

DESCRIPTION OF A NEW SPECIES OF SUBFOSSIL
EAGLE FROM MADAGASCAR: *STEPHANOAETUS*
(AVES: FALCONIFORMES) FROM THE DEPOSITS
OF AMPASAMBAZIMBA

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Abstract.—Several bones recovered from subfossil deposits at Ampasambazimba, Madagascar, are described as a new species of eagle, *Stephanoaetus mahery*. These bones presumably date from the Holocene. *S. coronatus*, occurring on the African mainland, is the only extant member of this genus, and throughout much of its range feeds extensively on primates weighing up to about 12 kg. Bones of a remarkable assortment of lemurs have been recovered from Ampasambazimba and it is suggested that *S. mahery* may have preyed upon primates. Further, the legendary *Rokh*, a giant bird reputed to have occurred on Madagascar, from the tales of Sinbad and Marco Polo, may have been derived from *S. mahery*.

Résumé.—Une nouvelle espèce d'aigle, *Stephanoaetus mahery*, fait l'objet d'une description réalisée à partir de divers ossements provenant des dépôts subfossiles d'Ampasambazimba, Madagascar. L'âge estimé de ces ossements est de l'holocène. *Stephanoaetus coronatus*, qui se rencontre sur le continent africain, est actuellement l'unique espèce connue dans ce genre. Cette espèce se nourrit communément de primates pesant environ 12 kg. De remarquables ossements de lémuriens ont été retrouvés à Ampasambazimba et il a été suggéré que *S. mahery* pourrait être un prédateur de primates. Par ailleurs, la légende de l'oiseau rock, célèbre oiseau-géant ayant été vécu à Madagascar dont on trouve des détails dans l'Histoire de Sinbad le marin et de Marco Polo pourrait être celle de *S. mahery*.

Famintinana.—Taolambiby maro hita avy tao amin'ny faritra misy taratsiefan-taolambiby ao Ampasambazimba, Madagasikara, no noheverina fa karazamboromahery vaovao, *Stephanoaetus mahery*. Araka ny tombatombana mikasika ireo taolana ireo, dia efa hatramin'ny vanimpotoana jeozolozika "Holocène" no nisian'izy ireo tao ambanin'ny tany. *S. coronatus*, hita any amin'ny kaotinantana afrikana, no hany karazana mitovy amin'io mbola velona ankehitriny izay mivelona ara-dalana amin'ny fihinanana karazana varika milanja sahabo ho 12 kg eo ho eo izay hitany ao amin'ny faritra iainany. Mbola nahitana karazan-taolambiby voafaritra ho varika ihany koa tao Ampasambazimba, noho izany azo heverina fa io *S. mahery* io dia nihaza sy nihinana karazambarika. Ankoatr'izany, ilay angano mikasika an'ilay hoe "Rokh" na ilay vorombe malaza niana tany Madagasikara, nalaina avy tao amin'ny Tantaran'i Sinbad sy Marco Polo dia mety tsy ho hafa fa'ity atao hoe *S. mahery* ity ihany.

The modern bird fauna of Madagascar is well-known for its high level of endemism, of the 201 extant resident species 105 (52%) are endemic (Langrand 1990). During the

course of the last few millennia the island has undergone drastic ecological change, a portion of which clearly is human induced (Perrier de la Bâthie 1921, Battistini & Vêr-



Fig. 1. Tarsometatarsus of *Stephanoaetus mahery*, new species, holotype, MAD 5491, Muséum National d'Histoire Naturelle, Service de Paléontologie, Paris, left dorsal and right ventral views.

in 1972, Burney 1987). In general, little is known about what effects these changes have had on the avifauna. The best known group of extinct birds on the island is the elephant birds (Family Aepyornithiformes) which consisted of at least seven species in two different genera (Brodkorb 1963). The exact sequence of events that led to their extinction is unknown, but at least one species may have been extant until the turn of the 17th-century, about the same time Europeans arrived on Madagascar (Flacourt 1658, p. 165). Other smaller bird species are known to have gone extinct in the past few millennia (Milne Edwards & Grandidier 1895, Andrews 1897, Goodman & Raavoavy 1993).

One of the best known subfossil localities on Madagascar is Ampasambazimba, located about 85 km west of the capital city of Antananarivo. The site is at the edge of a former lake created by the damming of a river by a lava flow. Subsequently, the lava barrier was downcut, and the lake drained

and successively infilled to form a marsh (MacPhee et al. 1985). During excavations at Ampasambazimba a large number of bird bones were recovered, which until now remained largely unstudied. The majority of this material consists of waterbirds, but bones of raptorial birds were also recovered. Within this material are elements of a large eagle previously unknown to science and here it is proposed to call it:

Stephanoaetus mahery, new species

Figs. 1, 2

Holotype.—Left tarsometatarsus, collections of the Laboratoire de Paléontologie, Museum National d'Histoire Naturelle, Paris, MAD 5491 (Figs. 1, 2). The element is complete except a portion of the hypotarsus is broken.

Locality.—Ampasambazimba, Madagascar, and accessioned in 1925 as part of a collection of over 750 specimens donated by "Gouvernement general de Madagascar

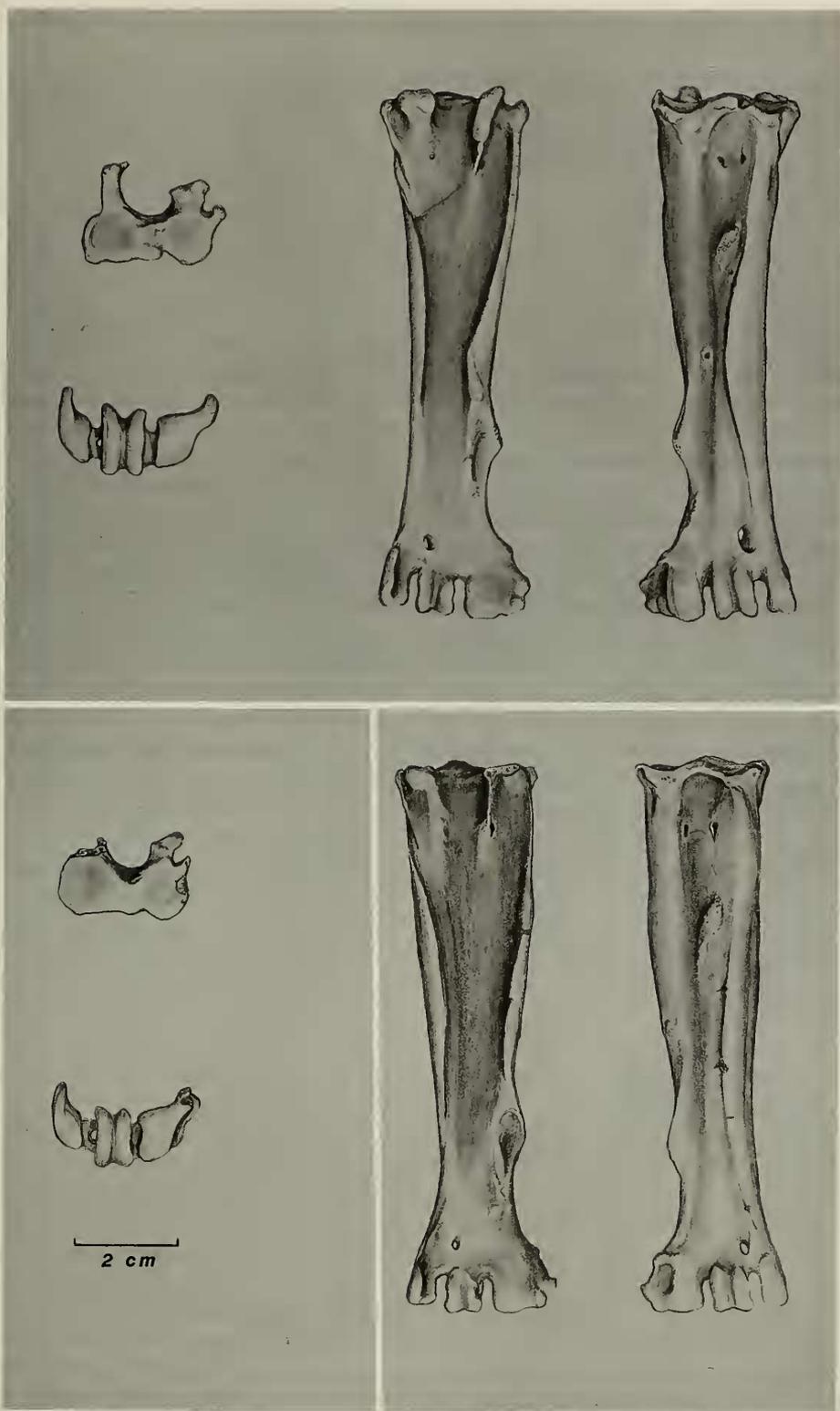


Fig. 2. Comparison of *Stephanoaetus coronatus* (MNHN 1901.209) tarsometatarsus (top) and *S. mahery* (MNHN MAD 5491) tarsometatarsus (bottom).

par l'intermediaire de M. Samat" and consisting of "ossements d'oiseaux sub-fossiles provenant d'Ampasambazimba, Antsirabe, et Morarano près de Betafo (W. d'Antsirabe)." The locality listed in the general catalog for the holotype is Ampasambazimba. Before 1925 several different excavations were conducted at this site and it is impossible to determine during which season the holotype was collected.

Chronology.—No radiometric date is available for the *Stephanoaetus mahery* remains. They are presumed to be Quaternary, probably Holocene. This is supported by material of *Megaladapis grandidieri*, an extinct lemur excavated from Ampasambazimba, that has yielded a radiocarbon date of 1035 ± 50 years B.P. (Tattersall 1973). However, since no stratigraphic information is available for the Ampasambazimba material reported on herein, it is unknown if the *Megaladapis* and *Stephanoaetus* remains were associated.

Measurements of holotype.—Greatest length 108.0 mm; proximal breadth 26.1 mm; and distal breadth 27.9 mm. (See von den Driesch 1976, fig. 62a–c for illustrations and descriptions of the measurements.)

Etymology.—The name *mahery* is from the Malagasy adjective meaning powerful. This is in reference to the presumed strength this eagle would have possessed.

Diagnosis.—The falconiform tarsometatarsus is one of the most distinctive osteological elements of raptors and has important systematic characters for diagnosing genera (Jolly 1977). The type specimen of *S. mahery* is exceptionally robust in both overall size and proportions. Articular surfaces and muscle attachments are exceptionally prominent. The specimen was compared to all genera of African eagles, and with the exception of *Stephanoaetus*, these are morphologically different. The Ampasambazimba tarsometatarsus is referred to the genus *Stephanoaetus* by the following characters (terminology follows Baumel [1979]): position of foramina vascularia

proximalia, particularly in reference to the crista plantaris mediana; configuration of the sulcus extensorius and associated muscle attachments; and proportion and morphology of the trochlea metatarsi I, fossa metatarsi, foramen vasculare distale, sulcus hypotarsi, and crista hypotarsi (medialis and lateralis). The holotype tarsometatarsus of *S. mahery* differs from comparative material of *S. coronatus* by being longer ($t_{10} = 2.15$, $P = 0.028$, Table 1). Further, the cristae plantares are more prominent and sulcus flexorius deeper in *coronatus* than *mahery*.

Paratypes.—All in collections of the Laboratoire de Paléontologie, Museum National d'Histoire Naturelle, Paris, and consisting of distal pedal phalanges (claws)—first digit of right side (MAD 5428) and left side (MAD 5423), distal one-quarter of left ulna (MAD 5587), and pelvic fragment (MAD 4944). Except for MAD 5428, which is from Ampasambazimba and is part of the same accession as the holotype, exact collection localities of the other bones are unknown, but are presumably from Quaternary deposits on Madagascar.

Discussion.—The genus *Stephanoaetus* was previously unrecorded on Madagascar, and *S. mahery* represents the largest known bird of prey to inhabit the island during the Quaternary. The extant raptor community contains distinctly smaller birds, except for the Madagascar Fish Eagle (*Haliaeetus vociferoides*), which in modern times is limited to the northern and northwestern portion of Madagascar, is one of the rarest eagles in the world (Langrand 1990).

The majority of raptors show sexual size dimorphism with females being larger than males, as is the case with *S. coronatus* (Brown et al. 1982). Since comparative material of *S. coronatus* used in this study is comprised of both sexes, and the holotype subfossil tarsometatarsus is larger than all of these modern specimens, it is concluded that *S. mahery* does not fall within size variation of *S. coronatus* (Table 1). Six of the eleven specimens of *S. coronatus* used in

Table 1.—Tarsometatarsus measurements (mm) of the holotype of *Stephanoaetus mahery* and a series of extant *S. coronatus*.

Taxa	Greatest length	Proximal breadth	Distal breadth
<i>mahery</i> , sp. nov.			
MAD 5491	108.0	26.1	27.9
<i>coronatus</i>			
Male (n = 2)	99.7, 102.4	22.2, 25.8	23.5, 27.2
Female (n = 2)	100.5, 102.9	25.2, 25.3	26.2, 27.2
Combined (n = 11) ¹	102.0 ± 2.7	25.1 ± 1.6	27.0 ± 1.4
	98.2–105.9	22.0–26.7	23.5–28.9

¹ Combined descriptive statistics presented as mean ± standard deviation and followed by range.

this study were captive birds; no significant difference in size or osteological characters was found between wild and captive individuals. The paratype material of *S. mahery* is difficult to distinguish from modern *S. coronatus*, at least in part due to the fragmentary nature of some of the bones.

One intriguing question associated with the discovery of *S. mahery* is what did it eat? Food habits of *S. coronatus*, the only extant member of this genus and which occurs throughout much of sub-Saharan Africa (Brown et al. 1982), have been studied in the Kibale Forest of Uganda (Skorupa 1989, Struhsaker & Leakey 1990), where this immensely powerful eagle feeds on an assortment of relatively large prey. This includes blue duiker (*Cephalophus monticola*) and Peter's duiker (*C. callipygus*), adults of the latter species weigh up to 20.5 kg (Kingdon 1982); red colobus (*Colobus badius*), adult males weigh between 9 and 12.5 kg (Kingdon 1974); black and white colobus (*C. guereza*), adult males weigh up to 10.5 kg (Struhsaker 1975); and a variety of smaller primates, carnivores, and birds. By number, over 80% of this eagle's diet at Kibale is composed of primates (Struhsaker & Leakey 1990).

On the basis of tarsometatarsus length, the general size of *S. mahery* is estimated to be comparable to that of *S. coronatus*, and it is assumed that the former species would have been capable of taking equivalent size prey. Further, the long hind talons

of *S. coronatus* are important to subdue large prey. The hind talons of *S. mahery* resemble those of *S. coronatus* in absolute size and massiveness (Fig. 3). Thus, it is assumed that *S. mahery* would have been as formidable a predator as modern *S. coronatus*.

Fourteen species of lemurs, seven of which are extinct, have been identified from the Ampasambazimba material (Tattersall 1973, Dewar 1984). If indeed these species were temporally sympatric, and there is evidence that they were, this assemblage would represent the highest primate species diversity known for any site, fossil or modern, on the island (Nicoll & Langrand 1989), and perhaps anywhere else in the world. Body weights of lemurs known from the deposits of Ampasambazimba and that might have been preyed upon by *S. mahery* include (from L. Godfrey, pers. comm. for extinct taxa [*] and Richard & Dewar [1991] for extant taxa): **Archaeolemur edwardsi* (24.5 kg), **Hadropithecus stenognathus* (16.7 kg), **Mesopropithecus pithecoides* (9.7 kg), **Pachylemur insignis* (10.0 kg), *Indri indri* (6 kg), and *Propithecus* spp. (3.6–5.8 kg).

Primatologists studying behavior of modern lemurs have observed that several large diurnal and social species have a strong stereotypic response to birds of prey flying overhead (Sauther 1989, Macedonia 1990). Evolution of this behavior is difficult to explain in light of little evidence of the extant raptors predated on this group of lemurs, young or old (Goodman et al. 1993). Recent

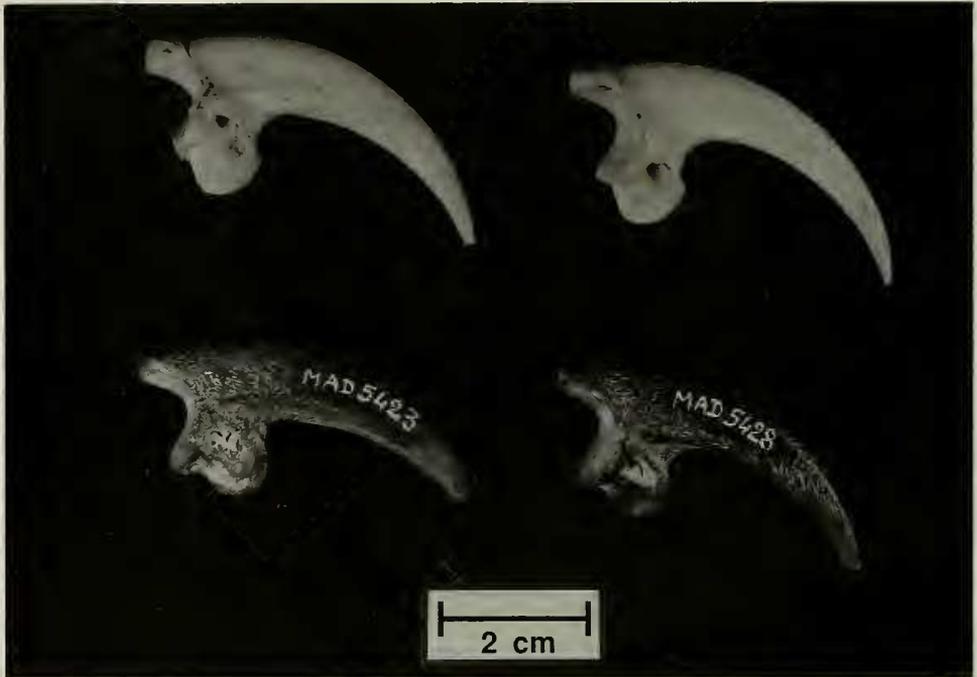


Fig. 3. Comparison of *Stephanoaetus coronatus* (MNHN 1901.209) first digit from left and right side (top) and *S. mahery* first digit left side (MNHN MAD 5423) and first digit right side (MNHN MAD 5428) (bottom).

discovery of another extinct eagle on Madagascar in the genus *Aquila*, and the possibility that it ate diurnal lemurs, has been interpreted as a potential evolutionary force in the development of this anti-predator behavior (Goodman 1994). Now that Quaternary deposits in Madagascar have yielded remains of *Stephanoaetus*, an eagle larger than *Aquila* and a presumed primate specialist, this explanation can be further supported. Hunting techniques used by *S. coronatus* such as puncturing the prey's heart with its massive and powerful hind talons or by flight blows (Brown et al. 1982, Leland & Struhsaker 1993) may leave no or subtle tell-tale marks in the victim's bone remains. However, a detailed study of food remains recovered from *S. coronatus* nests and feeding sites might reveal some characters that would help to diagnose how this eagle dispatches and dismantles prey. These characters could then be compared to lemur material excavated at Ampasambazimba to

determine if some of the bones recovered from the site are prey remains of *S. mahery*.

The legendary *Rokh* of numerous Middle Age travelers, including Marco Polo, and from the tales of Sinbad and *A Thousand and One Nights*, may have been a bird found on Madagascar. Several authors have equated the *Rokh* with elephant birds (e.g., Lavauden 1931), while others have rejected this idea and identified it as a bird of prey (Decary 1937, Allibert 1992). If indeed the *Rokh* is not totally imaginary, inhabited Madagascar, and was a large raptor, it may have been derived from *S. mahery*.

Comparative material examined.—Few skeletons of large eagles exist in the world's museum collections, and a substantial portion of these are those of birds that died in captivity (*). The holotype of *S. mahery* was compared to modern skeletal material of the following eagles (See Acknowledgments for definitions of acronyms.): *Haliaeetus vociferoides* (MNHN not cataloged; UA 77), *H. vo-*

cifer (BMNH 1954.38.51; MNHN 1908.60), *Ichthyophaga ichthyaetus* (BMNH not cataloged), *Terathopius ecaudatus* (UMMZ 158569), *Spilornis cheela* (MNHN A4025), *Morphnus guianensis* (FMNH 106705), *Harpia harpyja* (BMNH 1862.3.19.14, 1862.3.14.19; MNHN *1878.577), *Pithecophaga jefferyi* (BMNH 1910.2.11.1a, *1961.23.1; FMNH *106496), all extant *Aquila* spp. (excluding *A. gurneyi*), *Hieraaetus fasciatus* (MNHN *1870.326, *1910.424), *Lophaetus occipitalis* (FMNH 313295; MNHN 1880.32; USNM 431671), *Spizaetus cirrhatus* (BMNH 1850.8.15.13; FMNH *289556), *S. ornatus* (BMNH 1952.1.177; FMNH *288164; MNHN *1889.150), *Stephanoetus coronatus* (AMNH *4256; BMNH 1952.1.178, 1954.30.42; MNHN *1901.209; NMK OB125, OB849; USNM *345669, *346652, *346654, *346655, 432180), and *Polemaetus bellicosus* (BMNH 1853.10.21.1, 1952.1.179, 1954.30.43, 1957.9.1, 1984.101.1; USNM 430533).

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