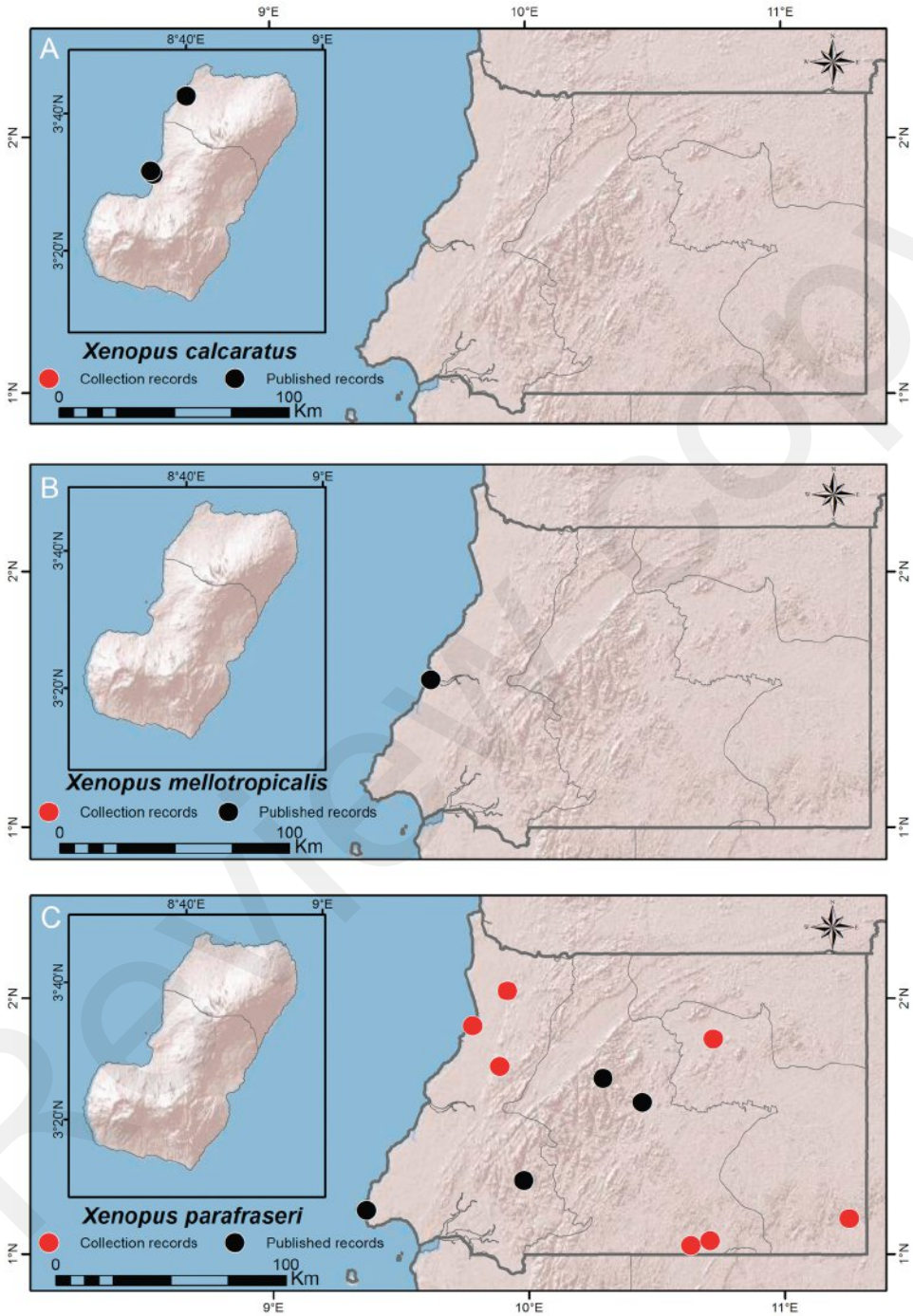
MAPS 21A–C. Distribution maps for Equatorial Guinean records of (A) *Petropedetes vulpiae*; (B) *Phrynobatrachus africanus*; (C) *Phrynobatrachus auritus*.



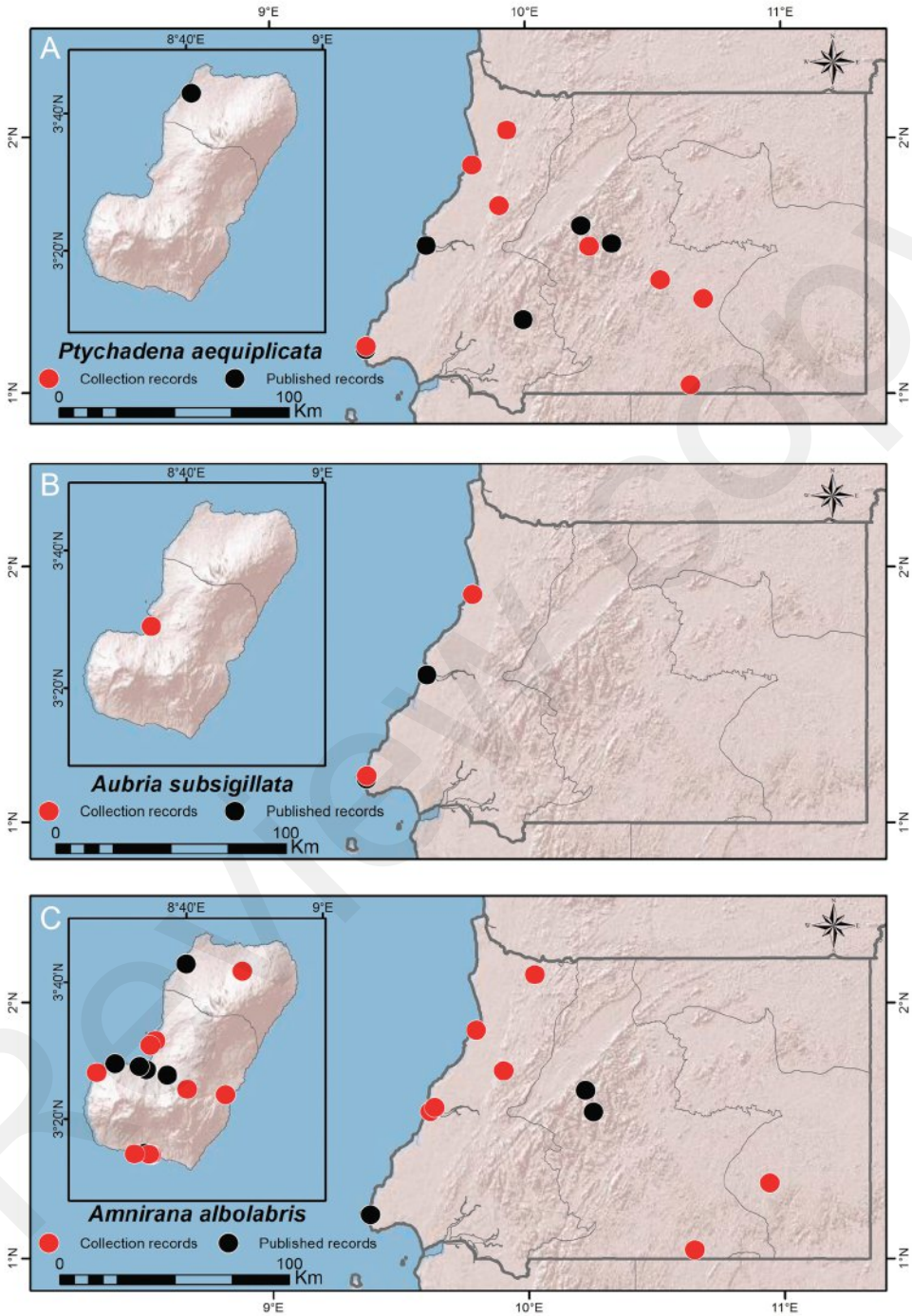
MAPS 22A–C. Distribution maps for Equatorial Guinean records of (A) *Phrynobatrachus batesii*; (B) *Phrynobatrachus calcaratus*; (C) *Phrynobatrachus cornutus*.



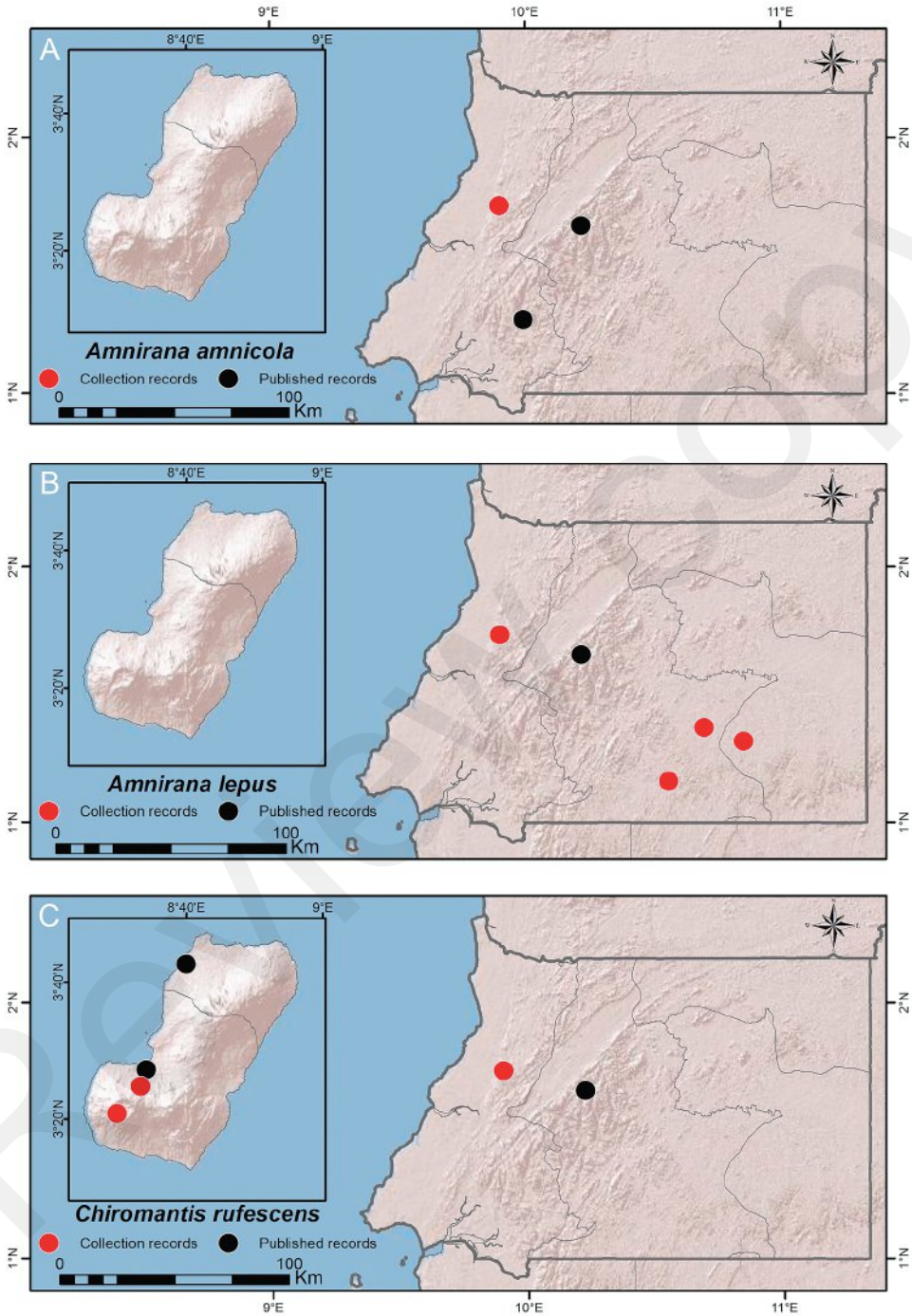
MAPS 23A–C. Distribution maps for Equatorial Guinean records of (A) *Phrynobatrachus sandersoni*; (B) *Hymenochirus boettgeri*; (C) *Xenopus allofraseri*.



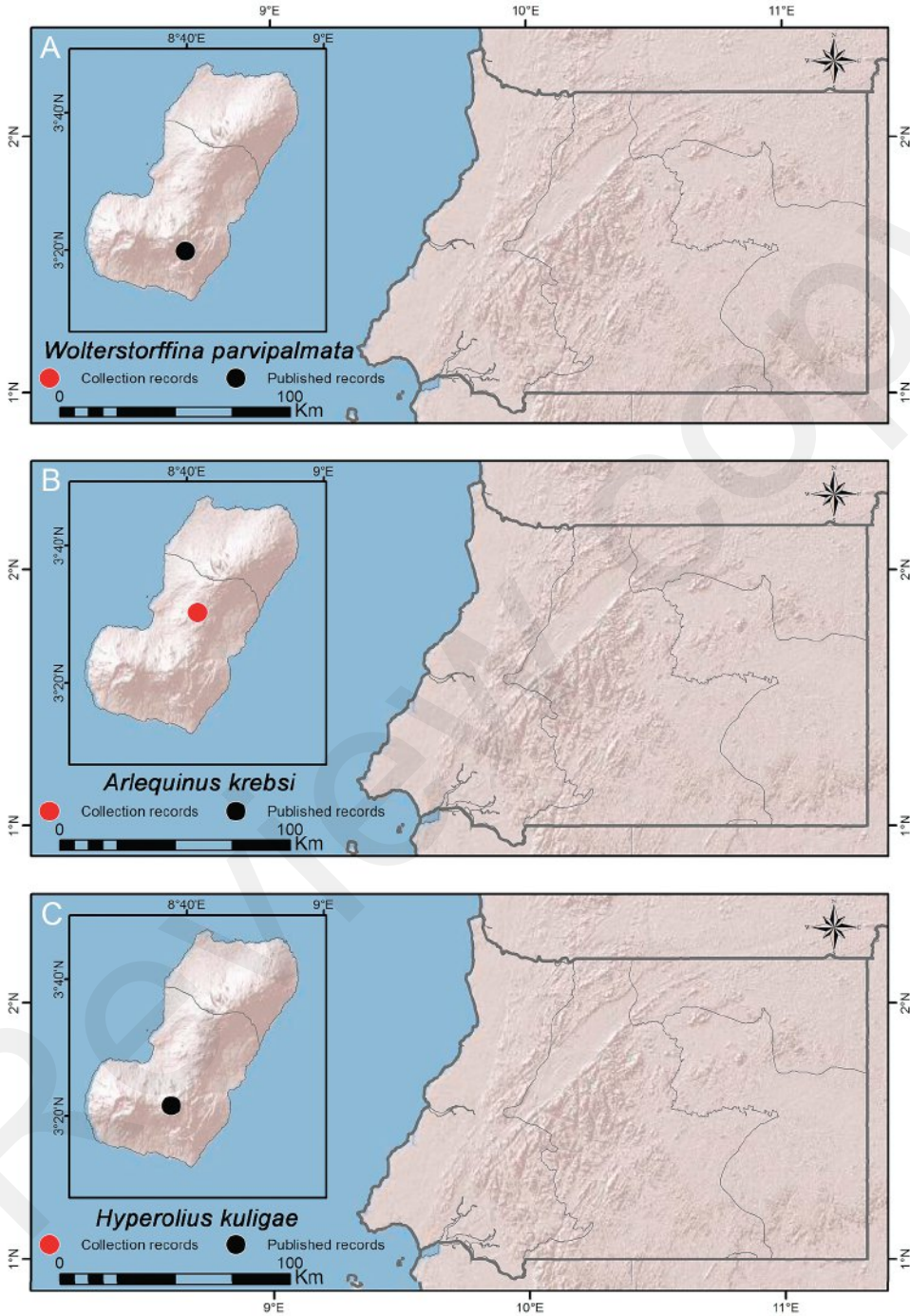
MAPS 24A–C. Distribution maps for Equatorial Guinean records of (A) *Xenopus calcaratus*; (B) *Xenopus mellotropicalis*; (C) *Xenopus parafraseri*.



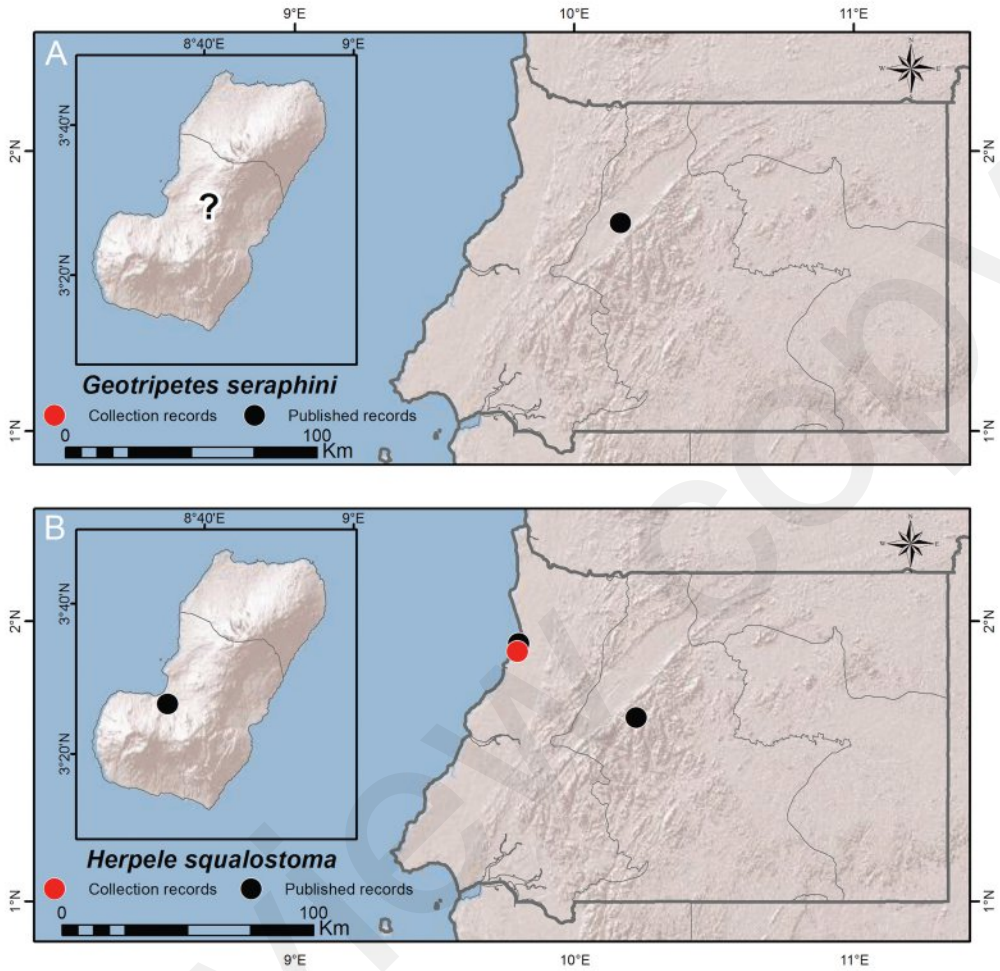
MAPS 25A–C. Distribution maps for Equatorial Guinean records of (A) *Ptychadena aequiplicata*; (B) *Aubria subsigillata*; (C) *Amnirana albolabris*.



MAPS 26A–C. Distribution maps for Equatorial Guinean records of (A) *Ammirana amnicola*; (B) *Ammirana lepus*; (C) *Chiromantis rufescens*.



MAPS 27A–C. Distribution maps for Equatorial Guinean records of (A) *Wolterstorffina parvipalmata*; (B) *Arlequinus krebsi*; (C) *Hyperolius kuligae*.



MAPS 28A–C. Distribution maps for Equatorial Guinean records of (A) *Geotripetes seraphini*; (B) *Herpele squalostoma* (the insular record of Elobey Island is not shown).

**Revision of the Grenadier Genus *Coelorinchus*
(Teleostei: Macrouridae) from the Mascarene Ridge,
Western Indian Ocean, with Description of Two New Species**

Artem M. Prokofiev^{1,2} and Tomio Iwamoto³

¹ A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii prospect 33, Moscow 119071, Russia; Email: prokartster@gmail.com; ² P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovsky prospect 36, Moscow 117218, Russia; ³ Section of Ichthyology, Institute of Biodiversity Science and Sustainability, California Academy of Sciences, 55 Music Concourse Drive, San Francisco CA 94118, USA; Email: tiwamoto@calacademy.org.

We recognize four species of *Coelorinchus* from the Mascarene Ridge, two of which are new, and none are known from outside the area. *Coelorinchus amirantensis* and *C. yurii* were in need of redescription based in part on discovered variation in morphological characters of *C. amirantensis*. The type series of *C. yurii* included a mix of two distinct species, leaving only the holotype as representative of the species. However, a search of the collections housed in the Institute of Oceanology (Moscow) revealed a second specimen of *C. yurii*, which is here described. All paratypes of *C. yurii* are referred to the new species *C. mascareneus*, which is most similar to *C. braueri*, but which can be easily distinguished by its narrow cleft-like external light organ lacking a naked dermal window. The second new species, *C. paraboliceps*, is most similar to *C. amirantensis* and *C. yurii* but differs in its (1) convex dorsal contour of snout, (2) sides of snout strongly and regularly convex in dorsal view, (3) terminal scute small and rectangular, (4) preoral region mostly scaleless, and (5) body squamation harsher. All Mascarene species belong to the “*Coelorinchus acanthiger*-group”, which is defined for 21 currently known species from all major ocean areas except the eastern Pacific. Keys are provided for the separation of Mascarene *Coelorinchus* species from other members of the *acanthiger*-group and from other Indian Ocean species that are characterized by their long snout that is incompletely supported by bone and no external evidence of a light organ or that is represented by a cleft or lens-like fossa in front of anus.

The genus *Coelorinchus* Giorna, 1809 is the most diverse lineage of the macrourid fishes comprising about 120 currently valid species (Fricke et al. 2019). This number is likely to grow as many more species await description. The species composition and taxonomy of macrourid fishes, and *Coelorinchus* in particular, are unequally investigated in different areas of the World Ocean, and the western Indian Ocean remains one of the least known regions in this respect. Seventeen currently valid species of *Coelorinchus* have been described or reported from the area (Alcock 1899; Brauer 1906; Barnard 1925; Iwamoto 1986; Cohen et al. 1990; Iwamoto and Anderson 1994; Iwamoto et al. 2004, 2006). The first author has identified a minimum of eight probably undescribed species of *Coelorinchus* collected during former Soviet Union investigations of Indian Ocean seamounts, including the two herein described from the Mascarene submarine ridge.

The Mascarene Ridge is the largest oceanic ridge or rise in the western Indian Ocean. It extends about 1250 nautical miles from north to south and includes the island chains of Amirantes, Seychelles, Cargados-Carajos, and Mascarenes. The ridge has a mostly flat top and is separated into several large banks (Mahé Plateau, Saya de Malha, and Nazareth Banks) (Fig. 1); it is treated as a structure of the continental type surrounded by the oceanic crust (a microcontinent) (Leontiev 1982). The earliest reports of Mascarene *Coelorinchus* contain no precise species identification (Shcherbachev 1984; Shcherbachev et al. 1986), and the reports of *C. acanthiger* Barnard 1925 and *C. karrerae* Trunov 1984 from the Saya de Malha Bank by Cohen et al. (1990) were misidentifications of subsequently described species. Iwamoto et al. (2006) described *C. amirantensis* and *C. yurii* from the Seychelles and Saya de Malha Bank. They noted that an additional undescribed species may exist in that area. In 2016 the first author made an attempt to identify the Mascarene *Coelorinchus* retained in the IOM collection and found the taxonomic situation even more complicated than was initially apparent. As a consequence, this new revision of Mascarene *Coelorinchus* was initiated.

MATERIAL AND METHODS

Grenadiers were sampled off the Mascarene Ridge (Fig. 1) by the former Soviet Union research vessels *Fiolent* and *Zvezda Kryma* in 1976 and 1977, *Rift* in 1982 (specimens collected during that expedition reported by Shcherbachev et al. [1986] were not available for this present study), and *Vityaz II* in 1989, and by the Israelitic expedition on the research vessel *Sea Surveyor* in 1998. Type specimens are deposited in the California Academy of Sciences (CAS), P.P. Shirshov Institute of Oceanology, Moscow (IOM), and Zoological Museum, Tel-Aviv University (TAU). Comparative materials used were from the extensive grenadier holdings of CAS and IOM; additional specimens were borrowed from AMS, CSIRO, NMNZ, SAIAB, SAM and ZMMGU (Institutional abbreviations follow Fricke and Eschmeyer [2019]).

Methods for taking counts and measurements follow Iwamoto (1970), Iwamoto and Sazonov (1988), and Nakayama et al. (2015). Anatomical terminology follows Okamura (1970a, b). We treat light organ as not evident externally when it is expressed externally only as a black ring around anus (periproct) but has no cleft-like, streak-like or fossa-like external window. The character of anterolateral snout margin fully or incompletely supported by bone can be determined by making a small incision on the underside and lifting a flap of skin to reveal the bony processes. In the descriptions, characteristics or values for the holotypes, when different from the other specimens, are enclosed in brackets. Abbreviations used are the following: HL, head length; TL, total length; n, number of specimens; FRV, fishery-research vessel; R/V, research vessel.

SYSTEMATICS

All Mascarene species of *Coelorinchus* (Fig. 2) belong to a diverse and rather loosely defined group of species characterized by the following combination of characters: snout long, incompletely supported by bone; flank scales with medial row of spinules much enlarged; rows of spinules parallel to slightly divergent, rarely strongly divergent (*C. gilberti*, *C. lasti*); scutes of head ridges conspicuously spinulose; premaxillary tooth band short, not reaching end of rictus, outer teeth weakly enlarged; light organ lacking external evidence of its presence or represented by a short cleft or dermal window in front of anus; no bands, stripes or spots on body. This group, here called *Coelorinchus acanthiger*-group, currently comprises 21 species distributed in all ocean regions except the eastern Pacific (Table 1). The Mascarene species can be distinguished from the extralimital ones by the following key.

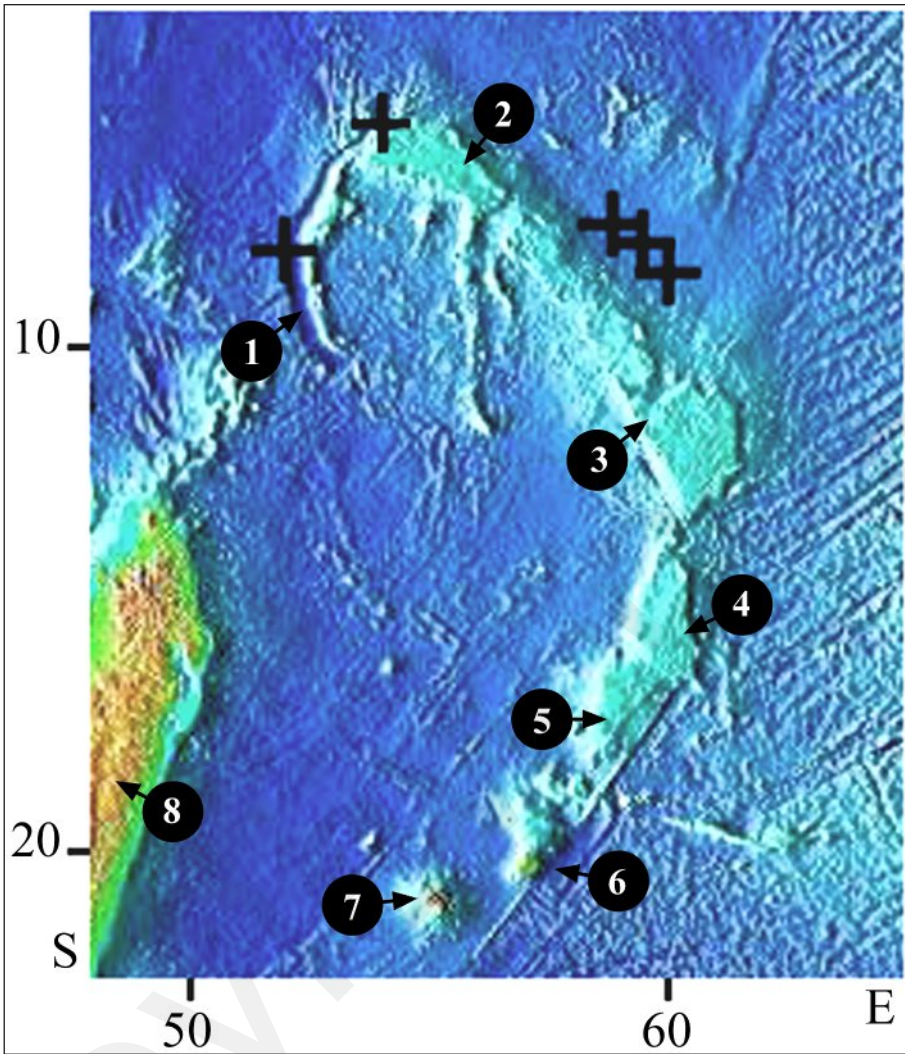


FIGURE 1. Station localities (+) on Mascarene Ridge at which grenadiers were collected (a single symbol may indicate more than one station). Abbreviations: (1) Amirantes Ridge, (2) Mahé Plateau, (3) Saya de Malha Bank, (4) Nazareth Bank, (5) Cargados-Carajos Islands, (6) Mauritius Island, (7) Reunion Island, (8) Madagascar Island.

- 1a. Underside of head fully naked.
 . *C. anisacanthus*, *C. aratum*, *C. doryssus*, *C. gilberti*, *C. labiatus*, *C. mediterraneus*, *C. occa*
- 1b. Underside of head at least partially scaled 2
- 2a. Scales between occipital ridges with a single keel-like row of spinules
 *C. parallellus*, *C. sparsilepis*
- 2b. Most of scales between occipital ridges with spinules arranged in 2-3 or more rows, or irregularly scattered 3
- 3a. Nasal fossa completely scaled *C. divergens*, *C. kermadecus*, *C. mycterismus*
- 3b. Nasal fossa naked or only partially scaled 4

- 4a. Triangular area between nasal fossa, orbit and suborbital ridge naked. *C. trachycarus*
 4b. Area between nasal fossa, orbit and suborbital ridge fully scaled 5
 5a. Lips, gums and mouth dark-dusky to black *C. lasti*, *C. obscuratus*
 5b. Lips, gums and mouth pale to light-dusky (but upper lip occasionally blackish in *C. yurii*) . 6
 6a. Scales between mid-base of first dorsal fin and lateral line 5.5–7.0. *C. acanthiger*
 6b. Scales between mid-base of first dorsal fin and lateral line 3–5 (rarely 5) 7
 7a. Tip of snout bluntly pointed in dorsal view, sides regularly convex; terminal snout scute small, 3.3 % HL, with medial element truncate, much wider than long (Fig. 15A); preoral region mostly scaleless in adults *C. paraboliceps* sp. nov.
 7b. Tip of snout acuminate in dorsal view, sides straight or concave in front of nasal fossa (but slightly convex in *C. yurii*); terminal snout scute elongate, 6+–12.2 % HL, its medial element somewhat diamond-shaped, with anterior extremity produced and acutely pointed; preoral region scaled to greater extent (usually completely scaly), except juvenile specimens. 8
 8a. Snout longer, 46–51 % HL; spinules of scales with buttresses strongly developed and forming concentric ridges even on scales below and in front of first dorsal fin; scales over interorbital region with spinules arranged in distinct keel-like rows. *C. amirantensis*
 8b. Snout shorter, 38–44 % HL; spinules of scales with or without buttresses; when prominent, buttresses not forming concentric ridges across scales at least from below and in front of first dorsal fin; scales over interorbital region mostly with spinules irregularly disposed and rows indistinct 9
 9a. Spinule rows on scales in front and below first dorsal fin clearly divergent, with medial row strongly raised; buttresses of spinules on flank scales strongly developed, often joined with those of neighboring rows; body scales strongly adherent; light organ not visible externally . *C. yurii*
 9b. Spinule rows on scales in front and below first dorsal fin parallel to slightly divergent, with medial row only slightly less inclined; buttresses of spinules on flank scales absent to weakly developed, never joined with those of neighboring rows; body scales deciduous; external light organ present 10
 10a. Light organ with dermal window (oval naked black fossa) in front of anus; terminal snout scute longer, 9.5–12.2 % HL; scales below midbase of first dorsal fin and lateral line 3.5–5.0 (usually 4.5); scales between origin of second dorsal fin and lateral line 4.5–6.5 (usually 5.0–5.5). *C. braueri*
 10b. Light organ externally represented by a short cleft in front of anus, with no dermal window present; terminal snout scute shorter, 6+–8.8 % HL; scales below midbase of first dorsal fin and lateral line 3.0–4.5 (usually 3.5); scales between origin of second dorsal fin and lateral line 4.0–5.0 (usually 4.5) *C. mascarenus* sp. nov.

***Coelorinchus amirantensis* Iwamoto, Golani, Baranes, and Goren, 2006**

Figures 2A, 3, 4, 5A–C, 6A–B, 7A–B, 8, 9.

Coelorinchus sp. A: Shcherbachev et al. 1986:201 (6°20'S, 54°23'E).

Coelorinchus amirantensis Iwamoto, Golani, Baranes, and Goren, 2006:438, figs. 4–5 (original description, Seychelles and Mascarene Plateau, 950–1900 m).

Holotype. — TAU P.11600 (157 mm HL, tail incomplete), Seychelles between Alphonse and Bijoutier islands, by trammel net in 1900 m, R/V *Sea Surveyor*, 17 Dec. 1998, collector M. Goren.

Paratypes. — TAU P.11603 (139.6 mm TL, 420+ mm TL), same data as for holotype. CAS 223467 (3, 96–126.5 mm HL, 285+–374 mm TL), IOM M.007–001 (1, 126 mm HL, 424+ mm TL) and IOM M.008–002 (1, 108 mm HL, 343+ mm TL), Mascarene Ridge, 8°26.4'S, 59°29'E, 1300–

1260 m, FRV *Fiolent*, cruise 7(9), trawl 52, 2 Sept. 1977. IOM M.005–020 (1, 79 mm HL, 250+ mm TL), Mascarene Ridge, 8°08'S, 59°37.6'E, 1247–1269 m, FRV *Zvezda Kryma*, cruise 1/6, trawl 210, 9 Nov. 1976. IOM M.006–019 (1, 85 mm HL, 260+ mm TL), Mascarene Ridge, 8°29'S, 59°35'E, 950–1150 m, FRV *Zvezda Kryma*, cruise 1/6, trawl 4, 19 June 1976. IOM M.009–010 (1, 41 mm HL, 147+ mm TL) and IOM M.010–009 (1, 80 mm HL, 265+ mm TL), Mascarene Ridge, 8°07'S, 59°18.6'E, 1300–1240 m, FRV *Fiolent*, cruise 7(9), trawl 53, 3 Sept. 1977.

DIAGNOSIS.— A species of the *Coelorinchus acanthiger*-group with light organ not evident externally; snout length 46–51 % HL, with sides in dorsal view straight to slightly concave and strongly converging anteriorly in front of nasal fossa; medial element of terminal scute long and diamond-shaped, 9.9–11.1 % HL; preoral region partially to almost completely scaled at 79 mm HL or greater; nasal fossa mostly naked, area between nasal fossa, orbit, and suborbital ridge fully scaled; scales over interorbital region with spinules arranged in distinct keel-like rows; scales on body firmly attached, bearing spinules with buttresses strongly developed, forming concentric ridges even on scales below and in front of first dorsal fin, but weaker on tail scales; 3.0–4.5 and 4.0–5.5 scales between midbase of first dorsal fin and between origin of second dorsal fin and lateral line, respectively; body dark-colored, fins darker, lips and gums pale.

DESCRIPTION.— Based on specimens 79–157 mm HL. General features of fish seen in Figs. 2A, 3, 4. Counts: first dorsal-fin rays ii + 7–8 [ii + 7]; pectoral-fin rays i + 16–19 [i + 17]; pelvic-fin rays 7; gill-rakers (inner) on 1st arch 6–8 [8]; gill-rakers on 2nd arch 5–7 (outer) / 6–8 (inner) [6 / 8]; transverse scale rows below origin of first dorsal fin 3.5–6.5 [5.5]; ditto, below midbase of first dorsal fin 3.0–4.5 [4.5]; ditto, below origin of second dorsal fin 4.0–5.5 [4.5]; ditto, between origin of anal fin and lateral line 10.0–10.5 [not counted]; lateral-line scales before origin of second dorsal fin 12(13); pyloric caeca not counted (stomachs everted).

Measurements shown in Table 2. Width of body across pectoral bases 79.3–84.5 % of greatest body depth (at dorsal-fin origin), 1.1–1.3 times smaller than greatest width of head (at preopercles). Head c. 3.0–3.6 times in TL. Snout long, 2.0–2.2 times in HL, 1.4–1.7 times greater than postorbital length of head.

Snout acute and horizontal in lateral view, with dorsal contour gently sloping toward the tip (Fig. 3A); usually distinctly convex at sides in dorsal view, with sides much more convergent toward the tip in anterior half to two-thirds of length of lateral nasal ridges; however, in some specimens (holotype and paratype IOM M.008–002) sides of snout regularly convergent toward the tip (Figs. 3B, 3C, 4). Snout tipped with long diamond-shaped terminal scute, which lateral elements form small (sometimes indistinct) “shoulders” on both sides of medial element at midlength of the latter. Anterolateral margins of snout not completely supported by bone. Orbit elliptical, its greatest diameter 4.0–4.9 times in HL, 1.8–2.3 times in snout. Suborbital shelf moderately angulated; shelf depth 1.4–1.5 times in suborbital depth. Lateral nasal ridge 2.7–2.9 times in length of suborbital ridge. Mouth large, posterior tip of maxilla extending to level of posterior quarter of orbit (rarely, to posterior third, but nearly to posterior border of orbit in largest IOM specimen), rictus below middle to posterior third of orbit. Preopercle inclined backward at about 50–70°, with moderately long, angularly rounded posteroventral lobe having crenate margin. Subopercle terminates ventrally in slender tip that extends somewhat beyond preopercle or completely hidden by preopercular lobe. Chin barbel short, slender, 3–4 times in orbit. Free neuromasts on snout, along head ridges and on underside of head prominent, more or less infuscated (more prominently on snout), surrounded by black hair-like papillae, poorly expressed on dorsal surface of head but densely covering preoral portion of snout, areas along upper jaw, and lower jaws. Inner side of gill opening usually without protrusion in its lower half (but present in 126-mm HL IOM specimen). Anus close to anal-fin origin. Light organ not externally visible.

Jaw teeth thin, conical, in narrow bands; premaxillary teeth larger than those on dentary; outermost teeth of premaxilla weakly enlarged. Premaxillary tooth band short, 1.9–2.2(2.6) times in length of rictus; dentary tooth band reaching end of rictus.

First dorsal-fin base 0.9–1.3 times shorter than the interdorsal space; second dorsal-fin spine with broken tip in all specimens examined. Pectoral fin narrow based, rather short, falling from just before anus (IOM M.007–001) to just behind anal-fin origin. Pelvic fins originate on same vertical with pectoral fins or (more often) behind it. Outermost pelvic-fin ray filamentous and extending to anus.

Squamation (Figs. 5A–C, 6A–B, 7A–B). All scales strong and adherent, those on body large. Scales on flanks, even in front of first dorsal-fin origin, with spinules arranged in parallel or slightly divergent rows; those on scales on top and lateral sides of head, in predorsal area, and on isthmus arranged in divergent rows. Spinules on scales below first dorsal-fin base arranged in 3–8 rows (usually 5–7), those on scales below origin of second dorsal fin arranged in 5–7 (smaller specimens) to 7–12 rows (largest specimens); predorsal scales with more erect and more separated spinules, arranged in 3–5 rows (Figs. 5A–C); lateral rows of spinules less complete on scales from anterior third of trunk and in specimens of smaller size; middle row of spinules distinctly enlarged, giving appearance of horizontal striations on body surface; spinules in rows gradually increasing in length posteriad, those of middle row longer and more erect in smaller specimens. Each spinule with prominent lateral buttresses often joined with those of neighboring rows to form low transverse ridges across exposed field of scale; buttresses strongly developed on scales elsewhere on trunk, in predorsal region, breast and belly, on top of head, on cheeks and gill cover (Figs. 5A–C, 6B, 7A), but becoming weaker on scales from tail region behind anterior third of anal-fin base, these scales show more depressed spinules with last spinule of medial row more greatly produced backward (Fig. 7B). Buttresses are better developed in larger specimens. Scales over interorbital region bearing spinules arranged in keel-like rows (Fig. 6A). Area between the orbit, nasal fossa, and suborbital ridge fully scaled, with spinules on scales arranged in 1–3 rows in larger specimens, in clusters to one short row in smaller specimens. Narrowest portion of suborbital shelf bearing 2–4 rows of tightly joined scales between lower rim of orbit and upper edge of suborbital ridge, scales in lowermost row much larger than 1–3 rows of small scales above it; number of rows decreasing with growth. Nasal fossa scaleless except for some cycloid scales along margins and sometimes a few spinulose scales in front of and/or below nostrils (from one side only in 126-mm HL IOM specimen, fully naked in holotype). Top of snout densely scaled. Underside of head usually densely scaled, but not gular region, branchiostegal membranes and small triangular area in front of premaxillary symphysis (Fig. 4A, 4B). Scales firmly adherent. In IOM specimens of 79 and 108 mm HL, underside of snout largely scaleless over anterior third to two-thirds of preoral length (Figs. 4C). Spinules on scales from underside of snout arranged in a single short row (up to 3–4 spinules in number in largest specimens). Density of spinulation of scales on top of head and arrangement of spinules variable. Scutes of head ridges strongly armed with numerous sharp, comparatively long, and rather stout conical spinules (thinner and longer in smaller specimens). Scutes forming medial nasal ridge 8–9 in number (including terminal scute), each with radiating rows of spinules bearing prominent buttresses. Supraoccipital scute small, coarsely spinulated, usually as large as neighboring scales but distinctly larger than same in 126-mm HL IOM specimen (slightly larger in 79-mm HL IOM specimen); postoccipital scute small, coarsely spinulated, about same size as anteriormost flank scales.

Body color brown, without markings; dark coloration formed by dense aggregations of brownish melanophores on epithelium covering exposed field of scales. When scales removed, scale pockets pure white with narrow dark-brown margins and sparse concentrations of brownish

melanophores, or rarely, isolated melanophores, much less expressed and much smaller on scale pockets from dorsal half of body and from caudal region. Distal third of scale pockets around periproct heavily pigmented by confluent brownish to blackish melanophores. Orbit encircled by dark-brown ring; anterior border of second naris blackish. Gular region and branchiostegal membranes darker than other parts of underside of head, upper reaches of branchiostegal membrane blackish. Lips and gums pale; mouth cavity pale to dusky; gustatory papillae pale, but minute papillae along margins of lower lip sometimes blackish; branchial cavity and peritoneum blackish; stomach pale. All fins dark or dusky; skin at bases of anal-fin rays sometimes darker than on adjacent scales.

VARIATION.— Specimens examined are variable in shape of snout, degree of scale covering of preoral region, and distribution of spinules on scales atop head. The holotype (157 mm HL) and paratype IOM M.008–002 (108 mm HL) show sides of snout regularly converging toward the tip, in contrast to the other specimens with sides of snout distinctly convex in dorsal view (compare Figs. 3B and 3C). However, this character does not correlate with other variable features. Paratype IOM M.005–020 (79 mm HL) is fairly distinct from the others in arrangement of scales in preoral region, which is largely scaleless along two-thirds of its length with scales cycloid laterally and behind scaleless area. However, in paratype IOM M.008–002, the anterior third of preoral region is also scaleless, though laterally and posteriorly from that area scales are spinulose. Paratype IOM M.005–020 shows less numerous spinules on scales on top of head in comparison to other specimens examined; however, density and arrangement of spinules on these scales are variable in all available specimens, and there are no specimens having these features nearly identical. We treat all these differences as individual variation.

The 41-mm HL paratype (IOM M.009–010; Fig. 8) differs from the adult and subadult specimens described above in having underside of head completely devoid of scales (Fig. 8B). It has body scales (Fig. 9) much less adherent than in larger specimens, with fewer but more raised spinules, 3–4 rows on scales in front and below first dorsal fin, in interdorsal area, and on isthmus; scales lost from other parts of body. The last spinule of medial row on scales from dorsal half of trunk conspicuously enlarged. Head ridges much more coarsely spinulated than in adults, but spinules on scales from head are less developed, and scales between the orbit and suborbital ridge are largely cycloid. Overall coloration is much paler than in adults but darkish circumorbital ring is already obvious. In proportions this juvenile is distant from all available larger specimens in the longer jaws and premaxillary tooth band, shorter terminal scute, much shorter lateral nasal ridges, and wider and somewhat shorter snout (Table 2).

ETYMOLOGY.— The species name is derived from the Amirantes Basin, the type locality of the species (Iwamoto et al. 2006).

COMPARISONS.— *Coelorinchus amirantensis* can be easily distinguished from all other Mascarene species of *Coelorinchus* by its distinctly longer and more acutely pointed snout, relatively shorter premaxillary tooth band, short-based first dorsal fin apparently lacking elongated filament of its second ray at all stages of growth, shorter interdorsal distance, and by details of squamation. Scales of *C. amirantensis* are strongly adherent with prominent lateral buttresses mostly confluent with each other to form low transverse ridges across exposed field of scale (vs. scales deciduous and buttresses weak or lacking in *C. mascarenus*) (Figs. 5A–F); buttresses forming transverse ridges on scales from predorsal area and flanks above lateral line, and before second dorsal-fin origin (vs. not forming transverse ridges in *C. yurii*) (Figs. 5A–C, 5J–L, 6B, 6F), becoming weaker on tail scales with transverse ridges disappearing, in contrast to *C. paraboliceps* (Figs. 7B, 7D). Scales on interorbital region possess spinules arranged in distinct keel-like rows in *C. amirantensis* instead of irregularly disposed spinules on most of scales in that area in the three other

Mascarene species (Figs. 6A, 6C, 6E). Morphometric differences between four Mascarene *Coelorinchus* species are summarized in Table 2. A comparison with similar extralimital species was provided by Iwamoto et al. (2006), see keys to species in current paper for additional data.

The 41-mm HL juvenile of *C. amirantensis* has underside of head completely scaleless and can be confused with *C. cf. labiatus*, which has the scaleless underside of head at all stages of growth. The 38-mm HL juvenile of *C. cf. labiatus* (IOM 00184) shows all lateral rows of spinules on scales in front, below and behind first dorsal fin complete and reaching distal margin of scale, in contrast to those in adults and similar to those of *C. amirantensis*. However, these spinules are much finer and more depressed than in juveniles of *C. amirantensis*, more numerous (usually in 5 rows, rarely in 4 or 6), with last spinule of medial row never much enlarged. The head ridges in juveniles of *C. cf. labiatus* are not so coarsely spinulated, and spinules on scales on top and sides of head are poorly developed (most scales cycloid and much more deciduous than in *C. amirantensis*). The 40–45 mm HL juveniles of *C. braueri* (IOM 00191) have underside of head also scaleless or with few scales at corners of mouth only, and the number and shape of spinules on their trunk scales is similar to those observed in the juvenile of *C. amirantensis*. However, spinulation of head ridges is much harsher in *C. amirantensis*, and the spinules on scales on top of head are arranged in parallel rows vs. rather irregularly disposed in juveniles of *C. braueri*. Furthermore, the juveniles of *C. braueri* possess a small naked dermal window in front of anus and a filamentous second dorsal-fin ray (both absent in *C. amirantensis*). We have no juveniles of three other Mascarene species for comparison. The 40–50-mm HL juveniles of *C. flabellispinis* and *C. trunovi* already have underside of head partially scaled.

***Coelorinchus mascarenus* new species**

Figures 2B, 5D–F, 10, 11A, 12B, 12D, 13A.

Coelorinchus yurii (partim.) Iwamoto, Golani, Baranes and Goren, 2006:434 (all paratype specimens; Saya de Malha Bank, Mascarene Ridge, 800–1130 m).

Holotype.— IOM M.011–007 (91 mm HL, 297+ mm TL), Mascarene Ridge, off Saya de Malha Bank, 8°32'S, 59°41'E, 960–1130 m, R/V *Vityaz-II*, station 2820, 29-m otter-trawl, 10 Jan. 1989.

Paratypes.— IOM M. 012–019 (1, 93 mm HL, 260+ mm TL) and CAS 66427 (2, 84.7–94.3 mm HL, 275+–313 mm TL), same data as for holotype. CAS 223466 (3, 72–76.5 mm HL, 245–290 mm TL) and IOM M.013–000 (7, 72–95 mm HL, 250+–330+ mm TL), Mascarene Ridge, Saya de Malha Bank, 9°32.7'S, 60°02'E, 800 m, FRV *Fiolent*, cruise 7(9), trawl 156, 26 Sept. 1977.

NOTE.— We could not find the 84.7-mm HL paratype of *C. yurii* (FRV *Fiolent*, cruise 7(9), trawl 156A) listed by Iwamoto et al. (2006) for the current study; thus, its identification remains uncertain.

DIAGNOSIS.— A species of *Coelorinchus acanthiger*-group with light organ externally represented by a short cleft anterior to anal surround, its length 3.0–9.9 % HL; snout length 39–43 % HL, length medial element of terminal scute 6+–8.8 % HL; preoral region partially to almost completely scaled at 72 mm HL or greater, nasal fossa scaleless, triangular area between nasal fossa, orbit, and suborbital ridge sparsely scaled; scales over interorbital space with irregularly disposed spinules, not forming clear keel-like rows; scales on body loosely attached, bearing spinules with buttresses weak or absent; 3.0–4.5 and 4.0–5.0 scales between midbase of first dorsal fin and between origin of second dorsal fin and lateral line, respectively; body color light, fins darker, lips and gums pale to dusky.

DESCRIPTION.— General features of fish seen in Figs. 2B, 10. Counts: first dorsal-fin rays

ii + 8; pectoral-fin rays $i + 16-18$ [$i + 17$]; pelvic-fin rays 7; gill-rakers (inner) on 1st arch 7 (8, as exception) [7]; gill-rakers on 2nd arch 5–6 (usually 5) (outer) / 7 (as exception, 8) (inner) [5 / 7]; transverse scale rows below origin of first dorsal fin 3.5–4.5 [4.5]; ditto, below midbase of first dorsal fin 3.0–4.5 [3.5]; ditto, below origin of second dorsal fin 4.0–5.0 (usually 4.5) [4.0]; ditto, between origin of anal fin and lateral line 10–15 [15]; lateral-line scales before origin of second dorsal fin 14–15 [14]; pyloric caeca 6–11 ($n = 5$).

Measurements shown in Table 2. Width of body across pectoral bases 74.3–86.4 % of greatest body depth (at dorsal-fin origin), 1.1–1.3 times smaller than greatest width of head (at preopercles). Head c. 2.8–3.5 (usually 3.3 or more) times in TL. Snout long, 2.4–2.6 times in HL, 1.1–1.3 times greater than postorbital length of head. Snout acute, slightly upturned (usually) to almost horizontal in lateral view, with dorsal contour very weakly concave (Fig. 10A); distinctly convex at sides in dorsal view, with sides much more strongly convergent toward the tip in anterior third of snout length (Figs. 10B, 10C). Snout tipped with moderately long, somewhat diamond-shaped terminal scute, which lateral elements form conspicuous “shoulders” aside medial element. Anterolateral margins of snout not completely supported by bone. Orbit elliptical, 3.7–4.3 times in HL, 1.5–1.7(1.8) times in snout. Suborbital shelf angulated (Fig. 13A); shelf depth 1.7–2.2 times in suborbital depth. Lateral nasal ridge 3.2–3.3 times shorter than suborbital ridge. Mouth comparably large, posterior tip of maxilla extending below posterior third to posterior quarter of orbit, rictus below middle of orbit. Preopercle inclined backward at about 60–70°, with moderately long posteroventral lobe more or less angularly rounded at tip. Subopercle terminates ventrally in slender tip that extends beyond preopercle. Chin barbel short, slender, 2.8–3.6 (usually 3.0–3.4) times in orbit. Free neuromasts on snout, along head ridges and on underside of head prominent, vary in color from whitish to blackish (always more or less infuscated on top and underside of snout), surrounded by isolated or scattered black hair-like papillae, more densely aggregated on preoral portion of underside of head below suborbital ridge and in front of upper jaw, few or absent in nasal fossa, behind mouth and on top of head above and behind orbits. Inner side of gill opening with or without fleshy protrusion in its lower half.

Anus close to anal-fin origin. Light organ externally evident as a short cleft, not forming scaleless black fossa, 3.1–10.4 times in pelvic-anus distance, its anterior end often poorly discernible, surrounded by scale pockets bearing dense aggregations of large black melanophores on silvery background (Fig. 11A). Area on belly occupied by such melanophores varies in size from specimen to specimen, at maximal development it covers scale pockets from anus anteriorly to a line between pelvic-fin origins and up to three longitudinal rows of scales on each side laterally from midventral line.

Jaw teeth conical, pointed, arranged in bands of nearly uniform width; premaxillary teeth larger than these on dentary; outermost teeth of premaxilla weakly to not enlarged. Premaxillary tooth band short, 1.7–2.0 times in length of rictus; dentary tooth band reaching rictus or nearly so.

First dorsal-fin base 1.2–1.6 times shorter than the interdorsal space; second dorsal-fin spine ending in filament, which length approximately equal to postrostral length. Pectoral fin narrow based, rather short, falling to or slightly before anal-fin origin. Pelvic fins originate more or less behind the vertical of pectoral-fin origin (rarely on the same vertical). Outermost pectoral-fin ray filamentous and extending to or just behind anal-fin origin.

Squamation (Figs. 5D–F, 12B, 12D). Body scales deciduous, those on head and predorsal region more adherent. Scales large with spinules in parallel rows (parallel to slightly divergent on scales in predorsal region). Spinules on scales below first dorsal-fin base arranged in 7–10 rows, some rows often incomplete; those on scales below beginning of second dorsal fin arranged in 9–12 rows, some often incomplete; middle row of spinules somewhat enlarged, giving appearance

of horizontal striations on body surface; spinules in rows gradually increasing in length posteriad (similarly expressed on flanks and in predorsal region). Lateral buttresses of spinules weakly developed to almost absent, never joined with those of neighboring rows. Predorsal scales with spinules only slightly more raised and less depressed than on flank scales; spinules on predorsal scales arranged in 5–8 (usually 6 or 7) rows. Scales on top of head, cheeks, and gill cover with parallel to slightly diverging rows of spinules (Fig. 12B); scales on interorbital space irregularly disposed, not forming clear keel-like rows; area between the orbit, nasal fossa, and suborbital ridge sparsely scaled, with spinules on scales arranged in clusters, rarely forming a single short row on some scales. Narrowest portion of suborbital shelf bearing 1 (rarely 0, in smallest specimen examined) to 2 rows of scales between lower rim of orbit and upper edge of suborbital ridge (Fig. 12D); these scales often separated from each other by bare interspaces, none enlarged. Nasal fossa completely scaleless. Top of snout densely scaled. Underside of head usually densely scaled except on gular region, branchiostegal membranes, and small triangular area in front of premaxillary symphysis (rarely middle portion of preoral region largely scaleless); scales strongly deciduous (mostly missing) in central area of preoral region and behind mouth. Scales from underside of head with spinules arranged in 1–4 short widely separated rows (1–4 spinules per row). Scutes of head ridges strongly armed with numerous stout conical spinules with pointed tips; scutes of medial nasal ridge with radiating rows of conical spinules lacking buttresses, 9–10 (11) in number (including terminal scute). Supraoccipital and postoccipital scutes very small (commensurable with neighboring scales), coarsely spinulated.

Body color pale brownish without markings. Light-brown coloration formed by dense aggregations of minute brownish melanophores on epithelium covering exposed field of scales. When scales removed, scale pockets pure white with narrow dark-brown margins and sparse melanophore peppering in posterior third of scale pocket (more conspicuous below lateral line). Orbit not encircled by dark ring; anterior border of second naris blackish. Scaled parts of underside of head darker than dorsal and lateral surfaces of head (coloration formed by dense aggregation of brownish melanophores); gular region and branchiostegal membranes from paler than, to as dark as, preoral region; distal margin of branchiostegal membrane blackish in its upper half. Lips and gums pale to dusky, mouth cavity dusky, gustatory papillae vary in color from white to brownish or blackish; branchial cavity and peritoneum blackish; stomach pale. All fins more or less dusky to blackish (rays of second dorsal fin pale), scale pockets at bases of anal-fin rays much more densely peppered with melanophores than neighboring ones.

ETYMOLOGY.— Named from its distribution area, Mascarene Ridge.

REMARKS.— All paratypes of *C. yurii* (Iwamoto et al., 2006:434) are referred to this species. Although it was formerly believed that differences between the holotype and paratypes can be attributed to size-related changes (Iwamoto et al., 2006:438), some of these differences (presence or absence of external light organ, adherent vs. deciduous scales) are clearly not this case. Furthermore, the 81–85 mm HL (IOM 013–000) paratypes are adults with mature gonads (including females 81 and 82 mm HL with ripe eggs about 0.5 mm in diameter). As *C. mascareneus* is very similar and apparently very closely related to *C. braueri*, it is probable that our specimens of *C. mascareneus* attain sizes close to maximum for this species. Both the holotype and the second known specimen of *C. yurii* described herein are much larger (154 and 156 mm HL) than the type series of *C. mascareneus*; thus, it is not possible to compare these species with specimens of similar size. However, we have a graded size series of *C. amirantensis*, a species close to *C. yurii*, containing specimens of similar size to both *C. mascareneus* and *C. yurii*. Results of our analysis show that most differences between *C. mascareneus* and *C. yurii* are not correlated with growth in *C. amirantensis* or sometimes show opposed trends (Table 3).

COMPARISONS.— The new species is similar to *C. braueri* known from off South Africa and seamounts in the southwestern part of the Indian Ocean northward to about 25°S. The main difference between these species include the external manifestation of the light organ, narrow and cleft-like, lacking a dermal window in *C. mascareneus*, compared with oval black naked fossa in *C. braueri* (Fig. 11). Furthermore, the new species has more deciduous scales and less attenuated snout than *C. braueri*, with shorter terminal scute (length 6+–8.8 vs. 9.5–12.2 % HL, $n = 20$), a smaller orbit (23–27, usually 25 % HL vs. 26–34, usually 28–32 % HL, $n = 36$, in *C. braueri*), and on average fewer scales below midbase of first dorsal fin and lateral line (usually 3.5 vs. usually 4.5 in *C. braueri*, $n = 36$) and scales between origin of second dorsal fin and lateral line (usually 4.0–5.0 vs. usually 5.0–5.5 in *C. braueri*, $n = 36$). For comparison with *C. yurii*, see Table 3.

***Coelorinchus paraboliceps* new species**

Figures 2C, 5G–I, 6C–D, 7C–D, 14, 15

Coelorinchus sp. B: Shcherbachev et al. 1986:201 (6°20'S, 54°23'E).

Holotype. — IOM M.004–003 (120 mm HL, 410+ mm TL), Mascarene Ridge, 8°26.4'S, 59°29'E, 1300–1260 m, FRV *Violent*, cruise 7(9), trawl 52, 2 Sept. 1977.

DIAGNOSIS.— A species of the *Coelorinchus acanthiger*-group with light organ not evident externally; snout 40 % HL, with sides strongly and regularly convex in dorsal view; medial element of terminal scute small, its length 3.3 % HL; preoral region largely naked at 120 mm HL, nasal fossa mostly scaleless, area between nasal fossa, orbit, and suborbital ridge fully scaled; scales over interorbital space with spinules not forming clear keel-like rows; scales on body firmly attached, bearing spinules with buttresses strongly developed, forming concentric ridges even on scales below and in front of first dorsal fin and on scales from tail; 3.5 and 4.5 scales between midbase of first dorsal fin and between origin of second dorsal fin and lateral line, respectively; body medium brown, fins darker, lips and gums pale.

DESCRIPTION.— General features of fish seen in Figs. 2C, 14. Counts: first dorsal-fin rays ii + 6; pectoral-fin rays i + 18; pelvic-fin rays 7; gill-rakers (inner) on 1st arch 7; gill-rakers on 2nd arch 6 (outer) / 7 (inner); transverse scale rows below origin of first dorsal fin 4.0; ditto, below midbase of first dorsal fin 3.5; ditto, below origin of second dorsal fin 4.5; ditto, between origin of anal fin and lateral line 14; lateral-line scales before origin of second dorsal fin 12; pyloric caeca not counted (stomach everted).

Measurements shown in Table 2. Width of body across pectoral bases 78.2 % of greatest body depth (at dorsal-fin origin), 1.3 times less than greatest width of head (at preopercles). Head c. 3.4 times in TL. Snout moderately long and rather broad, 2.5 times in HL, 1.1 times greater than postorbital length of head. Snout bluntly pointed in lateral view, with dorsal contour gently declining toward the tip, slightly convex at level of nasal fossa (Fig. 14A); strongly convex at sides in dorsal view, with tip somewhat angularly rounded (Figs. 14B, 14C). Snout tipped with short rectangular terminal scute consisting of transversely extended medial element and small squarish lateral elements (Fig. 15A). Anterolateral margins of snout not completely supported by bone. Orbit elliptical, 4.3 times in HL, 1.7 times in snout. Suborbital shelf moderately angulated; shelf depth 1.6 times in suborbital depth. Lateral nasal ridge 3.7 times shorter than suborbital ridge. Mouth large, posterior tip of maxilla extending below posterior quarter of orbit, rictus extending just behind vertical through middle of orbit. Preopercle inclined backward at about 65°, with moderately long, broadly and somewhat angularly rounded posteroventral lobe having roughly crenate free margin. Subopercle terminates ventrally in slender tip that extends somewhat beyond preopercle. Chin barbel short, slender, 3.1 times in orbit. Free neuromasts on snout, along head ridges and on underside of head prominent, more or less infuscated (brownish to blackish); black

hair-like papillae poorly developed on dorsal surface of head, numerous on underside below suborbital ridge and in preoral region (especially in area in front of premaxillary symphysis). Inner side of gill opening with shallow ridge-like protrusion in its lower half.

Jaw teeth conical, rather thin (needle-like), in narrow bands; premaxillary teeth larger than those on dentary; outermost teeth of premaxilla somewhat enlarged. Premaxillary tooth band short, 1.9 times in length of rictus; dentary tooth band reaching end of rictus.

First dorsal-fin base 1.5 times shorter than the interdorsal space; second dorsal-fin spine with very short filament (reaching origin of second dorsal fin only). Pectoral fin narrow based, short, falling well before anus. Pelvic fin originates behind the vertical of pectoral-fin base. Outermost pectoral-fin ray filamentous and extending to anus. Anus close to anal-fin origin. Light organ not externally visible.

Squamation (Figs. 5G–I, 6C–D, 7C–D). All scales strong and adherent, those on body large; those on flanks, on tail, and on belly with spinules arranged in parallel rows; those in predorsal region, on cheek, opercle, and isthmus arranged in more or less diverging rows. Spinules on scales below first dorsal-fin base arranged in 5–6 (7) rows; those on scales below beginning of second dorsal fin arranged in 6–8 rows; rows incomplete (except middle one); middle row of spinules distinctly enlarged and raised, giving appearance of horizontal striations on body surface; spinules in rows gradually increasing in length posteriad. Spinules on tail behind anterior quarter of anal-fin base with spinules more inclined backward and with last spinule of middle row much produced behind posterior margin of scale. Each spinule with prominent lateral buttresses often joined with those of neighboring rows to form low transverse ridges across exposed field of scale (buttresses well-developed and joined with those of neighboring rows even on tail scales). Predorsal scales smaller in size than those on flanks, with similarly erect but shorter spinules, arranged in 3–4 rows. Scales on top of head chiefly with more or less diverging rows of spinules; however, spinules often situated so irregularly that rows becoming indistinguishable; all spinules with prominent lateral buttresses. Area between the orbit, nasal fossa, and suborbital ridge fully scaled, with spinules on scales arranged mostly in clusters. Narrowest portion of suborbital shelf bearing about 4 rows of tightly joined scales between lower rim of orbit and upper edge of suborbital ridge (lowermost row consisting of scales much larger in size). Nasal fossa largely scaleless (few minute spinulose scales present on right side at anterodorsal and anteroventral margins of fossa, and two minute cycloid scales found on left side at anterodorsal margin of fossa). Top of snout densely scaled. Underside of head largely scaleless in preoral region except small area behind terminal scute and lateral quarters of posterior third of preoral length, where densely scaled (Fig. 15B); also densely scaled behind the level of premaxillary symphysis toward the preopercular lobe and on mandibular rami; naked on gular region and branchiostegal membranes; scales adherent. Spinules on scales from underside of head arranged in a cluster or in a single short row. Scutes of head ridges strongly armed with numerous rather long and stout conical spinules with pointed tips; scutes of medial nasal ridge with radiating rows of spinules having conspicuous lateral buttresses, 9 scutes in number (including terminal scute). Supraoccipital and postoccipital scutes small, not larger than neighboring scales, coarsely spinulated.

Body color medium brown without markings. Brown coloration formed by dense aggregations of melanophores on epithelium covering the exposed field of the scales. When scales removed, scale pockets pure white with narrow dark-brown margins and with variably expressed concentrations of brownish to blackish melanophores along posterior margins (poorly expressed on scale pockets from dorsal half of body and from breast and tail, conspicuous and broad on lower parts of trunk and on belly). Orbit encircled by dark-brown ring; anterior border of second naris blackish. Preoral area infuscated, gular region and branchiostegal membranes much darker, becoming black-

ish on upper reaches of branchiostegal membrane. Lips and gums as well as mouth cavity pale, gustatory papillae pale except minute dark-brownish papillae along outer margin of lower lip; branchial cavity blackish; stomach pale. Anal fin blackish; other fins less dark, more or less dusky, basal third of dorsal fin apparently much darker than rest of fin.

ETYMOLOGY.— Derived from “parabola” (a kind of graphics with all points equidistant from the given straight line) and “ceps” (Latin, a head), in allusion to the characteristically shaped snout in dorsal view; noun in apposition.

REMARKS.— Shcherbachev et al. (1986) reported as *Coelorinchus* sp. B two specimens, 59 and 73.6 mm HL, collected during the second cruise of R/V *Rift* at 6°20'S, 54°23'E. We were unable to find these specimens for the current study but a brief description provided by Shcherbachev et al. (1986) leaves no doubt as to their conspecificity with the holotype of *C. paraboliceps*. The *Rift* specimens have snout lengths of 40.8–44.1 % HL, preoral region almost scaleless, 4.0 scales between midbase of first dorsal fin and lateral line; flank scales with overlapping spinules, their rows not numerous; and external light organ absent.

The new species is notably different from all other Mascarene *Coelorinchus* in the shape of the medial element of the terminal scute of the snout, which is small and rectangular in shape in contrast to the acuminate and diamond-shaped element in the other species. However, the new species shows other differences (Table 4) that support its separation.¹

COMPARISONS — The new species is most similar to *C. yurii* but can be easily distinguished from that species in the preoral region largely scaleless (vs. completely scaled except for a small triangular area in front of premaxillary symphysis), and in the buttresses of spinules forming harsh transverse ridges even on scales in front and below first dorsal fin and on tail (vs. transverse ridges poorly developed to absent) (Figs. 5G–L, 6D, 6F, 7D, 7F). See Table 4 for additional minor differences and for comparison with *C. amirantensis*, another closely similar species. Overall, the buttresses of the scale spinules appear to be more highly developed, and the transverse crests across the scales formed by the buttresses are harsher in the new species than in any other Mascarene *Coelorinchus* (Figs. 5–7). The stability of these features requires confirmation with more extensive material.

Within the extralimital species, *C. paraboliceps* is reminiscent of *C. trachycarus* from the Tasman Sea and southern Australia; however, the latter species differs by its more extensive naked areas along the suborbital and lower preopercular margins, by its snout being sharply pointed and weakly convex at sides in dorsal view, and by its shorter postorbital length (22–32 % HL, orbit into postorbital 1.0–1.2 times vs. 36.7 % and 1.6 times in *C. paraboliceps*).

***Coelorinchus yurii* Iwamoto, Golani, Baranes, and Goren, 2006**

Figures 2D, 5J–L, 6E–F, 7E–F, 12A, 12C, 16, 17

Coelorinchus yurii (partim., holotype only) Iwamoto, Golani, Baranes, and Goren, 2006:434, figs. 2–3 (original description, Seychelles, 1900 m; all paratype specimens from Saya de Malha Bank herein referred to *C. mascarenus*).

¹ An anonymous reviewer stated that the “unusual character of [the] terminal snout [scute] is obviously attributable to a damage during early ontogeny. Fig. 14 clearly indicates that its snout is in [an] abnormal condition.” Furthermore, the reviewer suggests that the specimen is an “unusual variant of *C. amirantensis*.” We strongly disagree with that interpretation. The specimen is in good condition despite having been trawled from a bottom depth of 1260 to 1300 m; it suffered no major external damage, the snout is fully intact with associated bones unbroken, and the head overall is in a normal condition. The terminal scute is notably small and blunt, but there is nothing to suggest that an acuminate, sharply pointed scute such as found in the other species here treated could have been present at any earlier stage. Other differences supporting our species hypotheses are enumerated in the comparisons sections of each species and in the key to Mascarene species.

Holotype.—TAU P.11602 (154 mm HL, 541+ mm TL), Seychelles between Alphonse and Bijoutier islands, by trammel net in 1900 m, R/V *Sea Surveyor*, 17 Dec. 1998, collector M. Goren.

Other material examined. — IOM M.003–017 (c.156 mm HL [tip of snout damaged], 520+ mm TL), Mascarene Ridge, 8°29'S, 59°35'E, 950–1150 m, FRV *Zvezda Kryma*, cruise 1/6, trawl 4, 19 June 1976.

DIAGNOSIS.— A species of the *Coelorinchus acanthiger*-group with light organ not visible externally; snout 38–42 % HL, sides weakly convex in dorsal view; medial element of terminal scute diamond-shaped (tip broken in both known specimens); preoral region almost fully scaled, nasal fossa largely scaleless, area between nasal fossa, orbit, and suborbital ridge fully scaled; most scales over interorbital space with spinules irregularly disposed; scales on body firmly attached; flank scales bearing spinules with buttresses strongly developed, but not forming transverse ridges, at least on scales from below and in front of first dorsal fin, weakly developed to absent on scales from last three-quarters of tail; 4.5–5.0 and 5.5 scales between midbase of first dorsal fin and between origin of second dorsal fin and lateral line, respectively; body dark-colored, fins darker, gums and lower lip pale, upper lip pale to blackish.

DESCRIPTION.— General features of fish seen in Figs. 2D, 16A, 17. Counts: first dorsal-fin rays ii + 8; pectoral-fin rays i + 18; pelvic-fin rays 7; gill-rakers (inner) on 1st arch 8; gill-rakers on 2nd arch 6 (outer) / 8 (inner) in holotype, not counted in IOM specimen (gill arches damaged); transverse scale rows below origin of first dorsal fin 4.5 [5.0]; ditto, below midbase of first dorsal fin 4.5–5.0 [4.5]; ditto, below origin of second dorsal fin 5.5; ditto, between origin of anal fin and lateral line 12–15; lateral-line scales before origin of second dorsal fin 13; pyloric caeca not counted (stomach everted).

Measurements shown in Table 2 (IOM M.003–017; for holotype, see Iwamoto et al. 2006:Table 1). Width of body across pectoral bases 85.7 % of greatest body depth (at dorsal-fin origin), 1.2 times less than greatest width of head (at preopercles). Head c. 3.3 times in TL. Snout long, 2.6 times in HL, equal to postorbital length of head. Snout acute and horizontal in lateral view, with dorsal contour gently declining toward the tip; weakly convex at sides in dorsal view, with sides rather regularly convergent toward the tip (Figs. 16A–B, 17). Snout tipped with moderately long, somewhat diamond-shaped terminal scute, which lateral elements forming distinct “shoulders” on each side of medial element. Anterolateral margins of snout not completely supported by bone. Orbit elliptical, 4.3 times in HL, 1.7 times in snout. Suborbital shelf rather steep and feebly angulated (Fig. 13B); shelf depth 1.4 times in suborbital depth. Lateral nasal ridge 3.4 times shorter than suborbital ridge. Mouth large, posterior tip of maxilla extending below posterior quarter of orbit, rictus below middle of orbit. Preopercle inclined backward at about 60°, with moderately long, broadly and somewhat angularly rounded posteroventral lobe. Subopercle terminates ventrally in slender tip that extends somewhat beyond preopercle. Chin barbel short, slender, 2.1 times in orbit. Free neuromasts on snout, along head ridges, and on underside of head prominent, more or less infuscated (brownish to blackish), surrounded by isolated or scattered black hair-like papillae, more densely aggregated along anterior and lower margins of nasal fossa, in scaleless preoral area in front of premaxillary symphysis, along suborbital ridge below its posterior quarter, in area between the ends of upper jaw and horizontal limb of preopercle, and in scaleless area above gill cover. Inner side of gill opening lacking protrusion in its lower half.

Jaw teeth stout, conical, in narrow bands; premaxillary teeth larger than those on dentary; outermost teeth of premaxilla weakly enlarged. Premaxillary tooth band short, 1.5 times in length of rictus; dentary tooth band reaching rictus.

First dorsal-fin base 1.7 times shorter than the interdorsal space (equal in holotype); second dorsal-fin spine with broken tip in IOM specimen (1.3 times shorter than postrostral length in holo-

type). Pectoral fin narrow based, rather short, falling more or less before anal-fin origin. Pelvic fin originates on the same vertical with pectoral fins, or in the holotype, behind it. Outermost pectoral-fin ray filamentous and extending to anus. Anus close to anal-fin origin. Light organ not externally visible (Fig. 16C).

Squamation (Figs. 5J–L, 6E–F, 7E–F, 12A, 12C, 16D–E). All scales strong and adherent, those on body large; those on flanks in front of first dorsal fin and below its base above lateral line, in predorsal area, and on isthmus with spinules in more or less diverging rows; those on flanks below lateral line, behind first dorsal-fin base, and on belly with spinules in more or less parallel rows. Spinules on scales below first dorsal-fin base arranged in 5–8 rows, most rows complete (Fig. 5K); those on scales below beginning of second dorsal fin arranged in 7–10 [8–12 in holotype] rows, some of rows often incomplete (Fig. 5L); middle row of spinules somewhat enlarged, giving appearance of horizontal striations on body surface; spinules in rows gradually increasing in length posteriad (less conspicuous on anteriormost trunk scales); spinules of tail scales thinner than those of flank scales and somewhat needle-like, especially in lateral rows. Each spinule with prominent lateral buttresses, those of spinules of neighboring rows usually not joined with each other and not forming transverse ridges across exposed field of scale (Figs. 5J–K) (except some scales on flanks and abdomen: Fig. 7E); buttresses becoming weakly developed to absent on tail scales (Fig. 7F). Predorsal scales with more raised and more separated spinules, arranged in 3–5 rows (Fig. 5J). Scales on top of head, cheeks, and gill cover with diverging rows of spinules (Fig. 12A); most scales over interorbital space with irregularly disposed spinules not forming clear rows (Fig. 6E); area between the orbit, nasal fossa, and suborbital ridge densely scaled, with spinules on scales arranged in rows. Narrowest portion of suborbital shelf bearing about 4 rows of tightly joined scales between lower rim of orbit and upper edge of suborbital ridge; scales in lowermost row being much larger (Fig. 12C). Nasal fossa with few spinulose scales along anterior and lower margins (Figs. 16D–E). Top of snout densely scaled. Underside of head densely scaled, except gular region, branchiostegal membranes, and a small triangular area in front of premaxillary symphysis; scales firmly adherent (Fig. 16B). Spinules on scales from underside of head arranged in a cluster or in 1–2 short rows. Scutes of head ridges strongly armed with numerous stout conical spinules with pointed tips; scutes of medial nasal ridge with radiating rows of spinules bearing conspicuous buttresses, 9 scutes (including terminal scute). Supraoccipital and postoccipital scutes small (indistinctly larger than neighboring scales), coarsely spinulated.

Body color dark to medium brown without markings. Brown coloration formed by dense aggregations of melanophores on epithelium covering exposed field of the scales. When scales removed, scale pockets pure white with narrow dark-brown margins and sparse concentrations of brownish melanophores or rare isolated melanophores, often indistinct on flanks, most prominent on belly. Orbit encircled by dark-brown ring; anterior border of second naris blackish. Middle part of preoral area, gular region, and especially branchiostegal membranes darker than rest of head, distal margin of branchiostegal membrane much more infuscated in its upper half. Lips and gums pale, with a row of blackish papillae inside of premaxillary tooth band [upper lip blackish in holotype]; mouth cavity dusky; branchial cavity and peritoneum blackish; stomach pale. All fins dark; skin at bases of anal-fin rays much darker than on adjacent scales.

ETYMOLOGY.— The species was named in honor of the Soviet/Russian ichthyologist Yuri N. Shcherbachev (Iwamoto et al. 2006).

REMARKS.— Within the specimens listed in the original description (Iwamoto et al., 2006) only the holotype actually belongs to this species. All the paratypes are the new species *C. mascarenus*. However, we have discovered a second, previously overlooked specimen of *C. yurii* in the IOM collection; its characters match well with those of the holotype.

The photograph of the head in ventral view of the holotype of *C. yurii* was erroneously replaced by that of the holotype of *C. amirantensis* in the original description (Iwamoto et al. 2006:fig. 2c). Herein we publish a correct picture (Fig. 17).

COMPARISONS — The most obvious feature distinguishing *C. yurii* from the similar and co-occurring species *C. amirantensis* and *C. paraboliceps* is the absence of the continuous transverse ridges formed by buttresses of the spinules on the scales in front of and below the first dorsal fin, even in very large specimens (Figs. 5, 6). In addition, *C. yurii* can be easily distinguished from *C. amirantensis* in its shorter snout (38–42 % vs. 46–51 % HL), and from *C. paraboliceps* in the preoral region almost completely scaled (vs. scales present in small area behind terminal scute and in lateral quarters of posterior third of preoral length only). See Table 4 for more thorough comparison with the aforementioned species.

Within the extralimital species, *C. yurii* shares many common features with *C. lasti* from the Australasian waters (Iwamoto and Williams 1999), but can be easily distinguished from that species in the parallel to slightly divergent and more numerous rows of spinules on body scales (vs. strongly divergent, 3–5 in number in *C. lasti*), in the short (vs. high and blade-like in *C. lasti*) spinules on the scales from the underside of head, and in the somewhat longer snout (38–42 % HL, preoral length 35–37 % HL vs. 37–38 and 30–32 % HL in *C. lasti*). Although the body coloration is similarly dark in both these species, the lips, gums and mouth are generally light-colored in *C. yurii* (only upper lip can be conspicuously blackish) instead of blackish in *C. lasti*. Another similar species, *C. trachycarus* from the South Australian – New Zealand region (Iwamoto et al. 1999), can be distinguished by its much more extensive naked areas along the suborbital and the lower preopercular margins, more harsh and coarse spinulation of scales and head ridges, and by its smaller ratio of orbit into postorbital (1.0–1.2 vs. 1.5–1.7 in *C. yurii*).

**Key to the species of *Coelorinchus* from the western Indian Ocean
(eastward to Ninety East Ridge) with long snout (clearly exceeding orbital diameter
and upper jaw length) incompletely supported by bone, and with light organ externally
invisible or represented by a cleft or lens-like fossa in front of anus**

[NB: May not work for juvenile specimens less than 45 mm HL.]

- 1a. Underside of head fully naked. 2
- 1b. Underside of head at least partially scaled 3
- 2a. Trunk completely encircled by a broad dark band; body scales with median spinule row scarcely if at all larger than lateral rows; spinule rows complete and extending to distal margin of scale. *Coelorinchus kaiyomaru*
- 2b. Trunk not encircled by a dark band; body scales with median spinule row much larger than lateral rows; lateral rows incomplete, mostly not reaching scale margin *Coelorinchus* cf. *labiatus*
- 3a. Body scales with median spinule row scarcely if at all larger than lateral rows; all spinule rows complete and extending to scale margin; premaxillary tooth band extending nearly to end of rictus 4
- 3b. Body scales with median spinule row much larger than lateral rows; lateral rows variably expressed; premaxillary tooth band ending far before end of rictus 5
- 4a. Posterior nostril large, 2.3–2.7 times in orbit; outer premaxillary teeth not enlarged; scale spinules inclined; light organ not visible externally *Coelorinchus flabellispinis*
- 4b. Posterior nostril smaller, about 3.5 times in orbit; outer premaxillary teeth enlarged; scale spinules raised; light organ present as scaleless fossa in front of anus *Coelorinchus trunovi*

- 5a. Light organ externally not visible; buttresses of spinules of flank scales strongly developed at 79 mm HL or more 6
- 5b. External light organ present; buttresses of spinules of flank scales at most weakly developed even in largest fishes 8
- 6a. Snout length 46–51 % HL; spinules on scales over interorbital region arranged in keel-like rows; buttresses of spinules on tail scales less conspicuous than on trunk scales, but similarly developed on predorsal scales and on flank scales (Figs. 6B, 7A–B) *C. amirantensis*
- 6a. Snout length 38–44 % HL; spinules on scales over interorbital region mostly irregularly disposed; buttresses of spinules strongly developed on scales throughout the body or less conspicuous both on predorsal and on tail scales (Figs. 6D, 6F, 7C–F) 7
- 7a. Snout strongly and regularly convex toward blunt tip in dorsal view, convex at level of nasal fossa and gently declining toward the tip in lateral view; medial element of terminal scute small and rectangular; preoral region scaleless except small area behind terminal scute and lateral quarters of posterior third of preoral length; buttresses of spinules forming transverse ridges on scales in front of and below first dorsal-fin origin and on tail (Figs. 5G–I, 7D) *C. paraboliceps* sp. nov.
- 7b. Snout weakly convex and more rapidly convergent toward acuminate tip in dorsal view, almost horizontal in lateral view; medial element of terminal scute diamond-shaped; preoral region scaled except small area in front of premaxillary symphysis; buttresses of spinules not forming transverse ridges on scales in front and below first dorsal-fin origin and on tail (Figs. 5J–L, 7F) *C. yurii*
- 8a. Light organ with dermal window representing oval naked black fossa in front of anus (Fig. 11B); terminal snout scute longer, 9.5–12.2 % HL; scales below midbase of first dorsal fin and lateral line 3.5–5.0 (usually 4.5); scales between origin of second dorsal fin and lateral line 4.5–6.5 (usually 5.0–5.5) *C. braueri*
- 8b. Light organ cleft-like, without dermal window in front of anus (Fig. 11A); terminal snout scute shorter, 6+–8.8 % HL; scales below midbase of first dorsal fin and lateral line 3.0–4.5 (usually 3.5); scales between origin of second dorsal fin and lateral line 4.0–5.0 (usually 4.5) *C. mascarenius* sp. nov.

COMPARATIVE MATERIALS

Coelorinchus braueri: CAS-SU 31460 (1, 70 mm HL, 330+ mm TL), South Africa off Cape Colony, Herre 1934 Expedition, collector C. von Bonde. CAS 244464 (1, 101.5 mm HL, 385+ mm TL), 35°31'S, 18°50'E, 700 m, FRV *Violent*, cruise 5, trawl 68, 05 Nov. 1974. CAS 50145 (5 of 22 specimens, 52.1–68.6 mm HL, 209+–265+ mm TL), Mozambique off Maputo, 26°07'S, 34°11'E, 600–665 m, R/V *Anton Bruun*, cruise 8, station 397c, 29 Sept. 1964. IOM 00191 (20, 42–61 mm HL, 155+–230+ mm TL), 25°28'–25°29'S, 35°14'–35°11'E, 715–700 m, R/V *Vityaz-II*, station 2630, bottom shrimp trawl, 23 Nov. 1988. IOM 01864 (9, 86–98 mm HL, 322+–380+ mm TL), 20°46'–20°50'S, 35°59'–35°56'E, 950–900 m, R/V *Vityaz-II*, station 2621, bottom shrimp trawl, 20 Nov. 1988. IOM uncatalogued (2, 46+–53.7 mm HL, 212+–225+ mm TL), Atlantic Ocean off Cape Town, 33°52'S, 17°29'E, 460–425 m, FRV *Akademik Knipovitch*, trawl 276, 02 June 1965. IOM uncatalogued (3, 31.2–62.4 mm HL, 140–244+ mm TL), off south-western Africa, 700 m, FRV *Poltava*, trawl 423. IOM uncatalogued (1, 88.2 mm HL, 340+ mm TL), South Africa, Agulhas, FRV *Zvezda Kryma*, cruise 7, trawl 216. IOM uncatalogued (1, 78 mm HL, 315+ mm TL), off south-western Africa, FRV *Poltava*, station 429. IOM uncatalogued (1, 89.2 mm HL, 340+ mm TL), South Africa, 33°14'S, 17°04'E, 480 m, FRV *Poltava* (no other data). SAIAB 7270 (7, 55.3–

81.5 mm HL, 215+–313+ mm TL), South Africa off Natal, no precise data. SAIAB 30299 (3, 54.1–60 mm HL, 196+–232+ mm TL), Natal, 30°04'S, 31°13'E, 457 m, R/V *Africana*, A.4711-J-05, 26 Aug. 1986. SAIAB 34407 (1, 37.9 mm HL, 169 mm TL), South Africa NW Cape off Port Nolloth, 30°22.5'S, 15°02.7'E, R/V *Africana*, 02 Aug. 1990, collector M.E. Anderson. SAM 14032 (2, 53.9–87 mm HL, 230–245+ mm TL), 33°22.9'S, 17°29.1'E, 552 m, bottom trawl, 4 March 1988. SAM 17763 (1, 87.6 mm HL, 317+ mm TL), South Africa, no precise data.

Coelorinchus cf. labiatus: IOM 00184 (1, 38 mm HL, 147+ mm TL), 32°45'–32°41'S, 45°30'–45°31'E, 1750–1700 m, R/V *Vityaz-II*, station 2673, bottom shrimp trawl, 09 Dec. 1988. IOM (6, 87–132 mm HL, 267+–390+ mm TL), seamounts near West Australian Ridge.

Coelorinchus flabellispinis: IOM 00172 (15, 40–78 mm HL, 120+–257+ mm TL), off Socotra, 12°18'–12°14'N, 53°09'–53°06'E, 375–380 m, R/V *Vityaz-II*, station 2560, bottom shrimp trawl, 27 Oct. 1988.

Coelorinchus lasti: CSIRO H2615-02 (1 (holotype), 63 mm HL, 620+ mm TL), Western Australia: w. of Mandurah, 1140 m, SS1/91/83. CSIRO H1925-01 (1 (paratype), 142 HL, 455+ mm TL), southwestern Australia: w. of Temma, 41°15'S, 143°58'E; 959–1021 m; R/V *Petuna Endeavour*, 18 Nov. 1989.

Coelorinchus trachycarus: IOM uncatalogued (1, 50 mm HL, 170+ mm TL), Great Australian Bight, 37°28'S, 138°58'E, 1340–1320 m. CAS 228450 (2, 73.3–73.5 mm HL, 277+–279 mm TL), Australia: Tasmania: e. of Flinders Is., 39°52.9'S, 149°02.0'E, 1508–1426 m, FRV *Southern Surveyor* station SS1/00/259, demersal trawl, 29 Apr. 2009. CAS 98873 (1, 69.3 mm HL, 255 mm TL), Tasman Sea, Lord Howe Rise, 25°29'05"S, 163°13'10"E, 1315–1357 m, FRV *Tangaroa* Halipro 2, station 6, demersal trawl, 27 Nov. 1996. CAS 218302 (4, 38.4–70.7 mm HL, 148–235 mm TL), Tasman Sea, Lord Howe Rise, 32°11.59'S, 160°51.66'E, 1342–1361 m, FRV *Tangaroa* Norfanz station 72, demersal trawl, 24 May 2003. CAS 218453 (1, 71.9 mm HL, 267 mm TL), Tasman Sea, w. of North Cape, New Zealand, 33°46.55'S, 167°29.28'E, 1431–1460 m, FRV *Tangaroa*, Norfanz station 103, demersal trawl, 29 May 2003. CAS 218684 (1, 84.5 mm HL, 296+ mm TL), Tasman Sea, w. of North Cape, New Zealand, 34°58.85'S, 169°29.60'E, 1288–1294 m, FRV *Tangaroa*, Norfanz station 160, demersal trawl, 4 June 2003.

Coelorinchus trunovi: IOM 00176 (22, 35–114 mm HL, 130+–310+ mm TL), 21°11'–21°17'S, 35°42'–35°40'E, 490–550 m, R/V *Vityaz-II*, station 2622, bottom shrimp trawl, 21 Nov. 1988.

ACKNOWLEDGMENTS

We are sincerely indebted to the curators of the studied collections for their fruitful assistance. We thank an anonymous reviewer whose critical and detailed review pointed out weaknesses in the text that helped us focus and tightened our statements to the betterment of the manuscript. The work of the first author was supported by a grant (19–14–00026) of the Russian Science Foundation.

LITERATURE CITED

- ALCOCK, ALFRED. 1899. *A descriptive catalogue of Indian deep-sea fishes in the Indian Museum, collected by the Royal Indian Marine Survey Ship "Investigator"*. Indian Museum, Calcutta. iii+211 pp., 8 pls., 1 map.
- BARNARD, K.H. 1925. Descriptions of new species of marine fishes from S. Africa. *Annals and Magazine of Natural History*, ser. 9, 15(87):498–504.
- BRAUER, AUGUST. 1906. Die Tiefsee-Fische. I. Systematischer Teil. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia," 1898–1899* 15:1–432, text figs. 1–176, pls. 1–18.
- COHEN, DANIEL M., TADASHI INADA, TOMIO IWAMOTO, AND NADIA SCIALABBA. 1990. *Gadiform fishes of the*

- world. *An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date*. FAO Species Catalogue, vol. 10. FAO, Rome, Italy. 442 pp.
- FRICKE, RONALD, AND WILLIAM N. ESCHMEYER. 2019. *A guide to fish collections in the catalog of fishes*. Electronic version, updated 1 July 2019. <<http://researcharchive.calacademy.org/research/ichthyology/catalog/collections.asp>>. Accessed 17 July 2019.
- FRICKE, RONALD, WILLIAM N. ESCHMEYER, AND JON DAVID FONG, EDs. 2019. *Catalog of Fishes*. Electronic version, updated 1 July 2019. <<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcat-main.asp>>. Accessed 17 July 2019.
- IWAMOTO, TOMIO. 1970. The R/V Pillsbury Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65. 19. Macrourid fishes of the Gulf of Guinea. *Studies in Tropical Oceanography* 4(pt.2):316–431.
- IWAMOTO, TOMIO. 1986. Family No. 93: Macrouridae. Pages 330–341 in Smith, M. M. and P. C. Heemstra (eds.), *Smiths' sea fishes*. Macmillan South Africa, Johannesburg, South Africa. 1047 pp.
- IWAMOTO, TOMIO, AND M. ERIC ANDERSON. 1994. Review of the grenadiers (Teleostei: Gadiformes) of southern Africa, with descriptions of four new species. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* (61):1–28.
- IWAMOTO, TOMIO, DANIEL GOLANI, ALBERT BARANES, AND MENACHEM GOREN. 2006. Two new grenadiers (Teleostei, Gadiformes, Macrouridae) from the Seychelles and Mascarene Ridge, western Indian Ocean. *Proceedings of the California Academy of Sciences*, ser. 4, 57(13):433–442, 5 figs., 1 table.
- IWAMOTO, TOMIO, PETER McMILLAN, AND YURI N. SHCHERBACHEV. 1999. A new grenadier, genus *Coelorinchus*, from Australia and New Zealand (Pisces, Gadiformes, Macrouridae). *New Zealand Journal of Marine and Freshwater Research* 33(1):49–54. DOI: 10.1080/00288330.1999.9516855
- IWAMOTO, TOMIO, AND NIGEL R. MERRETT. 1997. Pisces Gadiformes: Taxonomy of grenadiers of the New Caledonian region, southwest Pacific. *Mémoires du Muséum national d'Histoire naturelle* 176:473–570.
- IWAMOTO, TOMIO, AND YURI I. SAZONOV. 1988. A review of the southeastern Pacific *Coryphaenoides* (sensu lato) (Pisces, Gadiformes, Macrouridae). *Proceedings of the California Academy of Sciences*, ser. 4, 45(3):35–82, figs. 1–9.
- IWAMOTO, TOMIO, YURI N. SHCHERBACHEV, AND BRYAN MARQUARDT. 2004. Grenadiers (Gadiformes, Teleostei) of Walters Shoals, southwestern Indian Ocean, with description of a new “West-Wind Drift” species. *Proceedings of the California Academy of Sciences*, ser. 4, 47(7):207–233, figs. 1–17.
- IWAMOTO, TOMIO, AND ALAN WILLIAMS. 1999. Grenadiers (Pisces, Gadiformes) from the continental slope of western and northwestern Australia. *Proceedings of the California Academy of Sciences*, ser. 4, 51(3):105–243.
- LEONTIEV, O.K. 1982. Relief, geological structure and geophysical fields of bottom. Pages 9–32 in V.G. Kort and S.S. Salmikov, eds., *Indian Ocean*. Nauka, Leningrad, Russia. 370 pp. [In Russian]
- NAKAYAMA, NAOHIDE, MIZUKI MATSUNUMA, AND HIROMITSU ENDO. 2015. Redescription of *Coelorinchus tokiensis* (Steindachner and Döderlein 1887) (Actinopterygii: Gadiformes: Macrouridae), with comments on its synonymy. *Ichthyological Research*. DOI 10.1007/s10228-015-0493-4
- OKAMURA, OSAMU. 1970a. *Fauna Japonica. Macrourina (Pisces)*. Academic Press: Tokyo, Japan. 216 pp., 64 pls.
- OKAMURA, OSAMU. 1970b. Studies of the macrouroid fishes of Japan. Morphology, ecology and phylogeny. *Reports of the Usa Marine Biological Station* 17(1–2):1–179, 85 figs.
- SHCHERBACHEV, YURI N. 1984. *Thalassobathyal ichthyofauna of the tropical western part of the Indian Ocean (composition and distribution)*. Dissertation submitted for the degree of Candidate of Biological Sciences, Institut Okeanologii AN SSSR, Moscow. 204 pp. [In Russian]
- SHCHERBACHEV, Y.N., N.V. PARIN, N.P. PAKHORUKOV, AND A.S. PIOTROVSKY. 1986. Mesobenthic and mesobenthopelagic fishes from submarine rises in the western Indian Ocean. *Trudy Instituta Okeanologii AN SSSR* 121:195–214. [In Russian]
- TRUNOV, I.A. 1984. A description of some species of the genus *Coelorinchus* Giorna (Macrouridae) from the southeastern Atlantic Ocean. *Voprosy Ikhtiologii* 23(6):894–904. [In Russian]

Review copy

Figures 2–17
(Specimen photographs)

Review Copy

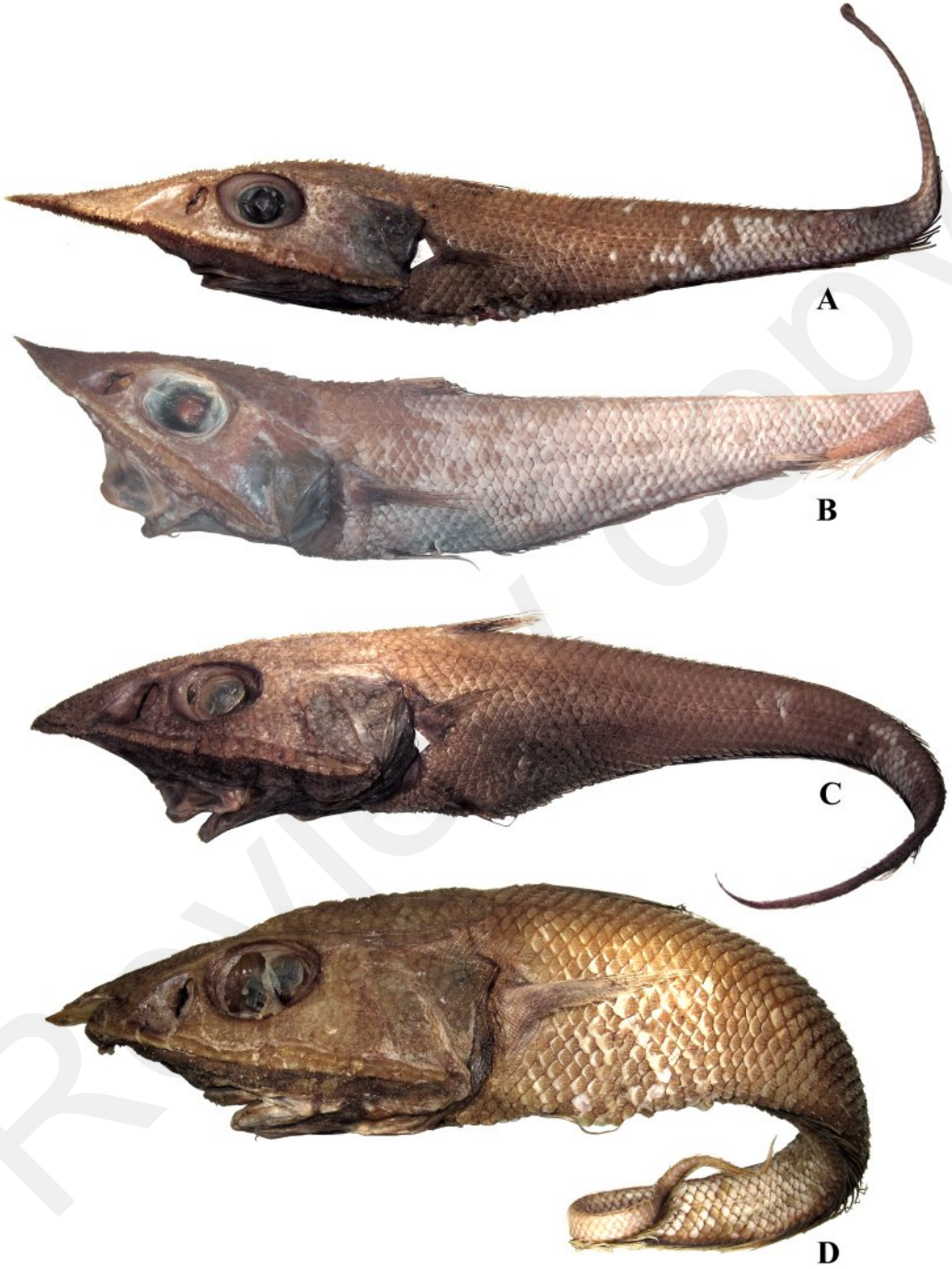


FIGURE 2. *Coelorinchus* spp., habitus, lateral view. A. *C. amirantensis*, IOM M.008–002, paratype, 108 mm HL. B. *C. mascarenus*, IOM M.011–007, holotype, 91 mm HL. C. *C. paraboliceps*, IOM M.004–003, holotype, 120 mm HL. D. *C. yurii*, IOM M.003–017, non-type specimen, c.156 mm HL.

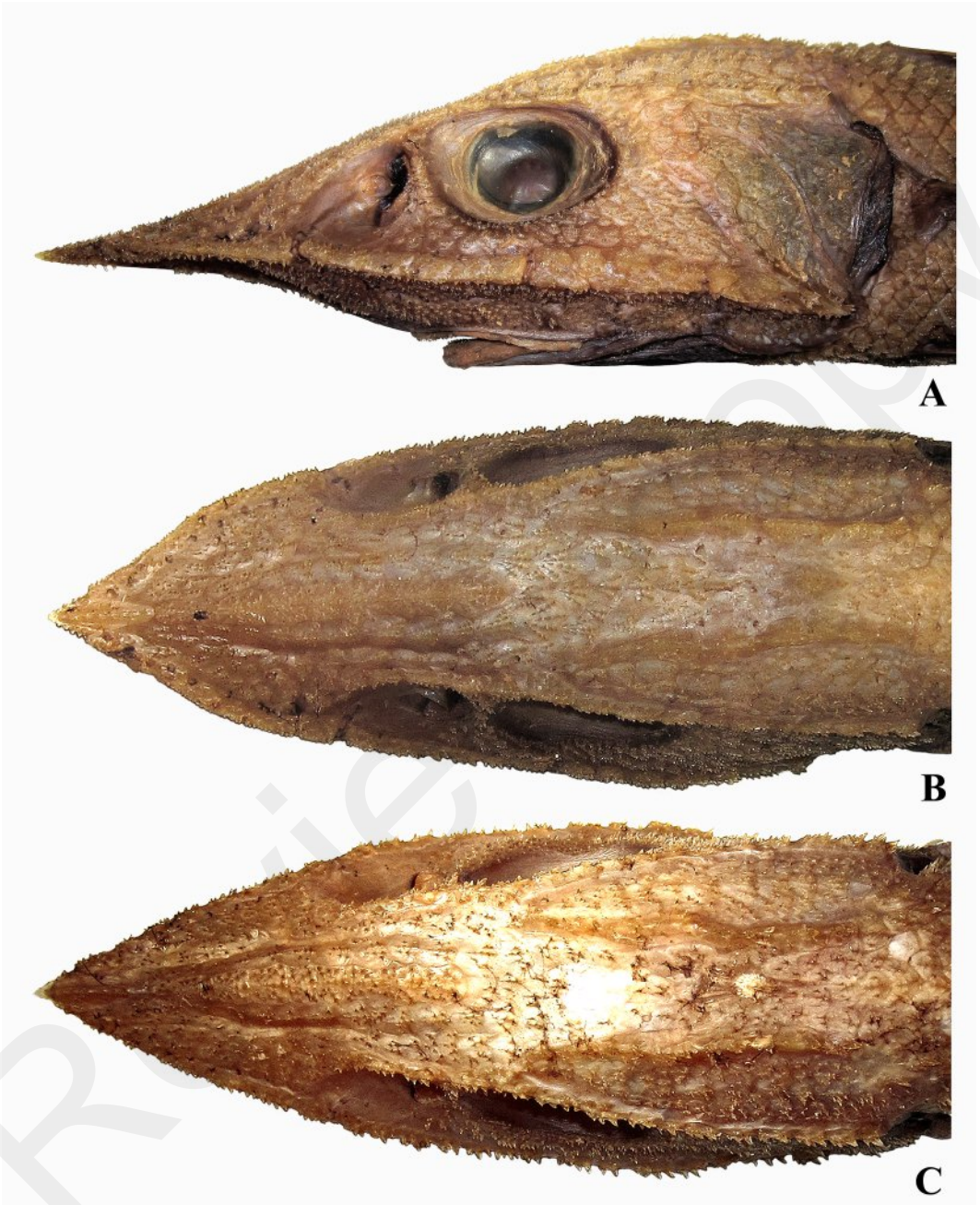


FIGURE 3. *Coelorinchus amirantensis*, paratypes, IOM M.007–001, 126 mm HL (A, B), IOM M.008–002, 108 mm HL (C). A. Lateral view of head. B, C. Dorsal view of head.

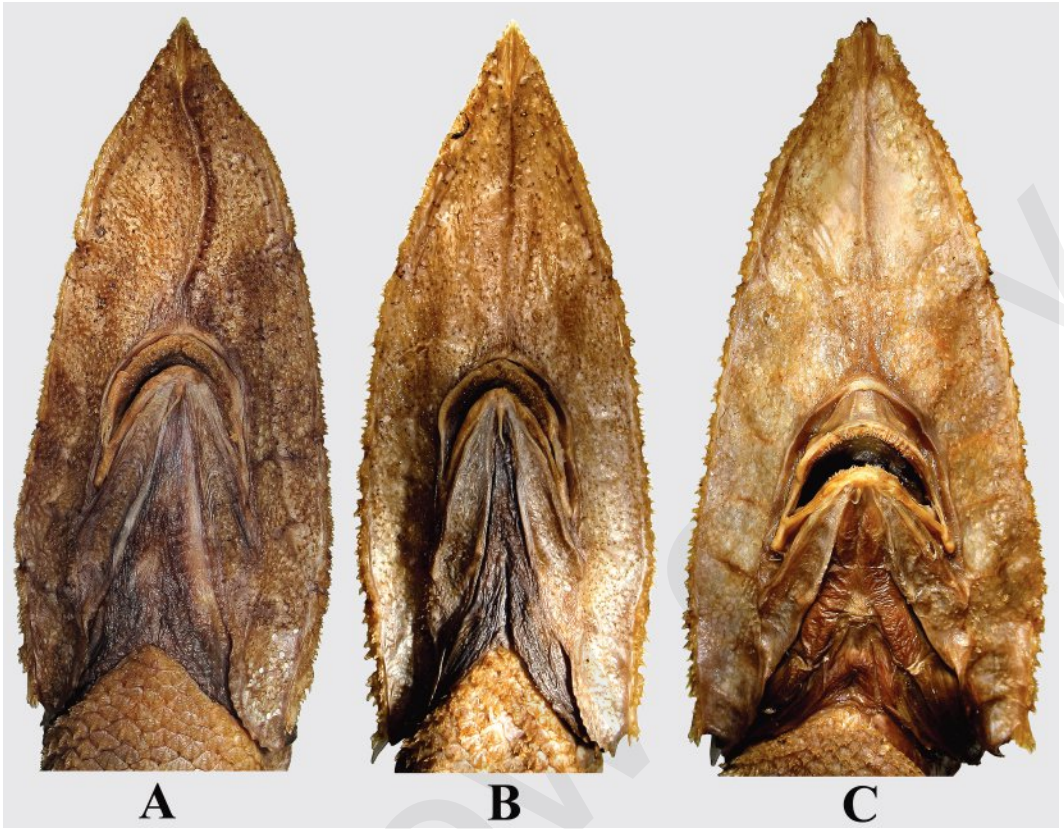


FIGURE 4. *Coelorinchus amirantensis*, paratypes, ventral view of head. A. IOM M.007-001, 126 mm HL. B. IOM M.008-002, 108 mm HL. C. IOM M.010-009, 80 mm HL.

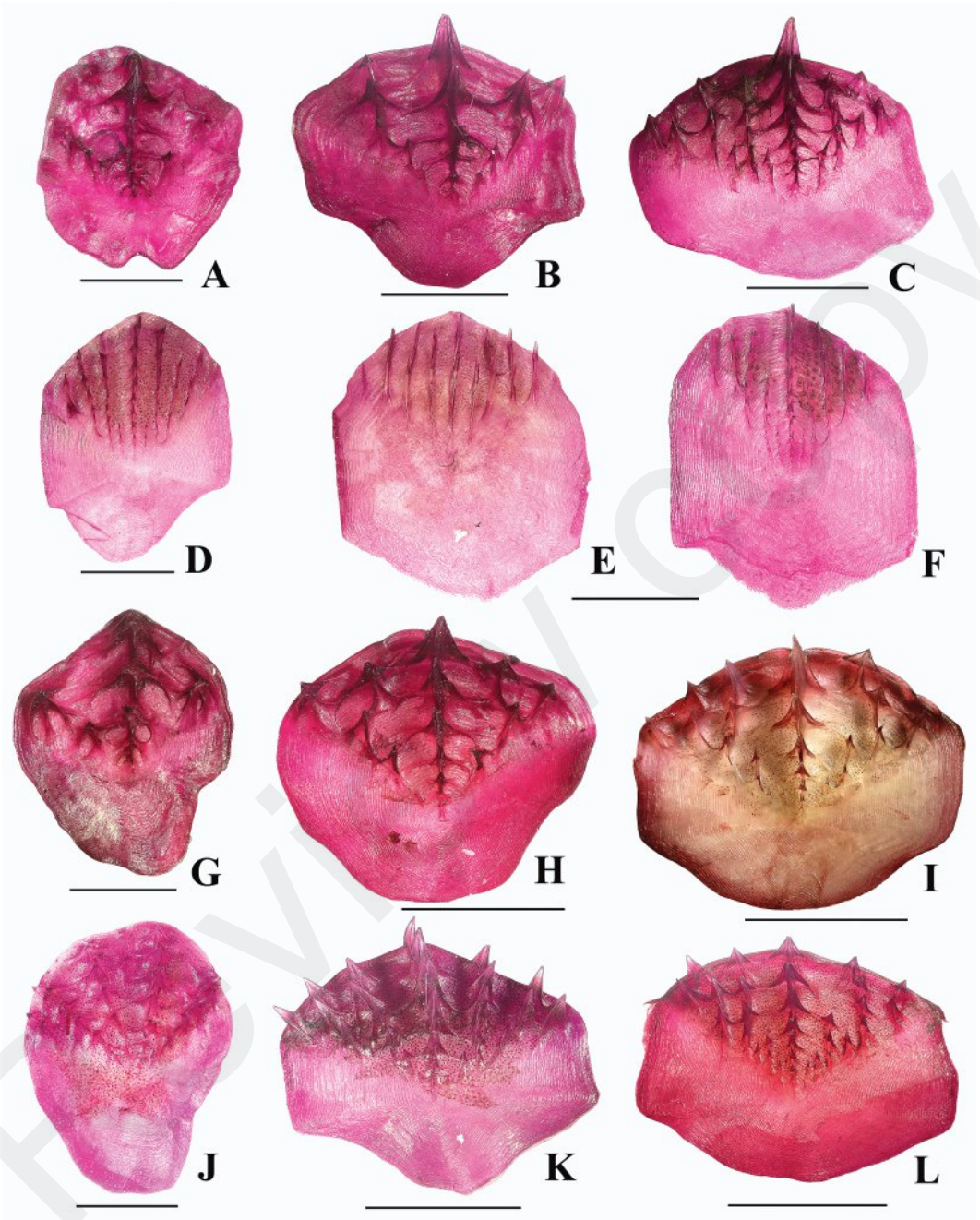


FIGURE 5. *Coelorinchus* spp., isolated scales from predorsal region (A, D, G, J), from flank between first dorsal-fin origin and lateral line (B, E, H, K), and from flank between second dorsal-fin origin and lateral line (C, F, I, L) (stained by alizarine red S for contrast). A–C. *C. amirantensis*, IOM M.007–001, paratype. D–F. *C. mascarenus*, IOM M.011–007, holotype. G–I. *C. paraboliciceps*, IOM M.004–003, holotype. J–L. *C. yurii*, IOM M.003–017, non-type specimen. Scale bars: A, J, 2.5 mm. B, C, E, F, H, K, 3.0 mm. D, 1.5 mm. G, 2.0 mm. I, L, 3.5 mm. Scale bar is common for E and F.

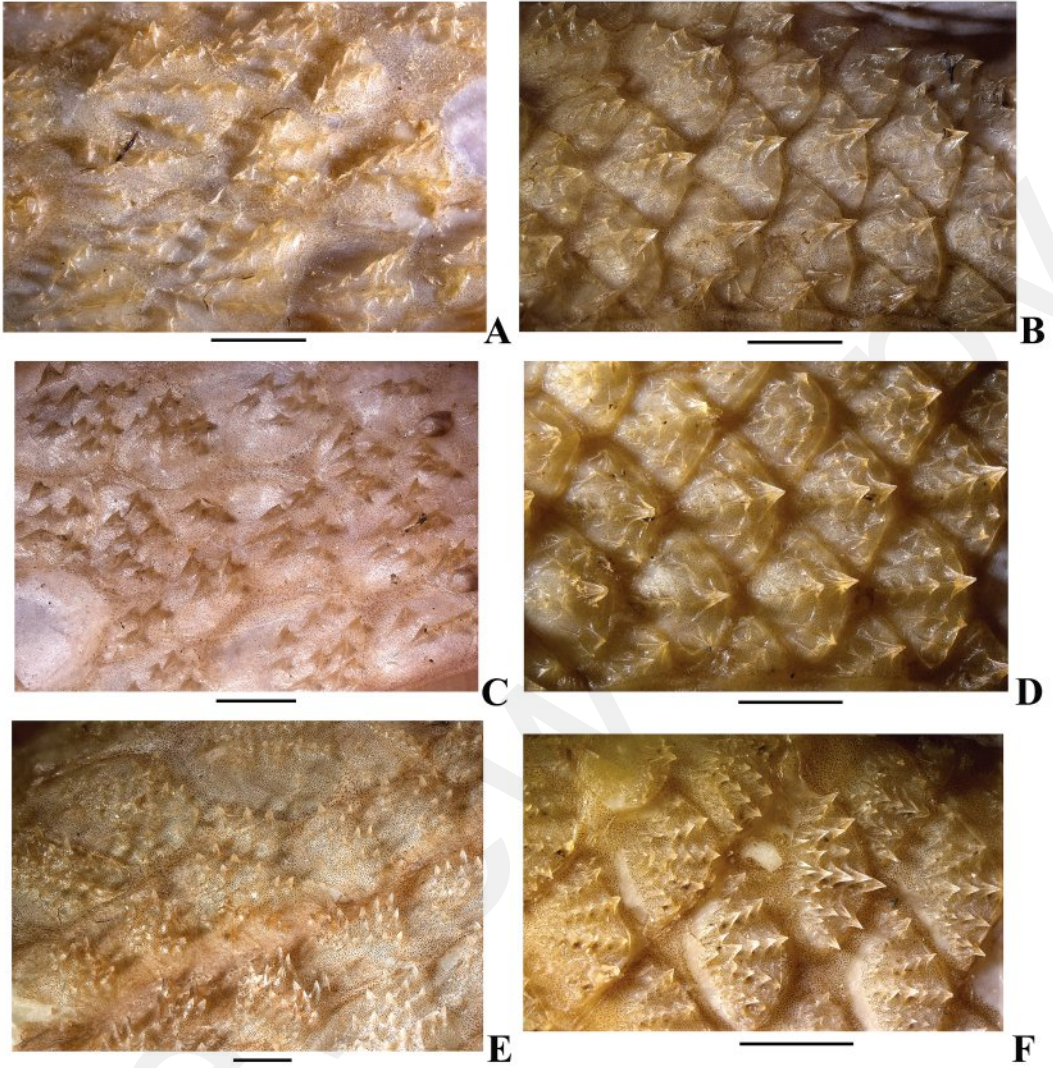


FIGURE 6. *Coelorinchus* spp., squamation of interorbital region (A, C, E) and of flank between mid-base of first dorsal fin and lateral line (B, D, F). A, B. *C. amirantensis*, IOM M.007-001, paratype. C, D. *C. paraboliceps*, IOM M.004-003, holotype. E, F. *C. yurii*, IOM M.003-017, non-type specimen. Scale bars: A, C, E, 2.5 mm. B, D, F, 5.0 mm.

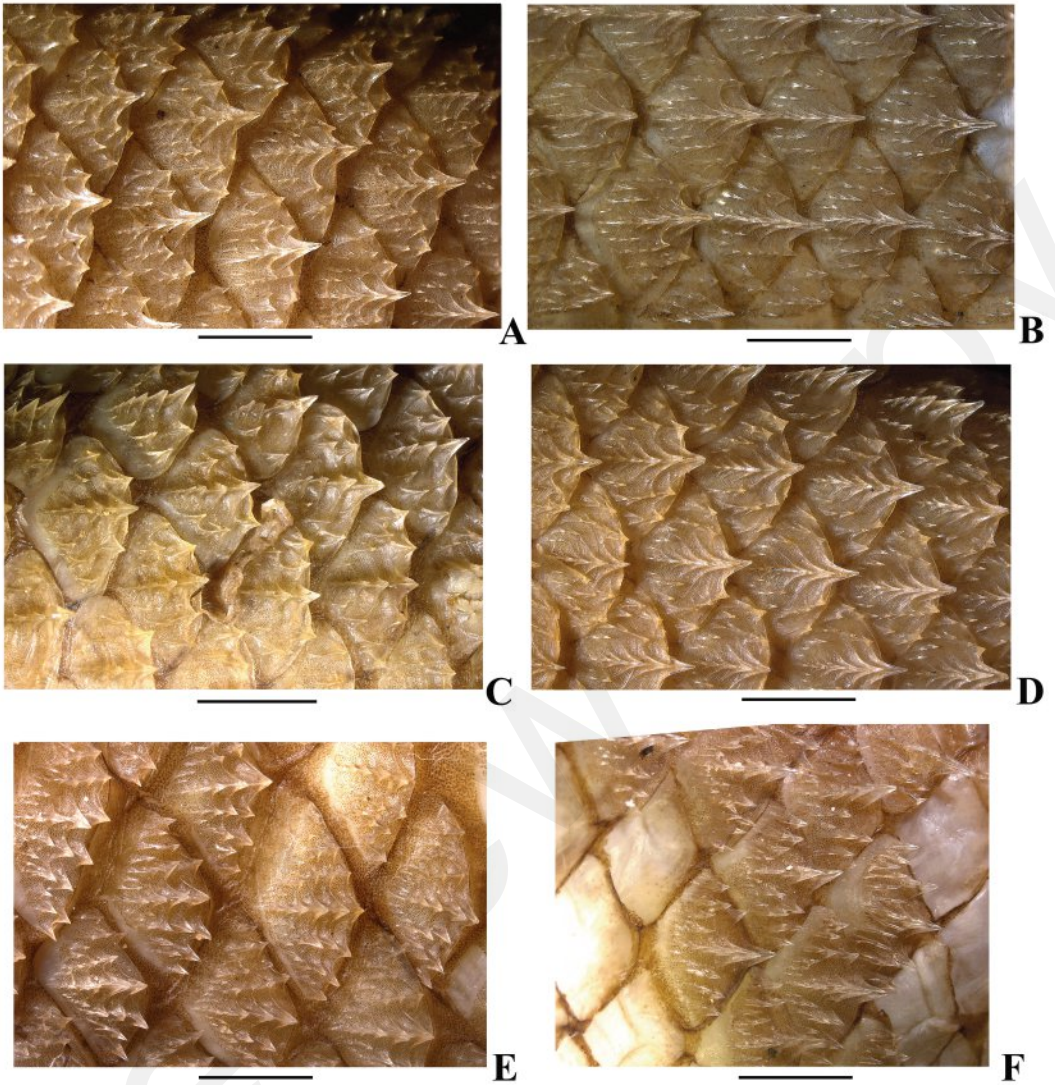


FIGURE 7. *Coelorinchus* spp., squamation of flank between origin of second dorsal fin and lateral line (A, C, E) and of tail behind anterior third of second dorsal-fin base (B, D, F). A, B. *C. amirantensis*, IOM M.007–001, paratype. C, D. *C. paraboliceps*, IOM M.004–003, holotype. E, F. *C. yurii*, IOM M.003–017, non-type specimen. Scale bars: 5.0 mm.



FIGURE 8. *Coelorinchus amirantensis*, IOM M.009–010, juvenile paratype, 41 mm HL. A. Dorsal view of head. B. Ventral view of head. C. Habitus, lateral view.

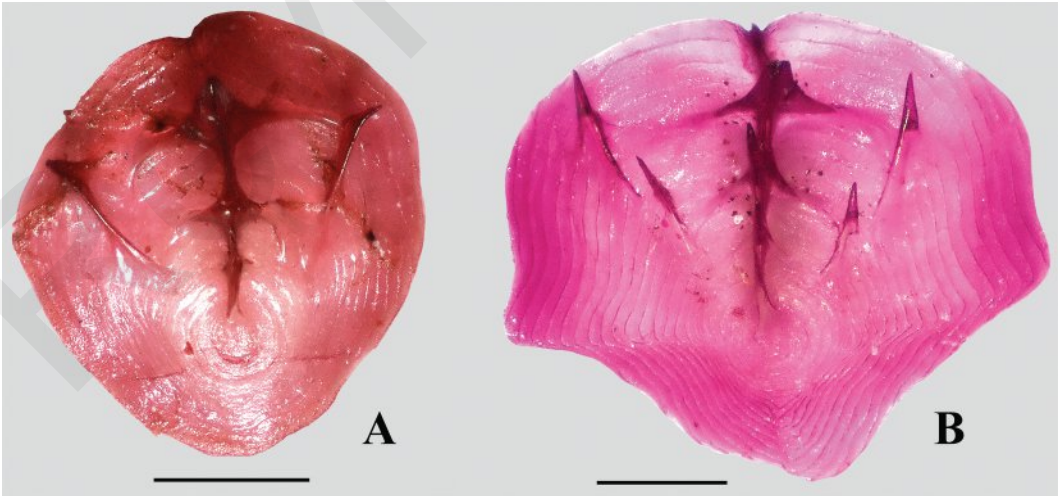


FIGURE 9. *Coelorinchus amirantensis*, IOM M.009–010, juvenile paratype, 41 mm HL, isolated scales from predorsal region (A) and from flank between mid-base of first dorsal fin and lateral line (B). Scale bars: 0.5 mm

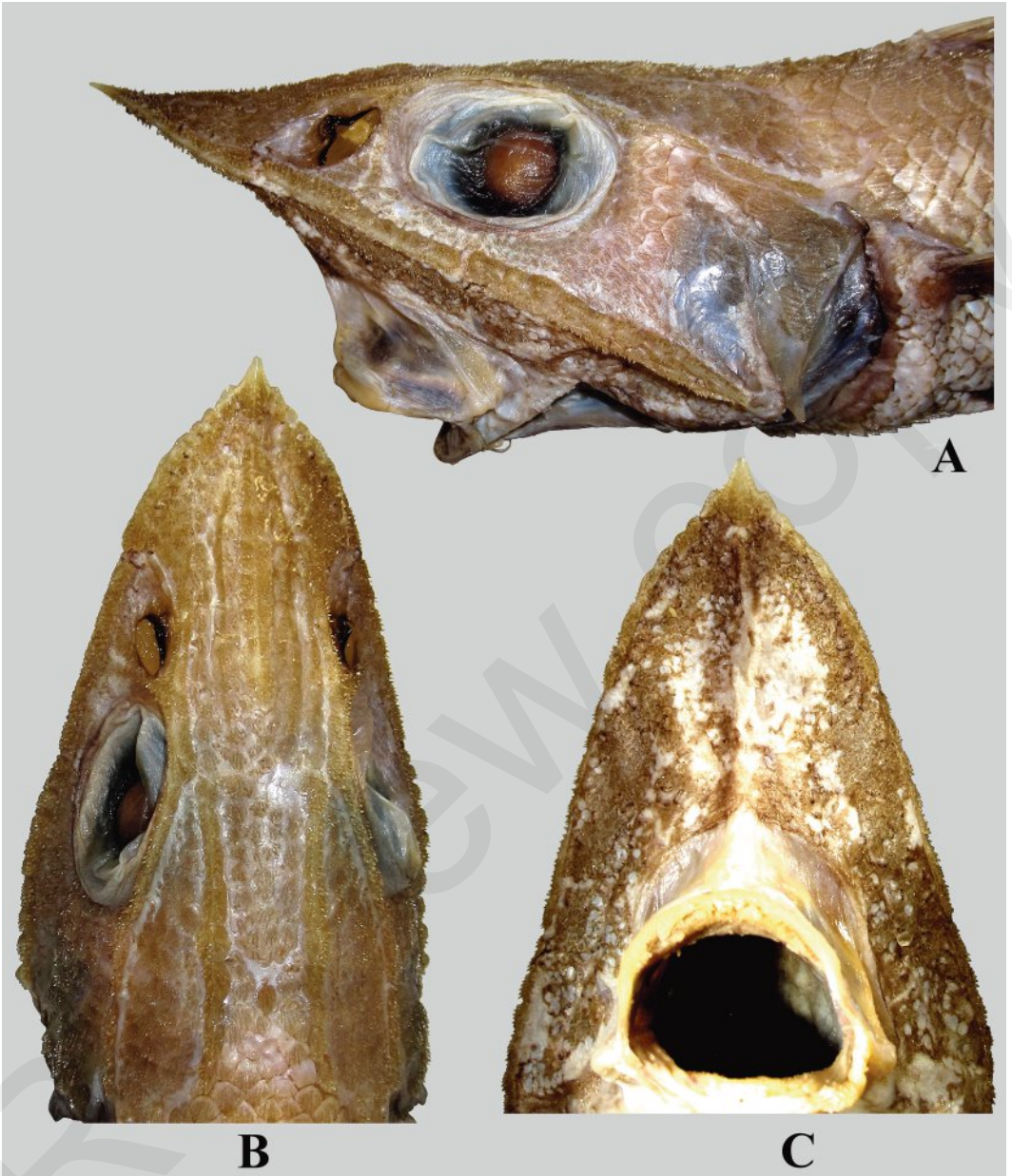


FIGURE 10. *Coelorinchus mascarenus*, IOM M.011–007, holotype, 91 mm HL. A. Lateral view of head. B. Dorsal view of head. C. Preoral region.

**A****B**

FIGURE 11. External evidence of light organ in *Coelorinchus mascarenus*, IOM M.011-007, holotype (A) and *C. braueri*, IOM 01864 (B). Scale bars: A, 3.0 mm. B, 2.0 mm

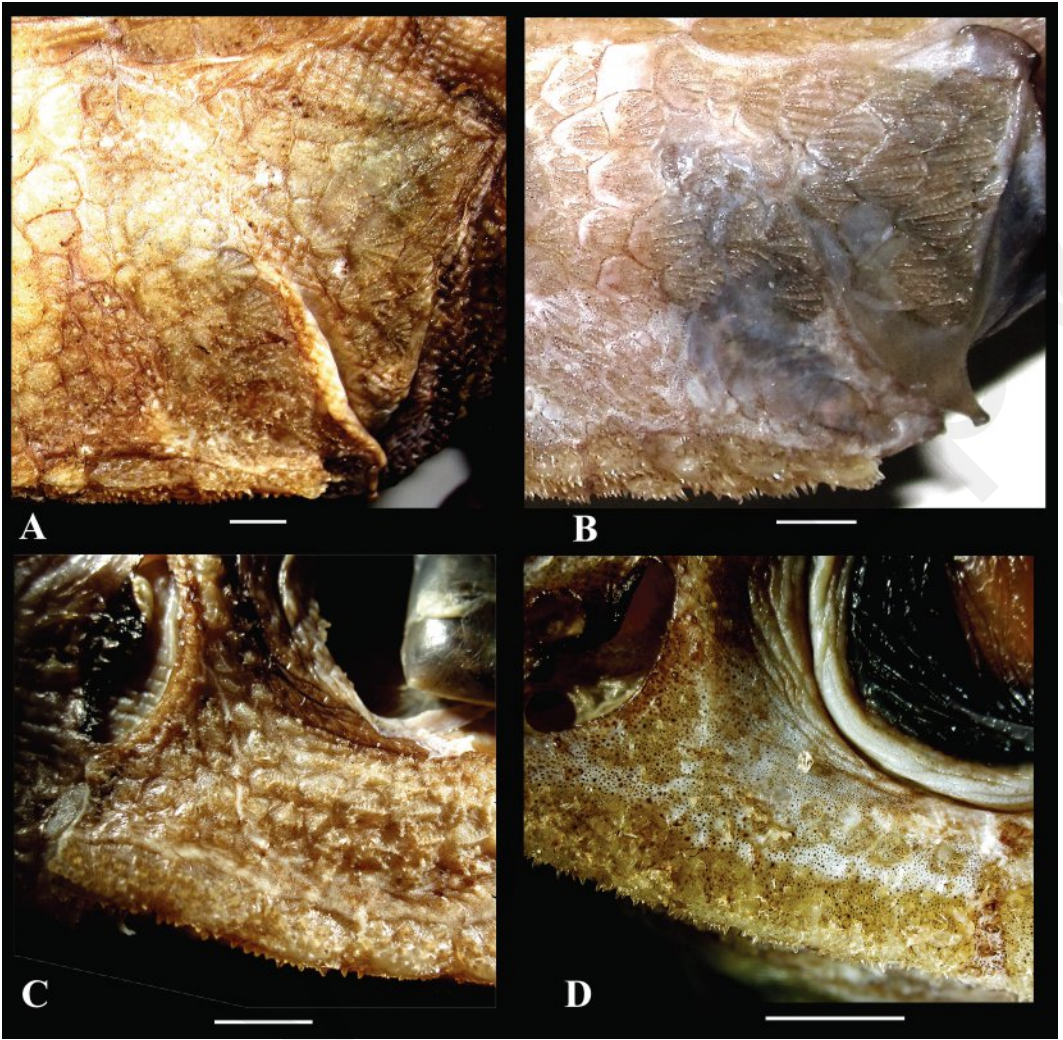


FIGURE 12. *Coelorinchus* spp., squamation of opercle (A, B) and of suborbital shelf (C, D). A, C. *C. yurii*, IOM M.003–017, non-type specimen. B, D. *C. mascarensis*, IOM M.011–007, holotype. Scale bars: 5.0 mm.

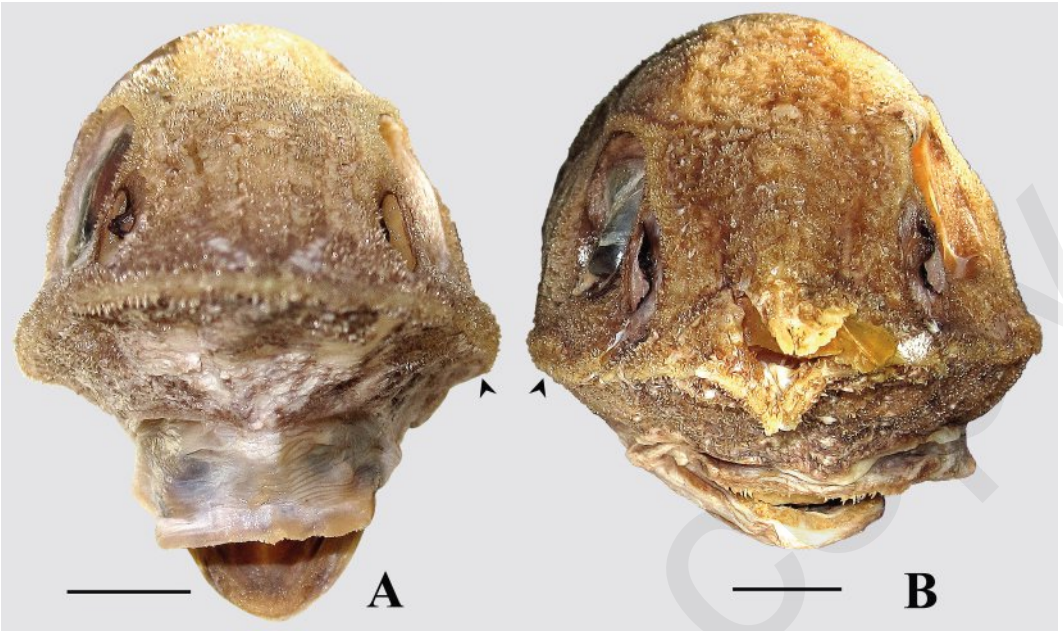


FIGURE 13. *Coelorinchus* spp., head, frontal view, suborbital shelf arrowed. A. *C. mascarenus*, IOM M.011–007, holotype. B. *C. yurii*, IOM M.003–017, non-type specimen. Scale bars: 10.0 mm.

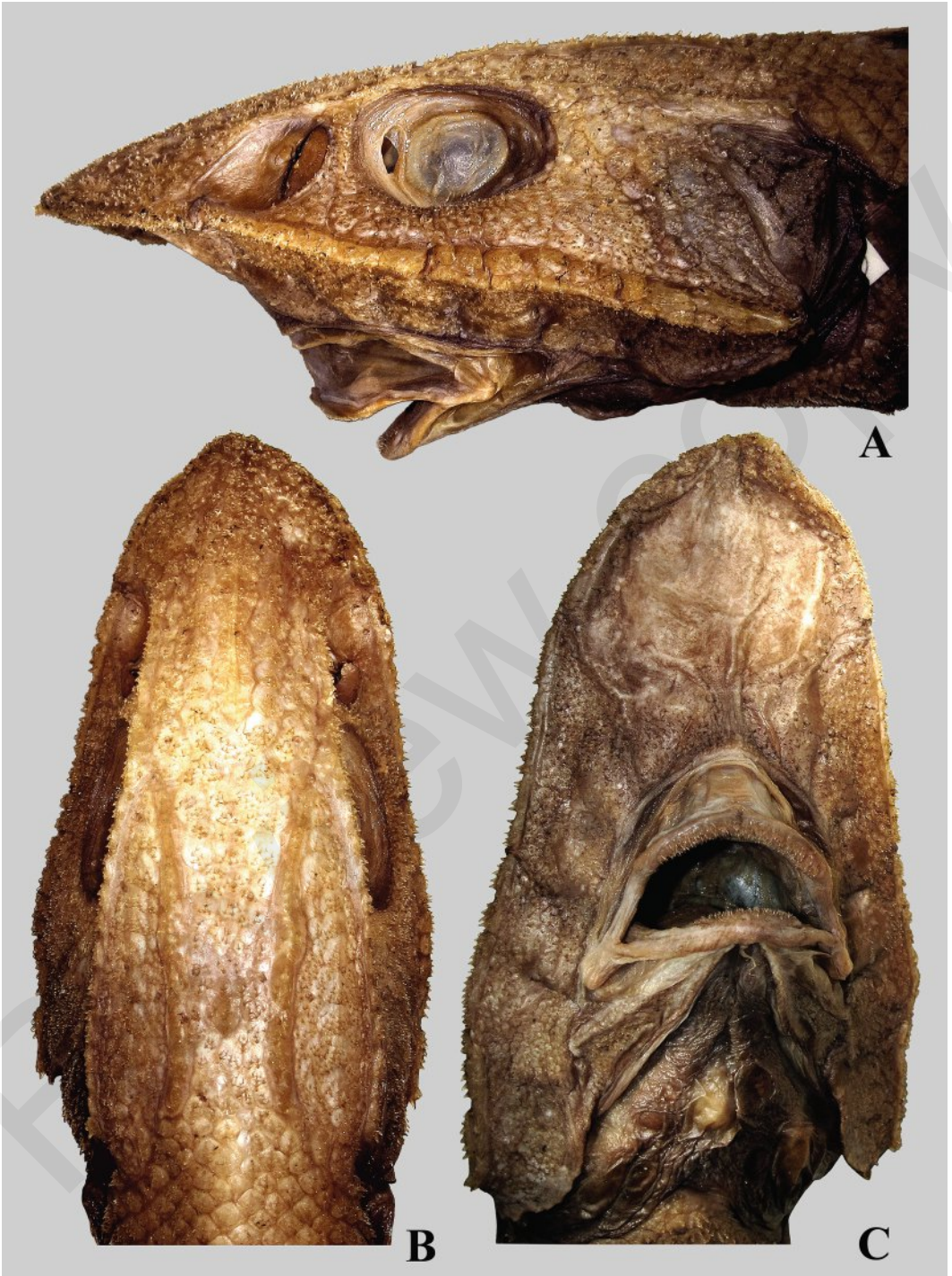


FIGURE 14. *Coelorinchus paraboliceps*, IOM M.004-003, holotype, 120 mm HL. A. Lateral view of head. B. Dorsal view of head. C. Ventral view of head.

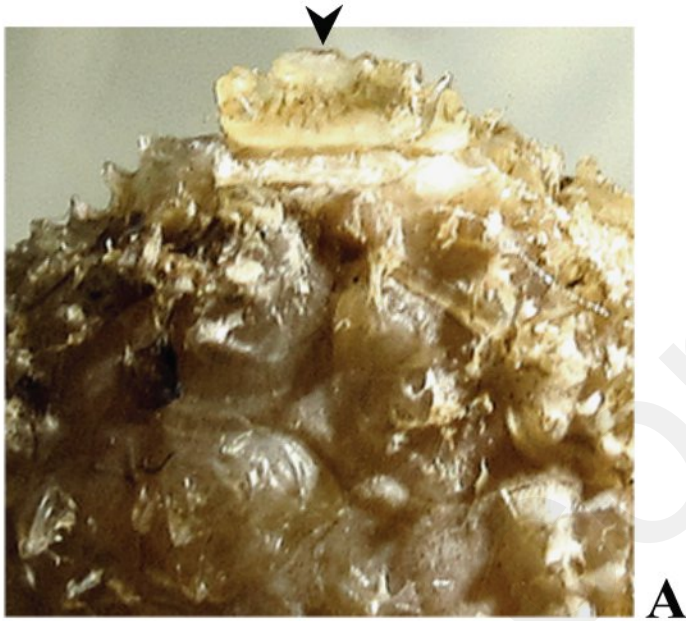


FIGURE 15. *Coelorinchus paraboliceps*, IOM M.004-003, holotype. A. Terminal scute of snout (arrowed), dorsal view. B. Preoral region. Scale bars: A, 1.5 mm. B, 5.0 mm.

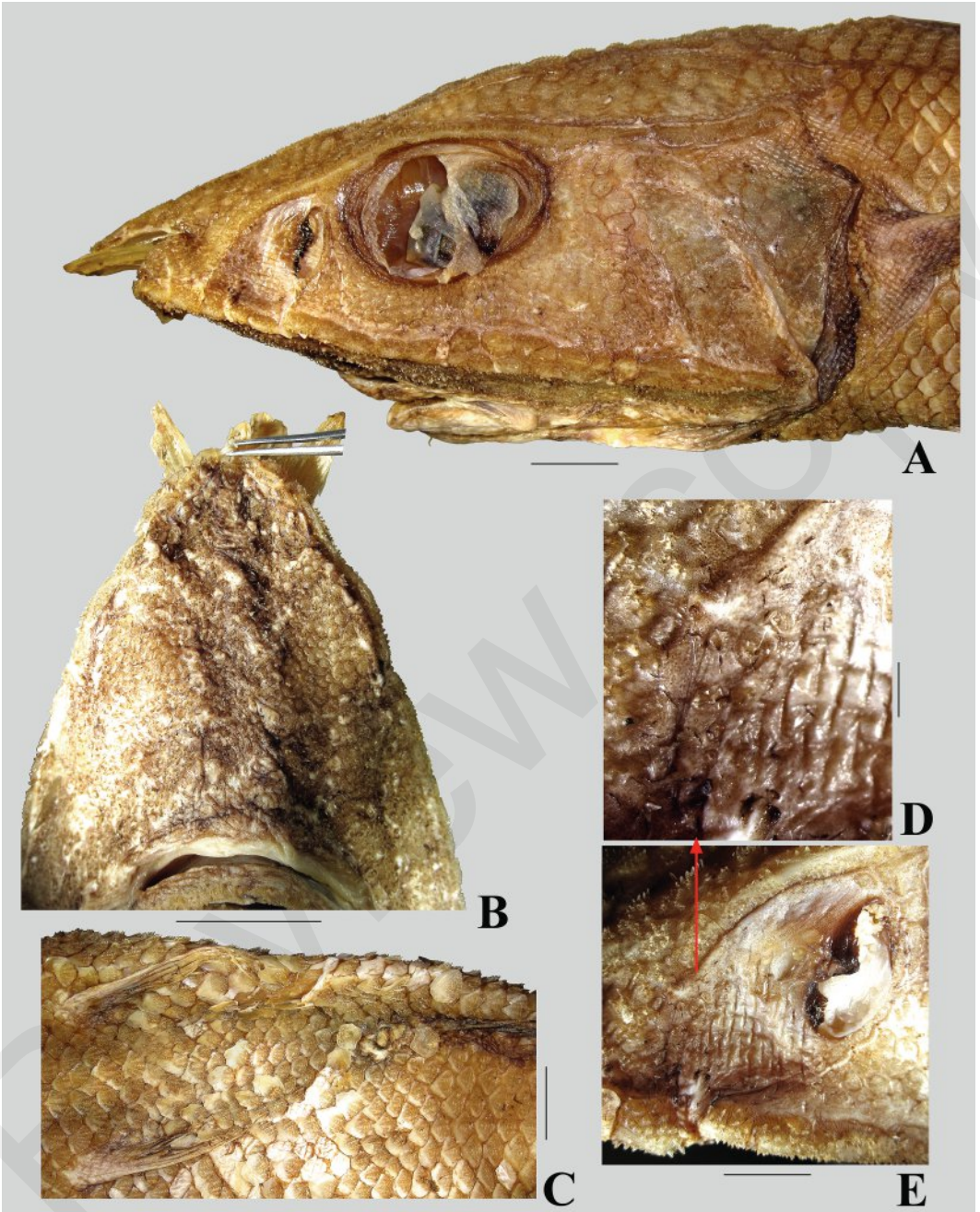


FIGURE 16. *Coelorinchus yurii*, IOM M.003-017, non-type specimen. A. Lateral view of head. B. Preoral region. C. Periproct. D, E. Nasal fossa and its squamation. Scale bars: A-C, 10.0 mm. D, 1.2 mm. E, 5.0 mm.

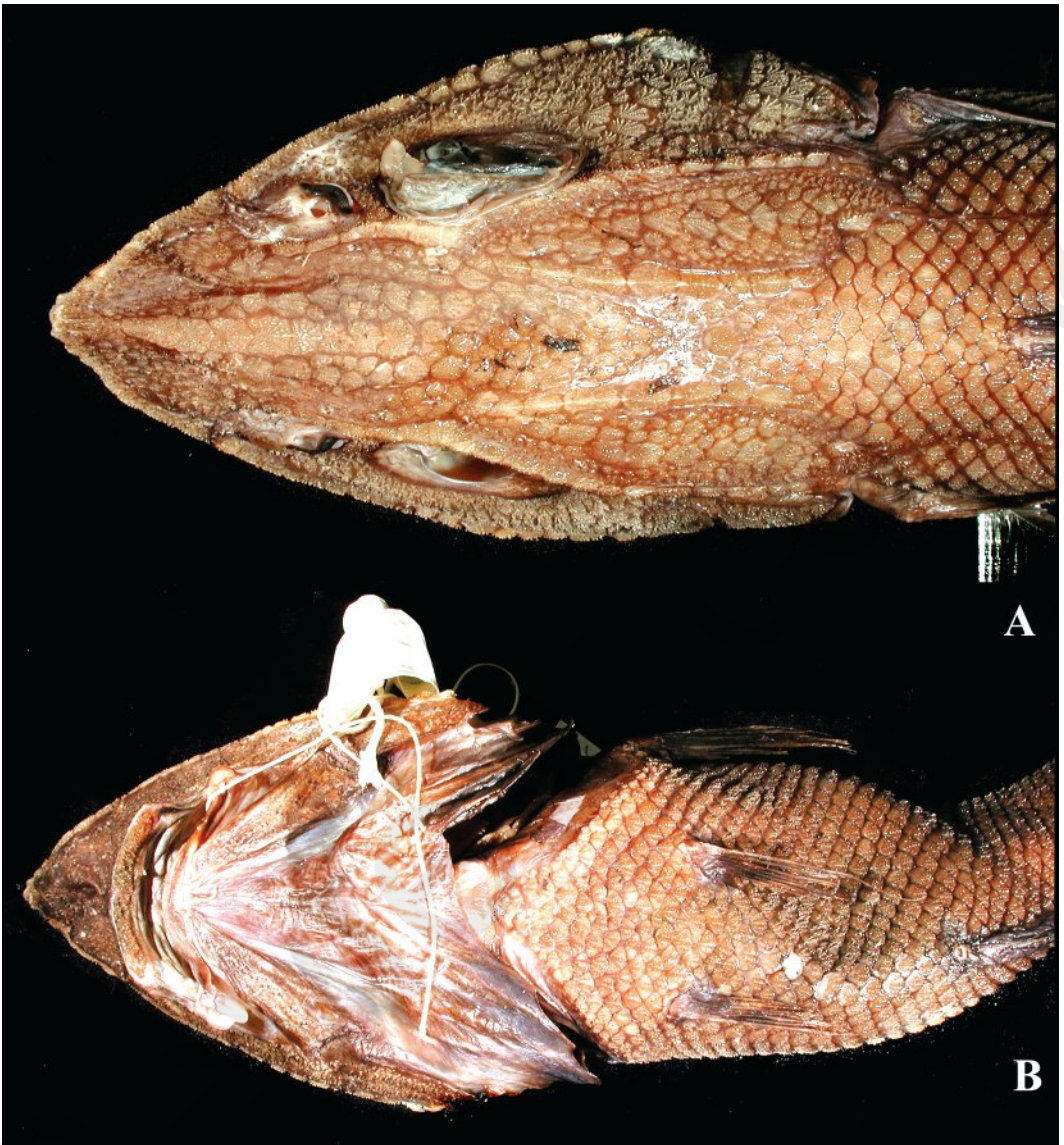


FIGURE 17. *Coelorinchus yurii*, TAU P.11602, holotype, 154 mm HL. A. Dorsal view of head. B. Ventral view of head and trunk.

Tables 1–4

Review Copy

TABLE 1. List of the currently valid species of the *Coelorinchus acanthiger*-group with their distributions.

Species	Distribution	Remarks
<i>Coelorinchus acanthiger</i> Barnard, 1925	Southern subtropical from off Argentina and South Africa to Australian – New Zealand region	<i>Coelorinchus pseudoparallelus</i> Trunov, 1983 is a synonym.
<i>Coelorinchus amirantensis</i> Iwamoto, Golani, Baranes and Goren, 2006	Mascarene Ridge	
<i>Coelorinchus anisacanthus</i> Sazonov, 1994	Central Pacific	
<i>Coelorinchus aratrum</i> Gilbert, 1905	Central Pacific	
<i>Coelorinchus braueri</i> Barnard, 1925	Off South Africa	Specimens from seamounts in south-western Indian Ocean at 25° S and from off South African coast and Agulhas show slight morphometric and structural differences and require thorough comparison.
<i>Coelorinchus divergens</i> Okamura and Yatou, 1984	Japan	
<i>Coelorinchus doryssus</i> Gilbert, 1905	Central Pacific	
<i>Coelorinchus gilberti</i> Jordan and Hubbs, 1925	Japan to Taiwan	<i>Coelorinchus kanetomoi</i> Matsubara and Asano, 1943 is a synonym (Okamura 1970a).
<i>Coelorinchus kermadecus</i> Jordan and Gilbert, 1904	South-western Pacific from New Caledonia to New Zealand	
<i>Coelorinchus labiatus</i> (Köhler, 1896)	North-eastern Atlantic	A very similar form (its differences from the nominal <i>C. labiatus</i> remain uncertain) is known from off South Africa and the seamounts of the south-western Indian Ocean. It was reported as <i>Coelorinchus</i> sp. 1b by Iwamoto et al. (2004).
<i>Coelorinchus lasti</i> Iwamoto and Williams, 1999	Australasia	
<i>Coelorinchus mascareneus</i> , new species	Mascarene Ridge	
<i>Coelorinchus mediterraneus</i> Iwamoto and Ungaro, 2002	Mediterranean Sea	
<i>Coelorinchus mycterismus</i> McMillan and Paulin, 1993	South-western Pacific from south of New Caledonia to New Zealand	
<i>Coelorinchus obscuratus</i> McMillan and Iwamoto, 2009	South-western Pacific from south of New Caledonia to New Zealand	
<i>Coelorinchus occa</i> (Goode and Bean, 1885)	Western central Atlantic	Specimens reported by Trunov (1984) from the South African waters belong to <i>Coelorinchus</i> sp. 1b (cf. <i>labiatus</i>).
<i>Coelorinchus paraboliceps</i> , new species	Mascarene Ridge	
<i>Coelorinchus parallelus</i> (Günther, 1877)	Japan to Taiwan	
<i>Coelorinchus sparsilepis</i> Okamura, 1984	Southern Japan (Okinawa Trough)	Separation from <i>C. parallelus</i> requires confirmation (Iwamoto and Merrett 1997).
<i>Coelorinchus trachycarus</i> Iwamoto, McMillan and Shcherbachev, 1999	Off southern Australia and New Zealand	
<i>Coelorinchus yurii</i> Iwamoto, Golani, Baranes and Goren, 2006	Mascarene Ridge	

TABLE 2. Measurements of the species of *Coelorinchus* from the Mascarene Ridge.

Character	<i>C. amirantensis</i>		<i>C. mascarenus</i>	<i>C. paraboliceps</i>	<i>C. yurii</i>
			n = 9	holotype	IOM M.003-17
			[holotype in brackets]		
SL, mm	147+	250-424+**	250-330+	410+	520+
		* (n = 5)	[297+]		
		** (n = 10)			
		*** (n = 9)			
HL, mm	41	79-157**	72-95	120	156
			[91]		
In % HL					
Snout length	45.1	45.9-50.5 (48.3)**	39.1-42.4 (41.5)	40	38.5
			[40.7]		
Orbit diameter	23.2	20.6-23.5 (21.9)**	23.5-27.0 (25.7)	23.3	23.1
			[26.4]		
Postorbital length	31.7	28.6-33.3 (30.5)**	31.9-35.3 (33.5)	36.7	38.5
			[33.0]		
Postrostral length	54.9	50.1-55.9 (52.5)**	57.6-61.5 (59.2)	60	61.6
			[59.4]		
Orbit-preopercle length	30.5	29.4-34.0 (31.4)**	30.6-35.3 (32.8)	36.7	38.5
			[33.0]		
Suborbital width	11.5	9.7-15.5 (12.1)**	10.6-12.9 (11.9)	12.5	12.8
			[11.5]		
Suborbital shelf width	6.6	6.5-7.9 (7.2)*	5.6-6.5 (6.1)	7.9	9
			[6.0]		
Upper-jaw length	24.4	19.8-23.0 (21.4)**	21.2-25.8 (23.5)	25	27.6
			[23.1]		
Length of rictus	19.5	14.8-17.5 (15.8)*	14.7-20.1 (17.6)	19.2	19.2
			[17.6]		
Length of premaxillary tooth band	9.8	6.3-8.7 (7.5)*	8.3-11.5 (9.8)	10	12.8
			[9.9]		
Preoral length	45.1	43.9-49.0 (45.4)**	36.8-40.0 (38.1)	33.3	35.3
			[37.4]		
Length of medial element of terminal snout scute	8.5	9.9-11.1 (10.6)*	6+-8.8 (7.4)	3.3	Broken
			[7.7]		

TABLE 2 (continued). Measurements of the species of *Coelorinchus* from the Mascarene Ridge.

Character	<i>C. amirantensis</i>		<i>C. mascarenus</i>	<i>C. paraboliceps</i>	<i>C. yurii</i>
			n = 9	holotype	IOM M.003-17
			[holotype in brackets]		
Width of medial element of terminal snout scute	3.7	3.1-3.7 (3.3)*	2.4-3.6 (3.0)	3.3	2.2
			[3.6]		
Length of posterior nostril	8.5	7.9-9.5 (8.6)*	8.2-10.8 (9.3)	10	7.7
			[8.8]		
Barbel length	6.6	3.7-7.0 (5.7)**	7.1-8.9 (8.0)	7.5	10.9
			[8.2]		
Length of lateral nasal ridge	26.8	33.3-35.4 (34.6)*	27.1-29.2 (28.3)	25	25.6
			[27.5]		
Length of medial nasal ridge	47.6	47.1-51.3 (49.7)*	38.8-43.5 (41.4)	41.7	38.5
			[40.7]		
Length of suborbital ridge	97.6	93.7-98.8 (95.7)*	88.2-93.1 (91.0)	91.7	86.5
			[90.1]		
Length of occipital ridge	36.6	31.7-37.3 (34.5)*	32.9-39.7 (37.2)	39.2	38.5
			[37.4]		
Snout width	31.7	25.9-28.8 (27.7)*	23.5-27.1 (26.2)	31.3	25.6
			[25.5]		
Internasal width	19.5	16.7-19.6 (18.1)**	16.7-19.4 (18.5)	20.8	19.2
			[18.7]		
Interorbital width	22	19.9-23.2 (21.7)**	17.7-22.2 (21.0)	25.8	23.7
			[21.4]		
Occipital width	13.4	11.2-12.7 (12.1)*	11.8-14.4 (13.1)	14.2	12.8
			[13.2]		
Greatest head width (at preopercles)	43.9	32.9-42.5 (36.0)*	40.0-49.5 (45.0)	45.8	44.9
			[49.5]		
Greatest body width (at pectoral-fin bases)	34.2	27.1-33.8 (29.9)*	34.1-41.8 (38.4)	35.8	38.5
			[41.8]		
Body depth at 1 st dorsal-fin origin	39	34.3-47.1 (39.5)***	43.5-50.7 (47.5)	45.8	44.9
			[48.4]		
Body depth at anal-fin origin	30.5	25.0-39.5 (31.3)*	34.7-43.7 (39.6)	39.2	35.3
			[42.9]		
First predorsal length	102.4	100.0-104.8 (101.8)*	101.1-110.5 (106.6)	104.2	109
			[105.5]		
Second predorsal length	128.3	120.0-132.5 (127.1)*	136.6-149.3 (144.5)	136.7	147.4
			[140.1]		
Preanal length	129.3	121.2-148.4 (134.8)**	136.6-152.1 (144.2)	140	147.4
			[145.1]		
Prepectoral length	100	100.0-101.6 (100.8)*	98.9-106.9 (102.0)	100	101.3
			[101.1]		
Prepelvic length	100	100.0-104.0 (102.2)*	103.5-112.1 (108.4)	105	101.3
			[112.1]		

TABLE 2 (continued). Measurements of the species of *Coelorinchus* from the Mascarene Ridge.

Character	<i>C. amirantensis</i>		<i>C. mascarenus</i>	<i>C. paraboliceps</i>	<i>C. yurii</i>
			n = 9	holotype	IOM M.003-17
			[holotype in brackets]		
Isthmus-pelvic length	17.1	16.3-19.4 (17.8)*	23.7-29.4 (26.5) [25.3]	21.7	25.6
Isthmus-anus length	44	44.3-54.0 (49.2)*	50.0-62.1 (54.4) [51.7]	57.5	62.2
Isthmus-anal length	45.2	45.6-55.6 (50.6)*	54.2-68.4 (59.7) [56.0]	59.2	67.3
Pelvic-anal length	28.1	29.1-46.8 (35.3)**	29.1-41.1 (33.0) [30.8]	37.5	41.7
Anus-anal length	1.2	1.2-1.9 (1.5)*	3.5-5.9 (4.9) [4.4]	1.7	4.5
Length of light organ	-	-	3.0-9.9 (6.5) [9.9]	-	-
Pectoral-fin length	31.7	27.1-30.4 (28.9)***	34.7-41.1 (37.8) [36.3]	30	35.3
Length of 1st pelvic-fin ray (with filament)	24.4	24.7-34.2 (28.8)***	32.3-38.4 (35.6) [36.3]	33.3	35.3
Length of 2nd pelvic-fin ray	c. 15	12.9-17.5 (16.0)*	17.2-21.8 (20.6) [damaged]	15.8	19.2
Length of 2nd ray of 1st dorsal fin (with filament)	Damaged	22.2-30.0 (27.0)*	53.8-59.0 (56.9) [57.1]	30.8	Tip missing
Length of 1st dorsal-fin base	11.5	9.4-15.3 (12.1)*	15.1-17.8 (16.4) [15.9]	12.5	14.4
Interdorsal length	13.4	9.4-15.6 (12.7)*	18.3-26.5 (22.4) [19.8]	18.3	24.4
Length of gill slit	11	7.9-12.7 (9.9)***	9.6-11.8 (10.9) [damaged]	10	Damaged

TABLE 3. Differences between *Coelorinchus yurii* and *C. mascarenus* in light of the ontogenetic variations in *C. amirantensis*.

Character	<i>Coelorinchus yurii</i>	<i>Coelorinchus mascarenus</i>	Ontogenetic variations in <i>Coelorinchus amirantensis</i> (HL 79–126 mm)
	(HL 154–156 mm)	(HL 72–95 mm)	
Light organ	Externally invisible; no bold melanophore pigmentation along midline of belly	Short cleft-like in front of anus; with bold melanophore pigmentation on silvery background along midline of belly	None [light organ externally invisible]
Spinule rows on scales from cheek and opercle	Strongly divergent (Fig. 12A)	Parallel to weakly divergent (Fig. 12B)	None [spinule rows divergent at all sizes]
Predorsal scales	Spinule rows divergent, 3–5 in number; medial row conspicuously raised in comparison with that of flank scales (Fig. 5J)	Spinule rows parallel to slightly divergent, (5)6–8 in number; medial row only slightly less inclined than that on flank scales (Fig. 5D)	None [spinule rows divergent at all sizes, 3–5 in number, medial row conspicuously raised, more strongly in smaller specimens]
Scales between first dorsal-fin base and lateral line	Spinule rows more or less divergent	Spinule rows clearly parallel	None [spinule rows always parallel to slightly divergent]
Lateral buttresses of spinules of flank scales	Strongly developed (Figs. 5K–L)	Small to absent (Figs. 5E–F)	Present [buttresses better developed in larger specimens]
Spinules on scales from area between nasal fossa, orbit and suborbital ridge	Arranged in 1 to 3 rows	Arranged in clusters, rarely in 1 short row on some scales	Present [in clusters or in 1 short row in smallest specimens to 1–3 rows in larger specimens]
Scales in nasal fossa	Present along anterior and lower border (Fig. 16D)	Absent	Present, but nasal fossa better scaled in smaller specimens
Scale rows in narrowest part of suborbital shelf	About 4; scales tightly joined, those in lowermost row enlarged (Fig. 12C)	Usually 1 (rarely 0 or 2); scales more or less separated by bare interspaces, all small (Fig. 12D)	Present, but number of rows decreasing with growth; scales tightly joined at all sizes, those in lowermost row enlarged
Scale attachment on flanks, breast and belly	Adherent	Deciduous	None [adherent at all sizes]
Scale attachment on underside of snout	Firmly adherent everywhere	Strongly deciduous in central portion of preoral region (or largely scaleless here in some specimens) and behind mouth	None [adherent]
Suborbital shelf	More steep (Fig. 13B)	More angular (Fig. 13A)	Similarly angular in all specimens examined
Suborbital shelf width	9.0 % HL	5.6–6.5 % HL (mean 6.1 %)	6.5–7.9 % HL, not corresponding with growth
Body color	Darker	Paler	Darker at all sizes

TABLE 4. Distinctions of *Coelorinchus amirantensis*, *C. paraboliceps* and *C. yurii*.

Character	<i>Coelorinchus amirantensis</i>	<i>Coelorinchus paraboliceps</i>	<i>Coelorinchus yurii</i>
Snout length, % HL	46–51	40–44	38–42
		[including data of Shcherbachev et al. (1986)]	
Dorsal contour of snout in lateral view	Horizontal (Fig. 3A)	Convex at level of nasal fossa, gently declining toward the tip (Fig. 14A)	Horizontal (Fig. 16A)
Sides of snout in dorsal view	Convex in basal half, straight to weakly concave in front of nasal fossa (Figs. 3B–C)	Strongly and regularly convex (Fig. 14B)	Weakly convex in front of nasal fossa (Fig. 17A)
Tip of snout in dorsal view	Acuminate	Rounded	Apparently acuminate (distal half of terminal scute broken in both known specimens)
Terminal scute of snout (medial element)	Elongate, diamond-shaped, 9.9–11.1 % HL (Figs. 3B–C)	Short, rectangular, 3.3 % HL (Fig. 15A)	Diamond-shaped (Fig. 17A)
Underside of snout (preoral region)	From almost completely scaled to largely scaleless in anterior third to two-thirds of preoral length	Scaleless except small area behind terminal scute and lateral quarters of posterior third of preoral length	Almost completely scaled
Spinules on scales over interorbital region	Arranged in keel-like rows (Fig. 6A)	Mostly irregularly disposed (Fig. 6C)	Mostly irregularly disposed (Fig. 6E)
Buttresses of spinules on trunk scales in front and below first dorsal fin	Forming transverse ridges (Figs. 5A–B, 6B)	Forming transverse ridges (Figs. 5G–H, 6D)	Not forming transverse ridges (Figs. 5J–K, 6F)
Buttresses of spinules on scales from tail	Not forming transverse ridges (Fig. 7B)	Forming transverse ridges (Fig. 7D)	Not forming transverse ridges (Fig. 7F)
Anus–anal length	1.2–1.9	1.7	2.8–4.5

Page intentionally left blank

Review Copy

Benthic Heterobranch Sea Slugs (Gastropoda: Heterobranchia) from Santa Barbara County, California

I. Review of the literature, and Naples Point, 2002–2019

Jeffrey H. R. Goddard^{1,2}, William M. Goddard², Zygmund E. Goddard²

¹ Marine Science Institute, University of California, Santa Barbara, California 93106-6150, USA.
Email: jeffg@ucsb.edu; ² Midland School, 5100 Figueroa Mountain Rd., Los Olivos,
California 93441, USA.

The shore at Naples Point is unique on the south coast of Santa Barbara County for its broad and gently sloping shale bench with permanent accumulations in the low intertidal of boulders and cobbles. From 2002 to 2019 we sampled these boulder fields intermittently for heterobranch sea slugs, recording a total of 12,193 individuals from 55 species, 48 of which were nudibranchs. The bubble snail *Haminoea virescens* was the most abundant species, followed by the sea hare *Aplysia californica*, and the nudibranch *Tritonia myrakeenae*. Southern species, with primarily Californian or Panamic biogeographic affinities, dominated the heterobranch assemblage at 35 species, while northern, primarily Oregonian species numbered 14. With two dips associated with La Niña events in 2010 and 2017, the prevalence of southern species increased steadily after 2008, in concert with an overall increase in the average yearly values of the Multivariate El Niño Southern Oscillation Index. During this same period, two of the initially more abundant northern nudibranchs, *Cadlina modesta* and *Tritonia festiva*, declined in abundance to zero, while conspicuous southern species, including *Doriopsilla gemela*, *Anteaeolidiella chromosoma*, and *Thordisa bimaculata*, markedly increased in abundance, with *A. chromosoma* and *T. bimaculata* peaking in abundance during both the 2009–10 and 2015–16 El Niño events. Many of the more frequently encountered species showed seasonal cycles in abundance, with *Tritonia myrakeenae*, *Hermisenda opalescens*, *Anteaeolidiella chromosoma*, *Triopha maculata*, and *Orienthella cooperi* peaking in abundance in the spring, and *Aplysia californica*, *Navanax inermis*, *Phidiana hiltoni*, *Diaulula sandiegensis*, and *Berthella strongi* peaking in the late fall or winter. The average total abundance of nudipleurans at Naples Point was one third to one half that reported from outer coast intertidal sites in central California, where potential or known predators of heterobranchs such as California spiny lobster, California cone snails, *Navanax inermis*, and Two-spot octopuses are less common or absent.

KEYWORDS: Heterobranch sea slugs, Nudibranchia, Gastropoda, intertidal zone, Naples Point, Southern California Bight, seasonality, population fluctuations, El Niño Southern Oscillation, Northeast Pacific Ocean

Santa Barbara County marks an abrupt turn in the California coast, from the primarily north-south orientation north of Point Conception to east-west in the Southern California Bight (SCB). The cool, south-flowing California Current dominates off northern California and along the westernmost Channel Islands, and is replaced in the SCB and the Santa Barbara Channel by cyclonic circulation and seasonally alternating poleward/equatorward flows (Harms and Winant 1998; Dong et al. 2009). This mixing of cool and warm waters forms part of the transition zone between the

Oregon and California Biogeographic Provinces (Briggs and Bowen 2012), and with a topographic complexity added by the northern Channel Islands and deep offshore basins, the Santa Barbara region supports a diverse marine biota comprised of both cool and warm temperate species, including approximately 100 species of heterobranch sea slugs (Sphon and Lance 1968; Lee and Brophy 1969; Gosliner 1996; Valdés 2019).

Sphon and Lance's (1968) annotated list of "nudibranchs and their allies" (= heterobranch sea slugs; hereafter heterobranchs) from Santa Barbara County was the first comprehensive list of heterobranchs for a California county. They included 71 species from 12 localities, as well as unspecified sites on Santa Cruz Island (which at 35 km long and 250 km² in area varies widely in physiography). However, Sphon and Lance (1968) did not review the primary literature on heterobranchs from the county and its surrounding waters, overlooking the significance of Santa Barbara as a collection and type locality for some of the better known heterobranch species from California, a role which stemmed from its importance as a settlement and port of call during the Mexican era in California (e.g., Dana 1840; Jepson 1934).

The first heterobranch mollusk collected from Santa Barbara documented by western science was *Bulla gouldiana*, found by the eminent botanist and naturalist Thomas Nuttall in 1836 (Carpenter 1857 [as *Bulla nebulosa*], and see Coville 1899 and Jepson 1934 for the chronology of Nuttall's first trip to California). The earliest published record of heterobranchs from Santa Barbara County (which until 1873 included what is now Ventura County) were Gould's (1853) descriptions of *Bulla culcitella* and *Bulla cerealis* (= *Acteocina culcitella* and *A. cerealis*, respectively) collected by Colonel Ezekiel Jewett, who spent ten weeks in 1849 collecting fossil and extant molluscs in the greater Santa Barbara area (Carpenter 1864). Ten years later Dr. James G. Cooper (1863) described the nudibranchs *Doris albopunctata* (= *Doriopsisilla albopunctata*), *Dendronotus iris*, and *Aeolis barbarentis* (= *Antiopella barbarentis*) based on specimens he collected subtidally and intertidally in the vicinity of Santa Barbara from May to July 1863. He also reported finding *Phidiana iodinea* (Cooper, 1863) (= *Flabellinopsis iodinea*), and *Chioraea leonina* Gould, 1852 (= *Melibe leonina*) from mainland Santa Barbara waters, and *Doris montereyensis* Cooper, 1863, *Doris sanguinea* Cooper, 1863 (= *Aldisa sanguinea*), *Doris sandiegensis* Cooper, 1863 (= *Dialulla sandiegensis*), and *Flabellina opalescens* (Cooper, 1863) (= *Hermisenda opalescens*) from rocky shores at Santa Barbara Island which, although closer to Ventura and Los Angeles Counties, is also part of Santa Barbara County. Although Cooper (1863) emphasized the physical and biological differences between the island and mainland, both MacFarland (1906) and O'Donoghue (1926) dropped the word "Island" in referring to Cooper's records of these latter three species, obscuring the precise collection locality. Carpenter (1864) briefly described *Volvula cylindrica* (= *Volvulella cylindrica*), which had been collected by Jewett from the Santa Barbara area but not examined by Gould. Gabb (1865) described *Tylodina fungina* based on a fresh but empty shell found by Cooper on the shore at Santa Barbara Island. From Cooper's (1867) catalogue of the Mollusca known from the western United States we can find three additional heterobranch taxa recorded specifically from Santa Barbara County: *Haminea vesicula* (Gould, 1855) (= *Haminoea vesicula*), *Tornatina carinata* Carpenter, 1857 (= *Acteocina inculta* (Gould, 1855)), and *Cylichna attonsa* Carpenter, 1865. Cooper (1867) also listed *Bulla quoyi* Gray in A. Adams, 1850 (= *B. punctulata* A. Adams in Sowerby 1850) from Santa Barbara, but this is a Panamic species not otherwise recorded north of Baja California Sur. Fewkes (1889) described *Cabrilla occidentalis* (= *Triopha occidentalis*) from Prisoner's Harbor on Santa Cruz Island, and Yates (1890), in his list of molluscs from Santa Barbara County, included 10 species of heterobranchs specified by Cooper (1867) as having been found in the County and added new Santa Barbara locality information for two others, *Neaplysia californica* Cooper, 1863 (= *Aplysia californica*) and *Phidiana iodinea* (= *Fla-*

bellinopsis iodinea). Dall (1902) described *Actaeon (Microglyphis) breviculus* (= *Microglyphis brevicula*), and Dall (1919) described *Volvuella californica*, both collected from 97 m depth off Santa Rosa Island during a cruise of the United States Fish Commission Steamer *Albatross*.

Nearly 50 years passed before the next publications documenting new records of heterobranchs from Santa Barbara County, when Lance (1966) noted *Okenia angelensis* Lance, 1966, *Trapania velox* (Cockerell, 1901), and *Cuthona alpha* Baba and Hamatani, 1963 (= *Catriona columbiana* (O'Donoghue, 1922) in the NE Pacific) from the Santa Barbara Yacht Harbor, and Lance (1967) extended the known range of *Aplysia vaccaria* Winkler, 1955 to Hammond's Point in Santa Barbara. One year later, Sphon and Lance (1968) published their aforementioned list, based primarily on their own collecting trips, but also on specimens from the Santa Barbara Museum of Natural History. They documented 42 taxa from the intertidal zone (or intertidal and subtidal), 26 species strictly from the subtidal, 2 species of Corambidae from floating kelp, and the pelagic *Fiona pinnata* (Eschscholtz, 1831). Lee and Brophy (1969) added 10 more heterobranch species to the county list, primarily from the subtidal, and Long (1969) recorded *Ancula pacifica* MacFarland, 1905 from Santa Cruz Island. Cowen and Laur (1978) described *Coryphella sabulicola* from subtidally off Santa Barbara, but it was synonymized with *Coryphella iodinea* (Cooper, 1863) (now *Flabellinopsis iodinea*) following the arguments of McDonald (1983). Since then, Behrens and Henderson (1981) described *Jorunna pardus* based in part on specimens from Santa Cruz Island; Gosliner and Behrens (1988) described *Phyllidiopsis blanca*, including a northern range limit at Santa Barbara Island; Millen and Bertsch (2000) described *Peltodoris mullineri* based in part on specimens from Santa Cruz Island; Engle and Richards (2001) reported *Polycera alabe* Collier and Farmer, 1964 subtidally from Santa Barbara Island and *Pleurobranchus areolatus* Mörch, 1863 (= *Pleurobranchus digueti* Rochebrune, 1895 in the NE Pacific Ocean; see Goodheart et al. 2015) from Anacapa Island during the 1997-98 El Niño; Goddard (2007) described feeding by *Berthella strongi* (MacFarland, 1966) on the slime sponge *Oscarella carmela* Muricy and Pearse, 2004 from Naples Point (as the Ellwood boulder field); Gosliner (2010) described *Flabellina goddardi* (= *Pacifia goddardi*) from Carpinteria, on the south coast of the county mainland; and Goddard and Hoover (2016) provided additional information on the distribution and biology of the latter. Lastly, a few additional species were noted from the County in recent papers on developmental mode (Goddard and Green 2013) and range shifts of heterobranchs in the North-eastern Pacific (Goddard et al. 2016, 2018).

Excepting the works of Dall (1902, 1919) and Lee and Brophy (1969), the papers cited above dealt primarily with shallow water fauna. Deep-water heterobranchs from Santa Barbara County waters were documented by Gosliner (1996), who worked on heterobranchs collected as part of the benthic reconnaissance and monitoring program conducted by the U.S. Minerals Management Service in the Santa Maria Basin and western Santa Barbara Channel. He documented the deep-water occurrence of 29 heterobranch taxa, including 25 from waters off Santa Barbara County. Fifteen of the latter were not previously recorded from the county and included undescribed species, as well as the first record of *Parvaplustrum* from the Pacific Ocean. The latter was described by Valdes et al. (2017) as *Parvaplustrum cadieni*. Valdes (2019), in his monograph on the benthic shelled sea slugs from the Northeast Pacific Ocean, described *Microglyphis michelleae* from 4100 m depth west of Point Arguello, Santa Barbara County. Three additional species — *Cylichnium cylindrellum* (Dall, 1908), *Scaphander interruptus* Dall, 1890, and *Acteon traskii* Stearnes, 1897 — are also reported for the first time from deep waters off of Santa Barbara County by Valdes (2019), who noted that *Acteon traskii* may be the same as *Acteon* sp. reported by Gosliner (1996).

Here, we document heterobranchs from the intertidal zone at Naples Point, a biologically diverse site encompassed by the Naples State Marine Conservation Area (Naples SMCA) and

located on the south coast of Santa Barbara County. Sphon and Lance (1968) included Naples Reef, a well-known dive site located approximately 1 km offshore of the point, as one of their localities, but do not appear to have included observations or records from the shore at Naples Point. Excepting the aforementioned papers by the senior author, none of the studies referred to above included Naples Point as a collection locality. However, during his studies of ecological succession and disturbance at Naples Point (as the Ellwood boulder field [see below]) Sousa (1979a) reported densities of the sea hare *Aplysia californica* of up to 155/1500 m² and described the seasonality of its egg-laying. Further, an unpublished field account in the James R. Lance Collection at the California Academy of Sciences documents 18 species of heterobranchs found at Naples Point (as Dos Pueblos Reef) by Jim Lance and Sam Spaulding in May 1972. To our knowledge this was the first time a survey focused on heterobranchs was conducted at Naples Point, and we include an annotated transcription of their account as Appendix A. The only other records of heterobranchs from Naples Point of which we are aware are specimens of seven species collected in 1983 (from “Rancho dos Pueblos Beach”) and deposited in the Malacology Department at the Santa Barbara Museum of Natural History (SBMNH). Four of these (*Haminoea vesicula*, *Navanax inermis* (Cooper, 1862) *Acanthodoris lutea* MacFarland, 1925, and *Spurilla chromosoma* Cockerell and Eliot, 1905 [= *Anteaeolidiella chromosoma*]) had not been recorded by Lance and Spaulding (see Appendix A).

In addition to species composition and abundance, we describe seasonal patterns of occurrence and egg-laying for some of the more abundant heterobranchs from Naples Point, as well as for the total number of species and individuals. We also include information on the prey of many species.

Our observations from Naples Point have so far spanned 17 years. During this period oceanographic fluctuations have included two strong La Niña events (2007–08, 2010–11) and one very strong El Niño (2015–16) (Null 2019). In the Northeast Pacific the 2015–16 El Niño followed an unprecedented marine heatwave beginning in late 2013, and together these events drove northward range shifts in numerous marine species (Cavole et al. 2016; Sanford et al. 2019), including at least 52 species of heterobranchs (Goddard et al. 2018). The latter study documented the appearance and population increases of the bubble snail *Bulla gouldiana* and the sea hare *Aplysia vaccaria* at Naples Point (as Naples) associated with these warm water events, and Goddard et al. (2016) described similar changes in abundance at Naples Point for the nudibranchs *Thordisa bimaculata* Lance, 1966, *Doriopsilla gemela* Gosliner, Schaefer and Millen, 1999, and *Anteaeolidiella chromosoma* (Cockerell and Eliot, 1905). We examine herein additional changes in the abundance and proportions of northern versus southern species associated with the above oceanographic fluctuations.

STUDY SITE

Naples Point is located on the south coast of Santa Barbara County, 24 km west of Santa Barbara (Fig. 1). Our study site spanned approximately 600 m of shore and consisted of tide pools, shallow channels, a few undercut rock outcrops, and three permanent accumulations of boulders and cobbles, all located on a broad, gently sloping, wave-cut bench of Monterey shale. The eastern-most of these boulder fields (Fig. 2) was our main study site and extends vertically from a tidal height of approximately +0.3 m above mean lower low water to -0.4 m. On a 0 m tide approximately 1500 m² of this boulder field is exposed to air (Fig. 2B). It is centered at 34.4339°N, 119.9500°W. Surfgrass, *Phyllospadix torreyi* S. Watson, 1879, dominates much of the surrounding bench. At low tide a shallow lagoon lies just landward of the boulder field, and behind that more shale bench, a narrow sand beach, and cliffs up to 25 m high consisting of Monterey shale overlain with terrestrial deposits. Sand levels on the beach and in the lagoon fluctuate seasonally, with near-

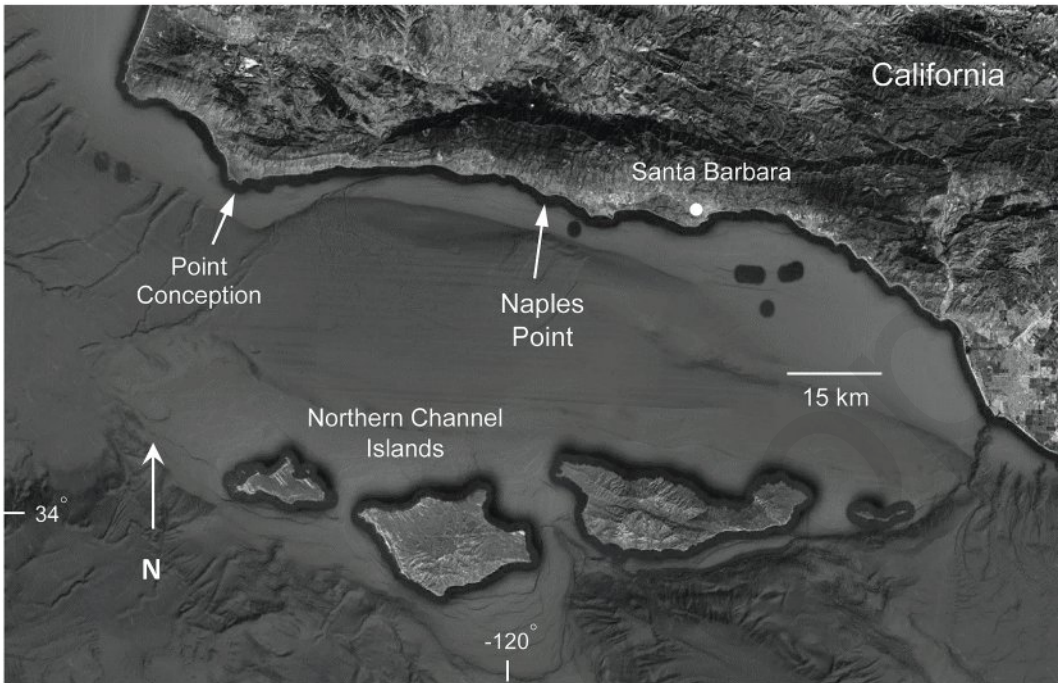


FIGURE 1. Map of southern Santa Barbara County showing the location of Naples Point in relation to Santa Barbara to the east, Point Conception to the west, and the northern Channel Islands to the south.

ly all of the sandy beach scoured away in winter. Although sand and detritus builds up between and underneath boulders during the summer, the boulder field as a whole is never significantly inundated by sand. Vertical relief in our study area is fairly low, with most boulders under 0.5 m diameter, and the tallest rock outcrop approximately 1 m high. Sousa (1979a) conducted ecological research in this same boulder field and provided an extensive description of the environment, including common algae and grazing invertebrates. Common mobile macro-invertebrates we observed in the boulder fields included Striped shore crab *Pachygrapsus crassipes* Randall, 1840, juvenile Bat stars *Patiria miniata* (Brandt, 1835), juvenile Purple sea urchins *Strongylocentrotus purpuratus* (Stimpson, 1857), Banded turban snails *Tegula eiseni* Jordan, 1936, chitons *Stenoplax conspicua* (Dall, 1879), *Lepidozona pectinulata* (Carpenter in Pilsbry, 1893), and *Leptochiton rugatus* Carpenter in Pilsbry, 1892, Tidepool ghost shrimp *Neotrypaea biffari* (Holthuis, 1991), and juvenile *Octopus* sp. Excepting a portion of the shore crabs and turban snails, at low tide we observed all of these species, and many others, solely underneath boulders and cobbles. Many of the low intertidal boulders were ringed at their bases by colonies of the Sand-castle worm *Phragmatopoma californica* (Fewkes, 1889).

The middle and western-most boulder fields are centered at 34.4341°N, 119.9520°W and 34.4346°N, 119.9554°W, respectively, and are each smaller in area than the main study site. We visited the middle area infrequently starting in 2006, and did not begin sampling the western-most area until June 2017.

Our study site lies within the Naples State Marine Conservation Area (Naples SMCA), a Marine Protected Area established by the California Fish and Game Commission in 2012 primarily to protect Naples Reef and its surrounding waters, and the shoreline on both sides of Naples Point. The point was named by the US Geological Survey after a town that existed briefly on the



FIGURE 2. Main study site at Naples Point. (A) Main study site, outlined in white, on a -0.3 m tide, 9 May 2015; (B) The same, from beach level, with the tide level at 0.1 m on 1 April 2019.

adjacent terrace in the late 19th century. The intertidal bench at Naples Point is unique on the Santa Barbara County coastline in its breadth and flatness. Elsewhere in the County the Monterey formation is significantly tilted and sometimes folded, dipping seaward as a result of the uplift of the adjacent Santa Ynez Mountains (Dibblee 1950).

Mean monthly coastal sea surface temperatures (SSTs) in the region typically vary from about 12°C in the winter to 19°C in the late summer, but were consistently elevated one to two degrees starting in 2014 (Fig. 3). During our study daily SST extremes in the Santa Barbara Harbor (about 24 km east of Naples Point) varied from 10.4°C on 22 February 2011 to 23.4°C on 31 August 2015 (Scripps Institution of Oceanography 2019).

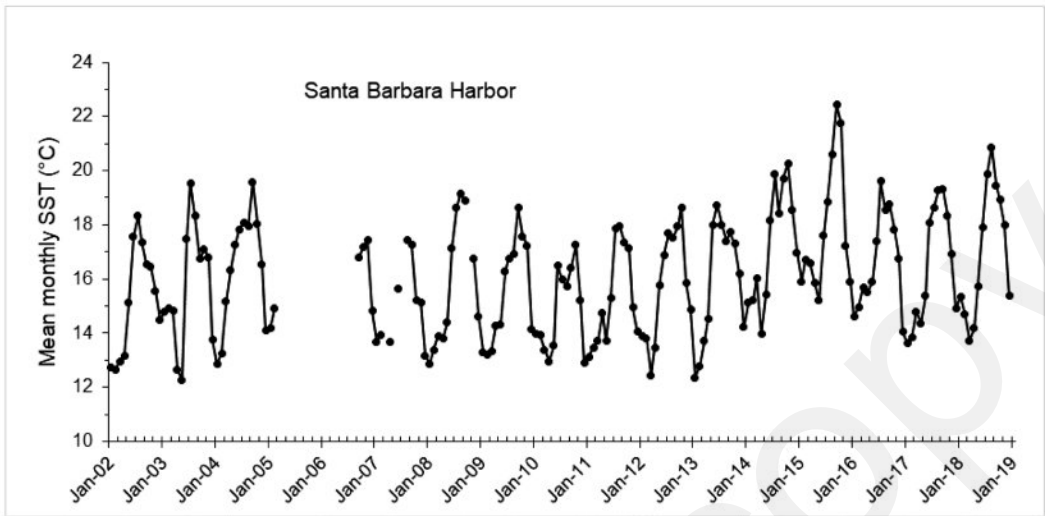


FIGURE 3. Mean monthly sea surface temperatures in the Santa Barbara Harbor, 2002–18. Data from Scripps Institution of Oceanography (2019).

Owing to the proximity just to the west of the Dos Pueblos Ranch and Dos Pueblos Creek, our study site has been referred to previously as Dos Pueblos Reef (see Appendix A). Our main study area has also been called the Ellwood boulder field (Sousa 1979a, b; Dean and Connell 1987a, b, c; Goddard 2007; Goddard et al. 2011), after the Ellwood Pier visible 2.5 km to the east.

METHODS

On low tides falling below +0.3 m JG, accompanied frequently beginning in 2008 by WG and ZG and occasionally other observers, searched pools and carefully turned cobbles and small boulders by hand, searching for heterobranchs. On each trip we recorded the number of individuals of each species found and the presence of their egg masses. For the bubble snail *Haminoea virescens*, a cryptic herbivorous bubble snail sometimes reaching very high densities, we counted all individuals encountered when sparse, but when its numbers were high we subjectively estimated its minimum abundance by order of magnitude. These values were entered in Excel as the order of magnitude plus one (e.g., 101 for 100, 1001 for 1000). For each sampling trip we recorded the time spent searching and the number of observers, with the latter adjusted subjectively by JG following each sampling trip depending on the search efforts by the junior authors and any other participants. A spreadsheet containing the sampling data over the course of our entire study is available via Research Gate: https://www.researchgate.net/publication/337195683_Heterobranch_sea_slugs_from_Naples_Point_Santa_Barbara_Co_CA_2002-19 or DOI: 10.13140/RG.2.2.22810.39362.

During the early years of this study we took photographs only of rare or unusual species, or species whose mode of development the senior author was examining. However, beginning in 2014, and using a Pentax WG III waterproof camera, we endeavored to photograph all species encountered, and sometimes each species found on each sampling trip, and since 2017 have posted these images on the online database iNaturalist (<https://www.inaturalist.org>). A few observations posted on iNaturalist are referenced below by their unique observation numbers.

After initially sampling Naples Point in February and June 2002, JG returned in October 2006. We sampled again in November 2006 and only once in 2007, in February. From 2008 through August 2019 we sampled more frequently, but still intermittently, averaging 6.7 months per year

(SD = 1.7, range 3–9 months per year). Across all years sampled we sampled 11 of the 12 calendar months from 2 to 11 times each (Mean = 7.8, SD = 2.6). Compared to the other seasons, summer was relatively under sampled, with no samples from July and only two from August. Multiple trips were sometimes made in a given month; for data summaries and analyses, the counts of species and individuals within months were combined and treated as one, as were the total number of hours searched per observer.

Owing to the intermittent nature of our sampling we utilize two types of time series in presenting results: (1) by calendar month, averaged across all years sampled, and (2) by year, averaged across all months sampled each year, starting in either 2006 for individual species, or 2008 for groups of species by geographic range group. Changes in abundance and number of species are standardized as numbers found per hour per observer. Unless stated otherwise, counts of individuals recorded and used in these analyses were by JG; counts of the number of species present were by all observers combined.

Incidental to our survey of heterobranchs we obtained information on their prey at Naples Point. Prey species were determined by observations in the field of close association of adult slugs and potential prey species (on sponges especially this would include evidence of feeding scars and for distinctively colored sponges like *Aplysilla glacialis* (Merejkowsky, 1878), observation of recently ingested sponge visible through the body wall of the slug) and direct observations in either the field or lab of feeding activity. Prey were identified to the lowest possible taxon using Carlton (2007).

Ranges and oceanographic indices

We assigned each species to a geographic range group as follows. Northern species as those ranging south only to San Diego or northern Baja California and northward to at least central Oregon. Southern species as those ranging south to at least Baja California Sur and northward usually only to southern, central, or northern California. Widespread species as those ranging from at least as far south as Baja California Sur and at least as far north as Washington. By this classification northern species are primarily from the Oregonian Biogeographic Province, and southern species are mainly from the Panamic or Californian Provinces. We tallied the number of species in each range group found each month and then converted those counts to proportions by dividing them by the total number of species found in each range group over the entire study. Because we did not sample every month or even every season in each year, we averaged these monthly proportions by year and then compared their changes over time to fluctuations in the Multivariate ENSO Index (MEI) (MEI.v2, NOAA Earth System Research Laboratory, available from: <https://www.esrl.noaa.gov/psd/enso/mei/>), the bimonthly values of which we also averaged by year.

Voucher specimens collected during this study were deposited in the Department of Invertebrate Zoology at the California Academy of Sciences (CASIZ) and in the Malacology Department at the Santa Barbara Museum of Natural History (SBMNH). Nomenclature follows the online database World Register of Marine Species (WoRMS) as of August 2019 (<http://www.marine-species.org/>).

RESULTS

Species composition and abundance

In 119 total trips to Naples Point from February 2002 to August 2019 we recorded 12,193 individual heterobranchs in 55 species (Table 1). These included 49 species of nudipleurans (48 nudibranchs, plus *Berthella strongi*), 3 cephalaspideans, 2 aplysiids, and 1 sacoglossan. Eight of the nudibranch species are shown in Figure 4. The Green bubble snail *Haminoea virescens* was the

FIGURE 4. Selected nudibranchs found at Naples Point during the present study. (A) *Trapania velox*, 2 January 2019. (B) *Doris* cf. *pickensi*, 19 January 2012. (C) *Thordisa bimaculata*, 22 April 2015. (D) *Doriopsilla gemela*, 3 December 2018. (E) *Tritonia myrakeenae*, 14 April 2018. (F) *Orienthella cooperi*, 28 February 2019. (G) *Hermisenda opalescens*, 1 April 2017. (H) *Austraeolis stearnsi*, 15 January 2017, found by ZG and photographed by WG.

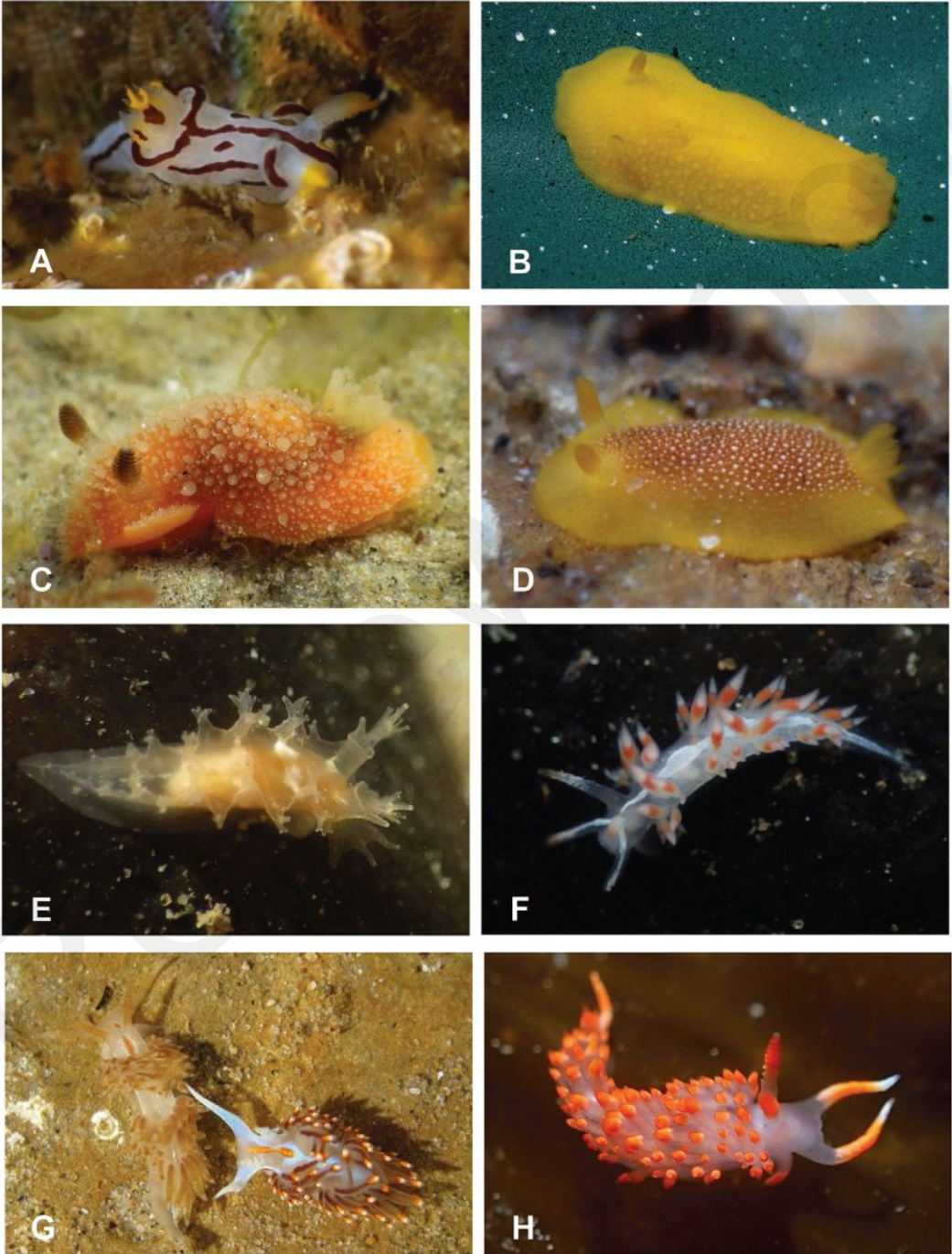


TABLE 1. Heterobranch sea slugs from Naples Point, 2002–2019. Frequency of occurrence calculated from number of months found out of 86 total months sampled.

Species	Total No. Inds.	Freq. Occur. (%)	Geog. Range	Prey observed at Naples Pt.
<i>Tritonia myrakeenae</i>	1286	81.4	S	Clavulariidae
<i>Aplysia californica</i>	2187	80.2	S	
<i>Haminoea virescens</i>	5349	68.6	W	
<i>Hermisenda opalescens</i>	541	62.8	S	
<i>Anteaeolidiella chromosoma</i>	334	55.8	S	<i>Diadumene</i> sp.
<i>Navanax inermis</i>	142	52.3	S	<i>Haminoea virescens</i> , <i>Hermisenda opalescens</i>
<i>Conualevia alba</i>	93	45.3	S	Poecilosclerida
<i>Phidiana hiltoni</i>	117	39.5	S	<i>Plumularia</i> sp., Campanulariidae, small aeolid and dendronotid nudibranchs
<i>Doriopsilla gemela</i>	84	37.2	S	<i>Cliona californiana</i>
<i>Diaulula sandiegensis</i>	74	36	S	Haliclonidae
<i>Triopha maculata</i>	101	34.9	S	Bryozoa
<i>Aegires albopunctatus</i>	49	32.6	W	<i>Lucilla nuttingi</i>
<i>Aplysia vaccaria</i>	170	32.6	S	
<i>Cadlina modesta</i>	83	31.4	N	<i>Aplysilla glacialis</i>
<i>Acanthodoris rhodoceras</i>	49	30.2	S	<i>Alcyonidium</i> sp.
<i>Aeolidia loui</i>	54	27.9	S	<i>Diadumene</i> sp., <i>Anthopleura elegantissima</i>
<i>Berthella strongi</i>	76	26.7	S	<i>Oscarella carmela</i>
<i>Orienthella cooperi</i>	82	25.6	S	Leptothecata
<i>Tritonia festiva</i>	32	22.1	N	Clavulariidae
<i>Anteaeolidiella oliviae</i>	29	19.8	S	
<i>Orienthella trilineata</i>	21	18.6	S	Leptothecata
<i>Doriopsilla albopunctata</i>	23	15.1	S	
<i>Doto kya</i>	76	14	N	<i>Plumularia</i> sp.
<i>Rostanga pulchra</i>	20	14	W	<i>Clathria (Thalysias) originalis</i>
<i>Cadlina sparsa</i>	19	12.8	S	<i>Aplysilla glacialis</i>
<i>Doto</i> form A of Goddard (1996)	49	11.6	S	Leptothecata
<i>Doris</i> cf. <i>pickensi</i>	12	10.5	S	<i>Hymeniacidon sinapium</i>
<i>Doris montereyensis</i>	23	10.5	N	
<i>Thordisa bimaculata</i>	11	10.5	S	
<i>Acanthodoris lutea</i>	11	8.1	S	<i>Alcyonidium</i> sp.
<i>Bulla gouldiana</i>	903	8.1	S	
<i>Flabellinopsis iodinea</i>	11	8.1	S	<i>Eudendrium</i> cf. <i>ramosum</i>

TABLE 1 (continued). Heterobranch sea slugs from Naples Point, 2002–2019. Frequency of occurrence calculated from number of months found out of 86 total months sampled.

Species	Total No. Inds.	Freq. Occur. (%)	Geog. Range	Prey observed at Naples Pt.
<i>Flabellinopsis iodinea</i>	11	8.1	S	<i>Eudendrium</i> cf. <i>ramosum</i>
<i>Ancula pacifica</i>	11	5.8	N	Kamptozoa
<i>Diaphorodoris lirulatocauda</i>	13	5.8	N	
<i>Tenellia albocrusta</i>	10	5.8	W	Leptothecata
<i>Cadlina flavomaculata</i>	3	3.5	S	<i>Aplysilla glacialis</i>
<i>Dirona picta</i>	4	3.5	S	Anasca
<i>Doto columbiana</i>	5	3.5	N	<i>Aglaophenia</i> sp.
<i>Eubranchius rustyus</i>	4	3.5	W	<i>Plumularia</i> sp.
<i>Ancula lentiginosa</i>	5	2.3	S	<i>Myosoma spinosa</i>
<i>Austraeolis stearnsi</i>	2	2.3	S	
<i>Babakina festiva</i>	2	2.3	S	
<i>Cuthona divae</i>	9	2.3	N	<i>Rhizogeton</i> sp.
<i>Antiopella barbarenaensis</i>	1	1.2	S	
<i>Aplysiopsis enteromorphae</i>	3	1.2	W	<i>Chaetomorpha</i> sp.
<i>Catronia columbiana</i>	1	1.2	N	<i>Ectopleura</i> sp.
<i>Dendronotus subramosus</i>	1	1.2	N	<i>Aglaophenia</i> sp.
<i>Dendronotus venustus</i>	2	1.2	S	Campanulariidae
<i>Diaphoreolis flavovulta</i>	1	1.2	N	
<i>Diaphoreolis lagunae</i>	1	1.2	S	<i>Symplectoscyphus turgidus</i>
<i>Doriopsilla fulva</i>	1	1.2	S	
<i>Hallaxa chani</i>	1	1.2	N	<i>Halisarca</i> sp.
<i>Melibe leonina</i> ¹	0	1.2	N	
<i>Peltodoris nobilis</i>	1	1.2	N	
<i>Trapania velox</i>	1	1.2	S	Kamptozoa
Total No.	12193			

¹ Observed only as an egg mass laid on *Macrocystis*.

most abundant species, followed by the sea hare *Aplysia californica*, the dendronatacean nudibranch *Tritonia myrakeenae* Bertsch and Mozqueira, 1986, the bubble snail *Bulla gouldiana*, and the aeolid nudibranchs *Hermisenda opalescens* and *Anteaeolidiella chromosoma*. *Tritonia myrakeenae* (Fig. 4E), found in 81% of the 86 total months sampled, was the most frequently encountered species, followed closely by *Aplysia californica*, at 80%. Twelve species were found only during single months, and most of these were represented by single specimens (e.g., *Trapania velox*; Fig. 4A). Southern species, as defined in the Methods section, dominated the assemblage at 35 species, followed by 14 northern species, and 6 widespread species (Table 1).

Voucher specimens of 21 species were collected during this study. The catalogue numbers and collection information for 20 of these can be found by searching the online CASIZ collection database (http://researcharchive.calacademy.org/research/izg/iz_coll_db/index.asp) using “Naples” as the Locality and Goddard as the Collector name. Voucher specimens of *Berthella strongi* from Naples Point are at SBMNH (catalogue numbers 369472 and 369473). Images were obtained at Naples Point of all heterobranch species except for *Ancula pacifica*, *Peltodoris nobilis* (MacFarland, 1905), *Dendronotus venustus* MacFarland, 1966, *Diaphoreolis flavovulta* (MacFarland, 1966), *Diaphoreolis lagunae* (O’Donoghue, 1926), and *Aplysiopsis enteromorphae* (Eliot, 1905) and can be found in the senior author’s observations on iNaturalist (<https://www.inaturalist.org/observations/jeffgoddard>) by searching for individual species, combined with the place name “Naples State Marine Conservation Area.”

The cumulative number of species we found at Naples Point climbed steeply through 2010 and then leveled off and appeared to be approaching an asymptote of about 48 species before jumping by 5 species in 2017 (Fig. 5). Since then we found 2 additional species, *Trapania velox*, in January 2019 and a juvenile *Antiopella barbarendis* in August 2019. The total number of species found each month varied from 2 to 28 (Mean = 10.4, SD = 5.3, N = 86).

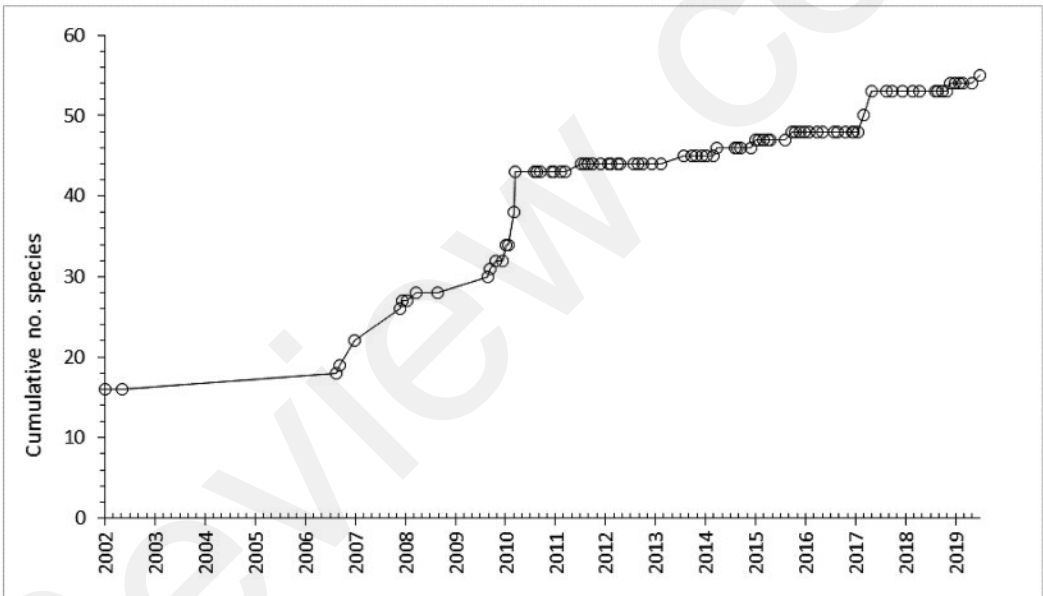


FIGURE 5. Cumulative number of species of heterobranchs found at Naples Point, 2002–19. Each point represents a sample month, with 86 total months sampled. Note that no months were sampled from 2003 through 2005.

Excepting *Geitodoris heathi* (MacFarland, 1905) and *Rictaxis punctocaelatus* (Carpenter, 1864), we found all of the species recorded by Lance and Spaulding in May 1972 at Naples Point (Appendix A). It should be noted however that Lance and Spaulding found only shells of *R. punctocaelatus*, and that these could have washed in from the subtidal, beyond our study area.

Prey

We obtained information on the prey of about two-thirds of the species of heterobranchs we observed (Table 1). Specialists included *Berthella strongi* feeding on the plakinid sponge *Oscarella carmela* (iNaturalist 33894759, 33894758; and see Goddard 2007); *Tritonia myra-*

keena, consistently found on the undersides of cobbles and boulders with an undescribed stoloniferous clavulariid octocoral locally common in the SCB (e.g., iNaturalist 19118368, 5396758); and the aeolid *Anteaeolidiella chromosoma*, frequently found in association with small *Diadumene* anemones on the sides and undersides of cobbles and boulders (iNaturalist 19133587, 19277689).

Seasonality and Egg-laying

The average number of species of heterobranchs we found each month ranged from 3.4 to 6.1 per hour per observer and tended to be lowest in August, November, and January (Fig. 6A). The total number of individuals of nudipleurans at Naples Point (= all nudibranchs, plus *Berthella strongi*) we found each month ranged from 7.3 to 42.4 per hour per observer (with a grand mean of 18.8 inds. h⁻¹ observer⁻¹) and showed a distinct peak in the spring (Fig. 6B).

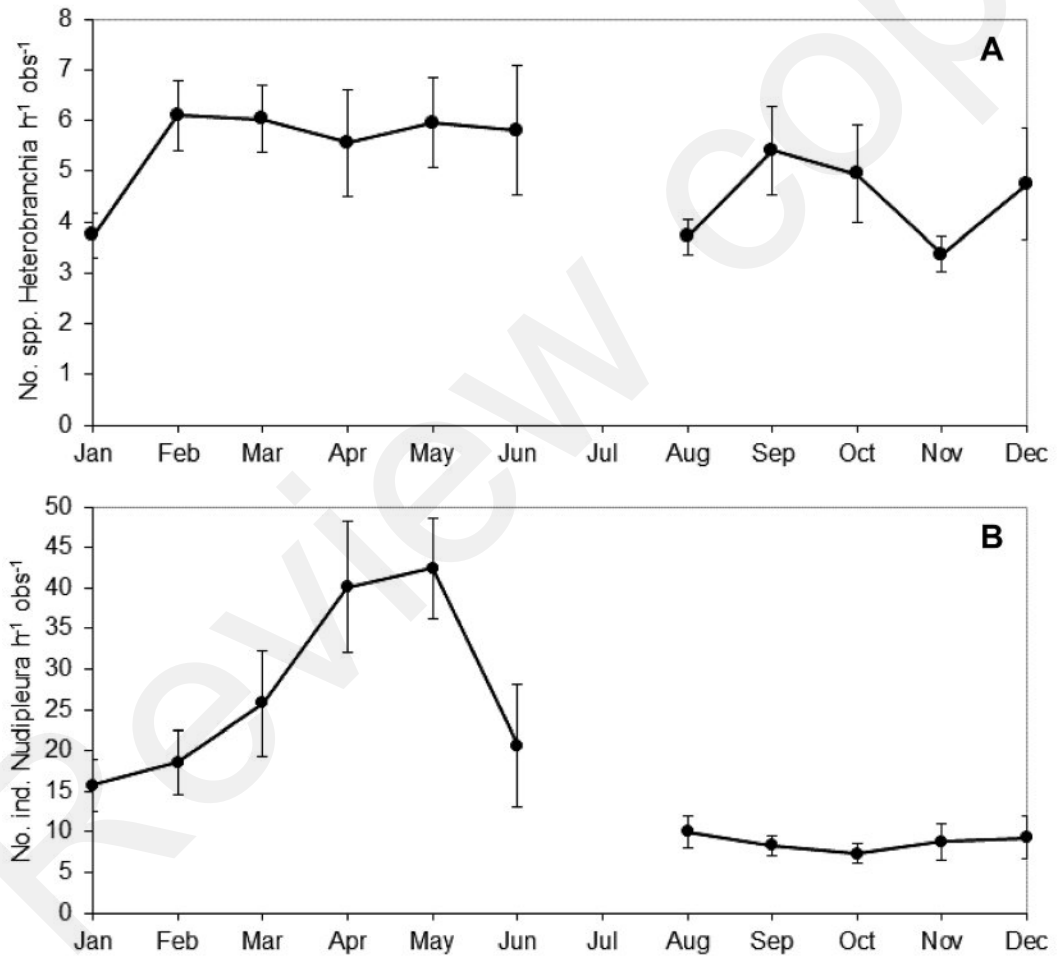


FIGURE 6. Monthly change in (A) total number of species of Heterobranchia, and (B) total number of individuals of Nudipleura at Naples Point, averaged across all years sampled. Values shown are means \pm 1 SE of monthly numbers per hour per observer, 2002–19.

The species most frequently observed in this study showed seasonal changes in abundance and fell into two groups, those peaking in abundance in late winter or spring (Fig. 7A–E), and those peaking in late fall or winter (Fig. 7F–J). *Haminoea virescens*, whose abundance was often estimated subjectively and is not shown, fell into the former group and exhibited high monthly variability in abundance. The high variability in abundance of *Anteaeolidiella chromosoma* in June compared to other months (Fig. 7C) was due to our finding an unprecedented number of individuals of this species (21 in 40 minutes of searching in the upper part of main study area) in June 2015, during a population peak in the midst of the 2015–16 El Niño (see next section).

We found egg masses of 37 species of heterobranchs at Naples Point (Table 2). Egg masses of *Haminoea virescens*, *Tritonia myrakeenae*, and *Anteaeolidiella chromosoma* were observed in 11/11 calendar months sampled, following by *Hermisenda opalescens* in 9/11 months sampled (Table 2; Fig. 7A–C). However, when the data from all 86 months sampled are taken into account, the egg masses of each of these four species were more prevalent in some months and seasons than others (Table 2). For example, egg masses laid by *Haminoea virescens* were most prevalent from March to September, those laid by *Tritonia myrakeenae* and *Hermisenda opalescens* in the spring and August, and those laid by *Anteaeolidiella chromosoma* in April and June (Table 2). In contrast, egg masses laid by *Phidiana hiltoni* (O'Donoghue, 1927) were found from September through April at fairly uniform prevalences.

Interannual variability

The proportion of southern species found each year exceeded that of northern species and the difference between the two proportions tended to track the El Niño Southern Oscillation as measured by the MEI (Fig. 8).

Coincident with the marine heat waves beginning in the NE Pacific in late 2013 and manifesting off Santa Barbara in mid-2014 (Fig. 3) two of what had been the most frequent northern species of nudibranchs at Naples Point, *Cadlina modesta* MacFarland, 1966) and *Tritonia festiva* (Stearns, 1873) (see Table 1), disappeared from our study site (Fig. 9A), while two conspicuous southern nudibranchs, *Anteaeolidiella chromosoma* and *Doriopsilla gemela*, greatly increased in abundance (Figure 9B). In addition to peaking in abundance during the 2015–16 El Niño, *A. chromosoma* also showed a lesser peak in abundance coincident with the moderate 2009–10 El Niño. *Thordisa bimaculata* was an order of magnitude less abundant than *A. chromosoma* (see Table 1) but exhibited a very similar yearly change in abundance (not shown), peaking in abundance with both the 2009–10 and 2015–16 El Niño events.

DISCUSSION

Including *Geitodoris heathi* and *Rictaxis punctocaelatus* recorded by Lance and Spaulding in May 1972 (Appendix A), 57 species of heterobranchs have now been recorded from Naples Point. This total is similar to those obtained from other sites in California and Oregon known for their species richness of heterobranchs (e.g., Nybakken 1978; Goddard 1984; Goddard et al. 2011). However, the grand mean of 18.8 individuals of Nudipleura we found per hour per observer at Naples Point was approximately one half to one third the values recorded from sites in central California (Goddard et al. 2011, Fig. 2; Schultz et al. 2011, Fig. 3; JG, unpublished data). Two factors appear to contribute to an overall lower abundance of nudipleurans at Naples Point compared to those sites: (1) relatively low abundances of sponges, hydroids, and arborescent bryozoans, many of which are consumed specifically by nudipleurans. This in turn may be related to low vertical relief and reduced habitat complexity of the study area, combined with the summer build-up

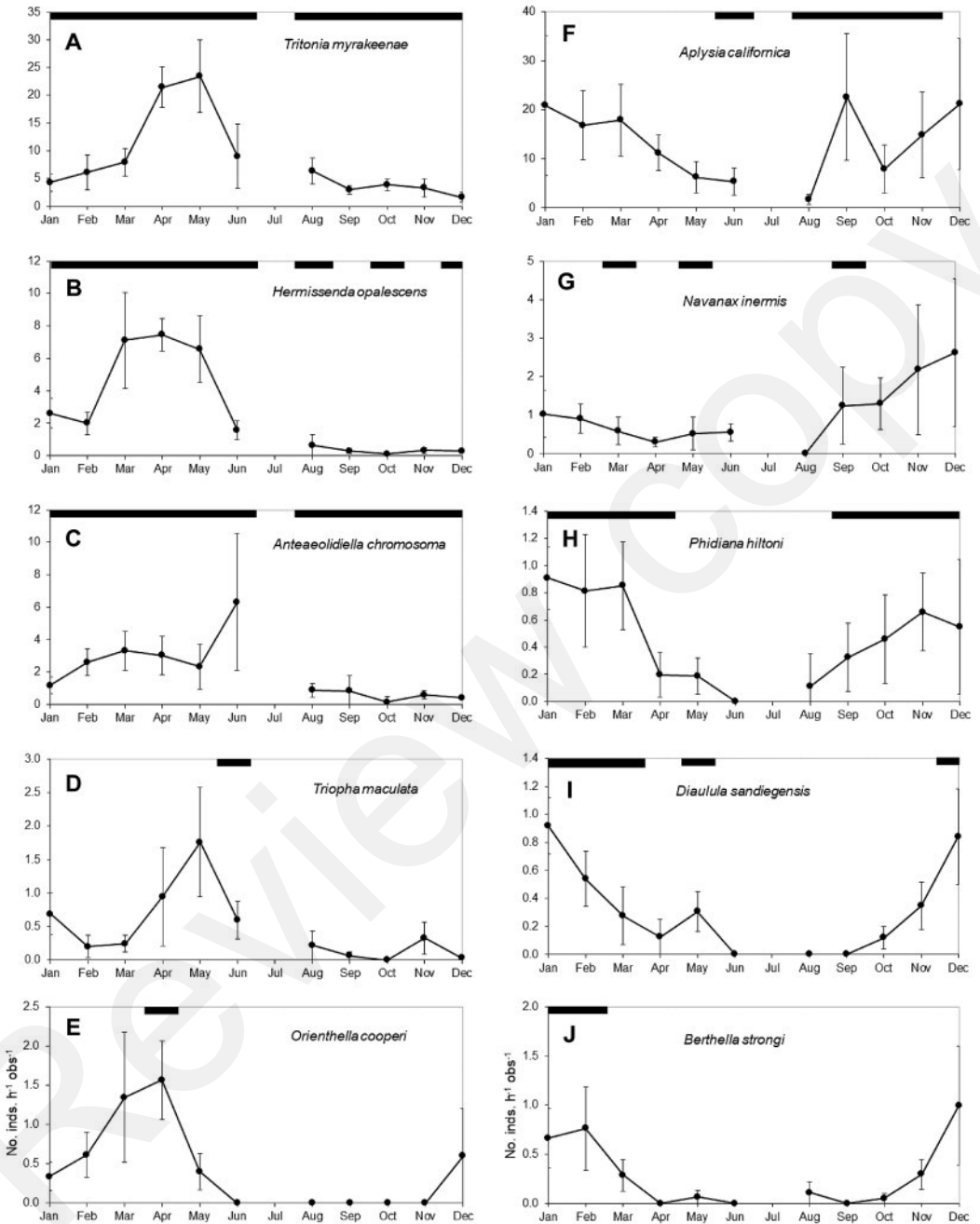


FIGURE 7. Monthly variation in egg-laying and abundance of 12 of the more frequently observed heterobranchs at Naples Point, averaged across all years sampled. Values shown are means \pm 1 SE of monthly number of individuals per hour per observer, 2002–19; black bars at top of graphs indicate monthly presence of egg masses.

TABLE 2. Months of occurrence of egg masses of heterobranch gastropods at Naples Point. Values are proportions calculated as the number of times egg masses were found in a given month out of total number of times each calendar month was sampled from 2002–19, with the latter values in parentheses in the top row. Blank cells indicate values of zero, and note that July was not sampled at all.

Species	Jan (11)	Feb (10)	Mar (8)	Apr (8)	May (7)	Jun (7)	Jul (0)	Aug (2)	Sep (8)	Oct (10)	Nov (10)	Dec (5)
Cephalaspidea												
<i>Bulla gouldiana</i>					0.14	0.14						
<i>Haminoea virescens</i>	0.18	0.3	0.75	0.88	0.86	1		1	0.63	0.4	0.3	0.2
<i>Navanax inermis</i>			0.13		0.14				0.13			
Anaspidea												
<i>Aplysia californica</i>						0.14		0.5	0.13	0.2	0.2	
<i>Aplysia vaccaria</i>				0.13						0.2	0.1	
Nudipleura: Pleurobranchida												
<i>Berthella strongi</i>	0.09	0.1										
Nudipleura: Doridina												
<i>Acanthodoris rhodoceras</i>				0.13	0.29							
<i>Aegires albopunctatus</i>									0.13			
<i>Ancula pacifica</i>					0.14			0.5				
<i>Cadlina modesta</i>		0.1			0.14							
<i>Conulaevia alba</i>									0.25		0.1	
<i>Diaulula sandiegensis</i>	0.09	0.1	0.13		0.14							0.2
<i>Doris montereyensis</i>	0.09											
<i>Doris cf. pickensi</i>		0.1										
<i>Rostanga pulchra</i>		0.2										
<i>Triopha maculata</i>						0.14						
Nudipleura: Cladobranchia												
<i>Aeolidia loui</i>	0.09	0.1		0.13								
<i>Anteaeolidiella chromosoma</i>	0.18	0.3	0.25	0.75	0.29	0.71		0.5	0.25	0.2	0.1	0.2
<i>Anteaeolidiella oliviae</i>										0.1		0.2
<i>Cuthona divae</i>				0.13								
<i>Doto columbiana</i>				0.13								
<i>Doto kya</i>			0.38	0.25	0.57	0.14						
<i>Doto form A</i>		0.1	0.25	0.25	0.29							
<i>Eubranchus rusticus</i>			0.13		0.29			0.5				
<i>Hermisenda opalescens</i>	0.27	0.5	0.5	0.63	0.57	0.14		0.5		0.1		0.2
<i>Melibe leonina</i>								0.5				
<i>Orienthella cooperi</i>				0.13								
<i>Phidiana hiltoni</i>	0.18	0.2	0.25	0.13					0.25	0.1	0.1	0.2
<i>Tenellia albocrusta</i>				0.13								
<i>Tritonia festiva</i>		0.1										
<i>Tritonia myrakeenae</i>	0.27	0.2	0.25	0.5	0.29	0.14		1	0.13	0.3	0.1	0.2

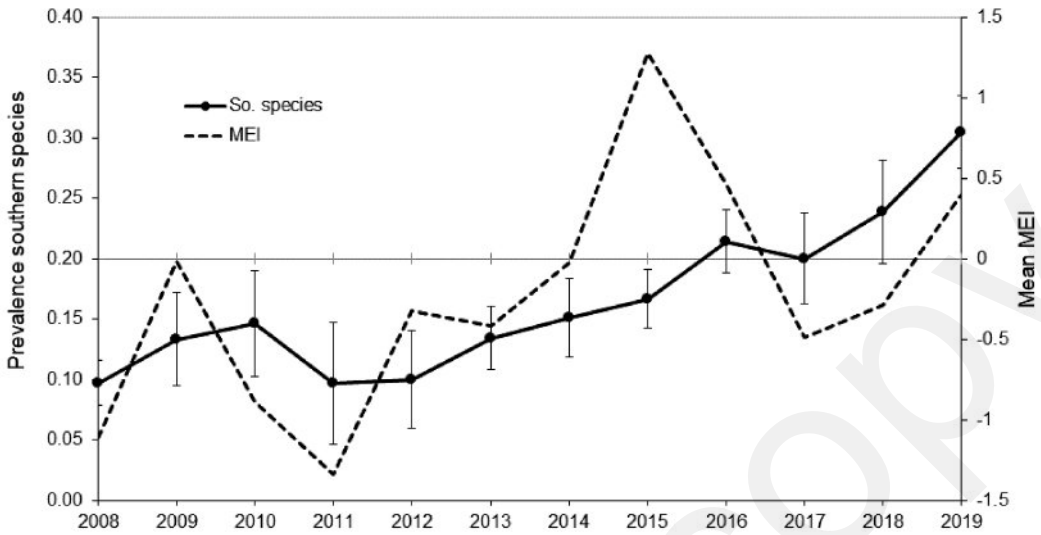


FIGURE 8. Change in relative prevalence of southern species of heterobranchs at Naples Point, with yearly mean of the Multivariate ENSO Index, 2006–19. Relative prevalence of southern species calculated as the proportion of southern species found each sample month out of the total number of southern species ($n = 35$) found throughout the entire study, minus the same proportion calculated each month for northern species. These monthly values were then averaged by year. Values shown are means \pm 1 SE.

of sediments underneath many of the boulders comprising the boulder fields. (2) Increased predation pressure, as indicated by the relative absence of nudipleurans and many other mobile macro-invertebrates from tide pools and other open habitat in our study area. Most of the heterobranchs we found at Naples Point occurred closer to mean lower low water (MLLW) than at the lowest tide levels. While we frequently found adult cephalaspideans (*Haminoea virescens*, *Bulla gouldiana* and *Navanax inermis*) and adult sea hares in the open, we rarely found juvenile sea hares and nudipleura of any life stage in the open, even on dawn low tides as is commonly observed for nudipleurans in tide pools in central and northern California (personal observations).

Potential or known predators of heterobranchs at Naples Point include: (1) *Navanax inermis*, which was the 6th most frequently observed heterobranch in our study area (Table 1). It is known to prey on bubble snails, *Aplysia californica*, and also consume soft-bodied nudibranchs (Paine 1963; Pennings 1990; personal observations). We have never observed *N. inermis* at outer coast, intertidal sites in central California. (2) The California cone snail *Californiconus californicus* (Reeve, 1844). This species was consistently found in our main study area and the adjacent lagoon and has been reported feeding on *Bulla gouldiana* and *Navanax inermis* (Saunders and Wolfson 1961; Kohn 1966) and has been observed once in the field attacking the dorid nudibranch *Triopha catalinae* (Cooper, 1863) (Valdés et al. 2013). (3) Decapod crustaceans including rock crabs (Canceridae), snapping shrimp (Alpheidae), and California spiny lobster *Panulirus interruptus* (Randall, 1840). We observed the latter under ledges at the lowest tide levels in our study area, and it is also abundant subtidally in southern Santa Barbara County, but not in central California. California spiny lobster are ecologically important nocturnal predators known to consume a wide variety of prey, especially mussels and sea urchins, but also sea hares (Tegner and Dayton 1983; Pennings 1990; Love-Chezem et al. 2013). (4) The sea stars *Patiria miniata* and *Astrometis sertulifera* (Xantus, 1860) have broad diets and have been reported to elicit escape behaviors in *Dendronotus iris* and *Aplysia californica*, respectively (Wobber 1970; Kandel 1979, Beeman and Williams 1980).

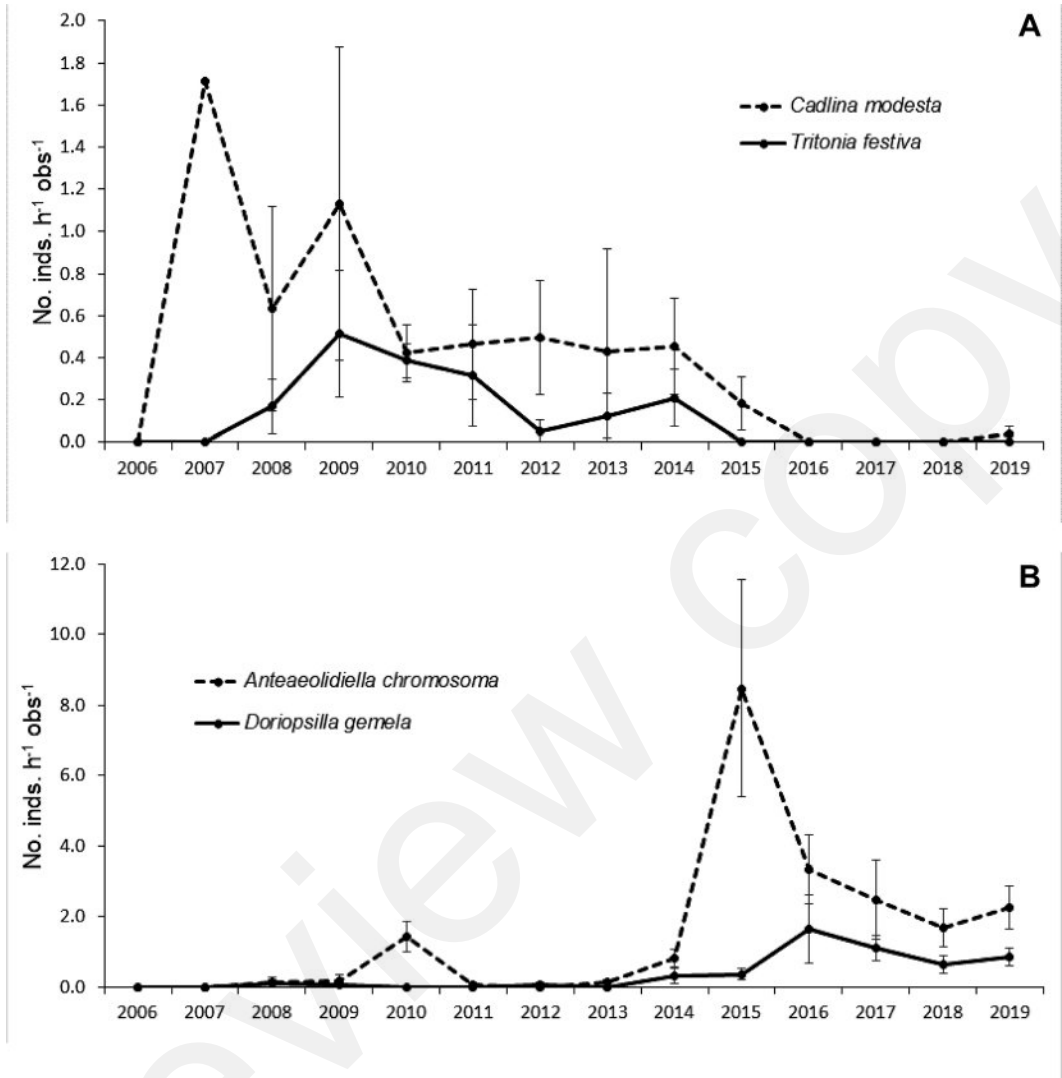


FIGURE 9. Yearly change in abundance of **A** two northern nudibranchs, and **B** two southern nudibranchs at Naples Point, 2006–2019. Values shown are yearly means \pm 1 SE of monthly number of individuals per hour per observer.

Juvenile *P. miniata* were the most common sea star under boulders at Naples Point, while *Astrometis sertulifera* was rare. (5) Juvenile Two-spotted octopuses, *O. bimaculoides* Pickford and McConnaughey, 1949 and *O. bimaculatus* Verrill, 1883, are frequently common under boulders at Naples Point and elsewhere in Southern California, but are rare intertidally north of Point Conception (Fawcett 1984; personal observations). Though known to exert significant predation pressure on shelled gastropods at Naples Point (Fawcett 1984), the only record we know of them consuming heterobranchs is from Ambrose (1984), who reported an unspecified number of *Bulla gouldiana* preyed on subtidally at Santa Catalina Island by *O. bimaculatus*. Two-spotted octopuses may have contributed to the rapid decline and complete disappearance of *B. gouldiana* at Naples Point, one year after its sudden appearance in 2015 (see Goddard et al. 2018). (6) Fishes, including species of sculpin (Cottidae) and surf perch (Embiotocidae), California clingfish, *Gobiesox*

rhessodon Smith, 1881, and Rockpool blenny *Hypsoblennius gilberti* (Jordan, 1882), all of which have been observed at Naples Point (Dean and Connell 1987c; personal observations).

The spring peak in total abundance of Nudipleura at Naples Point (Fig. 6B) largely reflects the timing of peak abundance of the three most abundant nudibranchs recorded during our study: *Tritonia myrakeenae*, *Hermisenda opalescens*, and *Anteaeolidiella chromosoma* (Fig. 7A-C; Table 1). Indeed, six out of 10 of the most abundant nudibranchs peaked in spring, while only one of those 10 - *Phidiana hiltoni* - showed a clear peak in the winter (Fig. 7H). The spring peak in total abundance of nudipleurans at Naples Point is similar to the spring/early summer peaks we have observed at sites in central California (JG, unpublished data), and similar to the late spring and summer peak in the total abundance of smaller non-dorid nudibranchs documented by Nybakken (1978) from the Monterey Peninsula. The timing appears to reflect spring peaks in the abundance of the hydrozoan and bryozoan prey of many of the more abundant nudibranchs.

Beginning in May 2010, when WG observed our first specimen of *Doris* cf. *pickensi* Marcus and Marcus, 1967 at Naples Point, we have found a total of 12 specimens of this distinctive species (see Fig. 4B) in our study area. Three of these have been deposited as vouchers at CASIZ (catalogue nos. 182710, 185189, 189305). Goddard et al. (2018) described some of the morphological features of these specimens and discussed their taxonomic status. We have no doubt that species no. 7 (“Cryptobranch sp.”) briefly described by Jim Lance from Naples Point (Appendix A) is the same species. The coloration, dorsal tubercles, labial tentacles, and size described by Lance all match those of our specimens. The senior author has also found this species at Point Fermin in Los Angeles County and Bird Rock, La Jolla in San Diego County, but a full study, including molecular genetics, is needed to determine if specimens from California are the same as or sister to those from the eastern tropical Pacific and those originally described by Marcus and Marcus (1967) from the northern Gulf of California.

We observed two color morphs of *Hermisenda opalescens* at Naples Point: (1) the common more brightly colored form with white-tipped, orange to brown cerata (Fig. 4G, right), and (2) a dull-colored form cryptic against sandstone and detrital-laden sediments (Fig. 4G, left; iNaturalist 22514917). This latter form frequently has a pale orange-colored head and rhinophores (e.g., iNaturalist 19452949), and is frequent in the SCB (personal observations). Its resemblance to the Northwest Pacific *Hermisenda emurai* (Baba, 1937) as pictured in Figure 3G of Lindsay and Valdes (2016) raised questions about its specific identity. However, specimens of this form from the SCB sequenced by Angel Valdes and colleagues confirmed its identity as *H. opalescens* (A. Valdes, personal communication to JG, 5 August 2016).

Our observations of egg-laying by *Aplysia californica* from June to November are similar to those by Sousa (1979a) who reported egg-laying by this species at Naples Point from May to December during a two year period in the mid-1970s. Sousa (1979a) also reported that during this same period the “abundance of sea hares fluctuated erratically with no clear seasonal trends.” Our data, obtained over a longer time period, suggest a peak in abundance in fall and winter, and a low in summer (Fig. 7F). However, as indicated by the large error of the monthly values, year to year variability is high, consistent with Sousa’s (1979a) results.

During our study southern heterobranchs increased in prevalence compared to northern species in concert with changes in the El Niño Southern Oscillation (ENSO) (Figs. 8 and 9). These results add to those reported recently for nudibranchs from elsewhere in California and Oregon (Schultz et al. 2011; Goddard et al. 2016, 2018; Sanford et al. 2019) during marine heat waves in general and positive phases of ENSO in particular. The sudden appearance at Naples Point of species like *Bulla gouldiana* and *Aplysia vaccaria* after years with none (Goddard et al. 2018, present study), combined with dramatic increases in abundance of species like *Doriopsilla gemela* and

Anteaeolidiella chromosoma (Figure 9B) are consistent with marine heat waves in the NE Pacific (1) increasing the transport of larvae from southern source populations, and (2) opening thermal windows conducive to the growth, reproduction, and development of southerly species. We expect many of these southern species to become permanently established in their newly acquired northern range as the frequency and intensity of marine heat waves increase in the region.

ACKNOWLEDGMENTS

We thank Liz Kools and Terry Gosliner for their help with our voucher specimens deposited at the California Academy of Sciences and for providing access to the James R. Lance Collection. Robin Agarwall, Brenna Green, Craig Hoover, Clark Marino, and Ken-ichi Ueda joined us on a few sampling trips, and we are grateful for their interest and search efforts. We thank Ángel Valdés for confirming the identity of the cryptically colored specimens of *Hermisenda opalescens*, and Peter Schuchert for identifying specimens of *Rhizogeton* consumed by *Cuthona divae*. We are especially grateful to Lise Goddard, without whose love and support this study would not have been possible. Voucher specimens were collected from Naples Point under Scientific Collecting Permit 005299 from California Fish and Game to JG prior to the establishment of the Naples SMCA.

LITERATURE CITED

- AMBROSE, R.F. 1984. Food preferences, prey availability, and the diet of the *Octopus bimaculatus* Verrill. *Journal of Experimental Marine Biology and Ecology* 77:29–44.
- BEEMAN, R.D., AND G.C. WILLIAMS. 1980. Opisthobranchia and Pulmonata: the sea slugs and allies. Pages 308–354 in R.H. Morris, D.P. Abbott, and E.C. Haderlie, eds., *Intertidal invertebrates of California*. Stanford University Press, Stanford, California, USA. ix + 690 pp.
- BEHRENS, D.W., AND R. HENDERSON. 1981. Two new cryptobranch dorids from California. *The Veliger* 24:120–128.
- BRIGGS, J.C., AND B.W. BOWEN. 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography* 39:12–30.
- CARLTON, J.T., ed. 2007. *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon*, 4th edition, completely revised and expanded. University of California Press, Berkeley, California, USA. xvii + 1001 pp.
- CARPENTER, P.P. 1857. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Pages 159–368 in *Report 26th Meeting of the British Association for the Advancement of Science*. .
- CARPENTER, P.P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Pages 517–686 in *Report 33rd Meeting of the British Association for the Advancement of Science*.
- CAVOLE, L.M., A.M. DEMKO, R.E. DINER, A. GIDDINGS, I. KOESTER, C.M.L.S. PAGNIELLO, M.-L. PAULSEN, RAMIREZ-VALDEZ, S.M. SCHWENCK, N.K. YEN, M.E. ZILL, AND P.J.S. FRANKS. 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: Winners, losers, and the future. *Oceanography* 29(2):273–285, <<http://dx.doi.org/10.5670/oceanog.2016.32>>.
- COOPER, J.G. 1863. On new or rare Mollusca inhabiting the coast of California. 2. *Proceedings of the California Academy of Sciences*, ser. 1, 3:56–60.
- COOPER, J.G. 1867. Geographical catalogue of the Mollusca found west of the Rocky Mountains between latitudes 33° and 49° North. Geological Survey of California, Towne & Bacon, Printers, San Francisco, California, USA. 40 pp.
- COVILLE, F.V. 1899. The botanical explorations of Thomas Nuttall in California. *Proceedings of the Biological Society of Washington* 13:109–121.
- COWEN, R.K., AND D.R. LAUR. 1978. A new species of *Coryphella* (Nudibranchia: Flabellinidae) from Santa Barbara, California. *The Veliger* 20:292–294.

- DALL, W.H. 1902. Illustrations and descriptions of new, unfigured, or imperfectly known shells, chiefly American, in the U. S. National Museum. *Proceedings of the United States National Museum* 24:499–562, pls. 27–40.
- DALL, W.H. 1919. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. *Proceedings of the United States National Museum* 56:293–371.
- DANA, R.H. 1840. *Two Years Before the Mast*. Harper & Brothers, New York. (1965 Edition, Airmont Publishing Publishing Co., New York, USA. 320 pp.)
- DEAN, R.L., AND J.H. CONNELL. 1987a. Marine invertebrates in an algal succession. I. Variations in abundance and diversity with succession. *Journal of Experimental Marine Biology and Ecology* 109:195–215.
- DEAN, R.L., AND J.H. CONNELL. 1987b. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. *Journal of Experimental Marine Biology and Ecology* 109:217–247.
- DEAN, R.L., AND J.H. CONNELL. 1987c. Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology* 109:249–273.
- DIBBLEE, T.W. 1950. *Geology of Southwestern Santa Barbara County*. Bulletin 150, Division of Mines, Department of Natural Resources, State of California. 95 pp.
- DONG, C., E.Y. IDICA, AND J.C. MCWILLIAM. 2009. Circulation and multiple-scale variability in the Southern California Bight. *Progress in Oceanography* 82:168–190.
- ENGLER, J.M., AND D.V. RICHARDS. 2001. New and unusual marine invertebrates discovered at the California Channel Islands during the 1997–1998 El Niño. *Bulletin of the Southern California Academy of Sciences* 100:186–198.
- FAWCETT, M.H. 1984. Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology* 65(4):1214–1230.
- GABB, W.M. 1865. Description of new species of marine shells from the coast of California. *Proceedings of the California Academy of Sciences*, ser. 1, 3:182–190.
- GODDARD, J.H.R. 1996. Lecithotrophic development in *Doto amyra* (Nudibranchia: Dendronotacea), with a review of developmental mode in the genus. *The Veliger* 39:43–54.
- GODDARD, J.H.R. 2007. *Berthella* (Opisthobranchia: Pleurobranchidae) from the northeast Pacific Ocean prey on plakinid sponges (Homoscleromorpha: Plakinidae). *The Veliger* 49:97–100.
- GODDARD, J.H.R., T.M. GOSLINER, AND J.S. PEARSE. 2011. Impacts associated with the recent range shift of the aeolid nudibranch *Phidiana hiltoni* (Mollusca: Opisthobranchia) in California. *Marine Biology* 158:1095–1109. (doi:10.1007/s00227-011-1633-7)
- GODDARD, J.H.R., AND B. GREEN. 2013. Developmental mode in opisthobranch molluscs from the northeast Pacific Ocean: additional species from southern California and supplemental data. *Bulletin of the Southern California Academy of Sciences* 112:49–62.
- GODDARD, J.H.R., AND C. HOOVER. 2016. Distribution, seasonality, and prey specificity of *Flabellina goddardi* Gosliner, 2010 (Gastropoda: Nudipleura: Aeolidina). *The Nautilus* 130:146–152.
- GODDARD, J.H.R., N. TRENEMAN, W.E. PENCE, D.E. MASON, P.M. DOBRY, B. GREEN, AND C. HOOVER. 2016. Nudibranch Range Shifts associated with the 2014 Warm Anomaly in the Northeast Pacific. *Bulletin of the Southern California Academy of Sciences* 115(1):15–40.
- GODDARD, J.H.R., N. TRENEMAN, T. PRESTHOLDT, C. HOOVER, B. GREEN, W.E. PENCE, D.E. MASON, P. DOBRY, J.L. SONES, E. SANFORD, R. AGARWAL, G.R. McDONALD, R.F. JOHNSON, AND T.M. GOSLINER. 2018. Heterobranch sea slug range shifts in the northeast Pacific Ocean associated with the 2015–16 El Niño. *Proceedings of the California Academy of Sciences*, ser. 4, 65(3):107–131.
- GOODHEART, J., Y. CAMACHO-GARCÍA, V. PADULA, M. SCHRÖDL, J.L. CERVERA, T.M. GOSLINER, AND A. VALDÉS. 2015. Systematics and biogeography of *Pleurobranchus* Cuvier, 1804, sea slugs (Heterobranchia: Nudipleura: Pleurobranchidae). *Zoological Journal of the Linnean Society* 174:322–362.
- GOSLINER, T.M. 1996. The Opisthobranchia. Pages 161–213 in P.H. Scott, J.A. Blake, and A.W. Lissner, eds., *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel*, vol. 9. *The Mollusca*, Part 2. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
- GOSLINER, T.M., AND D.W. BEHRENS. 1988. A review of the generic divisions within the Phyllidiidae with the description of a new species of *Phyllidiopsis* (Nudibranchia: Phyllidiidae) from the Pacific coast of North

- America. *The Veliger* 30(3):305–314.
- GOULD, A.A. 1853. Descriptions of shells from the Gulf of California and the Pacific coasts of Mexico and California. *Boston Journal of Natural History* 6(III):374–408.
- HARMS, S., AND C.D. WINANT. 1998. Characteristic patterns of the circulation in the Santa Barbara Channel. *Journal of Geophysical Research: Oceans* 103:3041–3065.
- JEPSON, W.L. 1934. The overland journey of Thomas Nuttall. *Madroño* 2(17):143–147.
- KANDEL, E.R. 1979. *Behavioral Biology of Aplysia*. W.H. Freeman, San Francisco, California, USA. 463 pp.
- KOHN, A.J. 1966. Food specialization in *Conus* in Hawaii and California. *Ecology* 47(6):1041–1043.
- LANCE, J.R. 1966. New distributional records of some Northeastern Pacific Opisthobranchiata (Mollusca: Gastropoda) with descriptions of two new species. *The Veliger* 9(1):69–81.
- LANCE, J.R. 1967. Northern and southern range extensions of *Aplysia vaccaria*. *The Veliger* 9(4):412.
- LEE, R.S., AND P. BROPHY. 1969. Additional bathymetric and locality data for some opisthobranchs and an octopus from Santa Barbara County, California. *The Veliger* 12(2):220–221.
- LINDSAY, T., AND Á. VALDÉS. 2016. The model organism *Hermisenda crassicornis* (Gastropoda: Heterobranchia) is a species complex. *PLoS ONE* 11(4):e0154265. doi:10.1371/journal.pone.0154265
- LONG, S.J. 1969. A note on the opisthobranchs of Santa Cruz Island, California. *The Veliger* 12(2):232.
- LOVE-CHEZEM, T., J.F. AGGIO, AND C.D. DERBY. 2013. Defense through sensory inactivation: sea hare ink reduces sensory and motor responses of spiny lobsters to food odors. *Journal of Experimental Biology* 216:1364–1372.
- MACFARLAND, F.M. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. *Memoirs of the California Academy of Sciences* 6:1–546.
- MARCUS, EV., AND ER. MARCUS. 1967. American opisthobranch mollusks. *Studies in Tropical Oceanography* (Institute of Marine Science, University of Miami) 6:viii + 1–256.
- MCDONALD, G.R. 1983. A review of the nudibranchs of the California coast. *Malacologia* 24:114–276.
- MILLEN S.V., AND H. BERTSCH. 2000. Three new species of dorid nudibranchs from southern California, USA, and the Baja California Peninsula, Mexico. *The Veliger* 43(4):354–366.
- NULL J. 2019. El Niño and La Niña Years and Intensities based on Oceanic Niño Index (ONI) Available from: <<https://ggweather.com/enso/oni.htm>>
- NYBAKKEN, J.W. 1978. A phenology of the smaller dendronotacean, arminaeae, and aeolidacean nudibranchs at Asilomar State Beach over a twenty-seven month period. *The Veliger* 16:370–373.
- O'DONOGHUE, C.H. 1926. A list of the nudibranchiate Mollusca recorded from the Pacific coast of North America, with notes on their distribution. *Transactions of the Royal Canadian Institute* 15:199–247.
- PAINE, R.T. 1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). *The Veliger* 6:1–9.
- PENNINGS, S.C. 1990. Multiple factors promoting narrow host range in the sea hare, *Aplysia californica*. *Oecologia* 82:192–200.
- SANFORD E., J.L. SONES, M. GARCÍA-REYES, J.H.R. GODDARD, AND J.L. LARGIER. 2019. Widespread shifts in the coastal biota of Northern California during the 2014–2016 marine heatwaves. *Scientific Reports* 9:4216 <<https://doi.org/10.1038/s41598-019-40784-3>>
- SAUNDERS, P.R., AND F. WOLFSON. 1961. Food and feeding behavior in *Conus californicus* Hinds, 1944. *The Veliger* 3(3):73–76.
- SCRIPPS INSTITUTION OF OCEANOGRAPHY. 2019. Shore stations program: Santa Barbara. Temperature data available from: <<https://scripps.ucsd.edu/programs/shorestations/shore-stations-data/data-santa-barbara/>> (Accessed 16 August 2019).
- SOUSA, W.P. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49(3):227–254.
- SOUSA, W.P. 1979b. Disturbance in Marine Intertidal Boulder Fields: The Nonequilibrium Maintenance of Species Diversity. *Ecology* 60(6):1225–1239.
- SPHON, G.G., AND J.R. LANCE. 1968. An annotated list of nudibranchs and their allies from Santa Barbara County, California. *Proceedings of the California Academy of Sciences*, ser. 4, 36(3): 73–84.
- VALDÉS, Á. 2019. Northeast Pacific benthic shelled sea slugs. *Zoosymposia* 13:242–304 <<http://dx.doi.org/10.11646/zoosymposia.13.1.21>>

- VALDÉS, Á., L. BLANCHARD, AND W. MARTI. 2013. Caught naked: First report a nudibranch sea slug attacked by a cone snail. *American Malacological Bulletin* 31(2):337–338.
- VALDÉS, Á., D.B. CADIEN, AND T.M. GOSLINER. 2016. Philinidae, Laonidae and Philinorbidae (Gastropoda: Cephalaspidea: Philinoidea) from the northeastern Pacific Ocean and the Beaufort Sea (Arctic Ocean). *Zootaxa* 4147 (5):501–537 <<http://doi.org/10.11646/zootaxa.4147.5.1>>
- VALDÉS, Á., T.M. GOSLINER, A. WARÉN. 2017. A new species of *Parvaplustrum* Powell, 1951 (Gastropoda: Heterobranchia: Aplustridae) from the northeastern Pacific. *The Nautilus* 131(1):97–100.
- WOBBER, D.R. 1970. A report on the feeding of *Dendronotus iris* on the anthozoan *Cerianthus* sp. From Monterey Bay, California. *The Veliger* 12:383–387.
- YATES, L.G. 1890. The Mollusca of Santa Barbara County, California. *Bulletin of the Santa Barbara Society of Natural History* 1(2):37–45.

Appendix

Field account from a binder of California field accounts in the James R. Lance Collection, Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, California. Updated taxonomic names, full names of those abbreviated by Lance, and other annotations by JG are given in brackets.

Santa Barbara – Dos Pueblos Reef [Naples Point]

13.V.72 [13 May 1972] Sam Spaulding + self [James R. Lance] -1.8['] 0430 PST

1. *Aplysia* calif. [*californica*] 50+, no eggs or crabs [probably Mottled pea crab *Opisthopus transversus*, known from a wide variety of hosts, including the mantle cavity of *Aplysia vaccaria*].

Large

2. *Rictaxis punctocaelatus* – 2 fresh crab shells

3. *R.* [*Rostanga*] *pulchra* – 5

4. *D. heathi* [*Geitodoris heathi*] 3 including a black dotted one

5. *D.* [*Diaulula*] *sandiegensis* – 4 small

6. *C.* [*Cadlina*] *modesta* – 3

7. Cryptobranch sp. – 1, 20 mm. superficially similar to *D. heathi* but a) tubercles very sparse, b) no black pigment net, c) *Diaulula*-like head [with small sketch showing grooved, auriform labial tentacles; *Doris* cf. *pickensi* of present study]

8. White gilled porostome [*Doriopsilla albopunctata*] – 8, 2 large

9. Yellow gilled porostome [*Doriopsilla gemela*] – 5

10. *A.* [*Aegires*] *albopunctatus*

11. *A.* [*Acanthodoris*] *rhodoceras* – 2

12. *Triopha* – small orange [*Triopha maculata*] – 2

13. *D.* [*Doriopsilla*] *fulva*

14. *Tritonia* sp. – 7, largest 15 mm, identical to those from Pt. Loma [*Tritonia myrakeenae*]

15. *Ae. papillosa* [*Aeolidia loui*] – 5, both white and brown phase

16. *H. crassicornis* [*Hermisenda opalescens*] – 50+, mostly small

17. *C. trilineata* [*Orienthella trilineata*] – 10, minute

18. *P. pugnax* [*Phidiana hiltoni*] – 4, orange and rose forms

Aphelandra verticillata transferred to *Holographis*
(Acanthaceae: Acantheae)

Thomas F. Daniel ^{1,3}, Lucinda A. McDade ², Carrie A. Kiel ²

¹ Department of Botany, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California 94118, USA; ² Rancho Santa Ana Botanic Garden, Claremont Graduate University, 1500 North College Avenue, Claremont, California 91711, USA;

³ Corresponding author: Email: tdaniel@calacademy.org

Aphelandra verticillata is transferred to *Holographis* based on molecular, macromorphological, and palynological data. Authorship and typification of the name are discussed. A key summarizing distinctions between *Aphelandra* and *Holographis* is provided.

KEYWORDS: New combination, pollen, morphological distinctions, field photos.

Taxonomy of the large (ca. 200 species) Neotropical genus *Aphelandra* R.Br. was revised by Wasshausen (1975), and the Mexican species were subsequently treated by Daniel (1991). In the latter account *A. verticillata* Hemsl., a species endemic to south-central Mexico, was noted to be somewhat intermediate in morphological characters with the smaller (17 species) Mexican genus *Holographis* Nees. Molecular phylogenetic analyses of Acantheae (McDade et al. 2005; fig. 4), which included multiple representatives of both genera, revealed *A. verticillata* to pertain to a clade containing all sampled species of *Holographis*. Based on this result, combined with morphological data as summarized below, *A. verticillata* is transferred to *Holographis*.

***Holographis verticillata* (Hemsl.) T.F. Daniel, L.A. McDade, and C.A. Kiel, comb. nov.**

Aphelandra verticillata Hemsl., Biol. Centr. Amer. Bot. 2:513. 1882. *Crossandra haenkeana* Nees in Alph. de Candolle, Prodr. 11:281. 1847, non *Aphelandra haenkeana* Nees, 1847. Type.—MEXICO. Western Mexico, 1791, *T. Haenke s.n.* (holotype: PR!; isotypes: GZU!, PRC!).

Descriptions of the species were provided by Wasshausen (1975) and Daniel (1991). Occurrences are known from four states in south-central Mexico (Guerrero, México, Michoacán, and Morelos; Daniel 1991). Although there are no illustrations of the species, plants were recently photographed in the southeastern-most portion of the state of México (Fig. 1).

The following additional collections have been studied since those cited by Daniel (1991). The distribution of this species, which is endemic to central Mexico, is shown in Figure 2.

ADDITIONAL SPECIMENS EXAMINED.— **Guerrero:** Mpios. de Iguala y Buenavista, Cañón de la Mano, entre Los Amates y El Naranjo, 10 km N de Iguala por el ferrocarril, sobre el cerro a SW de Los Amates, [ca. 18°24'50.86"N, 099°29'34.64"W], *C. Catalán C. 369* (L, MEXU, MO), *509* (MO); Mpio. Eduardo Neri, Cañada Carrizalillo, 1 km ESE de Amatlán, 17°52'N, 99°45'W, *R. Cruz D. 616* (FCME); Mpio. Taxco de Alarcón, 1 km N de La Cascada, 18°33'26"N, 99°39'35"W, *R. Cruz D. 2122* (FCME); Mpio. Taxco, alrededores de Acuitlapan, *B. del Río Luyando s.n.*



FIGURE 1. *Holographis verticillata*. Vegetative node showing quaternate leaves (top left). Habit with inflorescence (top right). Inflorescence (center left). Head-on view of floral limb (center). Upper lip of corolla with stamens and style/stigma (center right). Flower and buds on inflorescence with bracts and bracteoles (bottom). Photos courtesy of Dale Denham.

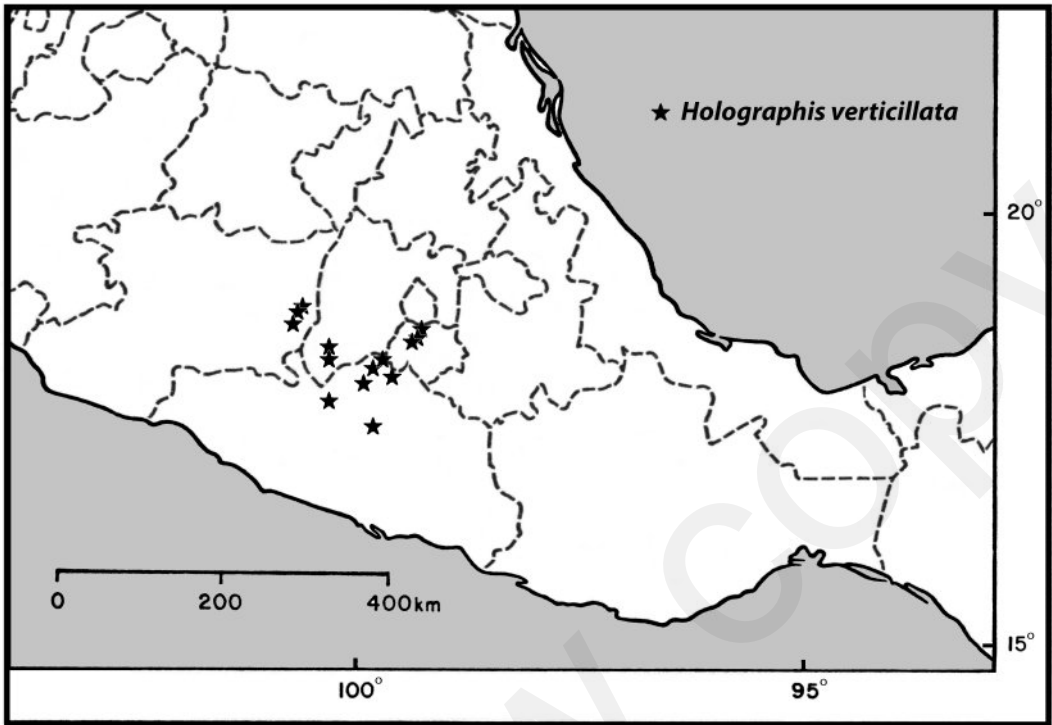


FIGURE 2. Map of central Mexico showing the distribution of *Holographis verticillata*.

(FCME). **México:** Tlatlaya y cercanías, *E. Matuda et al.* 29997 (MEXU). **Morelos:** Mpio. Xochitepec, E de Xochitepec a 100 m del Río Tetlama en la falda del Cerro El Capire, *I. de la Cruz* 1527 (MEXU).

AUTHORSHIP AND TYPIIFICATION.— Authorship of *Aphelandra verticillata* has been cited as “Nees ex Hemsl.” (e.g., Wasshausen 1975; Daniel 1991) and as “Nees” (e.g., IPNI 2019). In the protologue of *Crossandra haenkeana*, Nees (1847) cited in synonymy “*Aphelandra verticillata* N. ab E. in h. Haenk.!” using the name he wrote on some specimens of Haenke’s type collection. Owing to the prior existence of *A. haenkeana* Nees, Hemsley (1882) effectively published a new name for this species on its transference to *Aphelandra*, using the epithet of the name published as a synonym by Nees in 1847. Therefore, the publishing author of the name *A. verticillata* is Hemsley (or potentially “Nees ex Hemsl.”), but not Nees.

Wasshausen (1975) indicated that the holotype of *Aphelandra verticillata* was *Haenke s.n.* at PR and so annotated a collection there, which is mounted on two sheets (one bearing an original label with “*Aphelandra verticillata* N. ab E., Mexico, H. Haenke,” all in Nees’ handwriting, and the other bearing only plants and annotation labels). In the protologue of *Crossandra haenkeana*, Nees (1847) indicated merely a Haenke collection from Mexico in Haenke’s herbarium on which he had written “*Aphelandra verticillata* N. ab E.” The “original herbarium” or “main set” of Haenke’s herbarium has been indicated to be at PR (e.g., Lanjouw and Stafleu 1957; Stearn 1973). Both sheets at PR bear the same pair of reference numbers (305357 and 10480) to which “A” has been added on the label-bearing sheet and “B” has been added to the second sheet. In 1990, Daniel annotated both of these sheets as constituting the holotype. At PRC there are two isotypes, one of which (barcode 454829) bears “*Aphelandra verticillata* N. ab E.” in Nees’ handwriting. The isotype at

GZU (acc. 250616), also bears “*Aphelandra verticillata* N. ab E.” in Nees’ handwriting; in 2011, this specimen was erroneously annotated by Daniel as “*Aphelandra haenkeana*,” and as a probable isolectotype of *C. haenkeana*. Lectotypification would not appear to be necessary for the basionym of *A. verticillata*; however, if it is (e.g., if one interprets that Nees saw in Haenke’s herbarium all three of the specimens noted to bear the label data in his handwriting [i.e., those known to be at P, PRC, and GZU] and then these were subsequently dispersed with a division of Haenke’s herbarium, one of them might have to be designated as the lectotype), Wasshausen’s (1975) indication of the holotype at PR would serve to effectively lectotypify the name.

KEY CHARACTERISTICS.— The following key summarizes the known macromorphological, palynological, and cytological differences and tendencies that help to distinguish *Holographis* and *Aphelandra*:

- 1a. Leaves opposite (rarely subopposite) or quaternate; bracts entire and usually green; corollas often with colored linear nectar guides, 6.5–24 (–40 in *H. velutifolia* and *H. verticillata*, both of which have quaternate leaves) mm long; filaments of stamens often entirely included in corolla tube; pollen with colpi sometimes expanded or bifurcating toward poles, interapertural exine homogeneously sculptured; $x = 13$ *Holographis*
- 1b. Leaves opposite (rarely subopposite); bracts entire or dentate, green or variously colored; corollas rarely with linear nectar guides, mostly 25–85 mm long; at least distal portion of filaments of stamens usually exerted from corolla tube; pollen with colpi not expanded or bifurcating (usually narrowed) toward poles, interapertural exine usually heterogeneously sculptured; $x = 14$ *Aphelandra*

Morphological characteristics of *H. verticillata* that are suggestive of *Aphelandra* include a reddish coloration sometimes present on the bracts, relatively elongate corollas (25–38 mm long), and filaments and anthers of stamens exerted well beyond the mouth of the corolla. Each of these traits is also encountered in one or more species of *Holographis*. Characters of *H. verticillata* more typical of species of *Holographis* include its quaternate leaves (characteristic of 13 species of the genus, but unknown in *Aphelandra*) and pollen with homogeneous exine and colpi that expand or bifurcate toward the poles (known in at least five species of the genus, but essentially unknown in *Aphelandra*; see discussion of pollen below). *Holographis verticillata* can be distinguished from its congeners by the combination of having whorled leaves, elliptic bracts that are 11–19 mm long, yellow corollas that are 25–38 mm long, and pubescent capsules.

POLLEN.— Although there is variation in exine sculpturing among species of both *Aphelandra* (e.g., Wasshausen 1975; McDade 1984; Daniel 1991, 1998) and *Holographis* (e.g., Daniel 1983, 1988, 1998), at least two characteristics of pollen of *H. verticillata* more closely resemble grains of *Holographis* than those of *Aphelandra* bearing three colpi (Fig. 3). Like that of *H. verticillata*, pollen of at least five species of *Holographis* (e.g., *H. anisophylla* T.F. Daniel, *H. hintonii* (Leonard) T.F. Daniel, *H. ilicifolia* Brandegee, *H. pallida* Leonard & Gentry, *H. virgata* (Harv. ex Benth & Hook.f.) T.F. Daniel) have colpi that expand or bifurcate toward the poles. Colpi in most species of *Aphelandra* that bear three colpi either taper or do not expand poleward; distally bifurcating colpi have been documented in this genus only in some plants of *A. golfodulcensis* McDade (McDade 1984: fig. 26). It is noteworthy that colpi that expand toward the poles are also known in *Stenandrium* (e.g., *S. goiasense* Wassh., Wasshausen 1990: fig. 2c; some specimens of *S. dulce* (Cav.) Nees, Daniel 1998: fig. 2g), a Neotropical genus more closely related to *Holographis* than *Aphelandra* based on both molecular phylogenetic data (McDade et al. 2005) and putative base chromosome numbers (Daniel 1991; i.e., $x = 13$ in *Holographis* and *Stenandrium* vs. $x = 14$ in *Aphelandra*). The second characteristic linking pollen of *H. verticillata* to *Holographis* is the inter-

apertural exine sculpturing. In all species of *Holographis*, including *H. verticillata*, the interapertural exine is homogeneously sculptured, whereas in many or most species of *Aphelandra* with 3-colpate pollen, it is heterogeneous (Fig. 3).

Wasshausen (1975: fig. 18) shows pollen of *A. verticillata* (putatively of *Moore 5503* at US) that differs by having 3-colpate pollen with colpi tapering toward the poles, a prominent ridge within each colpus, and a 3-parted polar aperture. Similar pollen with intracolpal ridges and/or 3-parted polar apertures (cf. Daniel 1991: figs. 2e, g) are known among several species of *Aphelandra*, but not among any currently recognized species of *Holographis*. Examination of pollen from

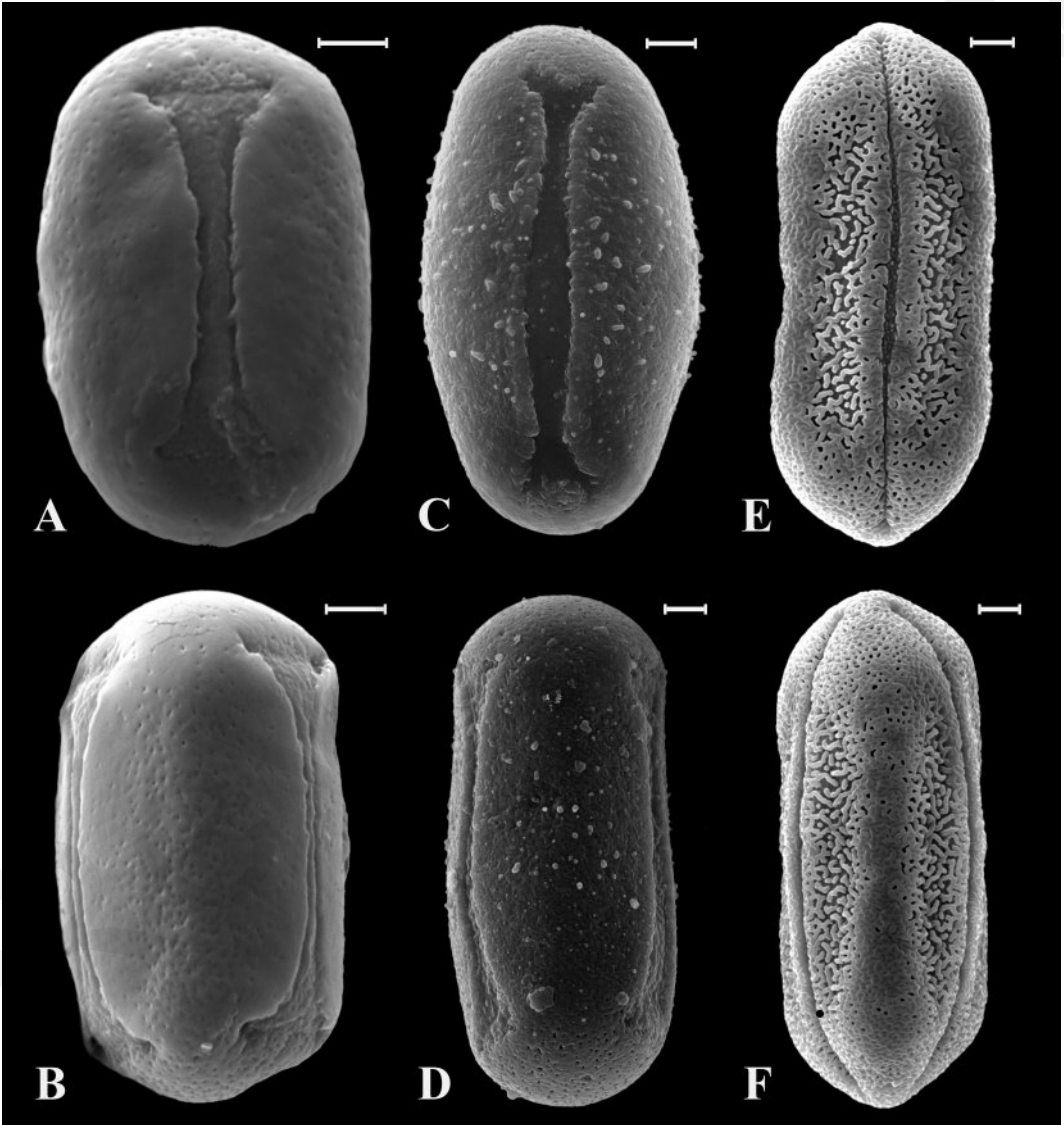


FIGURE 3. Examples of pollen of *Holographis* (including *H. verticillata*) and *Aphelandra*. A, B. *Holographis pallida* Leonard & Gentry (*Daniel 3382* from Sonora): A. Apertural view; B. Interapertural view. C, D. *Holographis verticillata*: C. Apertural view (*Daniel et al. 3295* from Michoacán); D. Interapertural view (*Moore 5503* from Guerrero). E, F. *Aphelandra castaneifolia* Britton (*Daniel & Wood 10175* from Bolivia): E. Apertural view; F. Interapertural view. Scales = 5 µm.

Moore 5503 at UC confirms pollen without intracolpal ridges or 3-parted polar apertures and with colpi expanded toward the poles (Fig. 3D). The image shown by Wasshausen (1975) likely represents contamination from a species of *Aphelandra*.

ACKNOWLEDGMENTS

Daniel's studies at European herbaria were funded by the In-house Research Fund of the California Academy of Sciences and the National Science Foundation (BSR-8609852); field studies in Mexico and Bolivia were funded by the National Science Foundation (DEB-8304790), the In-house Research Fund of the California Academy of Sciences, and the Botany Department's Rose Memorial Fund. We thank Dale Denham for permission to use his excellent photos, Otakar Šída (PR) for sending images of specimens, and the Academy's SEM laboratory. Gratitude is expressed to the following herbaria for hosting visits (TFD) or otherwise providing specimens for study: ARIZ, BM, CAS, ENCB, F, FCME, G, GH, GZU, K, L, MA, MEXU, MICH, MO, NY, PH, PR, PRC, TEX, UC, and US.

LITERATURE CITED

- DANIEL, T.F. 1983. Systematics of *Holographis* (Acanthaceae). *Journal of the Arnold Arboretum* 64:129–160.
- DANIEL, T.F. 1991. A revision of *Aphelandra* (Acanthaceae) in Mexico. *Proceedings of the California Academy of Sciences*, ser. 4, 47:235–274.
- DANIEL, T.F. 1998. Pollen morphology of Mexican Acanthaceae: Diversity and systematic significance. *Proceedings of the California Academy of Sciences*, ser. 4, 50:217–256.
- HEMSLEY, W.B. 1882. Botany, vol. 2. Pages 1–576 in F.D. Godman and O. Slavin, eds., *Biologia Centrali-Americana*. R. H. Porter, London, U.K.
- IPNI. 2019. International Plant Names Index. Website. <<https://www.ipni.org/?q=Aphelandra%20verticillata>> [accessed 27 September 2019]
- LANJOUW, J., AND F.A. STAFLEU. 1957. Index herbariorum, part 2, collectors. *Regnum Vegetabile* 9:175–295.
- MCDADE, L.A. 1984. Systematics and reproductive biology of the Central American species of the *Aphelandra pulcherrima* complex (Acanthaceae). *Annals of the Missouri Botanical Garden* 71:104–165.
- MCDADE, L.A., T.F. DANIEL, C.A. KIEL, AND K. VOLLESEN. 2005. Phylogenetic relationships among Acantheae (Acanthaceae): Major lineages present contrasting patterns of molecular evolution and morphological differentiation. *Systematic Botany* 30:834–862.
- STEARNS, W.T. 1973. An introduction to K. B. Presl's *Reliquiae Haenkeanae* (1825–1835). Pages 1–19 in K.B. Presl, *Reliquiae Haenkeanae* (reprint of edition Prague 1830–1831). A. Asher, Amsterdam, The Netherlands.
- WASSHAUSEN, D.C. 1975. The genus *Aphelandra* (Acanthaceae). *Smithsonian Contributions to Botany* 18:1–157.
- WASSHAUSEN, D.C. 1990. New species of *Stenandrium* (Acanthaceae) from the Planalto of Brazil. *Brittonia* 42:1–6.

The First Recognition of Cretaceous Deposits in California

Peter U. Rodda

Emeritus Curator, Department of Invertebrate Zoology and Geology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California 94118, USA; Courtesy Faculty, Earth Sciences Department, University of Oregon, Eugene, Oregon 97403, USA. Email: prodda@uoregon.edu.

Early in the year 1855, Dr. Henry Bates, of Shasta City, California, presented to the two-year-old California Academy of Sciences, a fossil said to be from Arbuckle's Diggings, a lode gold prospect in the southern Klamath Mountains, northwestern Tehama County, California.¹ At the Academy meeting of April 2, 1855, Dr. John Boardman Trask (Fig. 1) read a paper describing this fossil as a new species of fossil cephalopod, that he named *Ammonites batesi*; the description was published later that year in the Academy *Proceedings* (Trask 1855). Although Trask noted only that this fossil indicated the presence of "secondary rocks" (i.e., of the Mesozoic Era, encompassing the Triassic, Jurassic, and Cretaceous Periods), this was the first Cretaceous fossil described from California, and the entire Pacific Coast of North America.²

John Boardman Trask was a major figure in the history of geology in California. He conducted the first (unofficial) Geological Survey of California; he was an important pioneer in seismology; he was one of the founders of the California Academy of Sciences and a major contributor to its collections and activities; and he was among the earliest to describe California fossils (Leviton and Aldrich 1982; Rodda and Leviton 1983). Although he is credited with being the first to demonstrate the presence of Cretaceous rocks in California, Trask himself ironically failed to establish a definite Cretaceous age for any California fossils. For him this task proved elusive.

Trask (1855, 1856a, b) published three papers relating to Cretaceous fossils in California. In his first paper, on *Ammonites batesi*, Trask referred to the geological age of this specimen simply as "secondary", and he made no comparison or reference to any other ammonite or fossil of any age. *Ammonites batesi* is a representative of the world-wide ammonite family *Lytoceratidae*, fairly common fossils in both Jurassic and Cretaceous rocks, and somewhat similar, though more distantly related forms are found in Late Triassic strata. Trask presumably lacked the paleontological experience to recognize

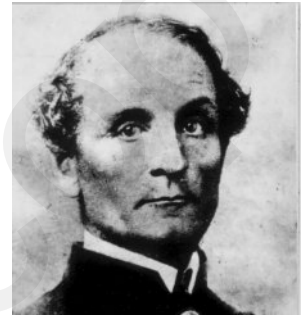


FIGURE 1. John B. Trask (Courtesy California Academy of Sciences Special Collections)



FIGURE 2. William M. Gabb (Nat'l Acad. Sci., *Biogr. Mem.*, 1909 [March] vol. VI, portrait [facing p. 347])

¹ Henry Bates was elected a corresponding member of the Academy in July 1855. He was a member of the California State Assembly, 1855–1856, and later State Treasurer, 1856–1857. In 1857 Bates was impeached by the state Senate and resigned his office.

² The first formal description of Pacific Coast fossils was published in 1848 by Timothy A. Conrad, of Philadelphia, based on mollusk specimens from Astoria, Oregon, and correctly assigned by Conrad to the Miocene Epoch (Moore 1963). Until 1855 all descriptions of California fossils were based entirely on specimens from Cenozoic rocks.

that *A. batesi* was a Cretaceous form. Trask did not include an illustration of the fossil, but his original specimen (the Holotype) was later illustrated by William More Gabb (Fig. 2) in the first volume of *Paleontology* issued by the second California Geological Survey [Whitney Survey], (Gabb 1864:67–68, pl. 13, fig. 16). *Ammonites batesi* is a distinctive, readily recognizable species, fairly common in part of the Lower Cretaceous sequence exposed in the drainage of Cottonwood Creek in Shasta County, California. Judging from Gabb's figure, the original specimen was mainly an internal mold with little original shell remaining (Fig. 3).

The following year Trask (1856a, b) published two more papers in the *Academy Proceedings* on California fossils. In the first, "Description of a New Species of Ammonite and Baculite from the Tertiary Rocks of Chico Creek" [Butte County], Trask described, named, and illustrated *Ammonites chicoensis* and *Baculites chicoensis*, based on fossils collected along Chico Creek by Andrew Randall, and deposited in the Academy collections³ (Fig. 4). Although the title of Trask's paper makes a startling statement regarding the age of these fossils, Trask was aware that ammonites similar to *Ammonites chicoensis* and *Baculites chicoensis* were generally considered indicators of the Late Cretaceous Period. He was, however, so struck by the modern appearance and beautiful preservation of the associated bivalves and gastropods — many appeared to him to be of living genera and species — that he concluded that the entire fossil assemblage from Chico Creek, including the ammonites, was much younger, possibly as young as Miocene, and that ammonites had not died out at the end of the Cretaceous but persisted well into the Cenozoic. He did indicate that he was "not without some hesitancy" in presenting his conclusions, and it is likely that his paleontological inexperience also led him astray here.

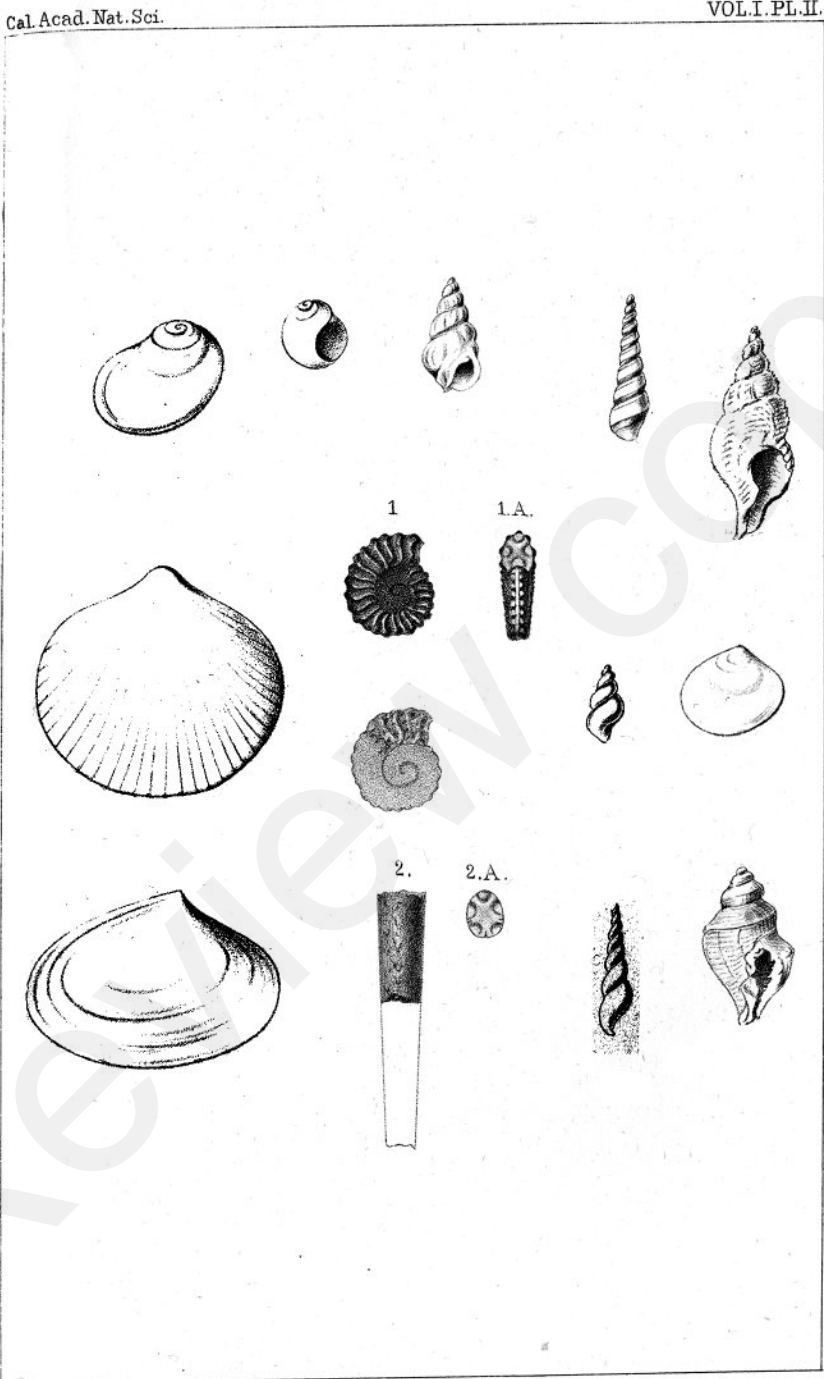
In the third paper, "Description of Three New Species of the Genus *Plagiostoma* from the Cretaceous Rocks of Los Angeles," Trask described and illustrated *Plagiostoma pedroana*, *P. annulatus*, and *P. truncata*, from coastal rocks near San Pedro. The fossils were external molds of bivalved shells preserved in fine-grained rock, from which Trask made casts for easier study. He definitely considered these fossils to be of Cretaceous age, even including "Cretaceous" in the title of his paper, but again he was mistaken. Trask misidentified these bivalve fossils as *Plagiostoma* (Superfamily Limacea), a genus found only in Mesozoic rocks. Trask's three species are now considered a single species, *Delectopecten pedroanus* (Trask), of a different, much younger, genus, (Superfamily Pectinacea), a mud pecten. Trask's specimens were almost certainly collected from what is now called the Monterey Formation of Miocene age, but no specimens of *Delectopecten pedroanus* have been found since Trask's time. In the San Pedro area a different species of mud-pecten has been reported from the Monterey Formation, and no fossiliferous rocks older than Miocene are present in this area (Woodring et al. 1946:37; Moore 1984:B18).

All of the original specimens on which these three papers were based were destroyed, along with nearly all of the Academy collections and library, in the San Francisco earthquake and fire of 1906. In 1938, F.M. Anderson (Fig. 5), then Honorary Curator of Paleontology at the Academy,



FIGURE 3. "*Ammonites Batesii*" Gabb

³ Andrew Randall was the first President of the California Academy of Sciences, serving from 1853 until 1856].



1. AMMONITE Chicoensis TRASK.

FIGURE 4. "Ammonite Chicoensis" Trask, plate 2 in Trask, J., B., 1856a, Description of a new species of ammonite and baculite from the Tertiary rocks of Chico Creek.

selected, from the Academy collections, a replacement type specimen, a Neotype (which Anderson called a “lectotype”), for *Ammonites batesi* [= *Lytoceras batesi* (Trask) (Anderson 1938:148, pl. 17, fig. 1) (Fig. 6). Neotypes for *Ammonites chicoensis* and *Baculites chicoensis* were selected, also from the Academy collections, by Taff, et al. (1940: 1320–1321, pl. 1, figs. 1–4) in a paper describing the stratigraphic sequence of the Chico Formation along Chico Creek. (Fig. 10). Neotypes have never been selected for the three species that Trask described as *Plagiostoma*, as no additional specimens have ever been found.

Even though Trask did not certainly recognize them as such, *Ammonites batesi*, *Ammonites chicoensis*, and *Baculites chicoensis* were the first three Cretaceous fossils described from California and from the Pacific Coast of North America. The first definite statement of the Cretaceous age of these fossils was made by John Strong Newberry (Fig. 7) in Volume VI of the Pacific Railroad Reports (Newberry 1856:24–25, 27). Newberry cites Trask’s papers, and he argues strongly for the Cretaceous age of the Chico Creek fossils (p. 24–25). In a footnote, he remarks that the well-known paleontologist F.B. Meek (Fig. 8) had recognized the diagnostic Cretaceous bivalve *Inoceramus* among the Chico Creek fossils and considered them of Late Cretaceous age. Newberry also notes (p. 27) that numerous ammonites of undoubted Cretaceous age were obtained from Arbuckle’s Diggings by Dr. Bates, one of which was the specimen of Trask’s *Ammonites batesi*. Newber-



FIGURE 5. Frank M. Anderson (Courtesy Photo Collection, Geology Dept., California Academy of Sciences)

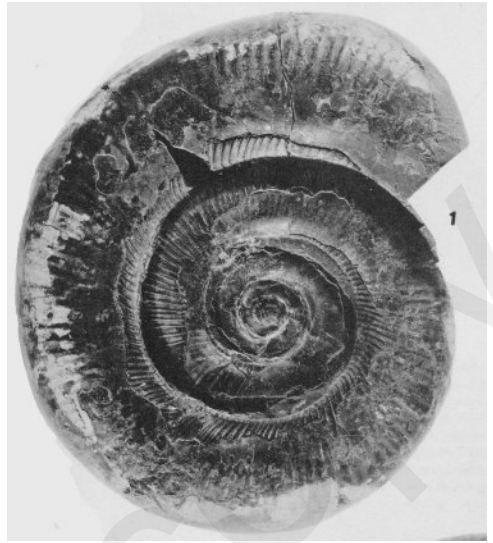


FIGURE 6. From Anderson (1938): “Plate 17.—Cretaceous Fossils from California. (1) *Lytoceras batesi* (Trask). Lectotype. Greatest diameter, 165 mm.; thickness of whorl, 51.5 mm. Argonaut zone, middle part of Horsetown group; Loc. 1347 (C,A,S.), east of Mitchell Creek, near Roaring River, Shasta County.”

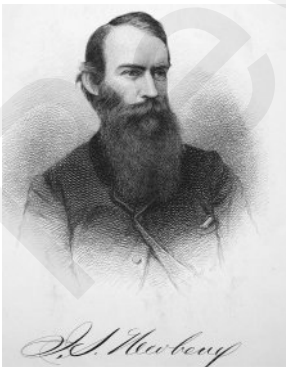


FIGURE 7. John S. Newberry (Courtesy Smithsonian Institution Archives, RU 7177, Box 8, Folder 25)

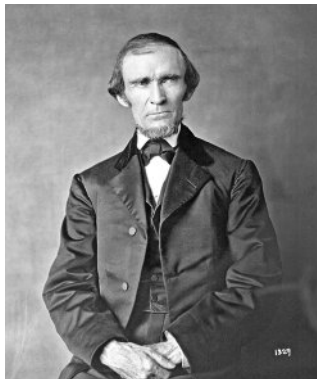


FIGURE 8. Fielding B. Meek (Courtesy Smithsonian Institution Archives, Image # AI-1329)

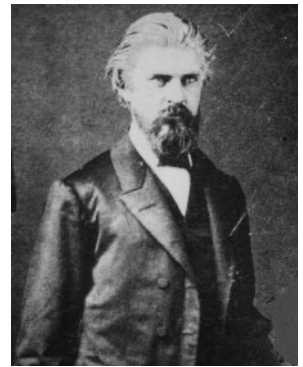


FIGURE 9. William P. Blake (Courtesy Smithsonian Institution Archives, RU 7177, Box 1, Folder 43)

BULL. GEOL. SOC. AM., VOL. 51

TAFF, HANNA & CROSS, PL. 1



FOSSILS FROM TYPE LOCALITY OF CHICO FORMATION

FIGURE 10. Plate 1 from Taff (1940).

1, 2. *Ammonites chicoensis* Trask. Neotype no. 5785, Calif. Acad. Sci. from loc 27838 (C. A. S.), Chico Creek, Butte County, California, 3.6 miles from "10 Mile House" on Humboldt Road (U. S. G. S. Topog. map). Chico Cretaceous. Greatest diameter, 79.6 mm.; least diameter, 60.5 mm.; greatest thickness, 26.0 mm. (p. 1320);

3, 4. *Baculites chicoensis* Trask. Neosyntypes nos. (fig. 3) and 5786 (fig. 4) 5787. Calif. Acad. Sci., from loc. 27838 (C. A. S.), Chico Creek, Butte County, California, 3.6 miles from "10 Mile House" on Humboldt Road (U. S. G. S. Topog. map). Chico Cretaceous. (3) Length of fragment, 78.8 mm.; greatest diameter, [of fragment], 18.0 mm.; (4) length of fragment, edge view, 77.7 mm.; least diameter, 11.0 mm. (p. 1321).

5, 6. *Cucullaea truncata* Gabb. Hypotype no. 5791, Calif. Acad. Sci., from loc. 28172 (C. A. S.) Chico Creek, Butte County, California, at bluff on creek due west of "10 Mile House" on Humboldt Road (U. S. G. S. Topog. map). Chico Cretaceous. Length, 65.5 mm.; height, 59.6 mm.; thickness, 36.2 mm. (p. 1321).

ry does not indicate that he had visited either Arbuckle's Diggings or Chico Creek. In another volume of the Pacific Railroad Reports, W.P. Blake (1857:154) (Fig. 9) in discussing some fossils of possible Cretaceous age from Benicia, California, notes that Cretaceous strata have been found in the northern part of the state, "Discovered and announced by Dr. J.B. Trask." Since Trask had not published a specific statement of the Cretaceous age, Blake either concurred with Newberry, or he may have heard Trask make such a statement at one of the regular Academy meetings that Blake attended.

Chico Creek, in Butte County, is a classic California locality for Upper Cretaceous fossils of the Campanian Period (Taff et al. 1940; Popenoe et al. 1960). The rocks at Arbuckle's Diggings, however, are pre-Cretaceous metamorphic rocks of Jurassic and pre-Jurassic age, part of the Klamath Mountains complex (Irwin 1960, 1994), and none of the Cretaceous ammonites purportedly from there could have been collected there.⁴ Arbuckle's Diggings was about a mile west of the nearest outcrop of Cretaceous strata, commonly an unfossiliferous basal conglomerate and sandstone, and two miles or so from the beginning of the ammonite-rich strata that extend eastward for another ten miles. (Murphy et al. 1964; Murphy et al. 1969). This sequence of Cretaceous strata, exposed in the drainage of Cottonwood Creek, 5,300 feet thick along the North Fork of Cottonwood Creek and 22,000 feet thick along Dry Creek, has long been famous for its Cretaceous fossils, especially ammonites (Gabb 1864, 1869; Anderson 1902, 1938, 1955; Murphy 1956; Popenoe et al. 1960; Murphy et al. 1969; Rodda, 1959; Rodda and Murphy 1985:3–14). (See reference maps, Figs. 11 and 12 showing locations of Arbuckle's Diggings, branches of Cottonwood Creek, Horsetown, and Cretaceous and Cenozoic deposits).

Gold was found at Arbuckle's Diggings in 1850 by twelve miners who had been working at Horsetown, an established placer gold mining area on Clear Creek in Shasta County, about 20 miles to the northeast.⁵ They were prospecting westward up branches of Cottonwood Creek, following earlier reports of gold by a prospector who had been driven from a discovery site by members of a local native tribe (The History of Shasta Co. and its communities, As written in 1881 by B.F. Frank and H.W. Chappell, published in 1881, book pages 5–36, 125–148, Transcribed by Kathy

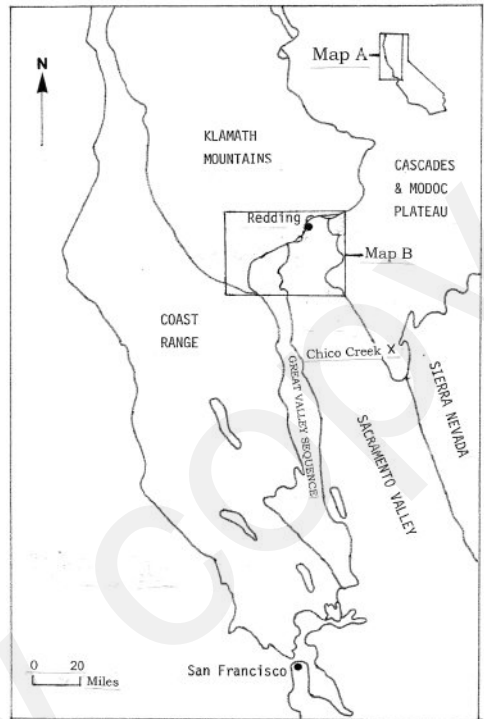


FIGURE 11. Index map to the Great Valley Sequence of Northern California. Map prepared by P.U. Rodda.

⁴ Arbuckle Basin, Arbuckle Gulch, and Arbuckle Mountain are indicated on the U. S. Geological Survey topographic map of the Chancellula Peak quadrangle (1951), but not the ephemeral Arbuckle's Diggings, which might have been named for either a pioneer settler, or for a later miner. In the Arbuckle area occasional prospecting and mining for gold continued under various names through the 1930s at least.

⁵ Horsetown was an important placer-gold mining camp established by Pierson B. Reading in 1848 at Reading Bar on Clear Creek in western Shasta County, eight miles southwest of the town of Redding. Both the town and the Bar were named for Reading, a prominent early settler. Clear Creek, an east-flowing tributary of the Sacramento River, heads in the Klamath Mountains, flows southeasterly to Reading Bar, then turns eastward and joins the Sacramento River six miles south of Redding.

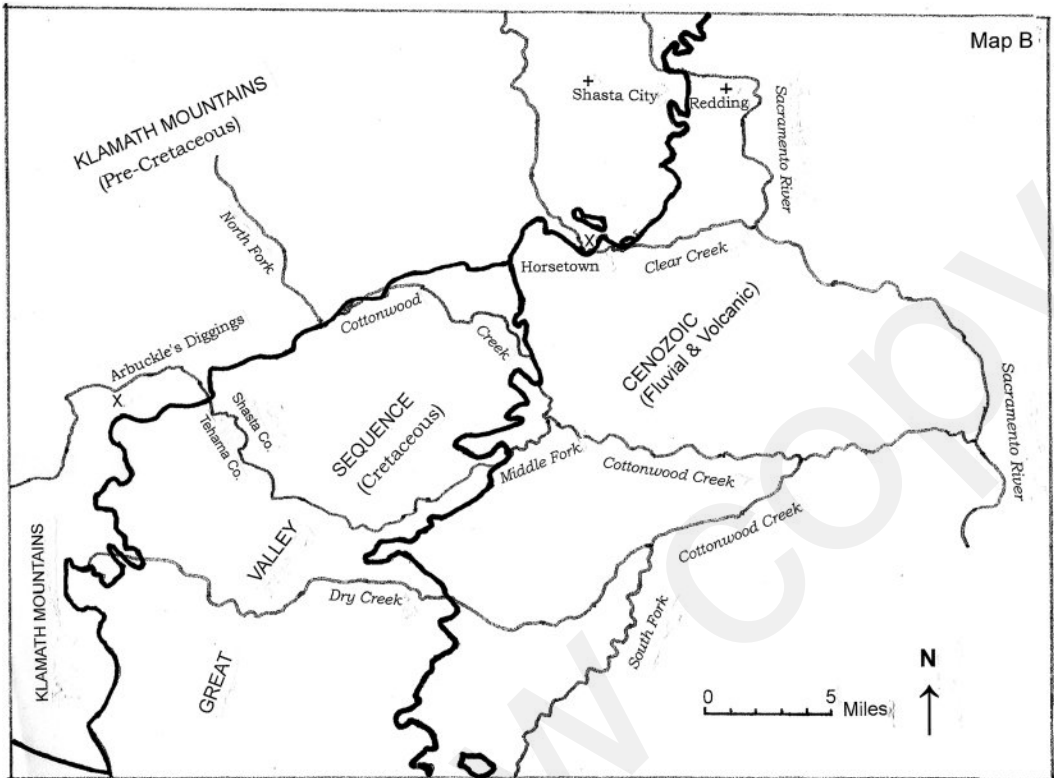


FIGURE 12. Map of northwest Sacramento Valley, showing generalized geology, branches of showing positions of Cottonwood Creek, and locations of Arbuckle's Diggings and Horsetown. Map prepared by P.U. Rodda.

Sedler, California Genealogy & History Archives, Southwest Shasta Historical Group, History & Happenings, <<http://HistoryandHappenings.squarespace.com/>>. ⁶ Horsetown was the likely supply center for Arbuckle Diggings. Wagon roads connecting Horsetown with other mining camps in the Cottonwood region crossed the ammonite-bearing strata, and off-road journeys between the two camps would have found ammonites, in-place in the creek banks or loose in the stream gravels, as they are still found today.

We do not know what connection Dr. Bates had with Arbuckle's Diggings, whether he was a miner, an investor, or just a visitor. In any case, Bates acquired a collection of Cretaceous ammonites either from the miners, or that he collected himself, or both. In addition to the original specimen of *Ammonites batesi*, Bates gave other Cretaceous fossils to the Academy. The Academy *Proceedings* for August 20, 1855 record, "From Dr. Henry Bates, a valuable collection of geological specimens, mostly Ammonites, from the vicinity of Shasta City."⁷ From this material Gabb described and illustrated four ammonite species, two of them new, based on specimens in the Academy collections, and purportedly from Arbuckle Diggings: [modern nomenclature in brackets] *Ammonites traskii* Gabb (Gabb 1864:63, pl. 11, fig. 10) [= *Simbirskites traskii* (Gabb)], *Ammonites*

⁶ The group of twelve included John S. Hittell, older brother of historian Theodore Hittell, who later prepared an unpublished manuscript history of the California Academy of Sciences to 1906 that was edited, revised, and enlarged by Leviton and Aldrich, 1997. John Hittell moved to San Francisco in 1852, where he became a well-known author, historian, and journalist. He died in San Francisco in 1901.

⁷ Shasta City is located in the southern Klamath Mountains five miles northwest of Reading, and ten miles north of the fossiliferous Great Valley Sequence.

batesi Trask (Gabb 1864:67, pl. 13, fig. 16)[= *Lytoceras batesi* (Trask)], *Crioceras percostatus* Gabb (Gabb 1864: 77, pl. 16, fig. 26)[= *Tropeum percostatum* (Gabb), and *Ancyloceras* sp. indet. (Gabb 1864:78, pl. 15, fig. 30) [= ?*Heteroceras* sp.]. (All of this material was lost in the 1906 San Francisco earthquake and fire that led to the destruction of the California Academy of Sciences' buildings, which at the time were located in downtown San Francisco. Neotypes have not been named for *Ammonites traskii*, or *Crioceras percostatus*.) This group of ammonites could not have come from any single locality as among them they range over a considerable stratigraphic interval, representing three consecutive Cretaceous Stages, Hauterivian, Barremian, and Aptian, further suggesting that these fossils were collected while traveling across the outcrop area of the Cretaceous strata. The basic stratigraphic and geographic distribution of Cretaceous ammonites in the Cottonwood District has been well established, and we know the stratigraphic age of each of these ammonites (Murphy 1956, 1975; Murphy et al. 1969). *Simbirskites traskii* occurs in the *agulla* zone of Hauterivian age (Murphy 1956), the fragmentary (?)*Heteroceras* sp. closely resembles forms from the *poniente* zone of Barremian age (Murphy 1956, 1975), and *Lytoceras batesi* and *Tropeum percostatum* are found only in the *wintunius* zone of Aptian age (Murphy 1956; Murphy et al. 1969).

It is somewhat surprising that the first California Cretaceous fossils to be described were not specimens from the Horsetown-Clear Creek area, rather than ones from Cottonwood Creek or Chico Creek. Ammonites and other fossil mollusks, were, and are, common at and near the site of Horsetown, in discontinuous outcrops of Cretaceous rocks on the north side of Clear Creek. Horsetown was an earlier-established, larger, and longer-lived mining district than Arbuckle Diggings, and mining operations would have uncovered many Cretaceous fossils. Josiah Dwight Whitney (Fig. 13), Director of the (Second) California Geological Survey, visited Horsetown in 1865, and noted that the Cretaceous rocks exposed there were "...well filled with fossils" (Whitney 1865:321). Gabb described several Cretaceous species from Horsetown, and many subsequent papers have described Cretaceous fossils from this area (Rodda 1959). Dr. Henry Bates seems to be the connection here, but what prompted him to go to San Francisco and give that fossil to the Academy? John Hittell may have been an intermediary; he was living in San Francisco at that time, and he and Dr. Bates likely had a connection through Arbuckle's Diggings.

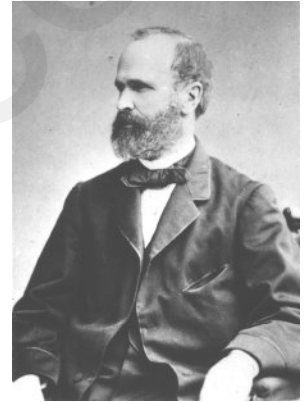


FIGURE 13. Josiah D. Whitney (Courtesy Smithsonian Institution Archives. Image # 78-106)

Cretaceous deposits are exposed over a large part of the Pacific slope of North America from Mexico to Alaska; they are notably fossiliferous, with ammonites and other mollusks especially well represented, and these have been the object of study for more than 150 years. Discovery was inevitable, of course, but the first recognition of the presence of Cretaceous strata and fossils in this vast area was due to the interaction of Henry Bates and John Boardman Trask.

ACKNOWLEDGMENTS

I wish to acknowledge with grateful appreciation the Smithsonian Institution Archivists Stephanie Ashley, Marisa Bourgoïn, and Heidi Stover for their prompt and efficient handling of my request to use images in the Smithsonian Institution Archives. I am also indebted to Gary Williams, who reviewed the submission, and Alan Leviton, who provided invaluable assistance in preparing the illustrations and readying the manuscript for publication.

REFERENCES CITED

- ANDERSON, F.M. 1902. Cretaceous Deposits of the Pacific Coast. *California Academy of Sciences, Proceedings* (Series 3, Geology), 2, 154 pp., pls. 1–12.
- ANDERSON, F.M. 1938. Lower Cretaceous Deposits in California and Oregon. *Geological Society America, Special Paper* 16. 339 pp., pls. 1–84.
- ANDERSON, F.M. 1958. Upper Cretaceous of the Pacific Coast. *Geological Society of America, Memoir* 71. 378 pp., pls. 1–75.
- BLAKE, W.P. 1857. Geological Report. *U. S. Pacific Railroad Reports*, 5(2), 370 pp.
- CONRAD, T.A. 1848. Fossils shells from Tertiary deposits on the Columbia River near Astoria. *American Journal of Science*, ser. 2, 5:432–433.
- DALL, WILLIAM H. 1909. Biographical Memoir of William More Gabb 1839–1878. National Academy of Sciences, *Biographical Memoirs* 6:347–361, portrait.
- GABB, W.M. 1864. Description of the Cretaceous Fossils. *Geological Survey of California, Palaeontology* 1(4):55–236, pls. 9–32.
- GABB, W.M. 1869. Cretaceous Fossils. *Geological Survey of California, Palaeontology* 2(2):127–254, pls. 19–34.
- IRWIN, P. 1960. Geologic reconnaissance of the northern Coast Ranges and Klamath Mountains, California, with a summary of the mineral resources. *California Division of Mines, Bulletin* 179. 80 pp., pl. 1.
- IRWIN, P. 1994. Geologic map of the Klamath Mountains, California and Oregon. *U.S. Geological Survey, Miscellaneous Investigation Series, Map* I–2148.
- LEVITON, A.E., AND M.L. ALDRICH. 1982. John Boardman Trask: Physician-Geologist in California 1850–1879, Pages 37–69 in A.E. Leviton, P.U. Rodda, E. Yochelson, and M.L. Aldrich, eds., *Frontiers of Geological Exploration of Western North America. Pacific Division American Association for the Advancement of Science.*
- LEVITON, A.E., AND M.L. ALDRICH. 1997. Theodore Henry Hittell's California Academy of Sciences, 1853–1906. *California Academy of Sciences, Memoir* 22. 623 pp.
- MOORE, E.J. 1963. Miocene marine mollusks from the Astoria Formation in Oregon. *United States Geological Survey, Professional Paper* 419. 109 pp., pls. 1–32.
- MOORE, E.J. 1984. Tertiary marine Pelecypods of California and Baja California: Propleamussiidae and Pectinidae. *United States Geological Survey, Professional Paper* 1228-B. B1-B112 pp., pls. 1–42.
- MURPHY, MICHAEL A. 1956. Lower Cretaceous stratigraphic units of northern California. *American Association of Petroleum Geologists Bulletin*, 40(9):2098–2119.
- MURPHY, MICHAEL A. 1975. Paleontology and stratigraphy of the lower Chickabally Mudstone (Barremian-Aptian) in the Ono quadrangle, northern California. *University of California, Publications in Geological Sciences* 113:1–52, pls. 1–15.
- MURPHY, M.A., G.L. PETERSON, AND P.U. RODDA. 1964. Revision of Cretaceous lithostratigraphic nomenclature, northwest Sacramento Valley, California. *American Association of Petroleum Geologists, Bulletin* 48(4):496–502.
- MURPHY, M.A., P.U. RODDA, AND D.M. MORTON. 1969. Geology of the Ono Quadrangle, Shasta and Tehama Counties, California. *California Division of Mines and Geology, Bulletin* 192:1–28, pl. 1.
- NEWBERRY, J.S. 1856. Report upon the geology of the route. *U.S. Pacific Railroad Reports, VI, Part II* (1): 1–68.
- POPENOE, W.P., R.W. IMLAY, AND M.A. MURPHY. 1960. Correlation of the Cretaceous Formations of the Pacific Coast (United States and Northwestern Mexico). *Geological Society America, Bulletin* 71:1491–1540, 1 pl.
- RODDA, P.U. 1959. Geology and Paleontology of a Portion of Shasta County, California. *University California, Los Angeles, Unpublished Ph.D. Dissertation*. 205 pp., 20 pls.
- RODDA, P.U., AND A.E. LEVITON. 1983. Nineteenth century earthquake investigations in California. *Earth Sciences History* 2 (1):48–56.
- RODDA, P.U., AND M.A. MURPHY. 1985. Paleontological Survey, Cottonwood Creek Project. *Unpublished report prepared for the U.S. Army Corps of Engineers, Sacramento District*: pages i-ix, 1–69, Appendix pages 1–359, pls. 1–8.

- TAFF, J.A., G D. HANNA, AND C.M. CROSS. 1940. Type locality of the Cretaceous Chico Formation. *Geological Society of America, Bulletin* 51:1311–1328, 2 pls.
- TRASK, J.B. 1855. [A new ammonite from Arbuckle's Diggins, Shasta County]. *California Academy of Natural Sciences, Proceedings*, ser. 1, (1):40.
- TRASK, J.B. 1856a. Description of a new species of ammonite and baculite from the from the Tertiary rocks of Chico Creek. *California Academy of Natural Sciences, Proceedings*, ser. 1, 1(2):85–86, pl. 2.
- TRASK, J.B. 1856b. Description of three new species of the genus *Plagiostoma* from the Cretaceous rocks of Los Angeles. *California Academy of Natural Sciences, Proceedings*, ser. 1, 1(2):86, pl. 3.
- WHITNEY, J.D. 1865. Report of Progress and Synopsis of the Field-Work from 1860 to 1864. *Geological Survey of California, Geology* 1:1–498.
- WOODRING, W.P., M.N. BRAMLETTE, AND W.S.W. KEW. 1946. Geology and paleontology of Palos Verdes Hills, California. *United States Geological Survey, Professional Paper* 207. 145 pp., pls. 1–37.