Revision of the Endemic Malagasy Cavefish Genus Typhleotris (Teleostei: Gobiiformes: Milyeringidae), with Discussion of its Phylogenetic Placement and Description of a New Species

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Revision of the Endemic Malagasy Cavefish Genus *Typhleotris* (Teleostei: Gobiiformes: Milyeringidae), with Discussion of its Phylogenetic Placement and Description of a New Species

JOHN S. SPARKS[1] AND PROSANTA CHAKRABARTY[2]

ABSTRACT

Troglobitic cavefishes of the genus *Typhleotris*, endemic to coastal southwestern Madagascar, are taxonomically reviewed and a new darkly pigmented species, *Typhleotris mararybe*, is described from an isolated karst sinkhole on the coastal plain below the Mahafaly Plateau. The new species, known only from Grotte de Vitane (Vitany) near the town of Itampolo, is unique among blind cavefishes in being uniformly darkly pigmented, rather than fully depigmented or exceptionally light in coloration. In addition to its dark coloration (vs. depigmented, translucent white body in congeners), the new species can be distinguished from its two congeners, *Typhleotris madagascariensis* and *T. pauliani,* by the sculpted, bony (vs. fleshy) appearance of its head with strongly protruding lateral ethmoid, sphenotic, and pterotic bones, and an elevated vertebral count.

KEY WORDS: Eocene, Grotte de Vitane, karst, Mahafaly Plateau, sinkhole, subterranean, *Typhleotris mararybe*, sp. nov., Vitany

INTRODUCTION

Troglobitic freshwater fishes, the typically blind and pigment-free obligate cave-dwelling lineages, represent an enigmatic and intriguing, yet poorly understood, group of vertebrates

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(Romero, 2001; Eigenmann, 1909). Worldwide, just over 150 species of subterranean fishes are known to science (Proudlove, 2010). Little is known regarding the basic biology of many of these lineages, primarily due to the precarious and remote locations of their habitats, including caves, sinkholes, and other isolated and difficult to access subterranean systems (Proudlove, 2006; Trajano, 2001). Due to the common features of these environments (e.g., frequent or perpetual darkness, lack of predators and competitors, limited trophic resources) many of these fishes have converged on similar morphologies characterized most commonly by the loss or degeneration of eyes, lack of pigment on the body, and the evolution of enhanced sensory systems, particularly on the head, which itself is frequently elongate and shovellike (e.g., Niemiller and Paulson, 2010).

A lack of basic knowledge is nowhere more pronounced than for the species of endemic Malagasy blind gobioids of the genus *Typhleotris*, which are restricted to a vast network of subterranean limestone (karst) habitats in remote arid regions of coastal southwestern Madagascar, as depicted in figure 1 (Sparks, 2003; also see Kiener, 1964). All known blind fishes from Madagascar are members of the suborder Gobioidei; however, there are two independent lineages of cave gobies on Madagascar, including the milyeringid genus *Typhleotris* Petit, 1933, and the gobiid genus *Glossogobius* Gill, 1859. Troglobitic freshwater fishes from Madagascar were first described by M.G. Petit (1933) in his account of *Typhleotris madagascariensis* collected from the Mitoho sinkhole within the Mahafaly Plateau, located to the south of the Onilahy River in southwestern Madagascar, and near the eastern shore of Lake Tsimanampetsotsa (figs. 2, 3). Twenty-six years later Arnoult (1959a) published the description of a second species, *Typhleotris pauliani*, from Grotte d'Andranomaly, located along the coastal plain to the south of Morombe near the town of Andalambezo, well to the north of the Onilahy River (figs. 4, 5). As shown in figures 2, 4, and 6, these two species differ substantially in the morphology and squamation pattern of the head, with *T. madagascariensis* exhibiting a fully scaled head, whereas the head of *T. pauliani* is asquamate (also see Kiener, 1963, and Arnoult, 1959b, for a comparison of the external morphology of these two species; fig. 6). A more recently described species of Malagasy blind goby, *Glossogobius ankaranensis* Banister, 1994, can be easily distinguished from *Typhleotris* by the presence of fused (vs. separate) pelvic fins. Similar to members of the gobioid family Eleotridae, the sister group of Milyeringidae (following the phylogeny of Chakrabarty et al., 2012, which recovered *Typhleotris* as the sister group to the endemic western Australian cavefish family Milyeringidae Whitley, 1945, we herein formally recognize Milyeringidae as comprising *Milyeringa + Typhleotris*), *Typhleotris* possesses separate pelvic fins. *Glossogobius ankaranensis* is restricted to subterranean pools and streams within Ankarana National Park in far northern Madagascar (Wilson et al., 1988; Banister, 1994).

Here we present a taxonomic revision of the endemic Malagasy cavefish genus *Typhleotris*, including diagnoses for all included species based on apomorphic anatomical features, and describe a new species from the coastal plain below the Mahafaly Plateau. This new troglobitic taxon exhibits seemingly contradictory features; the complete loss of eyes and an elongate, shovellike snout, with well-developed sensory canals and pores, typical of subterranean taxa, in combination with uniformly dark pigmentation, which is unique among all known blind troglobitic fishes.

MATERIALS AND METHODS

Collecting localities for the species of *Typhleotris* are listed with coordinates (where available) and brief habitat descriptions under comparative material for each included species. Collections were made using standard caving gear and small hand nets, given that some caves could easily be walked into, whereas others, such as sinkholes, required a more technical approach. The sheer walls of the sinkholes necessitated the use of basic rock-climbing gear for access to the water. All specimens collected were immediately photographed and preserved, including tissue samples for molecular analyses.

Osteological features of the new species and comparative gobioid taxa were analyzed using standard and digital radiographs, high-resolution digital images, via the examination of whole alcohol-preserved specimens, and specimens cleared and stained (C&S) for bone and cartilage (following the protocol of Taylor and Van Dyke, 1985). Point-to-point morphometric measurements were recorded to the nearest 0.1 mm using dial calipers. Counts and measurements follow Sparks and Nelson (2004), unless noted otherwise. For example, vertebral count excludes the ural centrum (i.e., the last half-centrum) and is presented as a total, in contrast to the standard convention for gobioid fishes (e.g., Birdsong et al., 1988). The commonly used abbreviations for standard length (SL) and body depth (BD) are used throughout. Body depth was measured at the origin of the first dorsal fin. Institutional abbreviations are as listed in Leviton et al. (1985) and Sabaj Pérez (2012).

FIGURE ABBREVIATIONS

ach	anterior ceratohyal
brs	branchiostegal rays
cl	cleithrum
dn	dentary
ect	ectopterygoid
fr	frontals
le	lateral ethmoid
me	median ethmoid
mx	maxilla
op	opercle
pal	palatine
pch	posterior ceratohyal
pmax	premaxilla
pt	posttemporal
qu	quadrate
rc	rostral cartilage
sc	supracleithrum
sym	symplectic

SYSTEMATIC ACCOUNTS

Typhleotris Petit, 1933

DIAGNOSIS: Members of Milyeringidae, comprising the subterranean genera *Typhleotris*, endemic to southwestern Madagascar, and *Milyeringa*, endemic to the northwestern cape of Western Australia, are distinguished from all members of their sister group, Eleotridae (except *Oxyeleotris caeca*, endemic to Papua New Guinea) by the complete loss of eyes, the presence of an elongate, shovellike snout, a well-developed system of sensory papillae on the head, and the loss of pigment throughout the body (apart from the new species, which is uniformly darkly pigmented, except for the distal portion of the fins). *Typhleotris* is distinguished from *Milyeringa* by the presence of scales extending onto the head (i.e., at least anteriorly onto the operculum in all species vs. head asquamate in *Milyeringa*), ctenoid scales at some point on the body (vs. cycloid only in *Milyeringa*), a fully scaled ventrum (vs. chest and belly asquamate from just ventral to pectoral-fin insertion laterally, and extending rostrally to anterior margin of chest and posteriorly [although posterior extent of asquamate region is variable] to slightly beyond pelvic-fin origin on ventrum in *Milyeringa*). All species of *Typhleotris* are fully scaled along the ventrum, as well as laterally below the pectoral fin. *Typhleotris* is distinguished from *Oxyeleotris caeca* by the presence of ctenoid scales on the operculum (vs. cycloid in *Oxyeleotris*) and a lower vertebral count (24–26 vs. 28 in *Oxyeleotris*).

TYPE SPECIES: *Typhleotris madagascariensis* Petit, 1933.

INCLUDED SPECIES: *Typhleotris madagascariensis, T. pauliani, T. mararybe,* new species.

Typhleotris madagascariensis Petit, 1933
Figures 2, 6A, 7A, 8A; table 1

LECTOTYPE: MNHN 1933-0060, 43.8 mm SL; Mitoho sinkhole (aven de Mitoho), underground waters in Mahafaly, southwestern Madagascar, coll. Perrier de la Bâthie. Lectotype designated by Bauchot et al. (1991).

NONTYPE COMPARATIVE MATERIALS: AMNH 245603, 1 ex., 44.8 mm SL, Mitoho Cave tourist camp, well at parking lot for Mitoho Cave, Parc National de Tsimanampetsotsa, northeast of Efoetse, 24°02′54.0″S, 043°45′07.6″E, southwestern Madagascar, MAD-6-2008, coll. J.S. Sparks, P.W. Willink, P. Chakrabarty, and S.B. Holtz, 7 June 2008. AMNH 245604, 1 ex., 43.6 mm SL, Andranomalaza (Vintany) sinkhole, Parc National de Tsimanampetsotsa, northeast of Efoetse, 24°02′37.6″S, 043°45′19.6″E, southwestern Madagascar, MAD-5-2008, coll. J.S. Sparks, P.W. Willink, P. Chakrabarty, and S.B. Holtz, 7 June 2008. AMNH 245605, 1 ex., 44.4 mm SL, Andranoilovy (Andranilove) Cave, Parc National de Tsimanampetsotsa, northeast of Efoetse, 24°03′15.9″S, 043°45′42.1″E, southwestern Madagascar, MAD-7-2008, coll. J.S. Sparks, P.W. Willink, P. Chakrabarty, and S.B. Holtz, 7 June 2008. AMNH 245606, 1 ex., 56.7 mm SL, Andriamaniloke Cave, Parc National de Tsimanampetsotsa, northeast of Efoetse, 24°03′15.9″S, 043°45′42.1″E, southwestern Madagascar, MAD-8-2008, coll. J.S. Sparks, P.W. Willink, P. Chakrabarty, and S.B. Holtz, 7 June 2008. AMNH 245607, 1 ex., 51.5 mm SL, data as for AMNH 245603. AMNH 245608, 1 ex., 45.2 mm SL, data as for AMNH 245604. AMNH 245609, 1 ex., 60.4 mm SL, data as for AMNH 245606. AMNH 245610, 2 ex., 39.0–45.0 mm SL, 1 ex. C&S, Mitoho Cave, Parc National de Tsimanampetsotsa, northeast of Efoe-

tse, 24°02′52.1″S, 043°45′11.5″E, southwestern Madagascar, MAD-4-2008, coll. J.S. Sparks, P.W. Willink, P. Chakrabarty, and S.B. Holtz, 7 June 2008. AMNH 245611, 1 ex., 25.4 mm SL, data as for AMNH 245610. AMNH 245687, 1 ex., 44.2 mm SL, data as for AMNH 245604. AMNH 245688, 1 ex., 54.3 mm SL, data as for AMNH 245605. BMNH 1981.11.9.21–22, 2 ex., Grotte de Lelia (Lalia), located north of Itampolo, southwest Madagascar, presented by J. Wilson. MNHN 1963-0174, 2 ex., 51.0–61.4 mm SL, Mikotsy [sic: should be Nikotsy sinkhole], just to the north of Itampolo, southwestern Madagascar, coll. De Saint-Ours. MNHN 1968-0167, 2 ex., 50.3–81.4 mm SL, Tulear (Toliara) (no additional data provided), southwestern Madagascar, coll. A Kiener.

DIAGNOSIS: Distinguished from congeners by the presence of scales extending fully onto the head. Head is more or less fully scaled, including opercle and subopercle, cheek (suspensorium), snout (extent of squamation variable), preorbital and interorbital regions, and nape. *Typhleotris madagascariensis* is further distinguished from the new species by the absence of pigment on the body and fins, a shorter second predorsal length (56.2–64.1 vs. 64.9–69.0 in new species), and a more or less rounded head and snout in dorsal and lateral view (vs. strongly concave/indented in orbital region), and from *T. pauliani* by a pelvic count of I, 5 (vs. I, 4 in *T. pauliani*) and the absence of spines in both the second dorsal and anal fins (vs. single spine present in both fins in *T. pauliani*).

DESCRIPTION: Selected proportional measurements and meristic data presented in table 1. A generally small ($\leq$ ~80 mm SL) and elongate (BD < 23% SL) gobioid, reaching relatively similar adult size as *T. pauliani*, although *T. madagascariensis* has a more elongate and less robust body. Body somewhat wide anteriorly and head dorsoventrally compressed, particularly rostrally. Head appearing smaller and more rounded than in congeners, which might be due to extent of squamation extending fully onto head. Body becoming progressively laterally compressed posteriorly. Caudal peduncle laterally compressed, elongate, and relatively shallow. Eyes lacking entirely, with ctenoid scales covering orbital opening in skull. Snout wide. Snout and anterior portion of head markedly elongate and shovellike, with a bony, armored appearance owing to enlarged sensory canals forming platelike subdivisions. On dorsal, lateral, and ventral sides of head numerous deep canals, lined with small pores. Anterior nostril short, wide, and tubular, located just posterior to upper lip; posterior nostril more or less slit like, but opening rather wide and oval. Lacrimal small, greatly reduced in size. Palatine elongate and very thin. Ventral margins of bones on cheek and operculum lined with densely arrayed short papillae, lending the bones a serrated appearance.

Mouth large, and gape wide. Oral jaw teeth small, conical, and slightly recurved; teeth numerous and arrayed in five or six closely set and irregular rows in anterior portion of mouth, and tapering to fewer rows of teeth posteriorly, as well as medially proximal to synthesis where tooth rows become noticeably constricted in both upper and lower jaws. Teeth present along full length of premaxillary arcade and dentary. Basihyal large, triangular, and fan shaped.

Nine or 10 thin, markedly elongate, medially denticulate, and distally tapering (to a point) gill rakers arrayed along lower limb of first arch. Four epibranchial rakers of similar morphology present on first arch. Gill rakers on arches 2–4 short, robust, and strongly denticulate dorsally; covered apically with short conical teeth. Fifth ceratobranchial elements separate, and densely toothed, as are upper pharyngobranchial toothplates. Fifth ceratobranchial and upper pharyngeal toothplates covered with small, robust conical teeth.

Head fully scaled, including snout (in some individuals scales extend rostrally almost to upper lip, to lateral ethmoid and median ethmoid). Squamation extends rostrally to anterior margin of frontal bones, where scale rows become constricted (narrow) medially. Scales sparsely arrayed over lateral ethmoid and median ethmoid (figs. 2, 6A, 7A, 8A). Laterally, ctenoid scales extend anteriorly over pterygoid elements to posterior portion of elongate, thin palatine. All scales on body and head strongly ctenoid, except on ventrum. Cycloid scales on ventrum extend from around anus and urogenital papilla to anterior margin of chest. Scales on belly and chest highly embedded and difficult to see in preserved specimens (i.e., can easily be seen in C&S individual, AMNH 245610, 39.0 mm SL). Scales on head, opercle, and dorsum strongly ctenoid. Scales becoming increasingly more embedded posteriorly on flank and dorsum, and on caudal peduncle to flexure, such that they may appear cycloid upon casual examination. All fins asquamate, except in some individuals a few scales may extend slightly onto base of caudal fin. Otherwise, body fully scaled to caudal fin, including regions both anterior and medial to pelvic fin. Scales arranged in irregular rows, uneven in size, with smallest on roof of head, and largest on operculum. Pectoral-fin axil and fleshy base asquamate.

It is worth noting that there is some intraspecific variation in scale morphology, as the two individuals from MNHN 1968-167 (50.3–81.4 mm SL, region: Toliara, locality: Tulear [no additional locality data provided], southwestern Madagascar, coll. A. Kiener) appear to have mostly cycloid scales covering the head (some ctenoid scales present on the operculum), whereas in all other available material the head is covered with ctenoid scales. Unfortunately, collection locality information for this lot is lacking, indicating only Tulear (Toliara), the largest city in the general region. These individuals may simply be aberrant in terms of scale morphology on the head, or this variation could be unique to an isolated population.

Two dorsal fins. First dorsal fin with five spines and second dorsal with eight or nine rays. Anal fin with eight rays. Spines lacking in both second dorsal and anal fins, only segmented and branched rays present. Pelvic-fin origin at about level or slightly anterior to vertical through pectoral-fin origin. Dorsal insertion of pectoral fin located just anterior to vertical through posterior margin of operculum. Pectoral fin with 14 to 16 rays. Anus located well anterior to vertical through origin of second dorsal fin. First dorsal fin small, rays feeble, and located at about level of vertical 1/3 distance through adducted pelvic fin. Anal-fin origin located posterior to vertical through origin of second dorsal. Urogenital papilla short, tubular, and narrow, not reaching anal fin when adducted. Pelvic formula I, 5. Pelvic and pectoral fins elongate, with long trailing rays. Pectoral-fin base well developed, portion surrounding proximal radials projecting from body as fleshy appendage. Caudal fin short, fanlike, and rounded distally. Vertebral count 24 or 25.

COLORATION AND PIGMENTATION PATTERN IN LIFE AND ALCOHOL (fig. 2): Body without pigment and uniformly white in coloration. In life, body is relatively translucent, whereas translucency is lost and body becomes an opaque white in alcohol. It is worth noting that all recently collected material is entirely lacking in pigment (e.g., fig. 2B), whereas some historical specimens (MNHN 1963-174, 2 ex., 50.3–81.4 mm SL; fig. 2C) appear to be somewhat light brownish overall. There is no way of knowing, unfortunately, whether this faint pigmentation is simply an artifact of preservation.

ETYMOLOGY: Named by Petit (1933) for the country of origin.

Distribution and Habitat (figs. 1, 3): Restricted to subterranean habitats (caves, sinkholes, wells) within the Mahafaly Plateau karst formation, as well as isolated locations with Eocene limestone along the coastal plain below and to the west of the plateau, to the south of the large Onilahy River drainage basin. The geographic range of *T. madagascariensis* extends from wells near Ambilahilalika (approx. 23°52′S), located about midway between Soalara and Efoetse in the north, southward to Nikotsy sinkhole, located just to the north of Itampolo (24°40′S) (fig. 1). Reports from locals indicate the presence of blind, pigment-free *Typhleotris* southward to just north of the Linta River, which could extend the southern range limit of *T. madagascariensis* if confirmed through additional fieldwork.

Remarks and Comparisons: *Typhleotris madagascariensis* can be distinguished from congeners by the presence of a fully scaled head, whereas both *T. pauliani* and *T. mararybe* have scales extending anteriorly only up to the roof of the head and onto the operculum, not fully covering the cheek and not extending onto the anterior portions of the head, such as the orbital region, snout, and anterior portion of the frontal bones. This species can also be distinguished from congeners by the presence of strongly ctenoid scales on the flank and dorsum (vs. cycloid in congeners).

Whereas all previous accounts in the literature report the presence of an initial spine in the second dorsal and/or anal fins in *T. madagascariensis* (e.g., Petit, 1933 [anal fin only]; Arnoult, 1959a, 1959b [anal fin only]; Kiener, 1963 [both fins]), careful examination of the available preserved material indicates that these elements are not true spines, but segmented rays. *Typhleotris pauliani* does have a single true spine preceding the rays in both the second dorsal and anal fins as previously reported (e.g., Arnoult, 1959a, 1959b; Kiener, 1963).

Typhleotris madagascariensis appears to have a rather widespread range, and is known from several localities throughout the southern portion of the Mahafaly Plateau, south of the Onilahy River, but, unfortunately, the species is not common or abundant anywhere within its range. These cave and sinkhole habitats are fragile and rather ephemeral systems, although most are so isolated that there is little danger from human encroachment. Only the collection localities within Tsimanampetsotsa National Park, including the Mitoho Cave tourist site, Andranomalaza (Vintany) sinkhole, Andranoilovy (Andranilove) Cave, and Andriamaniloke Cave, are afforded any official protection from the Malagasy government, and receive few visitors annually due to their relative inaccessibility.

Typhleotris pauliani Arnoult, 1959
Figures 4, 6B, 7B, 8B; table 1

Holotype: MNHN 1960-0258, 53.6 mm SL, Grotte d'Andranomaly, region of Andalambezo near Moromba, southwestern coastal Madagascar, coll. R. Paulian.

Paratype: MNHN 1960-0259, 1 ex., 42.8 mm SL, data as for holotype.

Nontype Comparative Materials: AMNH 245646, 1 ex., 49.2 mm SL, Andranomahiha Cave, southeast of Andalambezo, 22°17′23.6″S, 043°19′21.7″E, southwestern Madagascar, Mad-12-2008, coll. P. Chakrabarty and P.W. Willink, 11 June 2008. AMNH 245647, 1 ex., 43.7 mm SL, data as for AMNH 245646. AMNH 245648, 1 ex., 42.6 mm SL, data as for AMNH 245646. AMNH 245649, 1 ex., 49.8 mm SL, Safora Cave, southeast of Andalambezo, 22°19′18.4″S,
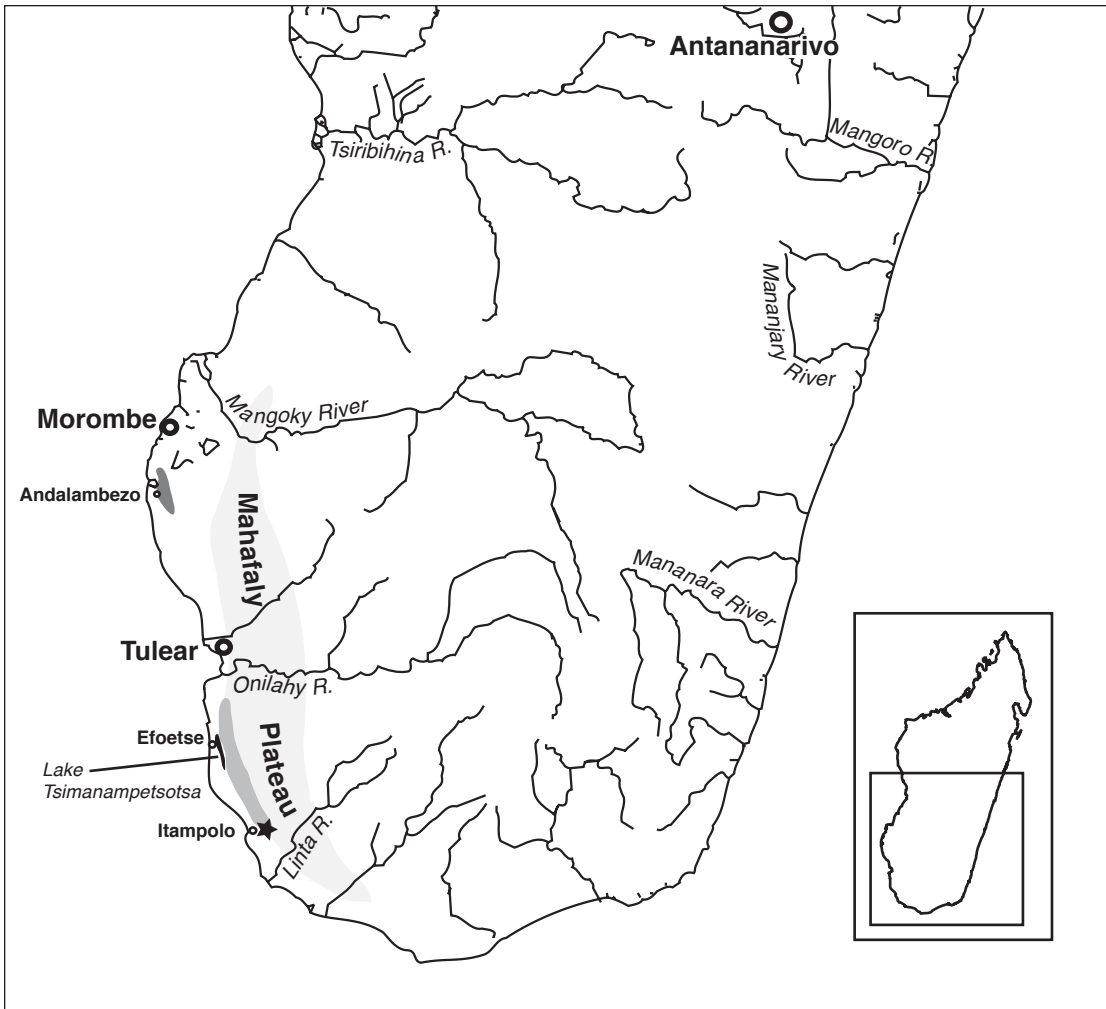
FIGURE 1. Map of Madagascar indicating the approximate geographic ranges for members of *Typhleotris*. The range of *T. madagascariensis*, extending from just north of Efoetse to Itampolo is indicated by medium gray shading, that for *T. pauliani*, in the region of Andalambezo, to the south of Morombe, is indicated by dark gray shading, and the type locality for *T. mararybe*, new species, Grotte de Vitane (Vitany) near Itampolo, is indicated by a black star. Andalambezo is the nearest major town to the type locality of *Typhleotris pauliani*, Efoetse the nearest major town to the type locality of *T. madagascariensis* (Mitoho Cave), and Itampolo the nearest major town to the type locality of *T. mararybe*, new species [Grotte de Vitane (Vitany)]. The approximate extent of the expansive Mahafaly Plateau is indicated in light gray shading.

043°19′22.9″E, southwestern Madagascar, Mad-13-2008, coll. P. Chakrabarty and P.W. Willink, 11 June 2008. AMNH 245650, 1 ex., 35.0 mm SL, Anona "shallow" cave in town of Andalambezo, 22°19′09.9″S, 043°19′21.4″E, southwestern Madagascar, Mad-14-2008, coll. P. Chakrabarty and P.W. Willink, 11 June 2008. AMNH 245651, 2 ex., 59.8–61.4 mm SL, data as for AMNH 245650. AMNH 245652, 1 ex., 41.0 mm SL, data as for AMNH 245650. AMNH 245653, 1 ex., 60.4 mm SL, Andakatomivola Cave, east of Andalambezo, 22°16′40.6″S, 043°19′02.0″E, southwestern Mad-
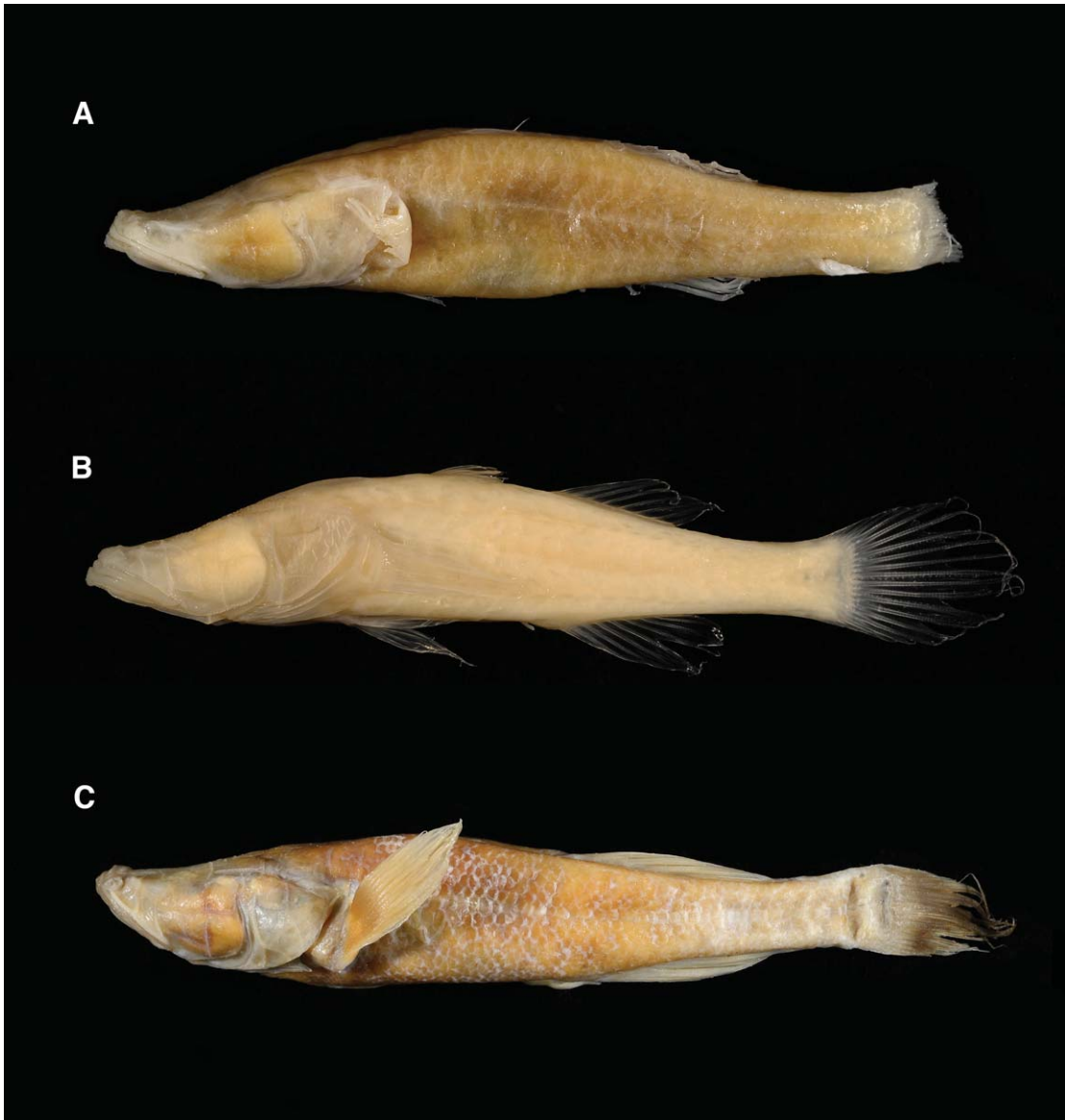
FIGURE 2. *Typhleotris madagascariensis*: **A.** Lateral view of lectotype, MNHN 1933-0060, 43.8 mm SL; Mitoho sinkhole, underground waters in Mahafaly, southwestern Madagascar. **B.** Recently collected specimen, AMNH 245610, from Mitoho Cave, 45.0 mm SL, in northern half of geographic range. **C.** Specimen from southern end of geographic range (Nikotsy sinkhole), near Itampolo, MNHN 1963-174, 61.4 mm SL.

agascar, Mad-16-2008, coll. P. Chakrabarty and P.W. Willink, 11 June 2008. AMNH 245654, 1 ex., 45.3 mm SL, data as for AMNH 245653. AMNH 245655, 1 ex., 44.3 mm SL, data as for AMNH 245653. AMNH 245656, 1 ex., 42.8 mm SL, data as for AMNH 245650. AMNH 245657, 1 ex., 50.3 mm SL, data as for AMNH 245650. AMNH 245658, 1 ex., 43.1 mm SL, data as for AMNH 245650. AMNH 245659, 1 ex., 39.7 mm SL, C&S, data as for AMNH 245650. AMNH 245660, 1 ex., 66.3 mm SL, Anona "deep" cave in town of Andalambezo, 22°19′09.9″S, 043°19′21.4″E, south-
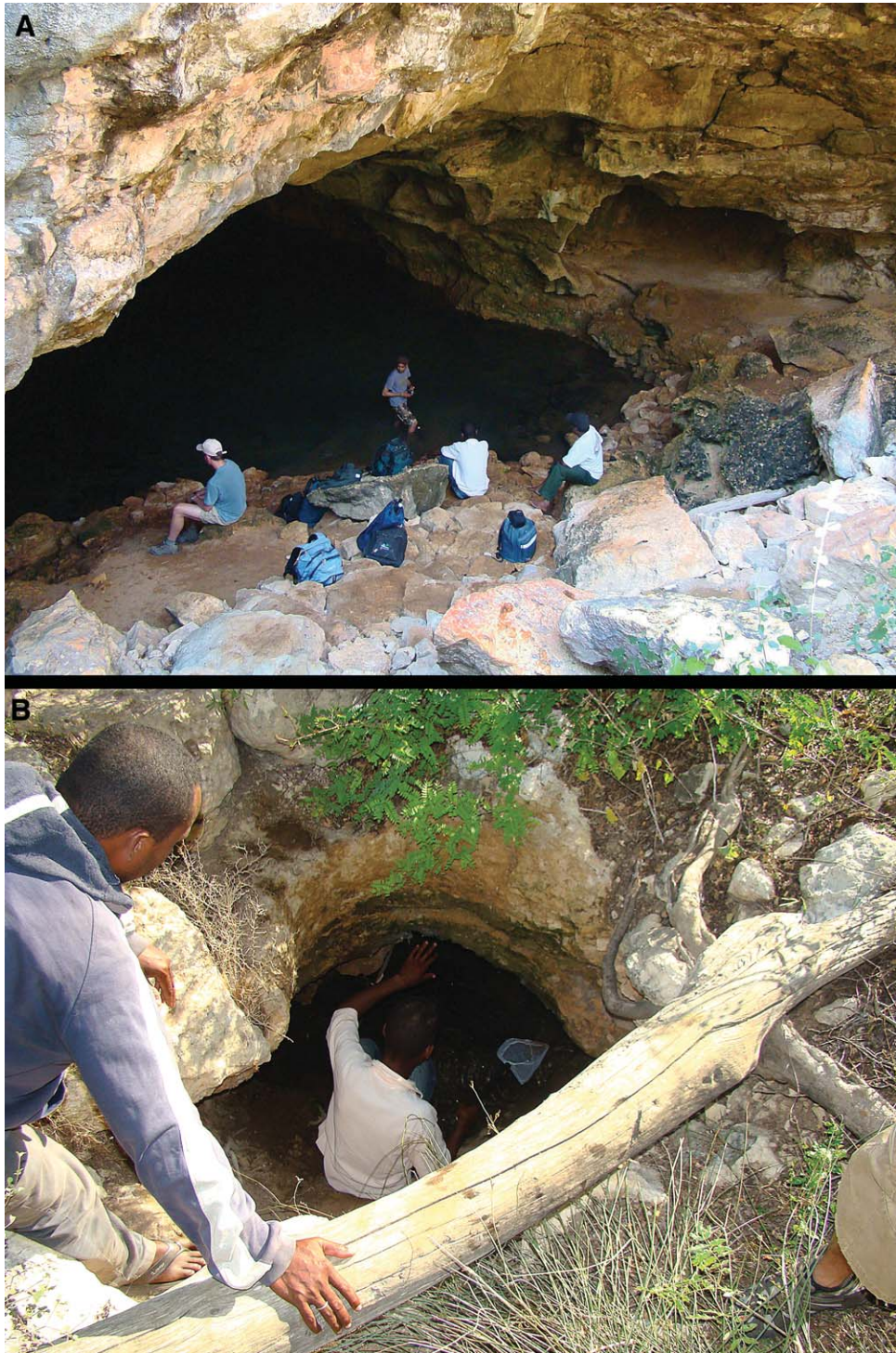
FIGURE 3. **A.** Mitoho Cave, type locality of *Typhleotris madagascariensis*. **B.** Fishing for *T. madagascariensis* in a small well near Mitoho Cave.

FIGURE 4. *Typhleotris pauliani*: **A.** Lateral view of holotype, MNHN 1960-0258, 53.6 mm SL; Grotte d'Andranomaly, Andalambezo region near Morombe, southwestern Madagascar. **B.** Paratype, MNHN 1960-0259, 42.8 mm SL; data as for holotype. **C.** Recently collected specimen, AMNH 245651, 61.4 mm SL; Anona "shallow" cave in town of Andalambezo.

western Madagascar, Mad-15-2008, coll. P. Chakrabarty and P.W. Willink, 11 June 2008. AMNH 245661, 1 ex., 71.2 mm SL, data as for AMNH 245660. AMNH 245662, 1 ex., 53.2 mm SL, data as for AMNH 245646. AMNH 245663, 1 ex., 47.7 mm SL, data as for AMNH 245646. AMNH 245664, 1 ex., 47.3 mm SL, data as for AMNH 245649. AMNH 245665, 1 ex., 44.7 mm SL, data as for AMNH 245649. AMNH 245666, 1 ex., 43.1 mm SL, data as for AMNH 245649. AMNH 245667, 1 ex., 58.6 mm SL, data as for AMNH 245653. AMNH 245668, 1 ex., 47.8 mm SL, data as for AMNH 245653. AMNH 245669, 1 ex., 41.5 mm SL, data as for AMNH 245653. AMNH

FIGURE 5. Cave near type locality of *Typhleotris pauliani*, near the town of Andalambezo, within which the authors collected fresh material.

245670, 1 ex., 55.8 mm SL, data as for AMNH 245653. AMNH 245671, 1 ex., 52.6 mm SL, data as for AMNH 245653. MNHN 1968-0168, 1 ex., 71.4 mm SL, Tulear (Toliara) (no additional data provided), southwestern Madagascar, coll. A. Kiener.

DIAGNOSIS: Distinguished from congeners by the absence of scales on the head, less the operculum (a scaled operculum is common to all species of *Typhleotris*), the presence of single and feeble leading spines in both the second dorsal and anal fins (vs. soft rays in *T. madagascariensis* and *T. mararybe*), a pelvic formula of I, 4 (vs. I, 5 in *T. madagascariensis* and *T. mararybe*), the presence of an enlarged, bony operculum, and an overall more robust and heavier body, particularly in adults. *Typhleotris pauliani* is further distinguished from the new species by the absence of pigment on the body and a longer prepelvic length (34.1%–40.4% vs. 33.0%–33.9% SL in *T. mararybe*), and from *T. madagascariensis* by the absence of ctenoid scales on the flank and dorsum (ctenoid scales present only on operculum in *T. pauliani*), except for a few weak ctenoid scales midflank in some individuals, more or less along the lateral midline.

DESCRIPTION: Selected proportional measurements and meristic data presented in table 1. A robust and deep-bodied (BD > 26% SL) species of *Typhleotris*, growing to roughly similar adult size (>70 mm SL) as *T. madagascariensis*. Body wide anteriorly, particularly posterior to snout, and head dorsoventrally compressed, particularly rostrally. Operculum prominent and angular, yet head overall appearing more fleshy than congeners. Back (spine) appears arched in larger speci-
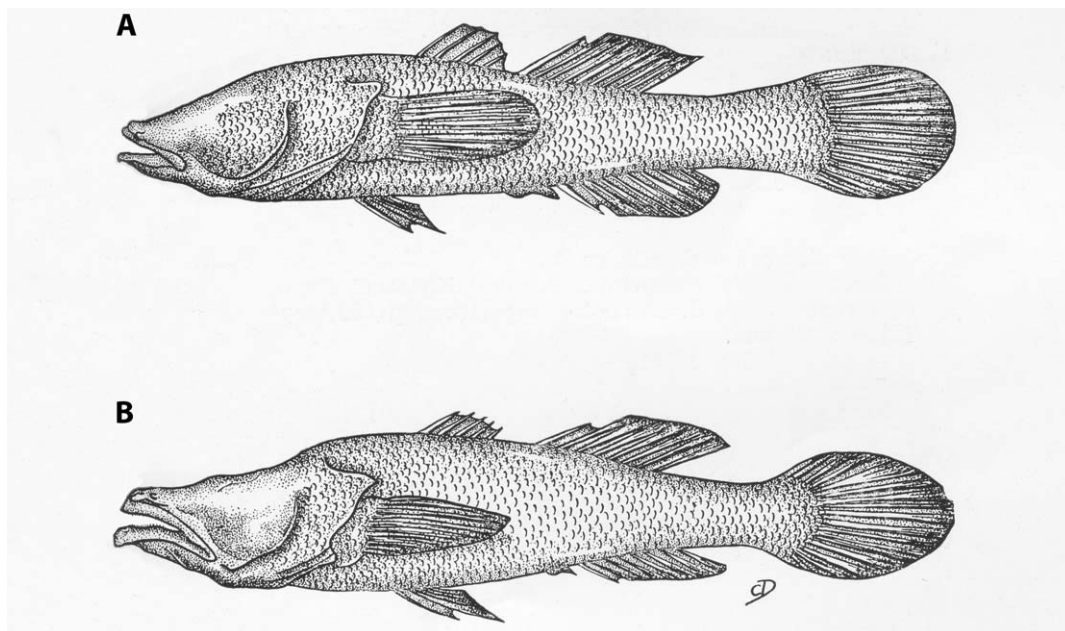
FIGURE 6. Illustration of **A.** *Typhleotris madagascariensis* and **B.** *T. pauliani* after Arnoult (1959b), showing general body and fin shape, as well as differences in extent of head squamation between species.

mens. Snout and anterior portion of head markedly elongate and shovellike (more so than congeners, creating a duck-billed look). Body becoming progressively laterally compressed posteriorly. Caudal peduncle laterally compressed and elongate. No eyes present; however, significant fat deposits present anteriorly over neurocranium, including orbital region. Anterior nostril relatively short, wide, and tubular, located just posterior to upper lip; posterior nostril very short and tubular, not slitlike. Lacrimal small, greatly reduced in size. Palatine elongate and very thin. Numerous deep grooves present on dorsal and ventral side of head; grooves lined with small pores.

Mouth large, and gape moderately wide. Oral jaw teeth small, conical, and moderately recurved; teeth numerous and arrayed in six to eight closely set and irregular rows along anterior portion of jaws, and tapering to fewer rows of somewhat smaller teeth posteriorly, as well as medially proximal to synthesis, where tooth rows become noticeably reduced and constricted, in both upper and lower jaws. Teeth present along full length of premaxillary arcade and dentary. Basihyal large, triangular, and fan shaped.

Gill rakers on lower limb of first arch somewhat thin, elongate, denticulate medially, and tapering distally, yet noticeably more robust and triangular than in *T. madagascariensis,* numbering 10 to 13. Two or three epibranchial rakers of similar morphology present on first arch. Gill rakers on arches 2–4 short, robust, and strongly denticulate dorsally; covered apically with short conical teeth. Fifth ceratobranchial elements separate, and densely toothed, as are upper pharyngobranchial toothplates. Fifth ceratobranchial and upper pharyngeal toothplates covered with small, robust conical teeth.

Head asquamate, except for presence of scales dorsally on posterior portion of neurocranium (figs. 4, 6B, 7B, 8B). Scales extending anteriorly approximately to posterior margin of frontals,

Table 1. Morphometric and meristic data for species of *Typhleotris*. Data corresponding to holotype of *T. mararybe*, new species, in **boldface**. Numbers in parentheses indicate either range (percentages) or number of individuals examined with a particular count (meristics).

	T. mararybe (*n* = 2)	*T. madagascariensis* (*n* = 16)	*T. pauliani* (*n* = 25)
Standard length (mm)	37.9–44.2	24.1–58.3	34.5–70.9
Percentage SL			
Head length (HL)	36.9 (**36.4**–37.5)	37.1 (33.6–39.7)	39.1(36.1–41.4)
Body depth	21.0 (19.8–**22.2**)	19.5 (17.1–22.9)	20.7 (16.3–26.4)
Caudal Peduncle length	25.1 (**23.5**–26.6)	22.5 (17.8–25.9)	22.4(17.2–26.7)
Caudal Peduncle width	3.3 (**2.7**–4.0)	4.9 (3.2–5.9)	5.6 (3.5–7.5)
Caudal Peduncle depth	10.1 (**9.7**–10.6)	9.3 (8.0–10.9)	9.4 (7.0–11.9)
Pectoral-fin length	21.5 (**19.5**–23.5)	23.6 (22.1–28.5)	22.8 (17.1–26.8)
Pelvic-fin length	14.1 (**11.5**–16.6)	15.9 (13.9–20.7)	16.3 (10.2–32.4)
Predorsal 1 length	45.8 (44.3–**47.3**)	44.1 (41.0–47.0)	47.7 (29.1–51.5)
Predorsal 2 length	67.0 (64.9–**69.0**)	61.1 (56.2–64.1)	64.5 (55.7–69.6)
Preanal length	67.7 (**67.6**–67.8)	62.4 (52.1–68.6)	66.1 (62.4–70.6)
Prepelvic length	33.5 (33.0–**33.9**)	35.4 (31.7–38.4)	36.8 (34.1–40.4)
Anal-fin base length	11.1 (**10.9**–11.3)	12.3 (9.5–14.3)	12.8 (8.3–17.1)
2nd Dorsal fin base length	12.7 (**12.0**–13.5)	13.7(11.7–17.8)	15.0 (12.0–21.1)
Percentage HL			
Head width (max)	51.1 (50.1–**52.2**)	49.3 (42.2–56.4)	51.1 (39.2–67.8)
Upper Jaw length	39.7 (**37.9**–41.5)	36.9 (32.5–42.6)	41.4 (38.3–50.2)
Lower Jaw length	56.8 (51.4–**62.1**)	48.5 (41.5–60.1)	52.2 (47.3–60.0)
Counts			
Gill rakers (lower limb)	**9** (1), 11 (1)	9 (2), 10 (1)	10 (1), 12 (1), 13 (1)
Vertebrae	**26** (2)	24 (2), 25 (13)	24 (4), 25 (18)
Dorsal fin 1	**V** (2)	V (16)	V (25)
Dorsal fin 2	**8** (2)	8 (13), 9 (3)	8 (23), 9 (2)
Anal fin	**8** (2)	8 (16)	8 (23), 9 (2)

and also onto operculum. Scales on opercle and subopercle strongly ctenoid, all others on body cycloid, including posterior roof of neurocranium, except for occasional weakly ctenoid scale on midflank (about at midline). Otherwise, body fully scaled to caudal fin, including along ventrum anterior of pelvic fin and on fleshy base of pectoral fin. Scales on ventrum cycloid, not well ossified and strongly embedded; difficult to visualize on whole alcohol-preserved specimens, but can easily be seen in C&S specimen (AMNH 245659, 39.7 mm SL). Pectoral-fin axil asquamate.

It is worth noting that as for *T. madagascariensis*, there is some intraspecific variation in head squamation in *T. pauliani*. The large individual from MNHN 1968-168 (71.4 mm SL, region: Toliara, locality: Tulear [no additional data provided]), also collected by Kiener, has cycloid scales extending anterior of the operculum and onto the cheek in two to four columns, whereas in all other available material, anterior lateral squamation is restricted to the operculum. Unfortunately, collection locality information for this lot is also lacking, indicating only Tulear (Toliara), the largest city in the general region. This individual may simply be aberrant in terms of scale morphology on the head, or this variation could be unique to an isolated population; however, we have no way of verifying given the limited information available for this lot.

Two dorsal fins. First dorsal fin with five weakly developed spines and second dorsal fin with one weak spine and seven or eight segmented, branched rays. Anal fin with one weak spine and seven or eight rays. First dorsal fin small, rays feeble, origin at vertical about 2/3 distance of adducted pelvic fin. Second dorsal-fin origin located at about midpoint of distance between posterior insertion of urogenital papilla and anal-fin origin. Pelvic formula I, 4. Pelvic-fin origin slightly posterior to vertical through dorsal margin of pectoral-fin insertion. Pectoral-fin origin slightly anterior to vertical through posterior margin of opercle. Pectoral base well developed, portion with proximal radials projects considerably from body as fleshy appendage. Pectoral rays 13 or 14. Urogenital papilla robust, relatively short and tubular, not reaching anal fin when adducted in smaller specimens, reaching anal-fin origin in larger specimens ($\geq$ ca. 55 mm SL). Pelvic and pectoral fins elongate and produced, with filamentous trailing rays, particularly in larger individuals. Caudal fin short and moderately rounded on distal end; in larger specimens ($\geq$ ~60 mm SL) caudal becoming more lanceolate in appearance (e.g., fig. 3C). Vertebral count 24 or 25.

Coloration and Pigmentation Pattern in Life and Alcohol (fig. 4): Body without pigment and uniformly white in coloration in all recently collected individuals. In life, body is relatively translucent, whereas translucency is lost and body becomes opaque white in alcohol. As reported above for *T. madagascariensis*, it is worth noting that although all recently collected material is entirely lacking in pigment (e.g., fig. 4C), some historical specimens (MNHN 1968-168, 1 ex., 71.4 mm SL) appear to exhibit a grayish or light grayish-brown coloration in alcohol. Unfortunately, it is impossible to know whether this faint pigmentation was visible in life or is simply an artifact of preservation. The fact that pigmentation is not mentioned in the original description of either *T. pauliani* or *T. madagascariensis* is certainly telling, but inconclusive.

Etymology: Named in honor of the prominent French entomologist and former deputy director of the Institut de Recherche Scientifique de Madagascar, Renaud Paulian, who collected the specimens on which the original description is based and who did much seminal work on western Indian Ocean biogeography (Aberlenc, 2008).

Distribution and Habitat (figs. 1, 5): Restricted to subterranean habitats in coastal regions to the south of Morombe in the vicinity of Andalambezo, extending from about 22°19′S northward to 22°16′S. *Typhleotris pauliani* is restricted to caves and sinkholes to the north of the large Onilahy River drainage. The type locality listed by Arnoult (1959a, 1959b) is "Madagascar Sud Ouest: Morombe, plateau de la baie des Assassins, grottes d'Andranomaly." Goodman and colleagues (personal commun.) have determined the location of the cave that Paulian (1959) explored

at Andalambezo (22°16′S; 43°17′E, cave at 15 m), and from which the type series was collected. Recently, additional specimens, presumably of *T. pauliani* based on digital images, have been collected from caves inland and just south of Andavadoaka (22°04′S) (S. Barley, personal commun.). Based on historical records, the geographic range of *T. pauliani* is considerably more restricted than that of *T. madagascariensis*; however, these new records extend the northern limit of the range of *T. pauliani*, suggesting that the species is more widely distributed.

Remarks and Comparisons: *Typhleotris pauliani* can be distinguished from *T. madagascariensis* by the absence of scales extending onto the anterior portions of the head and snout (*T. pauliani* and *T. mararybe* have scales extending anteriorly only up to the roof of the neurocranium, not extending onto the cheek [suspensorium], except a few rows in rare individuals, or more anterior portions of the head [e.g., snout, orbital region, or anterior portion of frontal bones]; *T. madagascariensis* has a fully scaled head) (figs. 2, 4, 6–7), and by the presence of cycloid scales covering the flank, roof of the neurocranium, dorsum, and posterior portion of ventrum (vs. ctenoid in *T. madagascariensis*). In addition to the lack of pigmentation, *Typhleotris pauliani* can further be distinguished from *T. mararybe* by the presence of a more or less smooth outline of the snout and anterior portion of the head in dorsal view (fig. 7B), versus the head appearing greatly constricted in the orbital region due to enlarged and projecting lateral skull elements (i.e., posteriorly the pterotic and sphenotic, and anteriorly the lateral ethmoid) and a strongly sunken, concave orbital region (fig. 7C). In addition, large individuals of *T. pauliani* ($\geq$ ~60 mm SL) can be distinguished from congeners by more elongate second dorsal and anal fins, and to a lesser degree, caudal fin, with produced and filamentous trailing rays.

Typhleotris mararybe, new species
Figures 7C, 9–10; table 1

Holotype: AMNH 245601, 44.2 mm SL; Grotte de Vitane (Vitany), sinkhole near Itampolo, coastal plain below and to west of Mahafaly Plateau, southwestern Madagascar, 24°42′07.1″S, 043°57′51.3″E, MAD-1-2008, coll. J.S. Sparks, P.W. Willink, P. Chakrabarty, and S.B. Holtz, 5 June 2008. Hologenetypes CytB, COI, and ND1 (following the nomenclature of Chakrabarty, 2010a) are available on GenBank under accession numbers JQ619660, JQ619665, and JQ619670, respectively.

Paratype: AMNH 245602, 37.9 mm SL, data as for holotype.

Diagnosis: The new species is characterized by uniformly dark brown pigmentation throughout the body, and extending onto the fins for 1/3 of their length; only the distal 2/3 of each fin lacks pigment, apart from the dorsal fins, which are dark brown (vs. an all white body and fins in both congeners). In addition, *T. mararybe* can be distinguished from congeners by the presence of prominent and protruding anterior skeletal elements. Protruding lateral ethmoid, sphenotic, and pterotic projections, in combination with a strongly sunken and concave orbital region, lend the head a sculpted and angled bony appearance (vs. relatively smooth and more or less fleshy in congeners), particularly in dorsal view (figs. 7C, 9), a shorter pectoral fin not reaching a vertical through the anus when adpressed (vs. pectoral fin extending to anus in congeners), and an elevated vertebral count (26 vs. 25 or fewer in congeners). The new species is further distinguished from *T. madagascariensis* by the absence of scales fully covering the head (vs. head fully scaled

in *T. madagascariensis*) and a longer second predorsal length (64.9%–69.0% vs. 56.2%–64.1% in *T. madagascariensis*), and from *T. pauliani* by a shorter prepelvic length (33.0%–33.9% vs. 34.1%–40.4% in *T. pauliani*), a pelvic formula of I, 5 (vs. I, 4 in *T. pauliani*), and the absence of a single leading spine in both the second dorsal and anal fins (vs. leading spines present in *T. pauliani*).

DESCRIPTION: Selected proportional measurements and meristic data presented in table 1. Based on the specimens available, a small (<45 mm SL), elongate (BD < 25% SL) and overall thin gobioid. Body wide anteriorly and head dorsoventrally compressed, particularly rostrally. Head bony, and sculpted in appearance, not fleshy, rounded, and smooth. Toothed margins of both upper and lower jaws visible externally when mouth closed. Inside of mouth white. Mouth large, and gape wide. No eyes. Snout and anterior portion of head elongate and shovellike, with a bony, armored appearance, creating a duck-billed appearance. Body becoming progressively laterally compressed posteriorly. Caudal peduncle laterally compressed, shallow, and elongate. Anterior nostril small, tubular, located near upper lip; posterior nostril short, somewhat slitlike and fleshy, but opening more or less oval. Numerous deep canals present on dorsal, lateral, and ventral surfaces of head; canals lined with numerous small pores.

Oral jaw teeth small, recurved, and conical; teeth numerous and arranged in six or seven closely set and irregular rows anteriorly in both
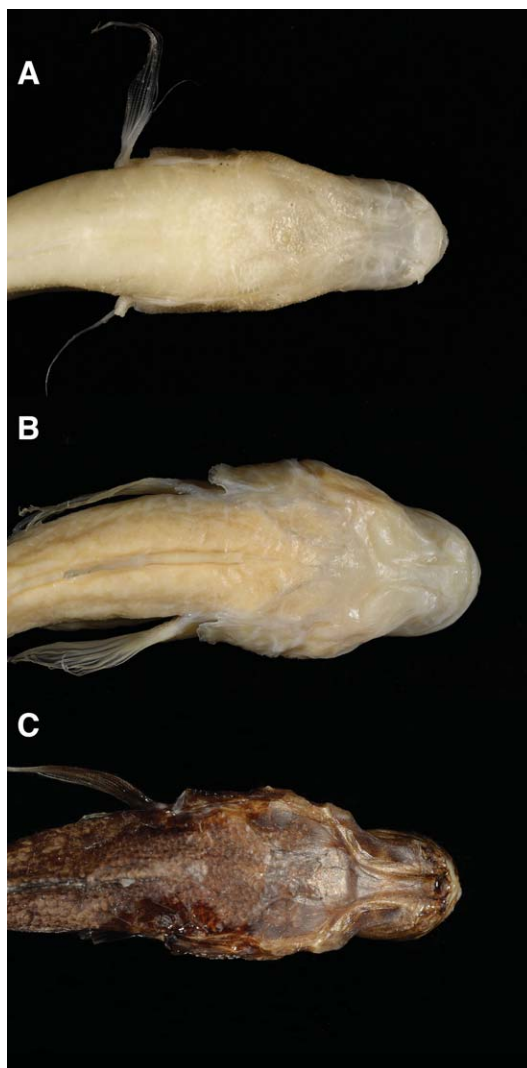

FIGURE 7. Dorsal view of the anterior portion of the head in the three described species of *Typhleotris*: **A.** *T. madagascariensis*, AMNH 245603; **B.** *T. pauliani*, AMNH 245651; **C.** *T. mararybe*, AMNH 245601, holotype.

upper and lower jaws. Teeth tapering to fewer rows of somewhat smaller teeth posteriorly, as well as medially proximal to synthesis, where tooth rows become noticeably reduced in number and constricted, in both upper and lower jaws. Teeth present along full length of premaxillary arcade and dentary. Porelike structures present on basihyal (tongue).

Nine or 11 thin, elongate, triangular, and medially denticulate gill rakers arrayed along lower limb of first arch. Epibranchial rakers on first arch of similar morphology, numbering four in holotype.
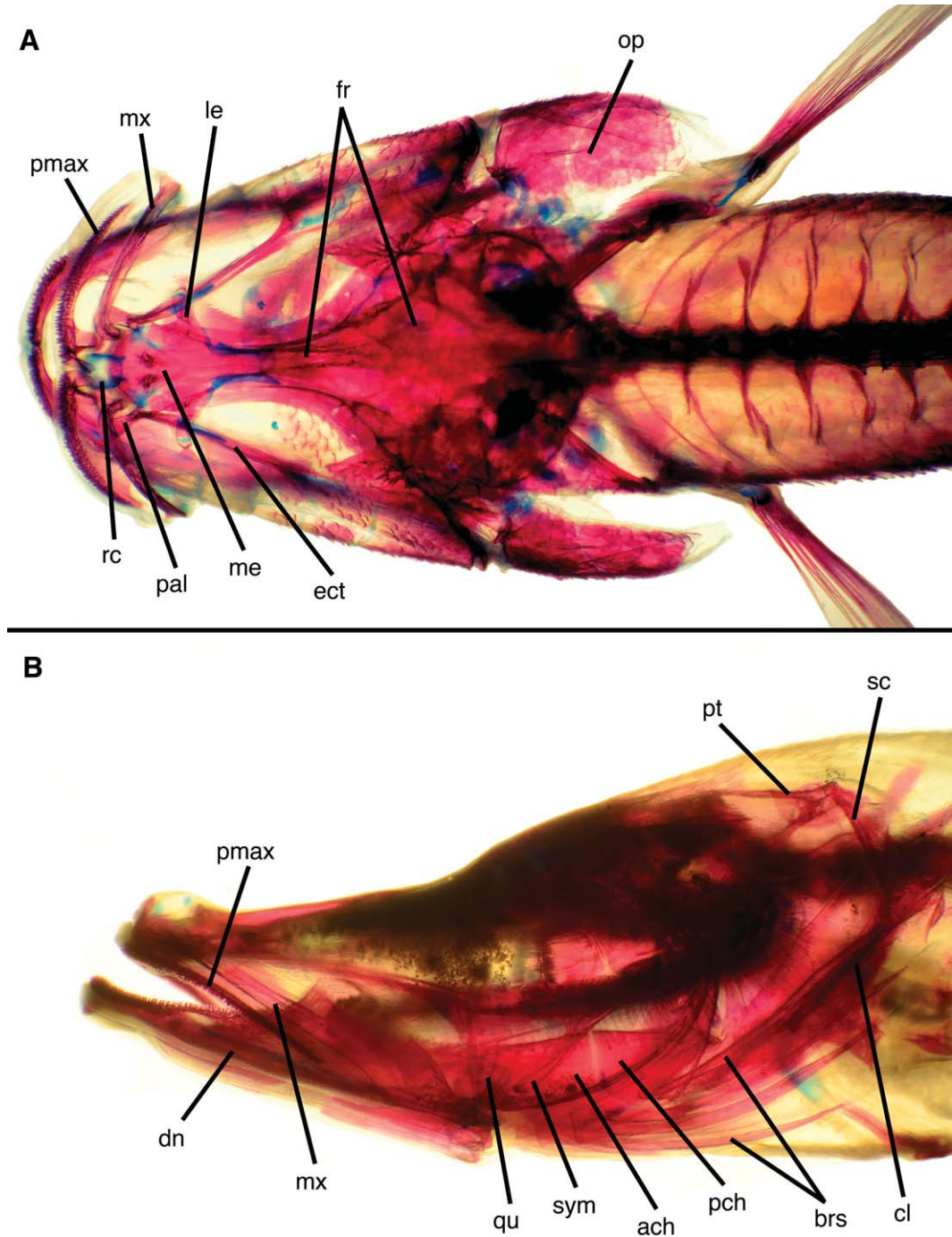
FIGURE 8. Dorsal view of head of cleared-and-stained individuals of: **A.** *Typhleotris madagascariensis*, AMNH 245610, 39.0 mm SL; Mitoho Cave. **B.** *Typhleotris pauliani*, AMNH 245659, 39.7 mm SL; Anona "shallow" cave, Andalambezo. Showing morphology (elongation) of anterior portion of head, snout, and jaws, and anterior extent of squamation on head in *T. madagascariensis*.
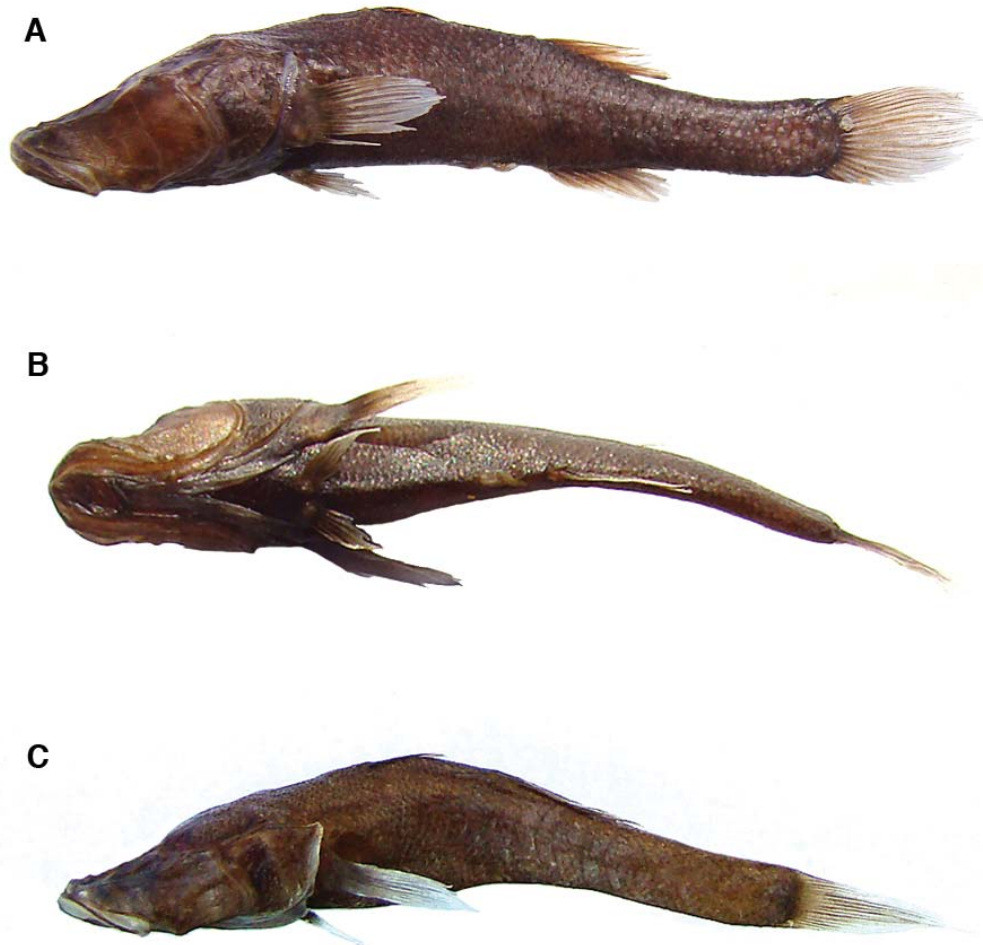
FIGURE 9. *Typhleotris mararybe* photographed in field immediately after collection: **A.** Lateral view of holotype, AMNH 245601, 44.2 mm SL; Grotte de Vitane (Vitany), sinkhole to the east of Itampolo, southwestern coastal Madagascar. **B.** Ventral view of holotype. **C.** Lateral view of paratype, AMNH 245602, 37.9 mm SL; data as for holotype.

FIGURE 10. Holotype of *Typhleotris mararybe*, AMNH 245601, 44.2 mm SL. In preservation.

FIGURE 11. **A.** Type locality for *Typhleotris mararybe*, Grotte de Vitane (Vitany) near Itampolo, southwestern coastal Madagascar. **B.** Snorkeling for the new species in Vitany sinkhole.

Head asquamate, except scales extending anteriorly onto roof of neurocranium and also covering operculum (note: in paratype ctenoid scales extend onto the cheek and comprise about 4–6 columns; no scales extending onto cheek in holotype, i.e., anteriorly terminate on operculum). Although scales on top of head do not extend nearly as far forward as in *T. madagascariensis*, squamation does extend to anterior margin of neurocranium, but scales do not extend anteriorly onto snout (as in *T. madagascariensis*). Otherwise, body fully scaled to the caudal fin, including chest region anterior to the pelvic fin and inner margin of pectoral fin. Cycloid scales present ventrally on chest and belly. Scales cycloid on body, except operculum, which is covered with strongly ctenoid scales. All other scales on body appear to be cycloid. Scales arranged in irregular rows, uneven in size, with smallest on roof of head and largest on operculum. Fleshy pectoral base covered with ctenoid scales. Pectoral-fin axil asquamate.

Two dorsal fins. First dorsal fin with five spines and second dorsal fin with eight rays. Anal fin with eight rays. Pelvic-fin origin anterior to vertical through origin of pectoral fin and slightly anterior to vertical through distal margin of opercle. Pectoral fin with 14 or 15 rays. Anus located anterior to vertical through anterior insertion of second dorsal fin. First dorsal fin small, spines feeble, and located posterior to vertical through pectoral-fin origin. Urogenital papilla small, not reaching anal fin when adducted. Pelvic fin short. Pectoral fin elongate, but not reaching level of urogenital papilla when adducted. In congeners pectoral fin extends well posterior of urogenital papilla when adducted. Caudal fin short and slightly rounded distally. Vertebral count 26.

Coloration and Pigmentation Pattern in Life and Alcohol (figs. 9, 10): Body uniformly dark brown. All fins dark brown proximal to base, whereas distal 2/3 of caudal, pelvic, pectoral, and anal fins depigmented and white. First and second dorsal fins more or less dark brown. In alcohol, the white coloration on the distal portion of the fins becomes an opaque off-white, whereas the dark brown base coloration of the body remains more or less unchanged.

Etymology: From the Malagasy *marary* ("ill or sick"), and *be* ("big"), meaning "very sick" or "big sickness" in reference to the strange debilitating viral illness or "sinkhole fever" members of our team contracted after snorkeling in Grotte de Vitane. The specific epithet, *mararybe,* is to be treated as an adjective.

Distribution and Habitat (figs. 1, 11): The type locality and only known habitat of *T. mararybe* is Grotte de Vitane (S: 24°42′07.1″; E: 043°57′51.3″), which is a sinkhole located near the town of Itampolo on the coastal plain below and to the west of the extensive, more or less north-south running, Mahafaly Plateau. Grotte de Vitane (fig. 11) is a karst formation with nearly vertical walls, whose water level at the time of our survey was approximately 10–15 m below the rim. The diameter of the sinkhole was approximately 100 m across at its widest, and 70 m at its narrowest, with more or less shear walls. The height of the sinkhole walls to the water level was approximately 50 m on its southern end, and much shallower on the northern end (approximately 20 m).

A chain ladder was used to climb down into the sinkhole to access the water where approximately five specimens of the new species were observed (fig. 11B). In a nearly four-hour effort, two of these fish (the holotype and paratype) were captured by the first author using a small

hand net while snorkeling. The two specimens were collected at or near the surface of the water, and dove straight down when approached. Another member of our group (P. Willink, FMNH, now at Shedd Aquarium) was able to observe additional individuals while snorkeling, but no additional specimens could be collected at the time of the survey.

Interestingly, in contrast to most other collection localities for *Typhleotris*, in which the water is generally quite shallow, the water in Grotte de Vitane was uniformly deep. At the time of collection (early June), the water was relatively clear, deep, and warm. Via several dives to inspect the substrate for fishes by the first author, it is estimated that the water level in the sinkhole was about 7.5–10 m deep on average. Although the water was clear, much suspended large particulate material was present in the water column. Apart from the new species of *Typhleotris*, the sinkhole water included an abundance of aquatic invertebrates, including water scorpions (Nepidae), shrimp, and water spiders. It is also interesting to note that all of the specimens observed, including those collected, were swimming in open water within 1–1.5 m of the surface. Upon being chased, all individuals immediately dove toward the bottom.

A portion of Grotte de Vitane is exposed to full sunlight, and there is a short (1 m) under-cut shelf along the otherwise sheer walls that was not directly exposed; however, the dark, subterranean portion of this particular system extended much further than one could snorkel on a breath of air, and remains unknown. Although we only encountered a few individuals in the sinkhole, all were darkly pigmented and blind. Given that portions of the sinkhole receive direct sunlight, possession of uniformly dark brown body coloration may function to camouflage individuals from predators or offer protection from UV radiation.

REMARKS AND COMPARISONS: *Typhleotris mararybe* can be distinguished from *T. madagascariensis* by the absence of scales on the anterior part of the head (compare figs. 2, 6A, and 7A with figs. 7C, and 9–10). Both *T. pauliani* and *T. mararybe* have scales extending only up to the roof of the neurocranium, not fully covering the cheek and orbital region (the paratype of *T. mararybe* and a single individual of *T. pauliani* were observed to possess a few scales on the cheek anterior of the operculum, with scales covering only the posteriormost portion of the cheek), or extending onto the anterior portions of head (i.e., anterior half of frontals or snout); *T. madagascariensis* has a fully scaled head. Although all three described species of *Typhleotris* are scaled along the ventrum anterior to the pelvic fin, these scales are both weakly ossified, compared to other body scales, and highly embedded in both *T. madagascariensis* and *T. pauliani*, making them quite difficult to discern in preserved material.

It is possible that the initial mention of the new species described herein was a consequence of a hydrological survey of the southwestern region of Madagascar (Guyot, 2002). Guyot (2002) notes that he encountered small blind fish, which he determined to be *Typhleotris madagascariensis*, at several locations on the Mahafaly Plateau. In reference to the locality named "F16" in his dissertation and referred to as Vintany sinkhole, Guyot (2002: fig. IV-2 and table IV-2) mentions that the fish appeared within the fluid expelled through drilling efforts. No further mention was made regarding the fish, nor was any description presented. According to information available to us through our guides, however, Vintany sinkhole (S: 24°02′37.6″; E: 043°45′19.6″) is located in the vicinity of Mitoho Cave, near Lake Tsimanampetsotsa and within Parc National de Tsima-

nampetsotsa. Vintany sinkhole did indeed yield depigmented and blind specimens referable to *T. madagascariensis* (table 1). The sinkhole near Itampolo where we collected the new pigmented species is called Grotte de Vitane (Vitany) (S: 24°42′07.1″; E: 043°57′51.3″), which seems to better match the placement of Guyot's (2002) Vintany sinkhole, according to his rather vague maps; however, given the limited data provided, we cannot be certain.

As discussed above, Grotte de Vitane is connected to an underground system of water via subterranean passages, but it is unclear whether the new species survives there. The dark brown pigmentation of *T. mararybe* makes them inconspicuous against the similarly dark background of the sinkhole walls and appears to provide effective camouflage. We hypothesize that the presence of a darkly pigmented blind species in an environment with significant exposure to direct sunlight is the result of this species being derived from a subterranean blind species that invaded this new habitat (Chakrabarty et al., 2012). As with other *Typhleotris*, individuals of the new species are relatively slow swimmers, but reacted quickly, diving toward the bottom when chased by our nets. It should be noted that individuals of *T. pauliani* were observed to move away from an approaching object with much more energy than *T. madagascariensis*.

Notably, Grotte de Vitane is regarded as a sacred site frequented by locals for prayer; the locals are apparently unaware that fish inhabit the sinkhole. Some locals are capable of using tree roots to lower themselves in and out of the sinkhole, but seemingly do this infrequently. For all of the other localities we sampled with cavefishes, local villagers were generally aware of the existence of these populations, which include all known blind fish localities in Madagascar discovered to date.

Both *T. madagascariensis* and *T. pauliani* are listed as "Endangered" in the IUCN Red List of Threatened Species (Loiselle et al., 2004). Accordingly, given the extremely circumscribed distribution of the new species, a single small sinkhole that is easily accessible, coupled with its rarity in that fragile habitat, we believe that *T. mararybe* should also be listed as threatened.

DISCUSSION

Although cavefishes of the genus *Typhleotris* have been known by the scientific community for nearly a century, they have not been studied in any detail with regard to their basic biology, phylogenetic relationships, or species diversity, which is in large part a result of their remote and difficult-to-access subterranean habitats in arid southwestern Madagascar. Although these subterranean systems and their inhabitants, both to the north and south of the Onilahy River, have attracted the interest of biologists since the first half of the last century (Petit, 1933, 1935, 1938; Paulian, 1953, 1955, 1959; Paulian and De Saint-Ours, 1953), there has been little focus on the taxonomy and diversity of the genus *Typhleotris* (e.g., Petit, 1941; Angel, 1949; Sparks, 2003) since its discovery and the description of its two included species. At the time of this field expedition (May-June, 2008), only a handful of specimens had ever been collected (primarily deposited at MNHN, Paris), most with only rudimentary locality data.

The karst formations of the Mahafaly Plateau are Eocene in age, yet much of the coastal plain is younger, comprising Quaternary sandstone (Guyot, 2002). At a few places along the coastal strip, shallow Eocene limestone has been located below Quaternary sandstone. Interestingly,

members of *Typhleotris* appear to be restricted to the older karstic limestone habitats of Eocene age (Guyot, 2002), and do not occur elsewhere in the region. *Typhleotris* have been observed and collected in many (most according to Guyot, 2002) localities with freshwater on the Mahafaly plateau, including wells in the paleovalleys, which are comprised of limestone of Eocene age, and have also been observed along the coastal plain to the west of the plateau in limestone formations of Eocene age (e.g., to the north of Lake Tsimanampetsotsa [= Tsimanampetsotse], in Nikotsy sinkhole located to the north of Itampolo, and in Grotte de Vitane (Vitany), located to the immediate south of Itampolo [Guyot, 2002]), all of which are western outcrops of Eocene-age limestone. For example, Guyot (2002) reports that near Itampolo, where both Nikotsy and Vitany sinkholes are located, there is an area several kilometers long of Eocene-age limestone, similar to that of the sinkholes on the plateau itself that was previously considered to be Quaternary in age.

Based on data presented by Chakrabarty et al. (2012), the new species is recovered as the sister taxon to *T. madagascariensis*. These two species share a pelvic-fin formula of I, 5 (vs. I, 4 in *T. pauliani*) as well as the absence of spines in both the second dorsal and anal fins (vs. leading spine present in both second dorsal and anal fin in *T. pauliani*). In addition, both *T. madagascariensis* and *T. mararybe* exhibit a squamation pattern in which scales extend well onto the head (fully in *T. madagascariensis* and anteriorly to about the midpoint of the neurocranium in *T. mararybe*). This clade is in turn recovered as the sister taxon to *T. pauliani*.

All three species of *Typhleotris* are easily distinguished by squamation pattern on the head and by the morphology of scales on the body. Interestingly, although the type locality of *T. mararybe* is encompassed within the southern extent of the geographic range of *T. madagascariensis*, its squamation pattern on the head and overall scale morphology on the body (i.e., cycloid except on opercle) is nearly identical to that of *T. pauliani*, whose geographic range is far to the north (fig. 1). What also distinguishes this new species from other blind cavefishes is that a significant portion of its only known locality, Grotte de Vitane (Vitany) near Itampolo in southwestern coastal Madagascar, is exposed to full sunlight. Whereas the dark pigmentation of this species is consistent with an exposed habitat, however, the absence of eyes is not. This uniformly dark pigmentation pattern is unlike that of any other known blind subterranean species.

Interestingly, a morphologically very similar genus, *Milyeringa*, is endemic to similar subterranean habitats in northwestern Australia (Humphreys, 2001). Despite the biogeographic implications of this potential transoceanic sister-group relationship for these troglobitic freshwater genera, the phylogenetic affinities of *Typhleotris* and *Milyeringa* have just recently been tested using nucleotide sequence data. *Typhleotris*, endemic to southwestern Madagascar, is recovered as the sister taxon to the endemic subterranean Australian genus *Milyeringa*, which is restricted to similar karst habitats in the arid northwestern cape of Western Australia (Chakrabarty et al., 2012).

Typhleotris can be distinguished from *Milyeringa* by the presence of scales extending onto the head (vs. head entirely asquamate in *Milyeringa*, including operculum), ctenoid scales at some point on the body (vs. cycloid scales only in *Milyeringa*), a fully scaled ventrum (vs. chest and belly asquamate). In *Milyeringa*, there is an asquamate region along the ventrum around the pelvic-fin base, extending rostrally to the anterior margin of the chest and posteriorly to just beyond (although variable) origin of the pelvic fin, and from just ventral to pectoral fin

insertion laterally. All species of *Typhleotris* are fully scaled along the ventrum, as well as laterally on the flank below the pectoral-fin base. Although all accounts in the literature to date (Romero and Vanselow, 2000; Chakrabarty, 2010b) note the absence of a pelvic-fin spine in *Milyeringa*, reporting the count as four rays only, there is, in fact, a rather feeble spine along the leading edge of the pelvic in all specimens examined, such that the formula should be I, 4. Thus, pelvic formula does not distinguish *Milyeringa* from *Typhleotris*. There is frequently also a single leading spine in the anal fin of *Milyeringa*, contrary to the results of prior studies, which report only segmented rays (Romero and Vanselow, 2000).

This notable new species, extraordinary for its uniformly dark pigmentation, in combination with the complete loss of eyes and the presence of other troglobitic anatomical specializations, is unlikely to be the last novel species discovered in this clade. The relative inaccessibility of much of the karst habitat of this lineage is quite challenging for expanding our survey work. Many of the sinkholes are incredibly deep, beyond the reach of all but the most experienced cavers, whereas others are located several days' journey, in a hostile arid climate, by oxcart from the nearest village. Nevertheless, an improved knowledge of the geology of these arid regions (e.g., Guyot, 2002) will surely facilitate the discovery of additional members of the genus.

COMPARATIVE MATERIALS

Milyeringa brooksi: WAM P28330-001, 1 ex., Pilgonaman Well, Western Australia, 8 July 1984; LSUMZ 13637, 1 ex., Pilgonaman Well, Western Australia, 21 May 2009; WAM P29242, 2 ex., 19 May 1983.

Milyeringa veritas: AMS IB.4481, 1 ex., Yardie Creek Station, Western Australia, May 1959; AMS I.2.1336-001, 4 ex., Milyering Well, Western Australia, Aug. 1963; AMS I. 20832-001, 5 ex., Northwest Cape, Western Australia, 13 Feb. 1979; AMS I.25504-001, 3 ex., south of Mangrove Bay, 13 Sept. 1985; AMS I.25502-001, 4 ex., 5 km south of Osprey Bay, 11 Sept. 1985.

Glossogobius ankaranensis: BMNH 1994.12.1.1, holotype, Ankarana Réserve Spéciale, northern Madagascar, coll. J. Wilson, 1 Jan. 1986; BMNH 1994.12.1.2, 1 ex., paratype, Ankarana (National Park), northern Madagascar, coll. J. Wilson, 1 Jan. 1986. AMNH 245679, 1 ex., Napolean Cave, 2 km from American campground, Ankarana National Park, northern Madagascar, Mad-25-2008, P. Chakrabarty and S.B. Holtz, 20 June 2008. AMNH 245680, 1 ex., data as for AMNH 245679. AMNH 245681, 1 ex., data as for AMNH 245679. AMNH 245682, 1ex., data as for AMNH 245679. AMNH 245683, 1 ex., data as for AMNH 245679. AMNH 245684, 1 ex., data as for AMNH 245679. AMNH uncat., 6 ex., cave within Ankarana karst formation, Ankarana National Park, northern Madagascar, Mad 11-13, J.S. Sparks, R.C. Schelly, Z.H. Baldwin, and C.B. Braun, June 2011. AMNH uncat., 5 ex., cave within Ankarana karst formation, Ankarana National Park, northern Madagascar, Mad 11-20, J.S. Sparks, R.C. Schelly, Z.H. Baldwin, and C.B. Braun, June 2011. AMNH uncat., 2 ex., large, deep subterranean pool within Ankarana karst formation, Ankarana National Park, northern Madagascar, Mad 11-21, J.S. Sparks, R.C. Schelly, Z.H. Baldwin, and C.B. Braun, June 2011.

Glossogobius, n. sp. (subterranean): AMNH 245685, 1 ex., Napolean Cave, 1 km from American campground, Ankarana National Park, northern Madagascar, Mad-29-2008, P.

Chakrabarty and S.B. Holtz, 22 June 2008. AMNH 245686, 1 ex., data as for AMNH 245685. AMNH uncat., 1 ex., large, deep subterranean pool within Ankarana karst formation, Ankarana National Park, northern Madagascar, Mad 11-21, J.S. Sparks, R.C. Schelly, Z.H. Baldwin, and C.B. Braun, June 2011.

Glossogobius, n. sp.: AMNH uncat., 1 ex., stream outside Ankarana karst formation, Ankarana National Park, northern Madagascar, Mad 11-14, J.S. Sparks, R.C. Schelly, Z.H. Baldwin, and C.B. Braun, June 2011. AMNH uncat., 2 ex., Milantety Cave, Ankarana karst formation, Ankarana National Park, northern Madagascar, Mad 11-15, J.S. Sparks, R.C. Schelly, Z.H. Baldwin, and C.B. Braun, June 2011.

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