Early Holocene fauna from a new subfossil site: A first assessment from Christmas River, south central Madagascar

Kathleen M. Muldoon\textsuperscript{I,II}, Brooke E. Crowley\textsuperscript{III}, Laurie R. Godfrey\textsuperscript{IV}, Armand Rasoamiananana\textsuperscript{V}, Adam Aronson\textsuperscript{VI}, Jukka Jernvall\textsuperscript{VII}, Patricia C. Wright\textsuperscript{VIII} and Elwyn L. Simons\textsuperscript{VIII}

ABSTRACT

We report on faunal remains recovered during recent explorations at 'Christmas River', the only subfossil locality known from Madagascar's south central plateau. Recovered remains of several extinct taxa date to approximately 10,000 \(^{14}C\) years before present (BP), including crocodiles, tortoises, the elephant bird \textit{Aepyornis}, the carnivoran \textit{Cryptoprocta spelea}, the lemurs \textit{Archaeolemur majori}, \textit{Pachylemur insignis}, and \textit{Megaladapis edwardsi}, and abundant remains of the dwarf hippopotamus, \textit{Hippopotamus lemerlei}. The presence of southern-limited, forest-dependent species at Christmas River supports the hypothesis that forest once extended, perhaps discontinuously, across the central highlands towards the west. One theory is that sites in the north central highlands, which are higher in elevation, maintained more mesic conditions during Plio-Quaternary climate shifts than those of the lower elevation sites of the south central highlands. Thus, elevation above sea level may have acted as a filter that limited species dispersal across the island in the past. Such a scenario would explain the distinction between more humid, higher elevation, northern highland subfossil communities versus more arid, lower elevation, southern subfossil communities. Continued exploration at Christmas River thus provides a remarkable opportunity for deciphering ecological changes that have taken place in south central Madagascar during the Holocene.

RÉSUMÉ

Malagasy is recognized as one of the regions of the most sensible of the world in which concerns the threats that were on its biodiversity, and that is the cause of levels of endemicity are inegalées, of a diversity varied and an impact important on the environment. Suite to the colonization by the Man he has more than 2000 years, extinction of masses of the fauna and an important recul forester have long been on the rivers that are important for the evolution, and the ecological changes that have taken place in south central Madagascar during the Holocene.

Correspondence:
Kathleen M. Muldoon
Department of Anatomy, The Geisel School of Medicine at Dartmouth, HB 7100, Hanover, New Hampshire 03755 U.S.A.
E-mail: kathleen.muldoon@dartmouth.edu
Madagascar Conservation & Development is the journal of Indian Ocean e-Ink. It is produced under the responsibility of this institution. The views expressed in contributions to MCD are solely those of the authors and not those of the journal editors or the publisher.

All the issues and articles are freely available at http://www.journalmcd.com

Contact Journal MCD
info@journalmcd.net for general inquiries regarding MCD
funding@journalmcd.net to support the journal

Madagascar Conservation & Development
Institute and Museum of Anthropology
University of Zurich
Winterthurerstrasse 190
CH-8057 Zurich, Switzerland

Indian Ocean e-Ink
Promoting African Publishing and Education
www.ioeink.com

Missouri Botanical Garden (MBG)
Madagascar Research and Conservation Program
BP 3391
Antananarivo, 101, Madagascar
pursuing vers l’ouest. Une théorie a proposé que les sites septentrionaux des haute-terres centrales, à des altitudes plus élevées, maintenaient des conditions plus humides au cours des changements du Plio-Quaternaire que les sites méridionaux de ces haute-terres centrales. Ainsi, dans le passé, l’altitude a dû agir comme un filtre qui empêchait la dispersion des espèces d’un endroit à l’autre de l’île. Un tel scénario expliquerait la distinction entre les communautés subfossiles du nord des haute-terres qui étaient plus humides à haute altitude et les communautés subfossiles du sud aride à basse altitude. La poursuite de l’exploration à Christmas River constitue une occasion unique pour décodier les changements écologiques qui sont intervenus dans le Sud de cette région centrale de Madagascar au cours de l’Holocène.

INTRODUCTION
Madagascar is considered a hotspot for endangered biodiversity, based on unequaled levels of endemism, species diversity, and human impact on the environment (Goodman and Benstead 2005). Following human colonization more than 2,000 years ago, Madagascar experienced well-documented megafaunal extinctions and widespread deforestation (Burney et al. 2004, Crowley 2010), leaving many elements of modern ecosystems in a state of ecological disruption. For example, endemic plants have lost important mutualists (Godfrey et al. 2008), animals have been forced to exploit resources or live in habitats to which they are poorly adapted (Cuozzo and Sauther 2006, Crowley et al. 2012, Godfrey et al. 2012), and both plants and animals have reduced, threatened, or entirely eliminated dispersal routes (Godfrey et al. 1999, Goodman et al. 2006, 2007, Muldoon et al. 2009, Muldoon 2010). Although humans are widely considered to be the primary trigger of megafaunal extinctions (Burney 1999, Burney et al. 2003, 2004, Godfrey and Irwin 2007, Crowley 2010), the relative contributions of climate change and human activities to this ecological transformation are contested (e.g., Virah-Sawmy et al. 2009a, b, 2010).

Isolated patches of modern forest that is markedly more humid than surrounding areas in the southwest at Analavelona (E44°10’0.1”, S22°38’60.0”), Betandraka (E45°12’43.2”, S22°47’34.8”), and Mikea (E43°28’0.12”, S23°18’0.0”) Forests, Zombitse-Vohibasia (E48°49’0.1”, S22°37’0.12”), and Isalo (E45°19’55.2”, S22°30’3.6”) National Parks, and in the southeast at Grand Lavasoa (E45°36’21.6”, S22°30’3.6”), 793 m above sea level; Figure 1). Christmas River is the only subfossil locality known from this region. All fauna recovered from this locality are therefore first known regional occurrences. Christmas River was discovered following on an observation by a sapphire miner, who located a bone bed 10–15 m deep in 2006. Sapphire miners focused on the collection of large macrofossils, and the younger layers of the pit have not yet been fully explored. A sample of sediment collected from the surface and subsurface at Christmas River indicates the presence of small vertebrate and botanical remains.

Approximately 600 vertebrate specimens, representing mammals, birds, and herpetofauna, have been collected from Christmas River to date. Skeletal remains in the mammalian assemblage demonstrate a high quality of preservation and include largely complete crania, jaws, isolated teeth, and post-cranial elements. All skeletal material recovered from Christmas

![Figure 1](image)

**Figure 1.** Map showing the position of Christmas River (red star), relative to modern forest sites (regular font, yellow dots) and other subfossil localities (bold font, red dots). Dashed green lines indicate the boundaries between ecoregions, following Burgess et al. (2004). Notice the unique position of Christmas River in the south central highlands, within the region of the hypothesized southern dispersal corridor.
River has been collected and studied as part of collaborative efforts between the Duke University Lemur Center, Division of Fossil Primates (Durham, North Carolina, U.S.A.), and Dartmouth College (Hanover, New Hampshire, U.S.A.), with the Département de Paléontologie et Anthropologie Biologique, Université d’Antananarivo (Antananarivo, Madagascar), respectively.

Morphological analysis of the Christmas River mammals was completed in comparison with reference material housed at the Département de Paléontologie et Anthropologie Biologique, Université d’Antananarivo (Antananarivo, Madagascar), the Natural History Museum (London, England), the Museum national d’Histoire naturelle (Paris, France), the Naturhistorisches Museum (Vienna, Austria), the American Museum of Natural History (New York, New York, U.S.A.), The Field Museum of Natural History (Chicago, Illinois, U.S.A.), the University of Massachusetts, Amherst (Amherst, Massachusetts, U.S.A.), as well as published descriptions. Qualitative comparisons and quantitative skeletal variables were recorded for each specimen examined following anatomical landmarks defined and illustrated in Steunes (1989) and Weston and Lister (2009) for *Hippopotamus*; Jouffroy (1963) for *Archaeolemur* and *Pachylermum*; Lamberton (1934) for *Megaladapis*; Goodman et al. (2004) for *Cryptoprocta*.

We selected several bones for radiocarbon dating. These bones were decalcified and gelatinized using EDTA and weak HCl, respectively (Crowley 2012). We confirmed collagen preservation using collagen yield and atomic C:N ratios (values falling between 2.9 and 3.6 were considered well preserved). Samples were radiocarbon dated at the University of Helsinki and the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory.

**RESULTS**

Christmas River differs from most open-air deposits in Madagascar in that it has the potential to yield a stratigraphic profile in the sense of vertical, chronological relations of sedimentary units. The deepest and most prolific layer reached so far at Christmas River is a grey-green clay containing the bones of several extinct taxa including crocodiles, tortoises, the elephant bird *Aepyornis*, and abundant remains of the dwarf hippopotamus, *Hippopotamus lemerlei*. Bones from this layer yielded AMS ¹³C dates of approximately 10,000 uncalibrated ¹³C years BP (Table 1). The *Hippopotamus* specimens from Christmas River therefore represent the oldest data for this genus in Madagascar.

The *Hippopotamus* specimens from Christmas River can be attributed to *H. lemerlei* on the basis of the following qualitative characters: a thick supraorbital margin that results from a large frontal sinus that extends laterally, an orbit that is taller than it is wide, the anterior margin of the orbit is situated above the third upper molar (M3), a long and flat mandibular symphysis (Figure 2a–c). The Christmas River specimens are intermediate in size between *H. lemerlei* and *H. madagascariensis* (Figure 3).

The extinct lemur *Megaladapis edwardsi* was recovered from lower levels, but did not have enough collagen to produce an accurate radiocarbon date (Figure 2g). *Megaladapis edwardsi* differs from both *M. madagascariensis* and *M. granddieri* in having significantly larger molars (especially the third molars, which are the longest and widest). Neither of the two partial mandible specimens recovered had intact molar rows. However, one specimen preserves m2 and a partial m3, and the approximate mesiodistal lengths of all three molars were estimated from the sizes of the alveoli for the two missing teeth (m1 = 18.0 mm, m2 = 24.0 mm, m3 = 35.0 mm). Based on these estimated size dimensions, both mandibles can be assigned to the larger species, *M. edwardsi* (m1 = 17.2 ± 0.6 mm [n = 43], m2 = 22.9 ± 0.9 mm [n = 63], m3 = 34.8 ± 1.5 mm [n = 70]).

Isolated remains found above the grey-green clay layer include the distal left humerus of *Archaeolemur sp. cf. majori* that is broken just below the deltoid crest, but with a largely intact distal epiphysis and olecranon fossa (DPC 24153a; Figure 2e). This specimen dates to 9,265 ± 30 ¹³C yr BP (Table 1). Additionally, *Pachylermum insignis* is represented by the distal two-thirds of a left femur that is broken at the level of the third trochanter (DPC 24156; Figure 2f), which yielded a date of 9,450 ± 30 ¹³C yr BP (Table 1). These specimens exhibit diagnostic features for each genus: for example, for *Archaeolemur*, a posteromedially deflected entepicondyle; and for *Pachylermum*, a relatively deep patellar groove with a raised lateral lip and anteroposteriorly compressed femoral shaft. Both of these specimens fall within the range of size variation of the southwestern species of their respective genus (e.g., *A. majori* and *P. insignis*), although the *Archaeolemur* humerus lies at the high end of its range (Table 2), while the *Pachylermum* femur falls at the low end of its range (Table 3). We note, however, that there is a distinct latitudinal body size gradient in *Archaeolemur*, such that body size tends to be smallest in the extreme south, and larger in the center and north of the island of Madagascar (Albrecht et al. 1990, Godfrey et al. 1990). The specimen from Christmas River is larger than most specimens at sites to the south and west, but similar in size to *A. majori* humeri from Tsirave (E45°7.1’, S21°49.6’, 745 m a.s.l.), a subfossil site just north of the Isalo Massif.

A distal humerus (DPC 24153b; Figure 2d) attributable to the extinct carnivore *Cryptoprocta spelea* on the basis of its large size was also recovered. The width of the distal humerus of DPC 24153b is 36.4 mm, which is larger than the same measurement in modern (27.9 ± 1.4 mm, n=12), or subfossil (32.1 ± 2.6 mm, n= 27) *Cryptoprocta ferox*, but similar in size to the larger-bodied extinct *C. spelea* (33.7 ± 1.7 mm; Goodman et al. 2004). Similar to the specimens of *Megaladapis*, collagen preservation for this specimen was too poor to produce a radiocarbon date (low yield, high atomic C:N).

### TABLE 1. Radiocarbon ages for vertebrate bones collected from Christmas River

<table>
<thead>
<tr>
<th>Genus and Species</th>
<th>Specimen #</th>
<th>¹⁴C yr BP ±1s</th>
<th>Cal yr BP ±1s</th>
<th>Lab #</th>
</tr>
</thead>
<tbody>
<tr>
<td>Archaeolemur sp. cf. <em>A. majori</em></td>
<td>DPC 24153a</td>
<td>925 ±30</td>
<td>10345 ±95</td>
<td>CAMS 147334</td>
</tr>
<tr>
<td><em>Pachylermum insignis</em></td>
<td>DPC 24156</td>
<td>9450 ±30</td>
<td>10615 ±95</td>
<td>CAMS 147038</td>
</tr>
<tr>
<td><em>Hippopotamus lemerlei</em></td>
<td></td>
<td>9655 ±60</td>
<td>10955 ±215</td>
<td>Hela-1828</td>
</tr>
<tr>
<td><em>Aepyornis sp.</em></td>
<td></td>
<td>9610 ±60</td>
<td>10920 ±230</td>
<td>Hela 1829</td>
</tr>
<tr>
<td><em>Aepyornis sp.</em></td>
<td></td>
<td>9535 ±70</td>
<td>10825 ±265</td>
<td>Hela 1774</td>
</tr>
</tbody>
</table>
FIGURE 2. Representative mammal fauna from Christmas River. *Hippopotamus lemerlei* (a) skull (08-CR-001a) in lateral view; (b) partial skull (08-CR-002n) in posterior view; (c) mandible (08-CR-006a) in anterior view; (d) *Cryptoprocta spelea* left distal humerus (DPC 24153b) in anterior view; (e) *Archaeolemur* sp. cf. *A. majori* left distal humerus (DPC 24153a) in anterior view; (f) *Pachylemur insignis* partial left femur (DPC 24156) in anterior view; (g) *Megaladapis edwardsi* (unnumbered) in occlusal and lateral views. Scale bars equal 1 cm.

FIGURE 3. Scatterplot showing separation of *Hippopotamus lemerlei* (red dots) and *H. madagascariensis* (green dots) based on femoral measurements. The Christmas River specimens (black stars) are significantly larger than *H. lemerlei* (t = -3.067, d.f. = 20, P < 0.05), and significantly smaller than *H. madagascariensis* (t = 4.165, d.f. = 10, P < 0.05) in femoral head diameter, but cannot be distinguished from either species based on femoral shaft width (for comparisons with *H. lemerlei*, t = -1.974, d.f. = 27, P = 0.05; for comparisons with *H. madagascariensis*, t = -0.270, d.f. = 14, P = 0.791). FES = flexor-extensor section; LMS = lateral-medial section (following Weston and Lister 2009).

TABLE 2. Descriptive measurements for south and southwest variants of *Archaeolemur majori*, compared with specimens from Tsirave and Christmas River. Measurements (in mm) are presented as mean ± standard deviation.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>South and Southwest</th>
<th>Tsirave</th>
<th>Christmas River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biepicondylar breadth</td>
<td>33.6 ± 1.5</td>
<td>35.7 ± 2.7</td>
<td>38</td>
</tr>
<tr>
<td>n = 6</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trochlea to medial epicondyle</td>
<td>27.8 ± 1.4</td>
<td>29.3 ± 2.0</td>
<td>29.2</td>
</tr>
<tr>
<td>n = 35</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trochlea + capitulum width</td>
<td>25.0 ± 1.4</td>
<td>26.0 ± 1.6</td>
<td>27.4</td>
</tr>
<tr>
<td>n = 33</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capitulum width</td>
<td>10.3 ± 0.8</td>
<td>10.9 ± 0.5</td>
<td>12</td>
</tr>
<tr>
<td>n = 34</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trochlear depth</td>
<td>11.9 ± 1.0</td>
<td>12.4 ± 1.6</td>
<td>12.4</td>
</tr>
<tr>
<td>n = 34</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olecranon fossa width</td>
<td>16.9 ± 1.2</td>
<td>17.5 ± 1.0</td>
<td>19.5</td>
</tr>
<tr>
<td>n = 37</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olecranon fossa height</td>
<td>9.2 ± 1.2</td>
<td>10.4 ± 0.8</td>
<td>11.4</td>
</tr>
<tr>
<td>n = 37</td>
<td>n = 6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3. Descriptive measurements for Pachylemur insignis and P. julyi, compared with specimens from Christmas River. Measurements (in mm) are presented as mean ± standard deviation. AP = anterior-posterior dimension.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>P. insignis</th>
<th>P. julyi</th>
<th>Christmas River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Midshaft AP diameter</td>
<td>11.8 ± 0.8</td>
<td>12.5 ± 0.7</td>
<td>10.4</td>
</tr>
<tr>
<td>Midshaft transverse diameter</td>
<td>13.0 ± 0.8</td>
<td>14.3 ± 1.8</td>
<td>14.6</td>
</tr>
<tr>
<td>Biepicondylar diameter</td>
<td>27.5 ± 1.4</td>
<td>29</td>
<td>28.4</td>
</tr>
<tr>
<td>Bicondylar diameter</td>
<td>26.4 ± 1.2</td>
<td>28</td>
<td>27.8</td>
</tr>
<tr>
<td>Intercondylar diameter</td>
<td>8.7 ± 0.8</td>
<td>9.5</td>
<td>8</td>
</tr>
<tr>
<td>Patellar breadth</td>
<td>12.8 ± 0.9</td>
<td>11.5</td>
<td>12.9</td>
</tr>
<tr>
<td>Medial condyle AP depth</td>
<td>23.3 ± 1.0</td>
<td>24.8</td>
<td>23.9</td>
</tr>
<tr>
<td>Lateral condyle AP depth</td>
<td>24.1 ± 1.1</td>
<td>25</td>
<td>24</td>
</tr>
</tbody>
</table>

DISCUSSION

The importance of Christmas River for understanding the paleo-ecological history of the south central highlands of Madagascar is demonstrated by its unique fauna. The mammalian subfossil assemblage is dominated by *Hippopotamus meridionalis*, an extinct species previously recovered almost exclusively from coastal areas in the southern region of the island (Steunes 1989, Jernvall et al. 2003). The distinguishing morphological characteristics of *H. meridionalis*, which include an orbit that is taller than it is wide, suggest an amphibious lifestyle similar to *H. amphibius* of modern Africa. This is in contrast to the terrestrial habits interpreted for *H. madagascariensis*, which has been recovered from Ampasambizimba and Antsirabe, subfossil localities that occur well to the north of Christmas River in the mid-central highlands (Figure 1, Steunes 1989). We note here that attributions of the Anjozorobe hipparion material to *H. meridionalis* (Burney et al. 1997, Samonds and Toomey 2010) should be corrected to *H. madagascariensis* (Weston and Lister 2009), emphasizing the geographic and ecological separation of these species that was described by Steunes (1989). The nearest subfossil localities to Christmas River are Ampoza (E44°42.3', S22°18.9', 570 m a.s.l.) and Anpanihy (E44°42.7', S22°19.8', 660 m a.s.l.), about 83 km further west (Mahé and Sourdot 1972, Jernvall et al. 2003). Although these localities yield much more recent dates (ca. 1,800 14C yr BP and 2,430 14C yr BP, respectively; Jernvall et al. 2003), the subfossil assemblages at these sites are also dominated by *H. meridionalis*.

The extinct lemur taxa shared between Christmas River and Ampoza include inferred southern forest-dwelling animals such as *Archaeolemur sp. cf. majori, Pachylemur insignis*, and *Megaladapis edwardsi* (Jernvall et al. 2003). This lemur assemblage is fundamentally different from the species composition of a string of subfossil sites forming a corridor crossing the central highlands well to the north of Christmas River, through the Antananarivo ex Province (especially the Vakinankaratra and Itasy regions; e.g., Ampasambizimba, Figure 1). The only characteristically southern giant lemur that is unequivocally found within this mid-central highlands corridor is *Hadropithecus stenognathus*, which is rare. Other primate taxa from the mid-central highlands include the extinct lemurs *Archaeolemur edwardsi*, *Megaladapis grandideri*, *Archaeolemur fontoynontii*, *Mesopropithecus pithecoideus*, *Pachylemur julyi*, and *Paleopropithecus maximus*, as well as the extant lemur *Prolemur simus*, *Indri indri*, *Propithecus diadema*, *Eulemur fulvus*, and *Cheirogaleus major*, among others. Sites in this more northern corridor, ranging from 914 m to over 1,645 m a.s.l., are higher in elevation than those in the south.

An east-west distance effect in extant mammal distributions has been interpreted as evidence that faunal exchange routes once crossed the southern portion of the central highlands (Godfrey et al. 1999, Muldoon and Goodman 2010). It has been hypothesized that this corridor was fragmented by shifts in vegetation associated with climate change, but given that much of the natural habitat across this zone no longer exists, it is difficult to reconstruct its former extent and type. Unfortunately, the Holocene fauna of the island’s eastern rainforests is currently unknown. However, the subfossil record of southern Madagascar demonstrates that several extant species currently restricted to humid forests once had more widespread geographic distributions (Goodman and Rakotondravony 1996, Goodman and Rakotofy 1997, Godfrey et al. 1999, Goodman et al. 2006, 2007, Muldoon et al. 2009, Muldoon 2010). Furthermore, the existence of relict patches of eastern rainforest flora and fauna in the west underscores recent habitat changes in southwestern Madagascar (Ramanamanjato et al. 2002, Goodman and Ramanamanjato 2007, Moat and Smith 2007). Elements of the extant fauna and flora of these areas have been used to suggest that these isolated humid and subhumid forests may serve as refugia for biota that had much more extensive distributions in southwestern Madagascar in the recent past (Goodman and Rakotondravony 1996, Goodman and Rakotofy 1997, Godfrey et al. 1999, Goodman et al. 2006, 2007, Muldoon et al. 2009, Muldoon 2010).

A preliminary paleoecological interpretation of the Christmas River site may offer an alternative explanation. One hypothesis is that the higher elevational distribution of sites in the north central versus south central highlands may have acted as a filter that limited species dispersal across the island in the past. Wilme et al. (2006) proposed that watersheds with sources at high elevation maintained mesic conditions during Plio-Quaternary climate shifts due to orographic precipitation. For forest-dependent mammals, such mesic conditions may have allowed dispersal across the more northern-central passage, but limited dispersal of moisture-restricted animals in the south. For example, *Megaladapis edwardsi* is the dominant species at coastal southern sites, and may be restricted to spiny thicket habitat. *Archaeolemur majori*, and *Pachylemur insignis* are also largely restricted to the southern quadrant of Madagascar. Such a scenario would explain the distinction between more humid, higher elevation, northern highland subfossil communities versus more arid, lower elevation, southern subfossil communities. This hypothesis requires further exploration using explicit biogeographic tools.

CONCLUSIONS

The presence of forest-adapted, characteristically southern species at Christmas River provides support for two hypotheses: first, that a dispersal corridor likely once extended across the
southern part of the central highlands. Preliminary evidence suggests that this corridor, perhaps discontinuously forested, could have been a northern extension of habitat typical of more southern regions, although a non-analog community of mixed eastern and southern plant communities cannot be excluded without paleoecological data. Second, it is clear that this corridor supported a primate assemblage that differed from primate communities further north. With further exploration, the faunal material from Christmas River will provide an unprecedented opportunity to decipher ecological changes that have taken place in south central Madagascar during the Holocene.

ACKNOWLEDGEMENTS

We appreciate the help of Désiré Randrialisatra, Angelin Gilbert Razafitrisahoarana, and local residents who participated in field work at Christmas River. Our work was carried out in collaboration with the Département de Paléontologie et Anthropologie Biologique, Université d’Antananarivo and the Centre ValBio (Centre de Formation International pour la Valorisation de la Biodiversité). We especially thank Thérèse Périn-Deville for assistance with the French abstract. We would also like to acknowledge three anonymous reviewers. We are grateful to our funding sources: American Philosophical Society Franklin Research Grant, American Association of Physical Anthropologists Professional Development Award, The Claire Garber Goodman Fund to KMM, UCOP Lab Fees No. 115818 to BEC, University of Helsinki to JJ, National Science Foundation (SBR 96-30350), National Geographic Society (7692-04) to ELS. This is DLC publication number 1222.

REFERENCES


ISSUE 1 — JUNE 2012