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LUNGFISH BURROWS FROM THE UPPER CRETACEOUS MAEVARANO FORMATION, MAHAJANGA BASIN, NORTHWESTERN MADAGASCAR

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ABSTRACT

An assemblage of large-diameter vertical burrows interpreted as lungfish estivation burrows is documented from the Upper Cretaceous (Maastrichtian) Maevarano Formation of northwestern Madagascar. These burrows suggest that lungfish were present in the Maevarano Formation paleofauna, and they are the first lungfish estivation burrows described from the rock record of Gondwana. Over 100 large-diameter burrows penetrate a pervasively cross-stratified fluvial sandstone body intercalated near the top of the Masorobe Member. The surface of this sandstone body was mapped and 74 burrows were documented in an area spanning ~110 m². Burrows cut through and deform surrounding foreset laminae, and in some cases impact surrounding strata up to 8 cm from the edges of individual burrows. In map view, the burrows exhibit three distinctive morphologies: circular, elliptical, and figure-eight shaped. These three map view cross sections are very similar to the modern burrow morphology of the African lungfish *Protopterus* when its burrow is exhumed along its full vertical expanse. Combined, these transverse-section views provide indication of lungfish estivation, and they are supplemented by several additional key characteristics, including spatial clustering (reflecting gregarious behavior), possible fin traces, and oxidized burrow margins. The localized occurrence of 100+ lungfish estivation burrows is consistent with previous reconstructions that posit a dryland paleoenvironment with a markedly seasonal wet-dry climate for the Maevarano Formation.

INTRODUCTION

The Upper Cretaceous (Maastrichtian) Maevarano Formation (Mahajanga Basin, northwestern Madagascar) is renowned for its exceptional preservation of vertebrate body fossils. Previously documented terrestrial and freshwater groups recovered from the unit include ray-finned fishes, anurans, turtles, snakes, nonophidian squamates (lizards), crocodyliforms, birds, dinosaurs, and mammals (Krause et al., 2006). Despite an abundant skeletal record that includes fish, lungfish have not been previously reported from the Maevarano Formation. This absence is somewhat puzzling because toothplates of ceratodontid lungfish have been recovered from the underlying Marovoay and Ankazomihaboka beds (Martin, 1981), and the aquatic paleoenvironments that lungfish inhabit are well represented in the Maevarano Formation.

In this report we describe the first large-diameter vertical trace fossils interpreted as lungfish burrows from the Maevarano Formation, and in doing so provide evidence that lungfish were members of the Maevarano Formation paleofauna. These same trace fossils also represent the first documented record of fossil lungfish burrows in the rock record of Gondwana. The large sample of lungfish burrows described includes a wide variety of morphologies and exposure views that closely parallel those documented for modern African lungfish (Johnels and Svensson, 1954). Moreover, the lungfish burrows described in this report occur in pervasively cross-stratified fluvial sandstone beds as opposed to massive mudstones or siltstones typical of most previous reports. This occurrence affords a uniquely informative view of lungfish bioturbation and expands the morphological inventory of lungfish burrows documented in the rock record.

LOCALITY AND METHODS

This ichnologic study is based on a sample of 132 large-diameter burrows exposed on bedding planes and, more rarely, in longitudinal cross sections in the Befandrama study area, which is located ~14 km northeast of the village of Berivotra, in northwestern Madagascar (Fig. 1). The majority of the burrows described herein are clustered in one locality (15°47′28.5″S, 46°40′25.7″E), although several additional burrows were documented within ~1 km of the main fossil locality. Most burrows occur in the Masorobe Member of the Maevarano Formation (Figs. 1–2), with the main burrow assemblage localized in a 1-m-thick sandstone body positioned ~5 m beneath the top of this member. The surface of the sandstone body hosting the clustered burrow assemblage was mapped with a 10-cm scale grid, and 74 burrows were documented in an area spanning ~110 m² (Fig. 3). Each burrow trace included on the map was numbered, photographed, and described in detail. Two burrows from the Masorobe Member were sampled for petrographic analysis, and thin sections were studied to discern any distinctions between burrow infills, burrow margins, and surrounding sedimentary rock. Several additional burrows were documented at the base of the overlying Anembalemba Member. Three detailed stratigraphic sections were measured to document the facies relations of the main burrow assemblage, and an additional section was measured to place the locality in overall stratigraphic context.

GEOLOGICAL SETTING

Rogers et al. (2000) described and formalized the Maevarano Formation, and subdivided the unit into three members, all of which crop out in the Befandrama study area. The basal Masorobe Member is ~80 m thick in its stratotype in the nearby Berivotra study area (Fig. 1), although its base is not exposed in Berivotra or Befandrama and, thus, its full thickness has not been ascertained. The Masorobe Member in Befandrama is characteristically pale red to gray in weathered exposures, and consists of coarse-grained, poorly sorted, clay-rich sandstone intercalated with thinner beds of claystone and siltstone. Evidence of pedogenesis in the unit includes color banding, superbly developed rhizoliths (with drab root halos and calcareous encrustations), pedogenic carbonate nodules, and slickensides (Rogers et al., 2000). The majority of the burrows described here (n = 120) are hosted by fluvial sandstone bodies in the upper 5 m of the Masorobe Member. The coarse-grained, poorly sorted, clay-rich sandstone body that preserves ~100 of these burrows ranges from ~1 to 3 m thick, and exhibits medium- to large-scale trough cross-stratification. Paleocurrents derived from exhumed trough axes trend to the northeast (13°, n = 36). Stringers of claystone pebbles mark some set boundaries, and drape the basal contact of this sandstone bed (Fig. 2).

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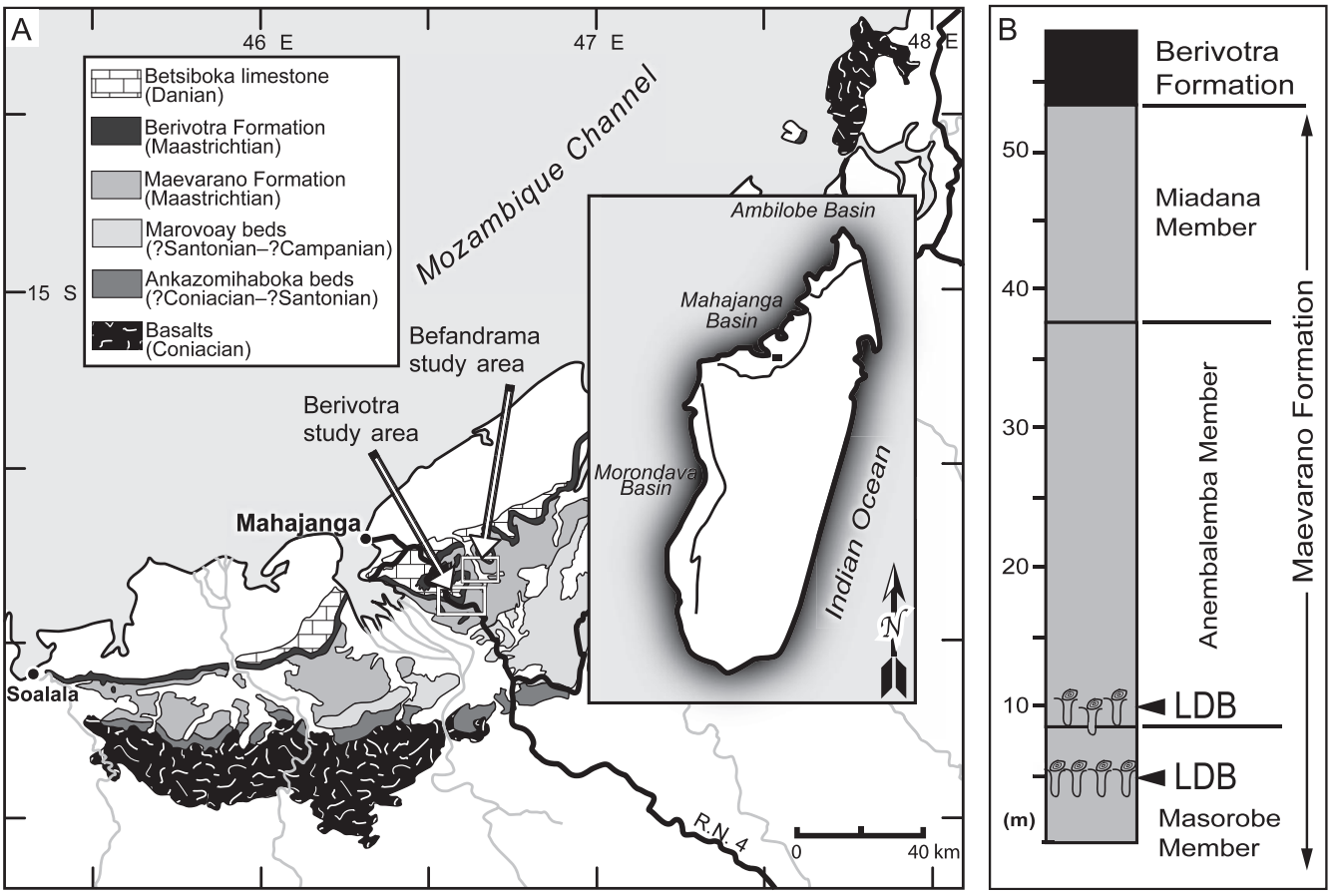

FIGURE 1—Regional stratigraphy and local section in Befandrama study area. A) Outcrop map of Upper Cretaceous and Tertiary strata and associated volcanic rocks in Mahajanga Basin of northwestern Madagascar, with locations of Befandrama and Berivotra study areas. Lungfish body fossils are known from the Marovoay and Ankazomihaboka beds, which underlie the Maevarano Formation. B) Schematic section of the Maevarano Formation in the Befandrama study area illustrating stratigraphic position of lungfish trace fossils described in this report. Only the upper ~10 m of the Masorobe Member are exposed in the study area. LDB = large-diameter burrows.

The Anembalemba Member caps the Masorobe Member throughout the exposure belt. In the Berivotra study area, the stratotype of the Anembalemba Member spans ~13 m. In the Befandrama study area, the Anembablemba Member attains a thickness of ~28 m. Rogers et al. (2000) recognized two predominant facies, designated facies 1 and facies 2, within the Anembalemba Member. Facies 1 consists primarily of light-colored, poorly sorted sandstones characterized by medium- to large-scale tabular and trough cross-bedding indicative of stream flow. Facies 2 is also comprised of poorly sorted sandstones, but they are greenish in color, have a much larger clay fraction, and are generally massive in structure. Rogers (2005) interpreted facies 2 as debris flow deposits related to torrential rainfall events that eroded sediments from nearby weathered basalts and the surrounding alluvial plain. Vertebrate fossils are remarkably abundant and exquisitely preserved in the Anembalemba Member, and are most common in facies 2. Twelve large-diameter burrows were documented in the basal 1 m of the Anembalemba Member in the Befandrama study area within a coarse-grained, poorly sorted sandstone bed that exhibits abundant small- to medium-scale cross-stratification. Some of these burrows penetrate the basal contact and extend into bioturbated facies of the underlying Masorobe Member.

The Miadana Member, initially described and heretofore only known from the Miadana Hills in the Berivotra study area (Rogers et al., 2000), consists of a mix of fine- to coarse-grained lithologies including claystone, siltstone, and sandstone. Unlike the underlying Anembalemba and Masorobe members, the Miadana Member is generally not well exposed and, to date, has not yielded abundant vertebrate fossils. Rogers et al. (2000) interpreted this unit to have accumulated in low-energy settings (e.g., sluggish rivers and associated floodplains) on the lower coastal plain. Approximately 16.5 m of the Miadana Member are exposed in the Befandrama study area. Deposits of the Miadana Member are sharply overlain by ~40 m of the Berivotra Formation (Maastrichtian), which accumulated on a clastic marine shelf. The Berivotra Formation is in turn capped by jumbled blocks of the Paleocene Betsiboka limestone (Rogers et al., 2000), which is also of marine origin.

Physical stratigraphic correlation of the Miadana and Anembalemba members of the Maevarano Formation with biostratigraphically zoned marine strata of the Berivotra Formation indicates that the Maevarano Formation is, at least in part, Maastrichtian in age (Besairie, 1972; Rogers et al., 2000; Gottfried et al., 2001; Abramovich et al., 2002; Rahantarisoa, 2007). The age of the Masorobe Member remains enigmatic, because there is presently no way to ascertain the location of the Campanian-Maastrichtian boundary in the local section. Despite many published reports that propose a Campanian or older age for the Maevarano Formation (e.g., Hoffstetter, 1961; Besairie, 1972; Russell et al., 1976; Obata and Kanie, 1977; Buffetaut and Taquet, 1979; Krause and Hartman, 1996; Papini and Benvenuti, 1998; Masters et al., 2006), there are simply no data at present that justify this interpretation. For this reason, we conclude that the burrows described in this report, which are known from both the Masorobe and Anembalemba members, are likely Maastrichtian in age (Rogers et al., 2007; Krause et al., 2010).

BURROW DESCRIPTIONS

The large-diameter burrows hosted within the Masorobe Member in the Befandrama study area are readily distinguished in longitudinal views (Fig. 4A). These nonbranching burrows are comprised of

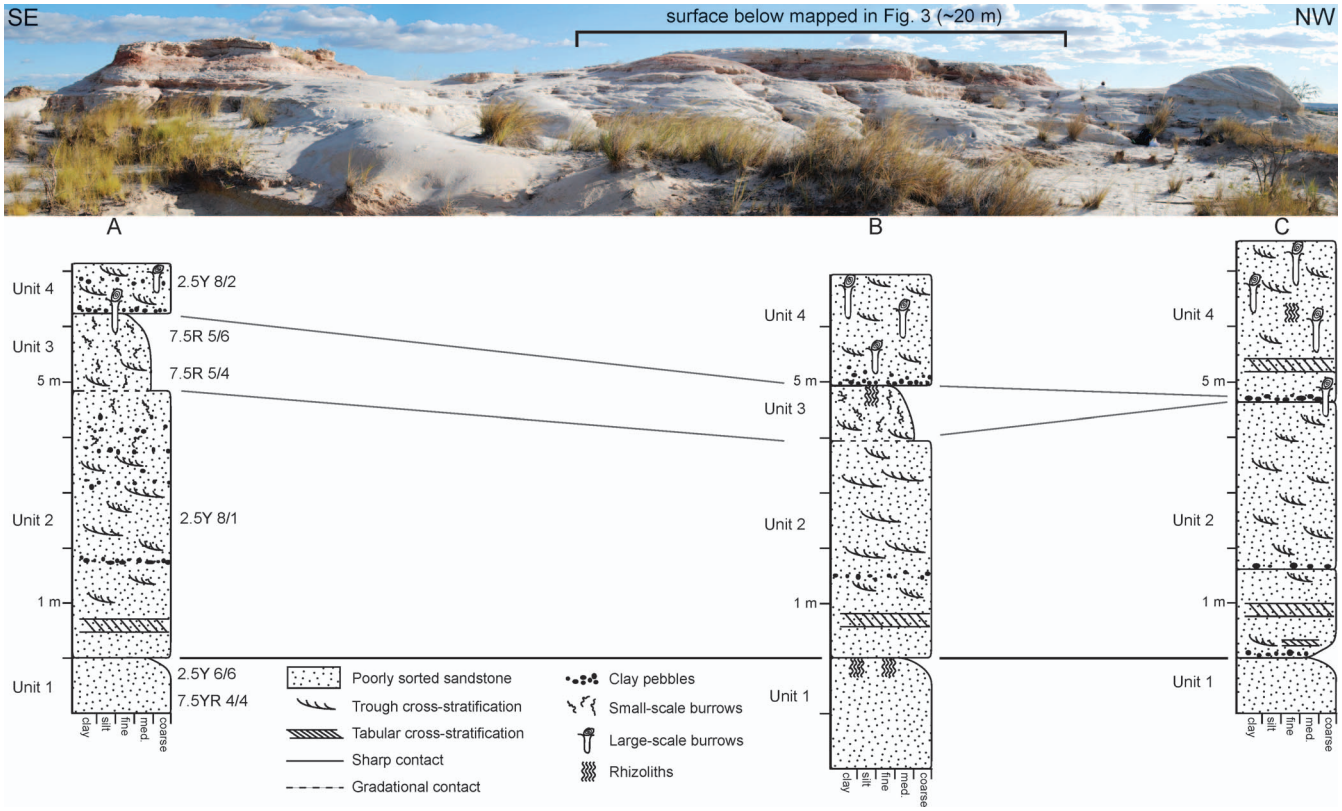

FIGURE 2—Exposures of the Masorobe Member that preserve abundant large-diameter burrows in the Befandrama study area (15°47′28.5″S, 46°40′25.7″E), with corresponding stratigraphic sections (labeled A, B, and C). Section B intersects the mapped surface (under bracket) detailed in Figure 3. Section C intersects outcrop that preserves the eight documented burrow longitudinal views illustrated in Figure 4A. The fluvial sandstone body that hosts the assemblage of large-diameter burrows (unit 4 in sections) truncates underlying beds as it thickens to the northwest.

subvertical cylinders with generally smooth walls, massive fills, and weathered or buried terminations. Penetration depths range from 15 to 60 cm, with an average of 34 cm (n = 9), although these are underestimates because the upper surfaces of burrows have been exhumed by erosion, and terminations are difficult to identify in our limited sample of longitudinal views. Channel diameters of the burrows exposed in longitudinal view range from 5 to 11 cm and average 7 cm. Along a single lateral transect, most burrows are spaced 40–50 cm apart, with a range of 20–76 cm between burrows. Burrows cut through and deform surrounding foreset laminae of clay-rich, coarse-grained sandstone (Fig. 4B), and in some cases impact surrounding strata up to 8 cm laterally from the edges of individual burrows, causing up to 15 cm of vertical deflection in a downward direction. Multiple burrows deflect stringers of cm-scale oxidized claystone pebbles, and one burrow exhibits an abrupt bend that coincides with its intersection with a stringer of red claystone pebbles (Fig. 4C).

Twelve additional large-diameter burrows are exposed in longitudinal view in a single outcrop at the base of the overlying Anembalemba Member. These burrows, which are spaced ~20–40 cm apart along a single lateral transect, have channel diameters and penetration depths comparable to the burrows described above from the Masorobe Member. They are generally vertical, with the upper channels of four of the twelve burrows subvertical in orientation. These burrows exhibit a greenish massive sandstone fill that is distinct from the light gray cross-bedded sandstone beds that host the burrows, and they cut through and deform surrounding foreset laminae in an identical manner to burrows in the Masorobe Member. Burrows that intersect the underlying Masorobe Member deform the contact between members, and disturb the bedding up to ~50 cm beneath the contact (Fig. 5).

In map view, the large-diameter burrows intercalated in the Masorobe Member exhibit three predominant morphologies: circular (Figs. 6A–B), elliptical (Figs. 6C–D), and figure-eight shaped (Figs. 6E–F). Edges of the burrows typically exhibit oxidized margins, or differential weathering, with a raised coarse-grained burrow margin. Many burrow cross sections are marginally depressed or raised relative to the surrounding matrix, with dark weathering rinds present in 21 of 74 cases (e.g., Fig. 6A). The oxidized margins that characterize some burrows cannot be distinguished from the surrounding matrix in thin section. The circular burrow cross sections (n = 3) have channel diameters of 10–15.7 cm, with an average of 13 cm (standard deviation of 2.5 cm). The elliptical burrow cross sections (n = 57) have major axis diameters of 9–26 cm, averaging 16.1 cm (standard deviation of 4.1 cm), and minor axis diameters of 5–15 cm, averaging 11 cm (standard deviation of 2.5 cm). The average ratio of the minor to major axes is 0.7. The figure-eight–shaped burrow cross sections (n = 14) resemble two overlapping ellipses. They have major axis diameters of 12–29 cm, averaging 18.8 cm (standard deviation of 3.8 cm), and minor axis diameters of 7.5–15 cm, averaging 10.6 cm (standard deviation of 2 cm). The average ratio of minor to major axes is 0.6 (see Table 1). One circular burrow cross section with a 10 cm diameter also exhibits two 1 cm projections spaced 7.5 cm apart in one hemisphere of the burrow (Fig. 6B).

The Masorobe Member in the Befandrama study area also exhibits smaller-scale trace fossils in beds that underlie the main burrowed stratum. Several vertical and U-shaped tubes ~10–30 cm deep with diameters of 0.5–1 cm crop out in a cross-bedded fluvial sandstone body ~2 m beneath the unit that hosts the clustered large-diameter burrows (Figs. 7A–B). These ichnofossils exhibit green, clay-rich passive fill and resistant entrances and exits that protrude a few mm above bedding planes. They are identified as *Arenicolites*, and presumably reflect the activity of insect larvae (Hasiotis, 2002; Buatois and Mángano, 2004). Additional small-scale ichnofossils consisting of

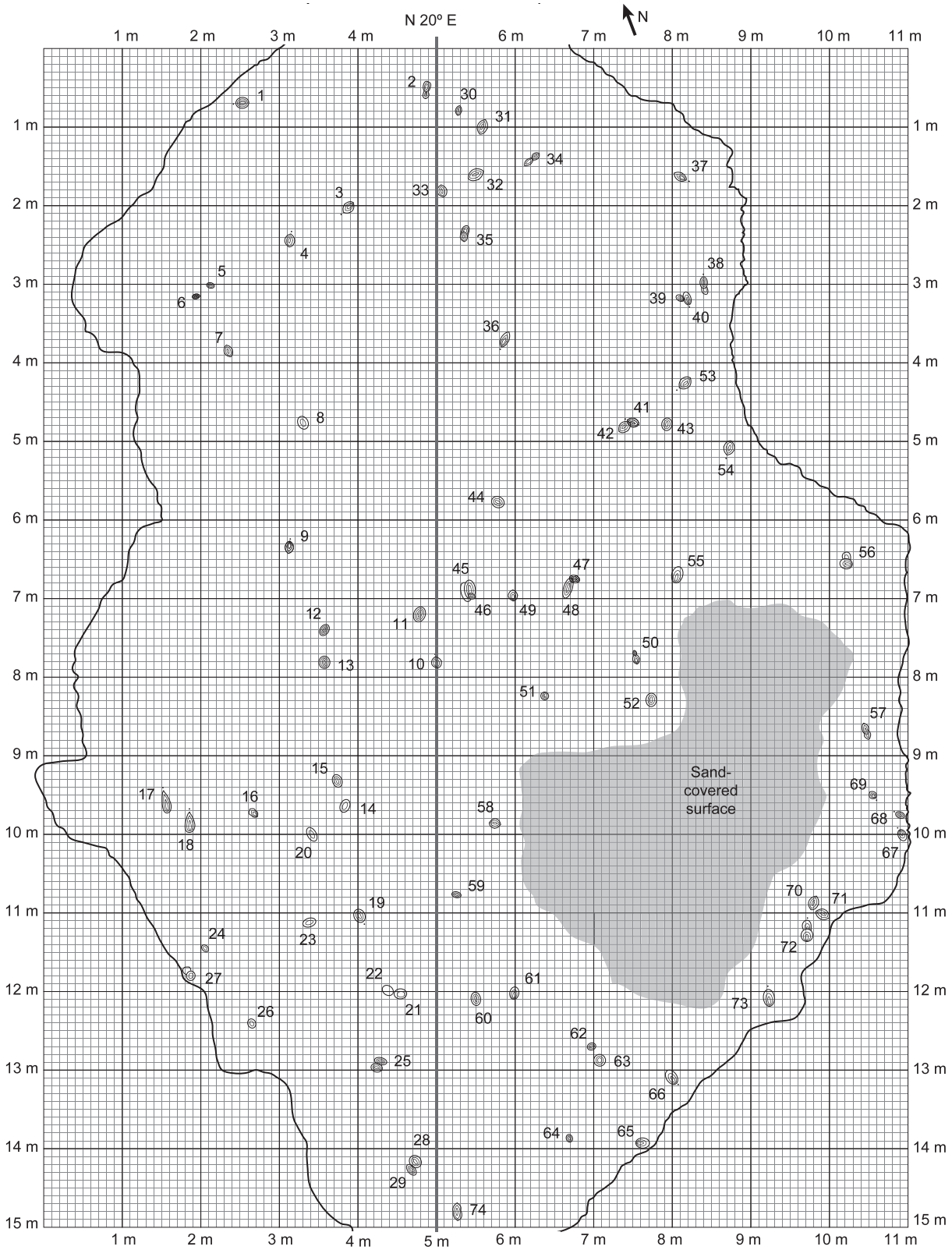

FIGURE 3—Map of large-diameter burrows (area under bracket in Figure 2). Large-scale grid has 1 m increments, with finer scale 0.10 m divisions. Circular, elliptical, and figure-eight burrow cross-section morphologies are mapped in their accurate orientations.

FIGURE 4—Longitudinal views of large-diameter burrows in the Masorobe Member in the Befandrama study area. A) Outcrop of cross-stratified fluvial sandstone with arrows indicating locations of large-diameter vertical burrows. B) Exhumed vertical exposure showing deflected laminae adjacent to burrow. C) Longitudinal view of burrow with sharp bend coinciding with an oxidized clay pebble stringer. Deflected laminae are visible near the base of this burrow.

dark red, subvertical to subhorizontal burrows 0.5–1 cm in diameter and 2–10 cm long are prevalent in the oxidized paleosol intercalated between these two fluvial sandstone bodies (Fig. 7C). The tracemaker of these burrows is unknown.

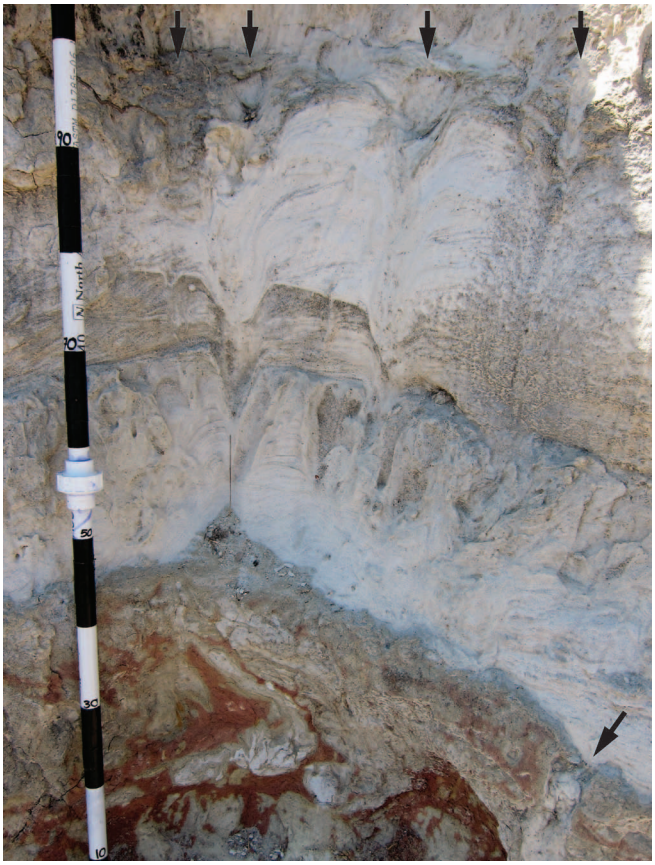

FIGURE 5—Longitudinal views of large-diameter burrows in the Anembalemba Member in the Befandrama study area. Burrows, indicated by arrows, penetrate through the basal meter of the Anembalemba Member (additional burrow and location of contact between members is indicated by arrow in lower-right corner). Cross-stratified beds of facies 1 of the Anembalemba Member are present above the contact. Contorted beds of the Masorobe Member, presumably an artifact of lungfish bioturbation, are present below the contact.

DISCUSSION

The animal responsible for the large-diameter burrows documented in the Maevarano Formation is impossible to unequivocally identify because body fossils are not found in direct association with the traces. However, a review of roughly comparable traces and their inferred tracemakers serves to narrow the focus: organisms typically linked to medium- to large-scale terrestrial burrows include crayfish, amphibians, bivalves, and lungfish. With regard to crayfish, their burrows, while having a wide range of lengths, generally exhibit diameters under 10 cm, with nearly circular cross sections (Hasiotis et al., 1993; Martin et al., 2008). Crayfish burrow architecture ranges from simple and vertical to complex, with branches and expanded chambers (Hasiotis et al., 1993; Martin et al., 2008). Additionally, the surfaces of crayfish burrows may preserve scrapes or hummocks, or have a mud or lag lining (Hasiotis et al., 1993). These features are not consistent with those of the traces described in this report, and thus crayfish are unlikely excavators of the Maevarano Formation burrows.

Lysorophid amphibian burrows tend to be vertical to subvertical elliptical tubes that taper downward, with lengths generally less than 15 cm (rarely ranging up to 32 cm) and diameters under 8 cm (Hembree et al., 2004; Hembree, 2010). They have been documented in densities of up to 20 per m^2, and may be preserved in multiple cross-cutting event layers (Hembree et al., 2004). Surfaces of lysorophid burrows are typically characterized by large irregular nodes, and amphibian body fossils are often found in association (Hembree et al., 2004; Hembree, 2010). The morphological characteristics of lysorophid burrows are inconsistent with those of the burrows documented in this report.

Bivalve-generated escape or dwelling traces from fluvial records generally consist of closely spaced to densely-packed vertical or subvertical burrows that, in map view, exhibit elliptical or bivalve-shaped morphologies (Hasiotis, 2004). The maximum diameters of bivalve-generated burrows, estimated from illustrations in Hasiotis (2004), are typically less than 5 cm, and while both bivalve- and brachiopod-generated burrows are sometimes associated with downward-deflected laminae in surrounding matrix (e.g., Zonneveld and Pemberton, 2003; Hasiotis, 2004), it is on a much smaller scale than that documented in the matrix surrounding the Maevarano Formation burrows (see Fig. 4). An animal considerably larger than a freshwater bivalve generated the sizeable, deep burrows (up to 60 cm deep) in the Maevarano Formation.

With regard to lungfish, the oldest purported lungfish burrows are known from the Devonian of Pennsylvania and Ireland (Woodrow and Fletcher, 1968; O'Sullivan et al., 1986; Hasiotis, 2002; Friedman and

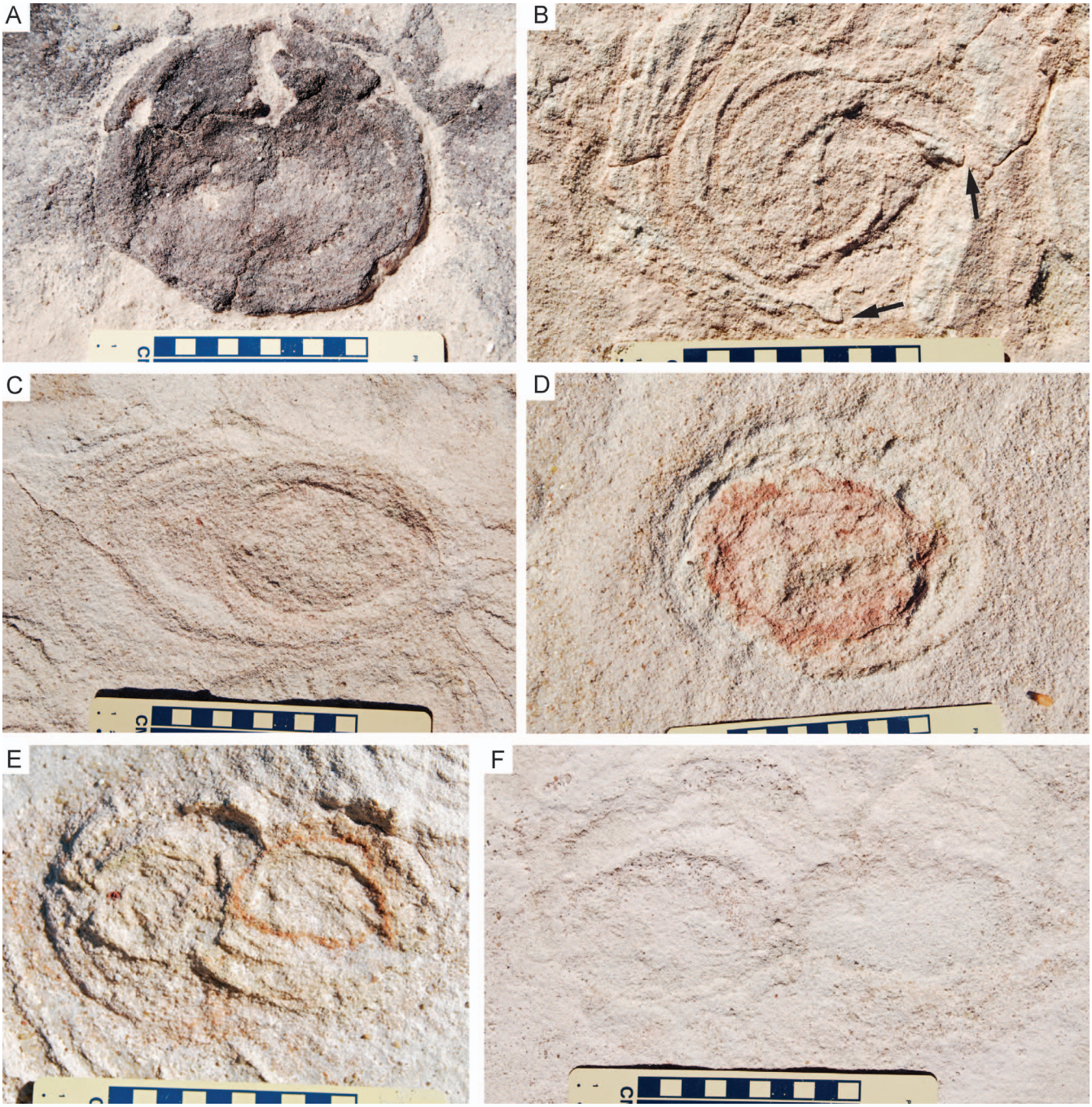

FIGURE 6—Burrow cross sections in map view. A) Circular burrow cross section with dark weathering rind (burrow #13 as shown in Fig. 3). B) Circular burrow cross section with two symmetrical projections indicated by arrows (#51, Fig. 3). C) Elliptical burrow cross section (#36, Fig. 3). D) Elliptical burrow cross section exhibiting localized oxidation (#44, Fig. 3). E) Figure-eight–burrow cross section with differential weathering and oxidation (on top of outcrop in Fig. 4A). F) Figure-eight–burrow cross section (#34, Fig. 3).

Daeschler, 2006; Jones and Hasiotis, 2010), with rare occurrences reported in the Mississippian of Kentucky (Horner and Storrs, 2002; Garcia et al., 2006) and the Pennsylvanian of Michigan and Kentucky (Carroll, 1965; Thomas and Blodgett, 1986). Lungfish burrows are more common in the Permian deposits of Texas, New Mexico, Oklahoma, and Kansas (Romer and Olson, 1954; Vaughn, 1964; Carlson, 1968; Dalquest and Carpenter, 1975; Olson and Bolles, 1975; Berman, 1976; Dalquest et al., 1989; Hasiotis et al., 1993, 2002). They have also been reported from the Triassic of the Colorado Plateau, New Mexico, and Texas (Hasiotis and Mitchell, 1989; Hasiotis et al., 1993; Gobetz et al., 2006), and the Cretaceous of Utah and Denmark (Orsulak et al., 2007; Surlyk et al., 2008). Nearly 80% of documented lungfish burrows (18 reports) are preserved in Paleozoic strata, with only five occurrences (~20%) reported in Mesozoic deposits. To date, no fossil lungfish burrows have been reported from Gondwana.

The identification of ancient lungfish burrows has been detailed and debated in the literature (Dubiel et al., 1987, 1988, 1989; McAllister, 1988; Hasiotis and Mitchell, 1989; Hasiotis et al., 1993, 2007; Miller et al., 2001; Hembree, 2010), and a universal diagnostic morphology remains controversial. For example, the Permian lungfish *Gnathorhiza* created both simple cylindrical burrows and burrows with enlarged terminal chambers (Hasiotis et al., 1993; Hembree, 2010). In contrast,

TABLE 1—Dimensions and morphological designations of mapped burrows.

Burrow #	Minor axis (cm)	Major axis (cm)	Ratio	Morphology
1	14	16.5	0.9	E
2	7	16	0.4	F
3	13	18	0.7	E
4	13	17	0.8	E
5	7	10	0.7	E
6	6	9.5	0.6	E
7	11	16.3	0.7	E
8	9	12	0.8	E
9	11	16	0.7	E
10	13	15	0.9	E
11	14	18	0.8	E
12	11	15.5	0.7	E
13	14	15.7	0.9	C
14	12	17	0.7	E
15	12	16.5	0.7	E
16	10.5	14	0.8	F
17	11	29	0.4	E
18	12.5	26	0.5	E
19	14	17.4	0.8	E
20	11	19	0.6	E
21	12.8	16	0.8	E
22	8	11	0.7	E
23	11	17	0.7	E
24	7.4	10	0.7	E
25	8	16	0.5	F
26	10	12	0.8	E
27	11	19	0.6	F
28	14.5	16.5	0.9	E
29	9.5	16	0.6	E
30	8	13	0.6	E
31	13	20	0.7	E
32	14.5	22	0.7	E
33	12.5	16	0.8	E
34	7	18	0.4	F
35	10	22	0.5	F
36	10.5	22	0.5	E
37	10.5	18	0.6	E
38	10	14.5	0.7	F
39	7.5	11	0.7	E
40	9.5	17	0.6	E
41	12	20	0.6	E
42	10	17	0.6	E
43	13	16	0.8	E
44	14	16.5	0.9	E
45	8	15	0.5	E
46	5	9	0.6	E
47	10	16	0.6	E
48	9.5	13	0.7	E
49	12	14.5	0.8	E
50	9	18	0.5	F
51	10	10	1.0	C
52	13.5	17	0.8	E
53	14	19.3	0.7	F
54	11.5	18.5	0.6	E
55	14	21	0.7	E
56	13	16	0.8	F
57	10	22	0.5	F
58	12.5	15	0.8	E
59	7.5	12	0.6	E
60	12	17	0.7	E
61	11.5	16	0.7	E
62	9	11	0.8	E
63	15	15	1.0	C
64	8	10	0.8	E
65	13	17.5	0.7	E
66	13.5	20	0.7	E
67	10.3	15	0.7	E
68	8	12	0.7	E
69	9.5	11	0.9	E
70	13	19	0.7	E
71	13.5	19	0.7	F
72	15	27	0.6	F
73	14	21.5	0.7	E
74	11	23	0.5	F

other ancient lungfish, especially in the Mesozoic record, apparently consistently formed burrows with flask-shaped or bulbous terminations, which served as the estivation chambers (McAllister, 1988; Hasiotis et al., 1993; Hasiotis, 2002; Gobetz et al., 2006; Orsulak et al., 2007). Nevertheless, over the past few decades numerous criteria have been proposed to facilitate the recognition of ancient lungfish burrows that lack directly associated body fossils. First and foremost, any burrows ascribed to lungfish should be compatible in size and shape with the dimensions and morphologies expected from the burrowing behavior of a medium to large fusiform fish. Prior studies have documented burrow lengths ranging from 10 to 50 cm (e.g., Olson and Bolles, 1975; Hasiotis et al., 1993, 2002; Gobetz et al., 2006) and burrow channel diameters ranging from 1 to 15 cm (e.g., Carroll, 1965; Carlson, 1968). The Maevarano Formation burrows range in length from 15 to 60 cm (n = 9) and have clearly defined channel diameters ranging from 5 to 15 cm (n = 74), and are, thus, consistent with the general scale of lungfish burrows reported elsewhere.

The clustering of burrows within a single bed is another feature that has been interpreted to represent gregarious estivation of lungfish (e.g., O'Sullivan et al., 1986; Gobetz et al., 2006; Hembree, 2010). The 74 burrows mapped in the Maevarano Formation are closely spaced (as many as 3 per m^2) within a single sandstone body, and their spatial packing is consistent with gregarious behavior. Whether they were all excavated at the same time is impossible to definitively ascertain, but it seems to be a reasonable conclusion given their scarcity in surrounding beds and the absence of apparent overprinting.

Several reports (Carroll, 1965; Hasiotis, 1991; Surlyk et al., 2008) describe lungfish burrows with dark oxidized rims, and 44 of the 74 mapped Maevarano Formation burrows exhibit oxidation in the

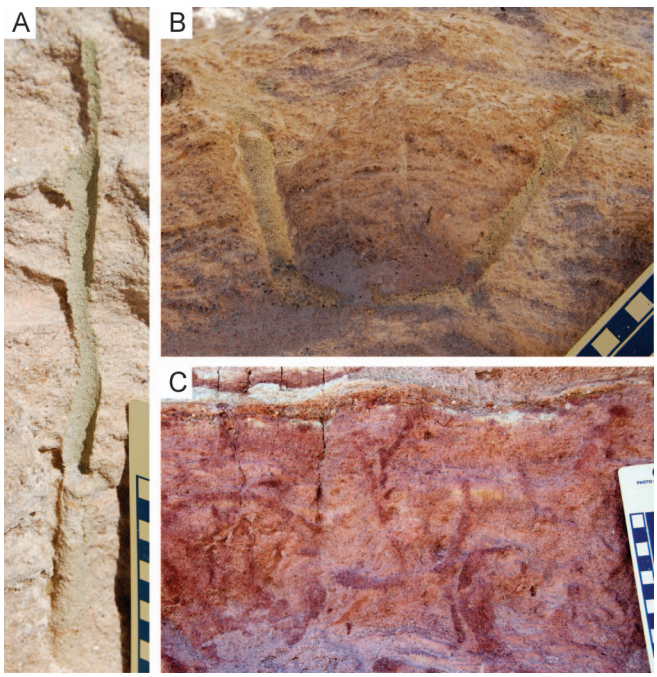

FIGURE 7—Associated trace fossils in the Masorobe Member. A–B) Vertical and U-shaped burrows with greenish clay-rich fill, identified as *Arenicolites*. These traces were documented in Unit 2 of Figure 2. C) Smaller-scale trace fossils in the oxidized paleosol (Unit 3, Fig. 2) subjacent to the sandstone hosting the large-scale burrows.

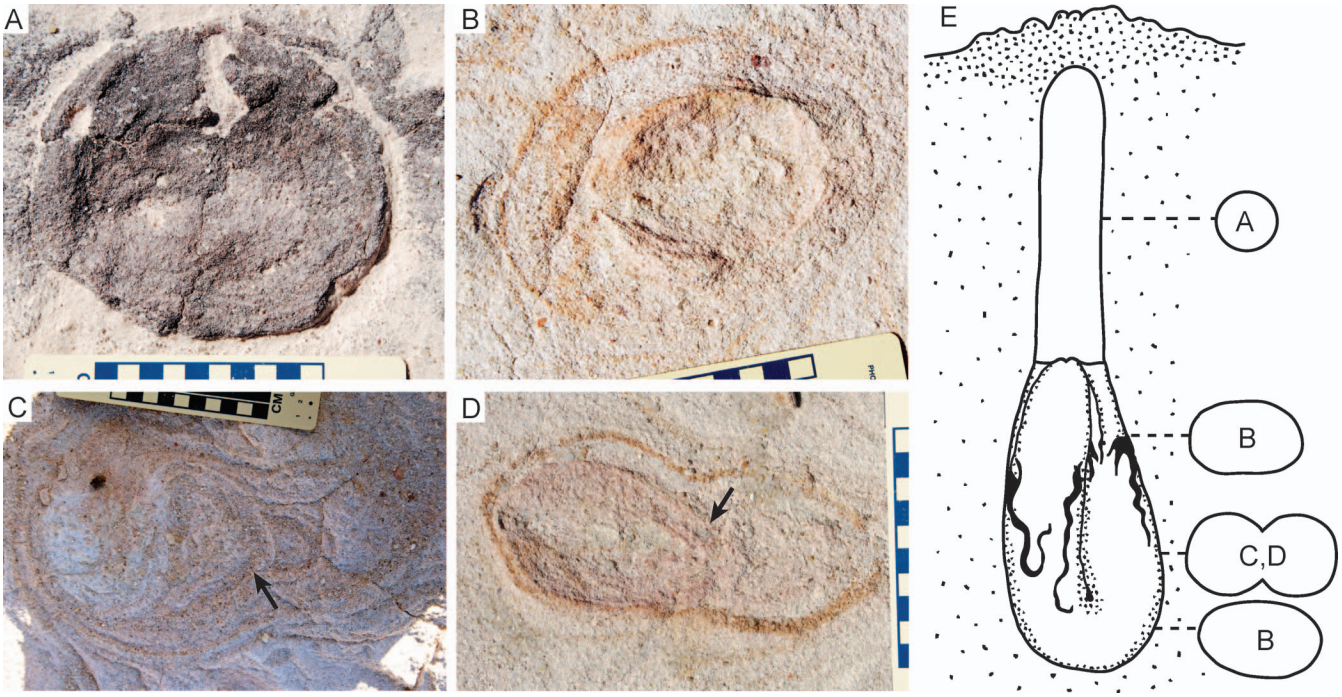

FIGURE 8—Map view exposures of ancient lungfish burrows (A–D) and schematic of a modern lungfish burrow (E). A) Circular burrow cross section (#13, Fig. 3). B) Elliptical burrow cross section with a locally developed oxidized margin (#3, Fig. 3). C, D) Burrow cross sections with figure-eight morphology (C = #72, D = #2, Fig. 3). The left side of each figure eight clearly cuts the right side (black arrows), and this is interpreted to reflect the position of the head end of the folded lungfish. Burrow D preserves an oxidized margin. E) Schematic of a lungfish estivation burrow with cross sections taken at various depths in the burrow profile (modified from Johnels and Svensson, 1954). Map views of the burrow traces from Madagascar presented in A–D exactly match the cross-sectional morphologies observed in modern lungfish burrows. Corresponding positions of various cross sections observed in outcrop are indicated on the schematic.

vicinity of burrow margins. In some purported lungfish burrows the infilled sediment shows differential weathering of alternating coarse and fine layers (Gobetz et al., 2006), and Carlson (1968) noted that a clay band of different color distinguished the inner chamber of the burrow. Many of the Maevarano Formation burrows display comparable features in map view, with a massive core often surrounded by more defined laminae. Alternating exposed laminae of coarse-grained sandstone and greenish clay-rich sandstone is a common occurrence (e.g., Fig. 6C), and differential weathering and oxidation within burrows is also prevalent (e.g., Fig. 6E). Fin traces have also been noted as an important identifying trait on the walls of lungfish burrows (Hasiotis et al., 1993; Hasiotis, 2002; Hembree, 2010), and the two symmetrical projections illustrated in Figure 6B are possible examples of fin traces, albeit in map view.

Comparability with modern traces is also critical (Hasiotis et al., 1993; Hembree, 2010), but there are unfortunately few studies that focus on modern lungfish and their interactions with sedimentary substrates. One notable exception is Johnels and Svensson's (1954) treatment of estivation by *Protopterus annectens* in Gambia. They documented burrow morphology in transverse sections along the full length of excavated burrows (Fig. 8E). In their study, *Protopterus* burrows were found in densities of up to 5 per m^2, with channel diameters ranging from 0.5 to 7 cm, and channel depths (measured from the sediment-water interface to the top of the chamber) ranging from 3 to 25 cm (Johnels and Svensson, 1954). The Cretaceous burrows of the Maevarano Formation are slightly larger than those reported for the modern *Protopterus*, but the overall morphology of the Malagasy sample is essentially identical. The circular cross sections can be correlated with the upper channel of the *Protopterus* burrow (Fig. 8A), and the elliptical cross sections match those from the top or bottom of this animal's flask-shaped estivation chamber (Fig. 8B). Perhaps most telling are the distinctive figure-eight–shaped burrow cross sections (n=14) in the Malagasy burrow assemblage. A transverse section taken by Johnels and Svensson (1954) through the midsection of the *Protopterus* chamber resembles two partially overlapping circles (our figure-eight morphology), reflecting the trace of a lungfish folded in half within its estivation chamber (Figs. 8C–D). Interestingly, Dalquest and Carpenter's (1975) brief report on Permian lungfish burrows from Texas also mentions a few burrows with hourglass cross sections, very similar to the figure-eight cross sections documented in modern-day Gambia and now the Maevarano Formation.

Differential erosion of the surface on which we mapped our burrows has fortuitously provided an opportunity to characterize these ancient burrows along their vertical expanse, and this in turn has afforded an excellent opportunity to identify the tracemaker (Fig. 8). Given the data outlined here, and after comparing our burrows with alternative tracemakers (including crayfish, bivalves, and amphibians), the ichnofossils from the Maevarano Formation of Madagascar were most likely made by gregarious lungfish that excavated >60-cm-deep estivation burrows with flask-shaped terminations.

SUMMARY AND CONCLUSIONS

This report provides the first evidence that lungfish were members of the Maevarano Formation paleofauna. The addition of lungfish to the Maevarano Formation vertebrate assemblage based on ichnofossils from the Befandrama study area enriches our understanding of the diversity of this ancient ecosystem, and is consistent with documented occurrences of lungfish tooth plates in immediately underlying strata (Marovoay and Ankazomihaboka beds: Martin, 1981). The apparent absence of both lungfish body and trace fossils in the Berivotra study area, which has been intensely prospected for vertebrate fossils for almost two decades (since 1993), may reflect the impact of different sedimentation patterns in the two field areas. In the Berivotra study area, the Maevarano Formation is characterized by abundant deposits of fine-grained debris flows that were emplaced in ancient channel belts

when the rains returned to the basin (Rogers, 2005). The thick, meter-scale packages of clay-rich sediment left by recurrent debris flows would arguably inhibit estivation behavior in the ancient channel belts of Berivotra. Interestingly, the fluvial sandstone bodies of the Masorobe Member in the Befandrama study area are larger in scale than their counterparts in Berivotra (thicker overall with larger-scale cross-bedding), and there are markedly fewer intercalated deposits of debris flows. Rocks in this part of the Maevarano Formation outcrop belt appear to intersect the record of a somewhat larger fluvial system where debris flows were less common. Bedding plane exposures of the uppermost Masorobe Member are also more expansive in the low relief outcrops of the Befandrama study area, and this too may influence the likelihood of discovery of lungfish trace fossils.

The burrows documented herein also provide abundant examples of lungfish estivation in the rock record. Several distinctive features of the numerous Malagasy burrows are noted, including the association of three distinct map view cross sections that are very similar to those documented in the burrows of extant lungfish (Johnels and Svensson, 1954). These cross sections are supplemented by several additional key observations, including spatial clustering and oxidized burrow margins. The pervasively stratified nature of the fluvial sandstone body hosting the Malagasy burrows also affords a unique view of lungfish estivation because most previous studies have focused on burrows embedded within massive fine-grained facies (e.g., Romer and Olsen, 1954; Carlson, 1968; Berman, 1976; Surlyk et al., 2008). The Maevarano Formation burrows provide an opportunity to document the impact of burrowing on surrounding sedimentary matrix. The deflection of laminae several cm beyond the margins of individual burrows (e.g., Fig. 4B) is indicative of an energetic and forceful excavation, and the downward deflection of strata in the proximity of burrows can now be added to the list of diagnostic features associated with lungfish bioturbation. The presence of only downward-deflected laminae adjacent to the burrows potentially reflects the variable physiological condition of lungfish that undergo estivation. At the time of excavation the lungfish are presumably in good physiological condition, and their strenuous exertions in the downward direction would be expected to have a significant impact on surrounding sedimentary structures. During estivation in dry environments, lungfish do not ingest any food or water, and undergo weight loss ranging from 3% to 15%, as shown in experimental studies (Smith, 1930; Janssens, 1964). Loss of body mass and lowered metabolism during a period of estivation, coupled with loss of fitness, would presumably make exiting the burrow a less forceful event, with less potential to deform surrounding sedimentary features. It is also possible that desiccation of the surrounding sediments during the dry season made deformation and upward deflection upon emergence less likely. One final explanation of the downward-only deflections could be that the ancient lungfish documented in this study died in their burrows, and thus never made the upward journey. However, the absence of lungfish body fossils in the vicinity of the burrows renders this interpretation unlikely.

Finally, previous studies have characterized the Maevarano Formation's paleoenvironment as a dryland setting where strong seasonality in the availability of water led to considerable stress and hardship among animal populations; bonebeds representing recurrent localized mass mortality abound in the formation. Both taphonomic and sedimentologic datasets support this general conclusion (Rogers et al., 2000, 2003; Rogers, 2005; Roberts et al., 2007; Rogers and Krause, 2007), as does the presence of spinicaudatan conchostracans, which are small branchiopod crustaceans that apparently required episodes of desiccation and rehydration to fulfill their reproductive cycle (Vannier et al., 2003; Stigall and Hartman, 2008). Lungfish can now be added to the array of animals that endured the hardships of the Upper Cretaceous Maevarano Formation ecosystem. Extant lungfish are known for their ability to survive prolonged drought, and today the African lungfish can survive in light torpor within their cocoon for months to years without food or water (Smith, 1930; Delaney et al., 1974; Fishman et al., 1992). From all indications, the Late Cretaceous of northwestern Madagascar was a harsh setting prone to drought and drought-related mortality, and the mass occurrence of 100+ lungfish estivation burrows is one more compelling line of evidence consistent with this paleoenvironmental reconstruction.

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