The early specimens of the potto *Perodicticus potto* (Statius Müller, 1776) in the National Museum of Natural History, Leiden, with the selection of a neotype

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The potto was first recorded and figured by Willem Bosman in 1704. The name *Lemur potto* Statius Müller, 1776 is exclusively based upon Bosman's account and figure, which are reproduced in full. The type locality is Elmina on the Gold Coast, the present Ghana. No type specimen was collected. The early pottos in the Leiden Museum are listed and their history is given, with special reference to the animals obtained by H.S. Pel. The publications on this material are reviewed. An adult female, RMNH 39375: mounted skin and skeleton acquired by Pel in 1849 at Dabocrom (Dabo Krom) near Sekondi, coastal Ghana, is designated the neotype of *Lemur potto* Statius Müller, 1776. The neotype is extensively described and figured. Taxonomic notes on the putative (sub)species of pottos are given, with a justification for establishing the neotype.

1. Bosman's Potto

The potto, *Perodicticus potto* (Statius Müller, 1776), was probably the first African "prosimian" that was seen by European travellers and traders. The earliest description and illustration of the animal was published in 1704 by Willem Bosman, in a popular treatise on the Gold Coast (the coastal districts of present Ghana) - a work overlooked by most 18th-century scientists including Linnaeus. It was the German/Dutch theologian and zoologist Philippus Ludovicus Statius Müller (often referred to as P.L.S. Müller or Muller), who realized that Bosman's "potto" was an animal that had escaped the attention of the scientific world. Statius Müller published a serial work in German on the animal kingdom, based on Linnaeus's classification. In the first volume of this work, dealing with mammals and published 1773, he made no reference to the potto, but he included the species in the first supplement, published in 1776 (not 1766 as stated by many authors; actually, the preface to this volume is dated 4 January 1776, one day before Statius Müller's sudden death). On p. 12 of this supplement, Statius Müller correctly arranged the species within the Order Primates under the name *Lemur potto* and described it as follows:

"I. a. Der Potto. Lemur Potto. Er ist dem Langschleicher (Lemur tardigradus oder Loris) sehr ähnlich[.] Es wird ihm aber vom Boßmann ein Schwanz zuerkannt, der jedoch kürzer als der Leib ist. Der Kopf ist unförmlich dick, der Körper grob und mit

rothen Haaren bedeckt. Das Vaterland ist Guinea". (I. a. The Potto. Lemur Potto. It is very similar to the long [= slow] crawler (Lemur tardigradus or Loris). It is described by Boßmann as having a tail which, however, is shorter than the body. The head is ungainly thick, the body coarse and covered with red hairs. The home country is Guinea).

From this very brief description, it would perhaps be hard to recognize a potto, were it not for Statius Müller's reference to Bosman (Germanized to Boßmann). In the second volume of his book on the Gold Coast, Bosman (1704b) deals with animal life in that country. On pp. 32-33 he gives a fairly extensive though most curious account of an animal that the indigenous people called "potto" and that he calls "Luyaerd" (Sluggard). It is illustrated by a crude but clearly recognizable figure (see Fig. 1) in the plate facing p. 35, fig. 4. Since this book is quite rare, the relevant paragraphs are cited here in full.

"Onder No. 4. bekoomt UE. De afteekening van een Beest, 't geen by de Negers de naem van Potto draegt / doch onder ons is 't bekend met die van Luyaerd; buiten twijfel wegens desselfs loomen en tragen aert; want om tien treeden voort te loopen, of liever kruipen, heeft het een geheelen dag van noden.

Eenige schrijven, dat so wanneer een deeser beesten op een boom geklommen is / hy daer niet weeder af sal koomen, voor dat hy niet alleen de vrugt, maer selfs ook de bladen heeft verteerd en opgegeeten; vervolgens glad en vet van denselven af klimmende / om op een anderen boom te klauteren, heeft hy tot dien arbeid so langen tijd van doen / dat hy / op den anderen koomende / t'eenemael vermagerd en uitgeteerd is; en byaldien beide die boomen wat ongemeen hoog waren / of wel datse een verre

Fig. 1. *Perodicticus potto*: Bosman's (1704b) drawing of the potto.

weg van den ander stonden / en dat onderweegen niets te eeten was / so sou hy / midden in de marsch, van honger moeten sterven. So als 't hier ter neder gesteld is / heb ik het by andere geleesen, sonder voor de waerheid daer van te derven instaen, alhoewel'er de Negers ook niet vreemd van zijn.

't Is soo een afschouwelijk en leelijk beest, dat ik geloof / desselfs wederga op den gantschen Aerdbodem niet te vinden is: de prent vertoond den selven heel eigentlijk en na het leeven: desselfs voorste pooten gelijken wonder wel na Menschen-handen: de kop is na evenmatigheid van sijn lighaem ongemeen groot: de geene / waer na deese prent geteekend is / was muisvael van couleur; doch den selven was noch geheel jong, dies hy sig ook met een gladde huid verbeeld; doch alsse oud worden / gelijk ik'er in den jare 1699. hier aen Elmina eenen gesien heb / so sijnse van een rosse couleur, als wanneer haer het hair even als met wolvlokken in malkander sit. Verders weet ik van deese beesten niet te seggen, als datse / sonder'er een afgrijsen van te hebben / niet konnen aengesien worden / en sonder dat'er anders eenige seldsaemheid, als desselfs sonderlinge leelijke gedaente, aen is."

An English edition of Bosman's work was published in 1705. The story on the potto is given on p. 250, accompanied by a reduced version of the plate, facing p. 248, fig. 4. It reads as follows:

"No. 4. Is a Draught of a Creature, by the *Negroes* called *Potto*, but known to us by the Name of Sluggard, doubtless from its lazy sluggish Nature; a whole Day being little enough for it to advance ten Steps forward.

Some Writers affirm, that when this Creature has climbed upon a Tree, he doth not leave it until he hath not only eaten up the Fruit, but the Leaves intirely; and then descends fat and in very good case in order to get up into another Tree; but before his slow pace can compass this, he becomes as poor and lean as 'tis possible to imagine: And if the Trees be high, or the way any thing distant, and he meets with nothing on his Journey, he inevitably dies of Hunger, betwixt one Tree and the other. Thus 'tis represented by others, but I will not undertake for the Truth of it; though the *Negroes* are apt to believe something like it.

This is such a horrible ugly Creature that I don't believe any thing besides so very disagreeable is to be found on the whole Earth; the Print is a very lively Description of it: Its Fore-feet are very like Hands, the Head strangely disproportionately large; that from whence this Print was taken was of a pale Mouse colour: but it was then very young, and his Skin yet smooth; but when old, as I saw one at *Elmina* in the Year 1699. 'tis red and covered with a sort of Hair as thick set as Flocks of Wool. I know nothing more of this Animal, than 'tis impossible to look on him without Horrour, and that he hath nothing very particular but his odious Ugliness."

Willem Bosman was chief "factor" (trader) of the Dutch "factory" (trade post) St George d'Elmina and, by the end of the 17th century, second in command of the Dutch trade posts in the Gold Coast, all of which were situated on the coast of present-day Ghana. He apparently had seen at least two pottos, a young animal (the one figured in his plate) and an adult. The latter he saw at Elmina in 1699. His description is very brief though not totally inadequate, but it is hard to see why Bosman took such a dislike to the animal. The story of its habits was based on hearsay, regarded as hardly credible by Bosman himself. Van Campen (1859: 5) remarks on Bosman's plate: "Eene afbeelding naar het levend dier bezitten wij niet, tenzij men de zeer onvoldoende figuur van Bos-

man, den eersten ontdekker der soort, als zoodanig wilde aanmerken, welke afbeelding evenwel naauwelijks eene aanhaling waardig is." (We do not possess an illustration of the living animal, unless one would regard as such the very inadequate figure by Bosman, the first discoverer of the species; this drawing, however, scarcely deserves to be mentioned). That may be so, but the animal figured by Bosman is nevertheless recognizable as a potto, so its identity is beyond doubt.

Since Statius Müller's description of the species was exclusively based on Bosman's account, the animals described and figured by that author are syntypes of *Lemur potto* Statius Müller, 1776. It is obvious that they were not preserved. The type locality may be restricted to Elmina in the present Ghana, the Dutch headquarters in the area in those days and the place where Bosman saw at least one of his pottos in 1699.

Several later authors overlooked Statius Müller's work, attributing the name *Lemur potto* to Linnaeus as, e.g., Geoffroy (1812: 165), or rather Gmelin (1788: 42) as, e.g., Jentink (1892: 60). Desmarest (1820: 104), referring to Bosman, Geoffroy and Gmelin, renamed the species *Galago guineensis*.

Bennett (1831) was the first to give a scientific description of the potto that was not based upon Bosman's story, but on a specimen in the London Museum collected in Sierra Leone by J. Boyle [in 1825]: "… a *Lemuridous* species, which is probably the animal noticed and imperfectly represented by Bosman under the name of *Potto*." He established a new genus *Perodicticus* and described the animal from Sierra Leone as *Perodicticus Geoffroyi*. Lesson (1840: 238-239), referring to Bosman, Gmelin and Bennett, renamed the species *Potto Bosmanü* [= *Bosmanii*], but confined its range to "Les environs de Sierra-Léone". He overlooked the Gold Coast and strangely confounded Bennett's (i.e. Boyle's) notes on the potto and on the giant rodent *Aulacodus swinderianus* Temminck, 1827 (*Thryonomys swinderianus*), inferring a diet of grains and groundnuts.

2. The early pottos in the Leiden Museum

The Primates in the National Museum of Natural History (Rijksmuseum van Natuurlijke Historie, RMNH) in Leiden were first catalogued by Schlegel (1876). Later, Jentink compiled three catalogues of the mammalian collections, published in 1887 (osteological material), 1888 (skins, first part) and 1892 (skins, second part including Primates). In 1892, the Leiden Museum had seven pottos. Jentink's entries are given here in full, with the present catalogue numbers added [RMNH 39375-39381]. The history of the specimens will be discussed in detail.

Jentink (1887: 52): *Nycticebus potto* E. Geoffroy.

a. Squelette d'une femelle adulte montée. Côte d'Or. Pel. Schlegel, Cat. Nº 6. [RMNH 39375]

b. Crâne d'une jeune femelle montée. Côte d'Or. De M. Spengler. Incomplet. Schlegel, Cat. Nº 7. [RMNH 39377]

Jentink (1892: 60-61): *Nycticebus potto* Gmelin.

a. Femelle adulte montée, figurée dans l'ouvrage intitulé: "Bijdragen tot de Dierkunde, 1852". Côte d'Or. Des collections de M. Pel. Schlegel, Cat. Nº 1. (Sq. *a* du Cat. Ost.). [RMNH 39375]

b. Mâle à-peu-près adulte monté. Côte d'Or. De M. Pel. Schlegel, Cat. Nº 2. [RMNH 39376]
c. Jeune femelle montée, figurée dans: van der Hoeven's Tijdschrift, 1844, pl. 2. Côte d'Or. Des collections de M. Spengler, 1823. Schlegel, Cat. Nº 3. (Cr. *b* du Cat. Ost.). [RMNH 39377]
d. Jeune femelle montée. Libéria, St. Paul's river, Soforé-place. Des collections des M.M. Büttikofer et Sala, 13 Mai 1880. [RMNH 39378]
e. (alc.). Jeune mâle. Libéria, Junk-river, Schieffelinsville. Des collections des M.M. Büttikofer et Stampfli, 14 Avril 1887. [RMNH 39379]
f. (alc.). Individu très adulte. Côte d'Or. 1875. Schlegel, Cat. Nº 4. [RMNH 39380]
g. (alc.). Individu à l'âge moyen. Côte d'Or. De M. Pel. Schlegel, Cat. Nº 5. [RMNH 39381]

Spengler's potto

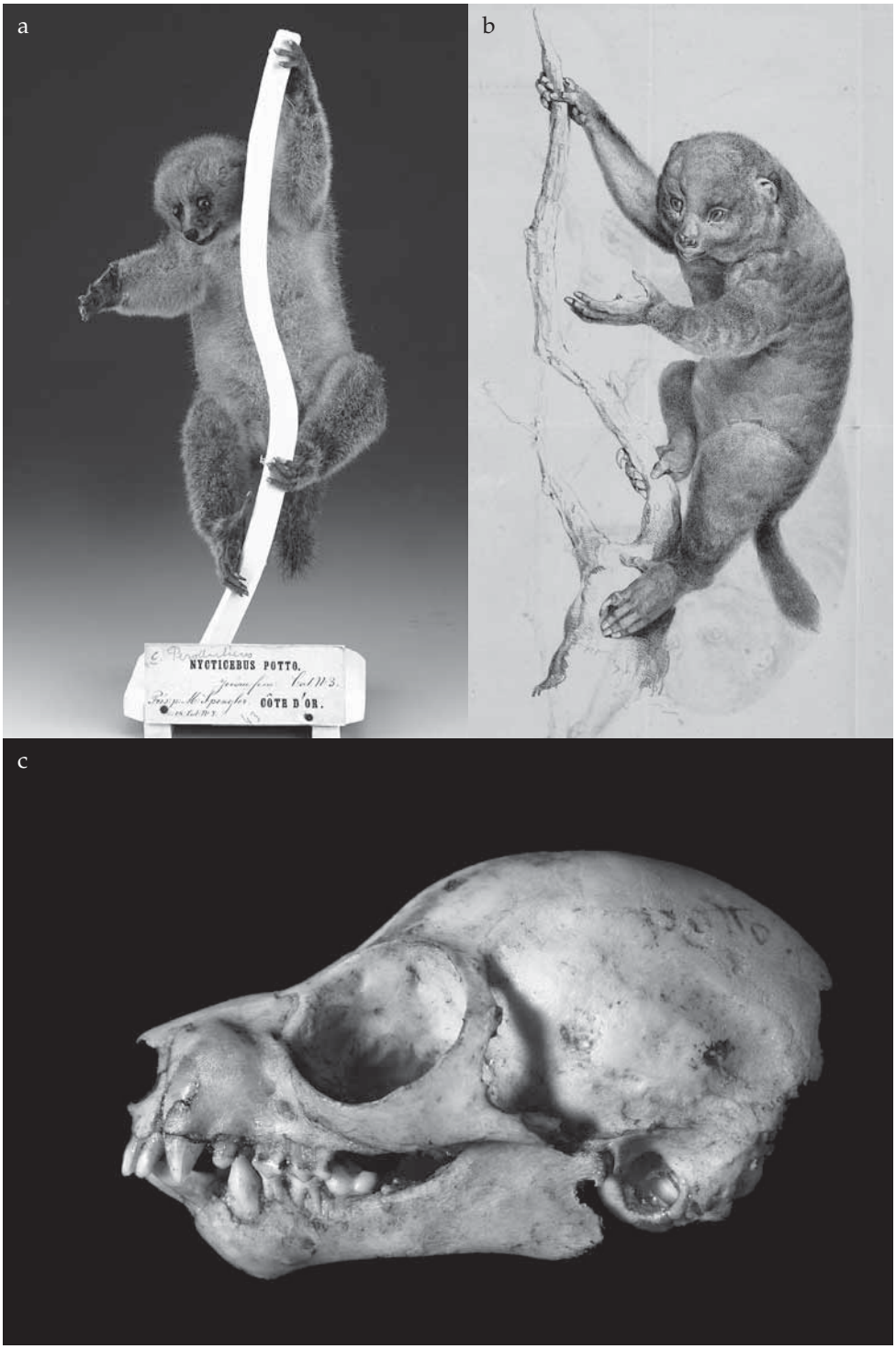
RMNH 39377. – Probably the earliest potto in any zoological collection is a juvenile obtained by the Leiden Museum in 1823. Unfortunately, nothing is documented besides the locality "Côte d'Or" (Gold Coast). It is attributed to M. (Monsieur) Spengler; the pedestal reads, in the handwriting of C.J. Temminck, the first director of the Leiden Museum: "Donné par L. Spengler". This probably was Lorenz Spengler from Copenhagen, who had a private zoological collection including material from West Africa. However, this Spengler had died in 1807, so cannot have donated the animal himself, though it may have originated from his collection. It is a beautifully preserved skin, with the back, flanks, legs and tail clad in the white-tipped fur so characteristic of young pottos; cf. Bosman's description of the difference in colouration between a young and an adult animal.

The skull of this specimen is briefly referred to by Van der Hoeven (1841: 341-342) who later, after having found the accompanying skin, published a detailed description of this potto, illustrated with two plates showing the mounted skin and the skull (Van der Hoeven, 1844: 24-27, pl. I fig. 3, pl. II). These are the earliest figures of a potto in the scientific literature. The skin and damaged skull of RMNH 39377 are immediately recognizable from these plates (see Fig. 2a-d).

In his zoological sketches of the Guinea coast, Temminck (1853: 47) writes of this specimen: "Ce ne fut qu'en 1833, que notre musée obtint un jeune individu, à peu-près de même âge que celui reçu à Londres; le même dont M. le Professeur van der Hoeven a fait mention et dont il donne une figure[2]." (It was only in 1833 [lapsus for 1823] that our museum obtained a young individual, of about the same age as the one received in London; this is the one that Professor van der Hoeven has mentioned and figured[2]). The footnote refers to Van der Hoeven's 1844 publication, though grossly misquoted.

Pel's pottos

Three pottos were collected by Hendrik Severinus Pel, also at the Gold Coast. Pel resided at several of the Dutch trade posts in that country between December 1840 and December 1850, when he went on leave, and again from January 1852 until March 1855, when he finally returned to the Netherlands. He made extensive zoological collections


a
NYCTICEBUS POTTO.
CÔTE D'OR.
b
c

for the Leiden Museum, mainly of vertebrates. The material collected during his first sojourn lies at the base of Temminck's (1853) Esquisses zoologiques sur la côte de Guinée, of which only the volume on mammals was published. Although most specimens were not very accurately documented in those days, additional data may often be found in the correspondence and shipment inventories preserved in the museum's archives, as is the case here. Holthuis (1968) gives a detailed account on Pel and his activities as a collector, including a map of the places where he worked.

Temminck had asked Pel specifically to look for the enigmatic potto, of which Spengler's specimen was the only one known to him. It took Pel many years to find it. In a letter of 24 August 1841 (p. 9) he wrote from Saccondé (Sekondi): "*Stenops Potto* heb ik slechts een gezien welke de doctor had dezelve komt ook diep uit het bosch…" (I have seen only one *Stenops potto* which the surgeon had; this too, comes from deep in the forest). And in February 1843 (p. 5) from Dabocrom (Dabo Krom): "Tot nog toe heb ik den Potto niet kunnen bekomen, en schynt alhier dus niet gemeen te zyn,…" (Until now I have been unable to obtain the Potto, so [it] seems to be uncommon here).

Apparently, Temminck had sent Van der Hoeven's 1844 treatise to Pel, whereupon the latter gathered some more information on the species. On 8 October 1847 (p. 2) Pel wrote from Boutry (Butre, between Sekondi and Takoradi): "… en het is voornamelyk de door Bosman gegeven naam van Potto. dat ik dit beest niet verkreeg. nergens aan de kust is dezelve onder dien naam bekend. eerst door de tekening van Professor van der Hoeven. is my de rechte negernaam bekend geworden, welke is *Aposô*. en waaronder dit beest zoowel te Elmina als in Ashanta bekend is. hoe of Bosman dus aan de naam van Potto gekomen is weet ik niet. thans heb ik over last gegeven dezelve optesporen, dezelve is echter zeer zeldzaam. zyne nocturne levenswyze maakt ook dezelve moeyelyk

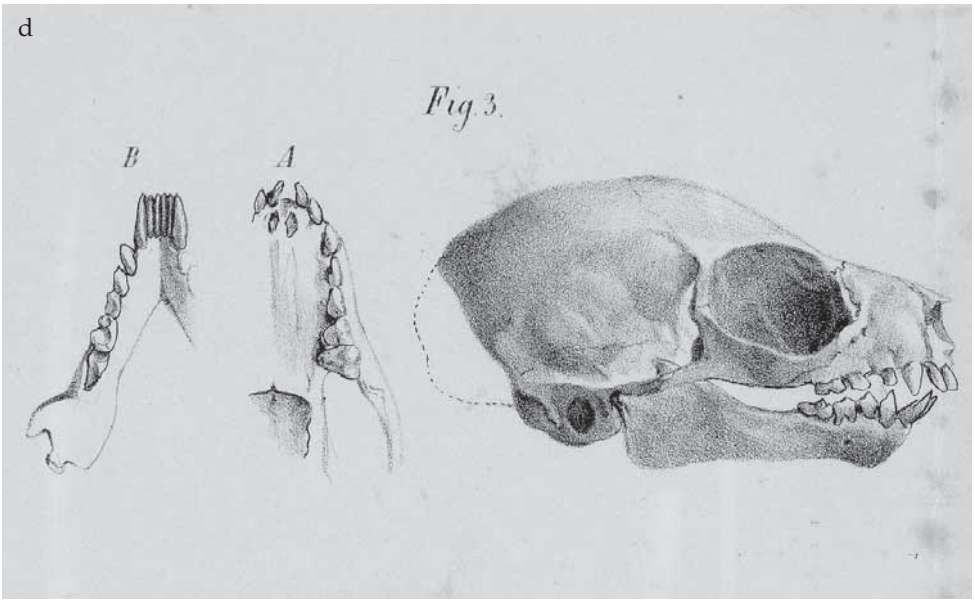


Fig. 2a-d. *Perodicticus potto*: Skin and skull of Spengler's potto RMNH 39377 compared to Van der Hoeven's (1844) pl. I fig. 3 and pl. II.

te krygen is. volgens de negers. is dit beest, zeer vasthoudend, eens iets in de poot hebbende. laat hy niet meer los. en zelf geschoten wordende, laat hy zich niet vallen alvorens de spieren ontbonden zyn. veel grooter als de teekening is wordt hy echter niet. ik hoop maar dezelve thans te zullen krygen." (… and it is mainly [due to] the name Potto given by Bosman that I did not obtain this animal. Nowhere along the coast is it known by this name. Only through Professor van der Hoeven's drawing have I learned the correct African name, which is *Aposô*, by which this animal is known both at Elmina and in Ashanta. How Bosman came upon the name Potto, I do not know. I have now given orders to trace it, but it is very rare. Its nocturnal habits too, render it difficult to obtain. According to the Africans, this animal is very tenacious; once it has got something in its paw, it does not let go. Even when it is shot, it does not drop itself before the muscles have relaxed. However, it does not grow much larger than is shown in the drawing. I just hope I will obtain it now).

RMNH 39376. – Eventually, Pel managed to find one. In his letter of 9 March 1849 to Temminck he wrote from Boutry that a shipment would be dispatched within a few days, stating (p. 1): "Hoewel niet vele nieuwe zaken bevattende, zyn er niet te min voorwerpen by welken in het Museum nog ontbraken, … Met den *Perodicticus aporô* was ik minder gelukkig aangezien de huid van het thans gezondene exemplaar eenigsins beschadigd is, het skelet en de ingewanden zyn echter in goede staat; eenige aanteekeningen over de levenswyze van dit dier ontvangt UWEGest hiernevens – ". (Though not containing many new things, it does include some specimens still lacking in the Museum, … I was less fortunate with the *Perodicticus aporô* [Pel clearly writes an r here], since the skin now dispatched is somewhat damaged; the skeleton and the intestines, however, are in good condition. Your Honour receives herewith some notes on the habits of this animal –). These notes are not in the museum's archives; probably, they were handed to Van der Hoeven (see below).

In his next letter, probably directed to the Leiden Museum's administrator J.A. Susanna and dated 10 March 1849, Pel added (p. 1): "De thans door my overgezondene bezending bevat veele goede zaken. onderde viervoetige dieren nog eene exemplaar van de groote *Anomalurus* welke thans van Dabocrom schynt verdwenen te zijn. ten minst is deselve zeldzaam en hoogst moeyelyk te verkrygen. evenzoo is het gelegen met den *Perodicticus potto Aposô* waarvan ik thans ook een voorwerp zend, ik verkreeg deselve levend. ongelukkig is deselve aan de staart beschadigd. veroorzaakt door eene wond welke het dier reeds had toen ik het verkreeg. niettegenstaande alle aangewende moeite, heb ik nog geen tweede exemplaar kunnen verkrygen." (The shipment now dispatched by me contains many good things. Among the four-footed animals [is] another specimen of the large *Anomalurus* which now seems to have disappeared from Dabocrom. At least it is rare and very difficult to obtain. The same holds true for the *Perodicticus potto Aposô* of which I also send a specimen, which I received alive. Unfortunately its tail is damaged, caused by a wound that the animal already had when I received it. Despite all efforts spent, I have still been unable to obtain a second specimen).

The animal is listed in Pel's shipping inventory for March 1849, packed in a stoppered bottle, which means that it was preserved in alcohol. Temminck acknowledged its receipt in a draft letter of 4 July 1849, in which he urged Pel: "Verzamel ook zooveel mogelyk in grooten getale Prodicticus en Anomalurij, kan het zyn, de huiden gedroogd

en ook de skeletten." (Collect as many Prodicticus [sic] and Anomalurij [flying squirrels] as possible and in large numbers; if possible, dry skins as well as the skeletons). Pel replied to this letter on 29 November 1849.

Since Pel had not mentioned a potto in his preceding letter to Temminck dated 1 August 1848, the present animal must have been obtained between that date and February 1849. The locality is Dabocrom (Dabo Krom), as can be inferred from Pel's letter of 10 March and as it is written, in Temminck's handwriting, on the pedestal of the specimen. This village is situated just northeast of Butre and west of Sekondi (Holthuis, 1968: 9, 22-23).

The skin of RMNH 39376, now mounted (see Fig. 3a), does indeed have a damaged tail. Strangely, its skeleton and skull have not been preserved, although Van der Hoeven (1851) published an extensive description of this animal, accompanied by a plate of the mounted skin and some organs (pl. I) and another of the skeleton, with details of the skull (pl. II). He writes (p. 1): "Eerst in de tweede helft des vorigen jaars (1849) ontving het Rijks Museum van Natuurlijke Historie te Leiden de huid van een volwassen voorwerp en tevens het dier zelf in wijngeest bewaard. Van het laatste waren de ledematen afgesneden, die afzonderlijk er bijgevoegd, door wegneming der spieren, behalve voor de vervaardiging van het skelet, onbruikbaar waren. Mijne onderzoekingen konden zich dus slechts tot enkele punten van de ontleding des diers bepalen. Maar ik ben intusschen thans in staat gesteld eene afbeelding van het volwassen dier te geven, tegelijk met eene afteekening van zijn geraamte." (Only in the second half of last year (1849) the National Museum of Natural History in Leiden received the skin of an adult specimen, as well as the animal itself preserved in spirit. Of the latter, the limbs had been severed and were added separately. Due to the removal of the muscles, these were of no use except for preparation of the skeleton. My observations thus had to be restricted to only some details of the animal's anatomy. But meanwhile I have been able to provide a figure of the adult animal, together with a drawing of its skeleton.)

On p. 11-12, Van der Hoeven adds: "De Heer Pel, die met de voorwerpen, waarvan wij thans melding maakten, tevens een kort berigt over den *Potto* naar *Nederland* overzond, waarvan de Directeur van het Rijks-Museum, ons medelid C.J. Temminck, de goedheid had mij een afschrift te bezorgen, vermeldt daarin, dat mijne vroeger gegevene afbeelding hem in staat gesteld had met den waren naam, die de Inlanders aan dit dier geven, bekend te worden. Zij herkenden mijne afbeelding voor die van den *Aporô**); dezen naam draagt het dier langs de geheele kust, zoo ver aan den Heer Pel bekend is." (Along with the specimens we have mentioned here, Mr Pel also sent a short note on the *Potto* to *the Netherlands*, of which the Director of the National Museum, our co-member C.J. Temminck, kindly let me have a copy. In this he mentions that my earlier published figure had enabled him to learn the correct name by which the Natives refer to this animal. They recognized my figure as that of the *Aporô**); as far as Mr Pel knows, this name is used for the animal along the entire coast). The footnote on p. 12 elaborates on the local name: "*) Het woord Aporô geeft in de Negertaal (de Fante- of Amina-taal?), volgens het berigt van den Heer Pel, *vasthoudend* te kennen, en is aan het dier gegeven, omdat het zich, zoo als de Negers zeggen, wanneer het eenmaal iets vast heeft, liever laat dooden, dan weêr los te laten. – Volgens een ander berigt, dat ik ontving, zou het dier *Aposo* of *Aposou* heeten, en ik geloof dat deze opgave vertrouwen verdient." (According to Mr Pel's note, the word *Aporô* in the African language (the

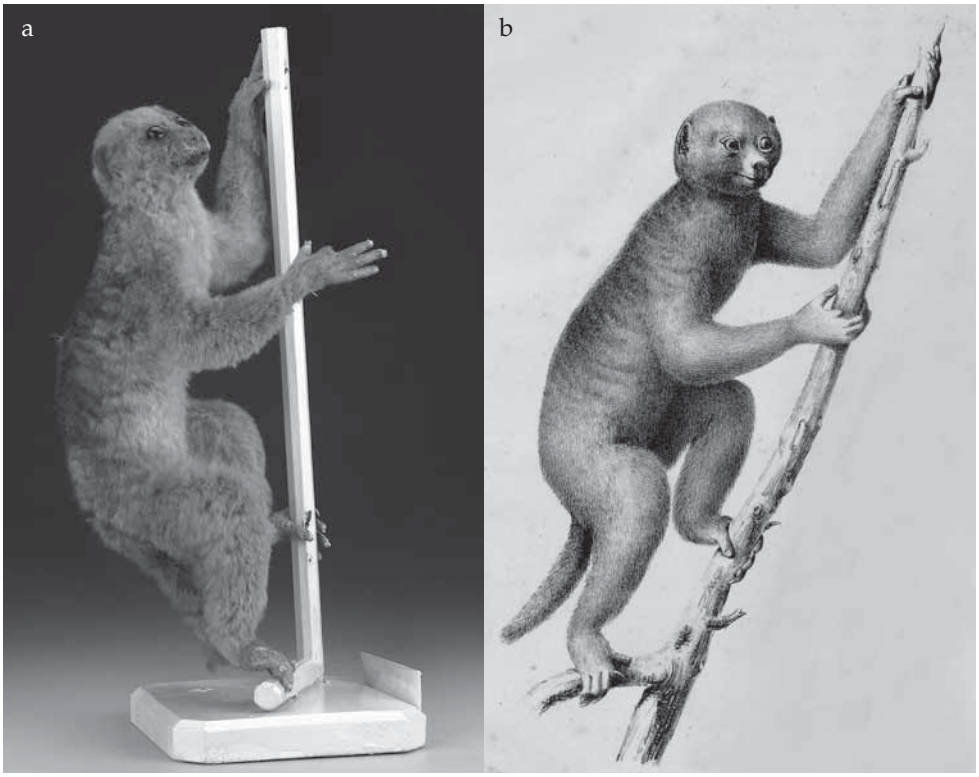
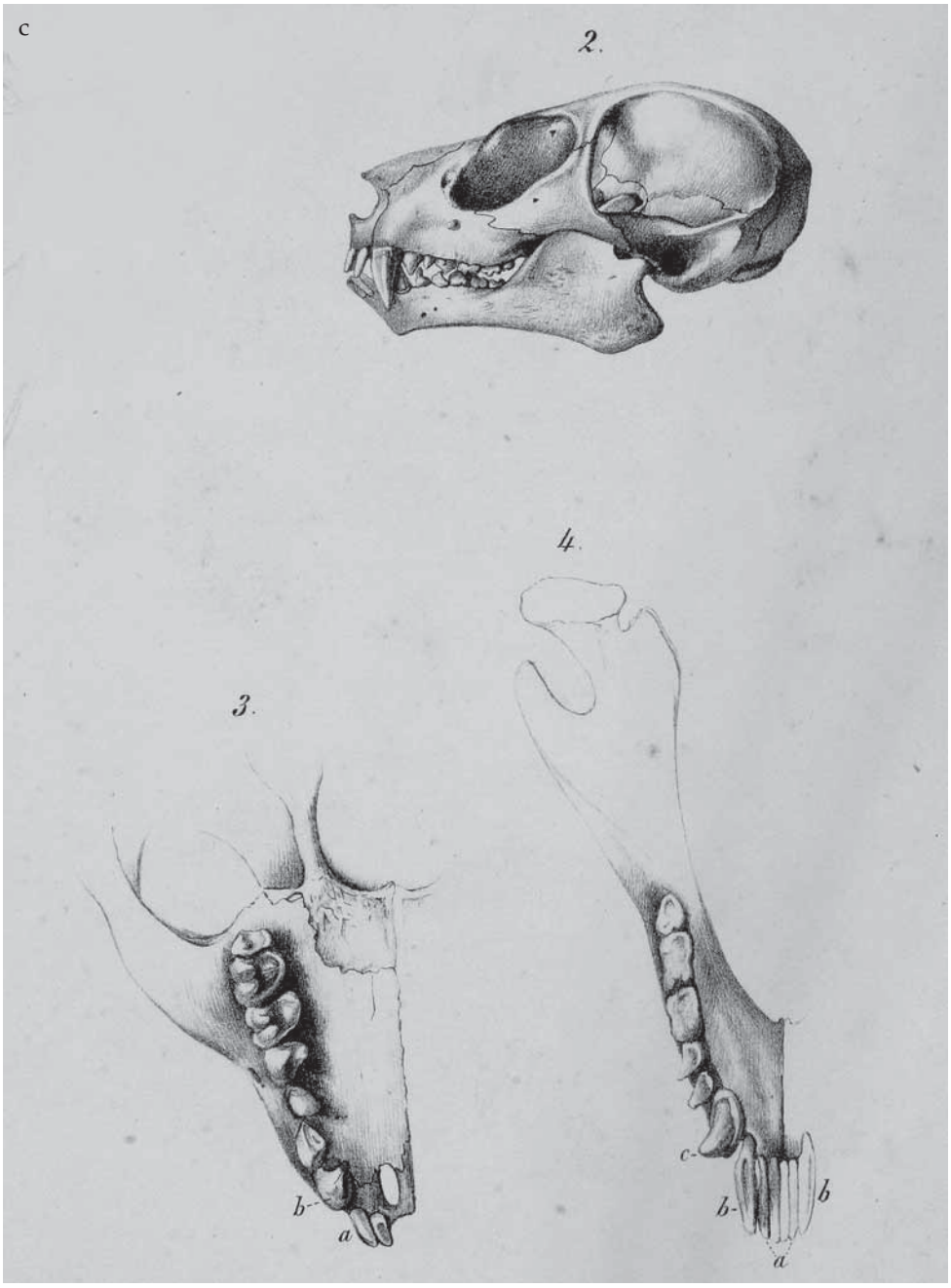


Fig. 3a-c. *Perodicticus potto*: Skin and skull of Pel's first potto RMNH 39376 and of Van der Hoeven's (1851) pl. I fig. 1 and pl. II figs 2-4.

Fante or Amina language?) means *tenacious*, because once it has got hold of something, it would have itself killed rather than releasing it. – According to another note I received, the animal is called *Aposo* or *Aposou*, and I believe that record is reliable).

On p. 12, Van der Hoeven concludes: "Het voorwerp, dat is overgezonden, werd eene maand levend waargenomen… Overigens is dit dier, waar het ook moge voorkomen, waarschijnlijk zeldzaam en van daar moeijelijk te bekomen, waaruit dan ook verklaard moet worden dat de Heer Pel, hoezeer hij reeds zeer vele jaren voor 's Rijks Museum op de kust van *Guinea* verzamelt, eerst in 1849 een voorwerp van dit dier naar *Nederland* heeft opgezonden." (The specimen that was sent had been observed alive for a month… Otherwise this animal is probably rare and thus difficult to obtain wherever it may occur, which would explain why only in 1849 Mr Pel sent a specimen of this animal to *the Netherlands*, despite having for very many years collected on the *Guinea* coast for the National Museum).

This all agrees with Pel's letters. Although on p. 11 Van der Hoeven speaks of "voorwerpen" (specimens), it is clear that, apart from Spengler's animal (RMNH 39377), he had only one specimen before him: the skin and skeleton collected by Pel. Strangely, he does not record its sex. Both the skin (pl. I, see our Fig. 3b) and the figure of the skull (pl. II, see our Fig. 3c), illustrate that the animal was not fully adult. The tail



has been "repaired" in pl. I, but for the rest, the mounted skin is recognizable as RMNH 39376. The skin is well preserved and of a bright russet colouration dorsally. It would seem that Van der Hoeven, who was based at Leiden University, never returned the skeleton to the museum, as Schlegel (1876: 288) did not include it in his catalogue. The

skeleton and skull, as well as the notes written by Pel, must be regarded as lost.

Temminck (1853: 47) writes of this specimen: "En 1848 nous parvint, par les soins de M. Pel, un mâle adulte conservé à l'esprit de vin, dont M. van der Hoeven obtint également la communication, et sur lequel il établit son mémoire cité dans nos synonymes." (In 1848 [lapsus for 1849] we received, by care of Mr Pel, an adult male preserved in spirit, which was also cummunicated to Mr van der Hoeven and on which he wrote his memoir cited under our synonyms). These synonyms (p. 49) do include a reference to Van der Hoeven's 1851 study, though again incorrectly quoted.

RMNH 39375. – Pel soon obtained another potto. Before he had received Temminck's acknowledgement of the first animal, he wrote on 27 September 1849 from Dabocrom (p. 1): "Door het spoedige vertrek uit Holland van den schoener Gouv. v d. Eb. ontving ik zeker geene tyding van myne vorige bezending, spoedig hoop ik hiervan echter met de spoedig te wachten schoener St George d'Elmina iets te vernemen. Hoewel eerstgemelde schoener van hier ook zeer haastig vertrekt, wil ik evenwel de gunstige gelegenheid niet laten voorbygaan alles wat ik sedert myne vorige verzamelde. weg te zenden. bestaande uit veele fraaye zaken… Onder de viervoetige dieren thans een heerlyk exemplaar van den Aposô." (No doubt due to the early departure of the schooner Gouv. v d. Eb from Holland, I have not received any news of my previous shipment. I soon hope, however, to learn about that through the schooner St George d'Elmina, which is expected soon. Although the first-mentioned schooner also departs from here very hastily, I do not want to miss the favourable opportunity to send off everything I collected since my previous [shipment], which consists of many fine things… Among the four-footed animals [there is] now a splendid specimen of the Aposô). Pel confirmed this dispatch by letter of 2 October 1849 from Dabocrom, again stating (p. 1): "Onder de zoogdieren bevindt zich thans een uitmuntend exemplaar van den *Perodicticus Aposô*,…" (Among the mammals there is now an excellent specimen of the *Perodicticus Aposô*).

This animal must have been obtained between March and September 1849. It is the adult female of which the mounted skin and skeleton have been preserved (see Figs 4-9). The pedestal of this skin also says "Dabocrom" in Temminck's handwriting, faintly readable. The invoice for this shipment, sent by the shipping agent to the Leiden Museum, is dated 7 December 1849.

Temminck (1853: 47) writes of this specimen: "En 1850 M. Pel nous adressa le troisième individu, une très-vieille femelle, ainsi que le squelette de cet animal remarquable. Ces animaux me servent à établir définitivement les caractères zoologiques qui font le sujet du présent article; l'ostéologie et la partie anatomique se trouvent suffisamment indiquées dans le travail de M. van der Hoeven. La Société Zoologique d'Amsterdam vient de publier dans ses actes, un portrait colorié et de grandeur naturelle, du bel individu femelle, déposé dans notre musée." (In 1850 [lapsus for 1849] Mr Pel sent us a third individual, a very old female, as well as the skeleton of this remarkable animal. These animals have enabled me to establish definitely the zoological characters that are the subject of the present article; the osteology and the anatomical details have been sufficiently treated in Mr van der Hoeven's work. The Zoological Society of Amsterdam has just published in its transactions a coloured portrait at natural size of the beautiful female individual deposited in our museum). After having described the

Fig. 4. RMNH 39375, Pel's second potto, neotype of *Perodicticus potto* (Statius Müller, 1776): mounted skin.

Leiden material, Temminck concludes (p. 50): "M. Pel a obtenu les sujets que nous venons de décrire, de la Fantie, dans les forêts voisines, de Dabocrom, côte de Guiné." (Mr Pel obtained the specimens we have just described from Fanti, in the nearby forests of Dabocrom, coast of Guinea).

Temminck refers here to a short note on the potto written by Pel during his leave in the Netherlands and published in 1852. The text was meant to be a comment on a drawing by Hermann Schlegel, curator of the Leiden Museum, sketched spontaneously after Pel's oral description of the species. At Pel's suggestion, this sketch was worked out with the three mounted skins in Leiden as examples; size and proportions were those of the largest animal, i.e., the old female. It is a most curious picture and it seems hard to see why Pel liked it so much. Pel briefly referred to Van der Hoeven's 1851 publication, stating: "Zoo als bekend is, heeft de Hoogleeraar J. van der Hoeven deze voorwerpen reeds voor mij onderzocht, en eene verhandeling over den *Aposô* bekend gemaakt." (I acknowledge that Professor J. van der Hoeven already examined these specimens before me, and has published a treatise on the *Aposô*). This is not quite accurate, as Van der Hoeven had not included the newly received large female.

Pel continues: "Daar het de bedoeling niet is, het reeds gedane werk nog eens over te doen, zoo verwijzen wij onze lezers op voornoemde verhandeling, en herhalen hier slechts, hetgeen wij in onze, den Heer van der Hoeven medegedeelde korte aanteekeningen van dit dier verzameld hebben. Het wordt door de negers der goudkust *Aposô* (niet *Aporô*, zoo als men verkeerdelijk gelezen heeft) genoemd, een woord, hetgeen vasthoudend betekent en treffend een dier kenschetst, bij hetwelk het klimvermogen in eenen zoo hoogen graad ontwikkeld is. Ik heb slechts twee voorwerpen van dit dier kunnen magtig worden, en die eerst in de laatste jaren van mijn verblijf aan de kust gekregen. Het eene werd mij levend in eene mand gebragt. Het bragt gewoonlijk den geheelen dag slapende door; het nam alsdan eene zonderlinge houding aan, en hield den kop tusschen de kruislings over den nek geslagen voor- en achterpoten. Des nachts was het dier rusteloos in beweging; die beweging was niet traag, zoo als Bosman opgeeft, maar veeleer bedaard en zeker te noemen. Het voedsel van dit dier bestond in vruchten, bananen en papaai (*Carica papaya*) en men kan veronderstellen, dat het in den natuurstaat van verschillende vruchten leeft; in dien staat houdt het zich steeds op boomen op, werpt zijne jongen in holle boomstammen en verschuilt zich ook daarin gedurende den dag.

Wij sluiten deze weinige regelen met de opmerking, dat onze afbeelding het dier in natuurlijke grootte daarstelt."

(Since it is not our intention to do again what has already been done, we refer our readers to the above-mentioned treatise and only repeat here what we have laid down in our short notes communicated to Mr. van der Hoeven. It is called *Aposô* by the Africans of the gold coast (not *Aporô* as it has been misread), a word that means tenacious and that accurately characterizes an animal of such highly developed climbing ability. I have only been able to obtain two specimens of this animal, and even these only during the last few years of my sojourn on the coast. One of these was brought to me alive in a basket. It usually spent the whole day sleeping; it then adopted a peculiar posture, holding its head between its fore and hind feet crossed over the nape. During the night the animal moved restlessly; its movements were not slow as Bosman records, but may rather be called quiet and deliberate. The food of the animal consisted of fruits, bananas

and papayas (*Carica papaya*) and one may suppose that in a natural state it lives on various fruits; in that state it always lives in trees, gives birth in hollow trunks and also hides there during the day.

We conclude these few lines by stating that our figure shows the animal at natural size).

Considering the loss of the first skeleton, it seems most fortunate that this specimen had arrived too late to be included into Van der Hoeven's 1851 study.

RMNH 39381. – During his second sojourn in the Gold Coast, Pel obtained one more potto. In a letter to Temminck of 14 June 1854 he wrote from Elmina (p. 2): "Gisteren kocht ik een zeer jonge *Aposô* die ik geloof dat de serie compleet zal maken". (Yesterday I bought a very young *Aposô* which I believe will complete the series). This must be the specimen preserved in alcohol, skull in situ. Its locality can be taken as the surroundings of Elmina, the place where Bosman had seen a potto in 1699. Probably, the animal was kept alive for some time, as it cannot be called very young any longer. It must have been sent to Leiden with Pel's last shipment in January 1855. Nothing has been published on this specimen besides the entries in Schlegel's (1876) and Jentink's (1892) catalogues.

Additional pottos, preserved and not preserved

In early 1857, two more pottos were received in Leiden. They had been collected in November 1856 by Mr Boomsma (no initials given), a health officer at Elmina. Their external and anatomical characters were studied extensively by F.A.W. van Campen, a student with Van der Hoeven. He died on 17 January 1859, before he had completed his work. His manuscript was edited by Van der Hoeven and published during the same year (Van Campen, 1859). These specimens were never transferred to the Leiden Museum. This may have been due to a serious conflict between Van der Hoeven and Schlegel, who had become the Director of the museum after Temminck's death in 1858.

It is very unfortunate that three skeletons of pottos (the one belonging with RMNH 39376 and the above two), which had reached Leiden in the 19th century and had been under Van der Hoeven's care, are lost.

RMNH 39380. – This is a very large animal preserved on alcohol, skull in situ. Nothing is documented except the provenance "Côte d'Or" (Gold Coast) and the year of acquisition, 1875.

Büttikofer's pottos

RMNH 39378 and 39379. – Two pottos were collected in Liberia in 1880 and 1887, during two expeditions by Johann Büttikofer and his assistants C.F. Sala and F.X. Stampfli, respectively (see Jentink, 1888). Their provenance is well documented: a young female, mounted skin with skull in situ, collected 13 May 1880 at Soforé Place on the upper St Paul's River, and a young male preserved in alcohol, obtained 15 April 1887 at Schieffelinsville on Junk River, northwest of Marshall; these localities can be found on the map published by Büttikofer (1888: pl. 5). After having listed these two specimens,

Jentink (1888: 13) quotes Büttikofer's notes on the potto: "Im Küstenstrich wird diese einzige Art, die ich aus dieser Gegend kenne, kaum angetroffen; ein verstümmeltes Exemplar erhielt ich aus dem Innern weit hinter Cobolia am Mahfa River. Man kennt das Thierchen überigens auch weiter unten; es wird in der Vey-sprache *Sofli* genannt, d.h. soviel als ein *schlauer Schleicher* – *Sofli-man* wird in dem verstümmelten Eingeborenen-english [sic] ein Spion im Kriege genannt. – Es wurde mir bei den Gola's erzählt, dass der *Sofli* ein [sic] ungeheure Kraft in seinen Händen habe, und dass ein festgehaltenes Thier sich nicht daraus losmachen könne." (This unique species, which I know from this area, is rarely found in the coastal strip; I received a mutilated specimen from the interior far inland of Cobolia on the Mahfa River. The animal is, however, also known further down; in the Veylanguage it is called *Sofli*, i.e. something like *cunning crawler* – in the natives' poor English a spy in the war is called *Sofli-man*. – I have been told by the Gola that the *Sofli* has extremely powerful hands and that an animal that it holds fast cannot wrench itself free). Apparently, the damaged specimen was not preserved; Schieffelinsville is situated in Liberia's coastal strip.

3. Designation of a neotype

As stated above, the syntypes of *Lemur potto* Statius Müller, 1776 are the animals mentioned by Bosman (1704b). For this reason, they are also the syntypes of *Galago guineensis* Desmarest, 1820 and belong in the type series of *Potto bosmanii* Lesson, 1840. They are no longer in existence. Moreover, Bosman's figure is very poor to say the least and quite obviously cannot be used for purposes of taxonomic comparison.

In view of this and of the fact that various other taxa have been distinguished within the genus *Perodicticus* Bennett, 1831, a neotype should be designated, preferably originating from the surroundings of Elmina or elsewhere in coastal Ghana. Although RMNH 39381, a young animal preserved in alcohol, is from Elmina, RMNH 39375 from Dabocrom (Dabo Krom) just west of Sekondi is far better suited, since it comprises the mounted skin of an adult female in good condition though probably somewhat bleached, with the complete skeleton preserved. We hereby designate it the neotype of *Lemur potto* Statius Müller, 1776 and therewith of *Galago guineensis* Desmarest, 1820.

The specimen is that of a female with full adult dentition (2.1.3.3/2.1.3.3) but with some postcranial epiphyses still fusing (e.g., distal femur, humeral head, epiphyses of the ankle and wrist) and cranial sutures visible (including the basioccipital, metopic, and sagittal). The teeth are relatively unworn. This individual is, however, fully grown and shows adult coat colouration (see Fig. 4). The postcranial epiphyses that are not yet fully fused are among the last to do so, and cranial sutures remain open or visible in pottos until well past full dental eruption. The neotype is a young adult.

Description of the neotype

RMNH 39375; *Lemur potto* = *Perodicticus potto potto* (Statius Müller, 1776), female, mounted skin and skeleton. Dabocrom (Dabo Krom) near Sekondi, Ghana, between March and September 1849; coll. H.S. Pel.

As can be seen in Fig. 4, *Perodicticus potto potto* is a stocky animal with short, dense fur, a broad, round head with a relatively short muzzle, and a tail of moderate length.

The eyes are large and protuberant. The ear pinnae are relatively small, round, and naked except at the lower end where wispy hairs occur both ventrally and dorsally. The rhinarium is brown, and the vibrissae are reduced so that there are no obvious whiskers. The upper jaw slightly overhangs the lower jaw. The pelage is tawny brown with reddish or cinnamon highlights on the limbs and darker highlights on the back, particularly in the shoulder region. The face is similar in colour to the limbs, although, in the region between the eyes and extending partially over the nasals, there is a light brown band with distinctly darker lateral borders. The ventral pelage is less dense than the dorsal and is a lighter grey-brown. A long brown tail ends in a black tuft. The hands and feet are grey-brown; they are darker and less tinged with red than the rest of the limbs. The pollex and hallux are widely divergent and robust, bearing flat nails. The second digit of the hand is rudimentary. The second digit of the foot is also reduced in length but sports an elongated grooming claw. The trunk is robust, and the upper and lower limbs are subequal in length. There is cornified skin in the mid-cervical and upper thoracic region of the back, but the guard hairs are short and sparse. Some basic osteological and dental measurements are provided in Table 1.

The skull and mandible

The skull is about two-thirds as wide as it is long (Fig. 5). The orbits are large and anteriorly oriented, the zygomatic arches are arcuate, and the bizygomatic breadth exceeds the biorbital. The interorbital breadth is relatively small. The orbital rims are moderately developed (less so than in pottos from other regions), as are the temporal lines.

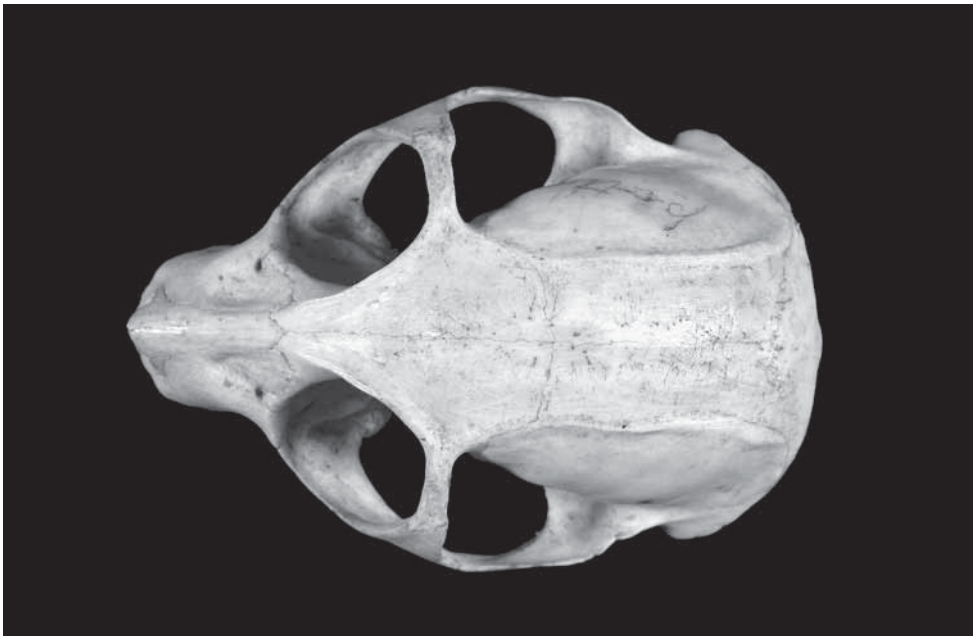


Fig. 5. Skull of RMNH 39375: dorsal view.

Table 1. *Perodicticus potto*: Metric dimensions of neotype RMNH 39375 (mm).

Maximum cranial length (prosthion-opisthocranion)	62.0	Height of the mandibular corpus at M_2	7.1
Bizygomatic breadth	43.9	Toothcomb length	4.4
Prosthion-staphylion	21.7	P_2 crown height	4.2
Interorbital breadth	7.8	P_2 mesiodistal diameter	3.9
Distance between anterior carotid foramina	7.2	P_2 buccolingual diameter	2.8
Length of the maxillary tooth row, C^1 to M^3	21.4	P_3 crown height	2.2
		P_3 mesiodistal diameter	2.3
		P_3 buccolingual diameter	1.7
C^1 height	7.1	P_4 crown height	2.4
C^1 mesiodistal diameter	4.5	P_4 mesiodistal diameter	2.7
C^1 buccolingual diameter	2.7	P_4 buccolingual diameter	2.7
P^2 crown height diameter	3.1	M_1 mesiodistal diameter	3.4
P^2 mesiodistal diameter	3.2	M_1 buccolingual diameter	2.7
P^2 buccolingual diameter	2.1	M_2 mesiodistal diameter	3.3
P^3 crown height	1.9	M_2 buccolingual diameter	2.8
P^3 mesiodistal diameter	2.7	M_3 mesiodistal diameter	3.2
P^3 buccolingual diameter	1.4	M_3 buccolingual diameter	2.6
P^4 crown height	2.3	Humerus length	67.6
P^4 mesiodistal diameter	2.8	Humeral midshaft transverse diameter	5.4
P^4 buccolingual diameter	3.4	Humeral midshaft anteroposterior diameter	5.9
M^1 mesiodistal diameter	3.7	Humeral midshaft circumference	18.4
M^1 buccolingual diameter	4.0	Femur length	79.9
M^2 mesiodistal diameter	3.4	Femoral midshaft transverse diameter	5.5
M^2 buccolingual diameter	4.5	Femoral midshaft anteroposterior diameter	4.5
M^3 mesiodistal diameter	2.4	Femoral midshaft circumference	16.4
M^3 buccolingual diameter	3.5	Length of 7^{th} cervical vertebral spine	13.7

The palate is narrow and rounded anteriorly (anterior to P^3) and broad in the region of the molars. It is widest across the second molars (Fig. 6). The nasals display a slight convexity in lateral profile, but protrude minimally beyond the anterior nasal spine, which in turn projects minimally beyond prosthion (Fig. 7). Beneath each orbit is a large infraorbital foramen. The lacrimal duct is located anterior to the inferior margin of the orbit (Fig. 5). On the basicranium, the postglenoid plate is thick but not tall; it is located just posterior to the anterior margin of the adjacent bulla. The auditory bullae are inflated anteriorly, and the distance between the anterior carotid foramina is relatively small. The lateral pterygoid wings are relatively short; the pterygoid plates are small and extend little more than half the distance between the distal end of the tooth row and the anterior border of the auditory bulla.

On the mandible, the anterior border of the ascending ramus slopes strongly obliquely posteriorly and the coronoid process is moderately hooked (Fig. 8). The coronoid rises well above the plane of the mandibular condyles. The gonial region is more strongly hooked, and the posterior border of the ascending ramus is distinctly notched between the mandibular condyles and the gonial processes. The condyles are situated only slightly above the occlusal plane in lateral view. In occlusal view (Fig. 9), the horizontal rami converge anteriorly so that the mandible is V-shaped. As in all lorises and most but not all lemurs, a moderately procumbent toothcomb comprises two incisors and a canine on either side, and the mandibular symphysis remains unfused in adults.

Dentition

On the upper jaw (Figs 6, 7), the central and lateral maxillary incisors are approximately equal in height. These teeth are long and slender (about a third as tall as the canine) but with blunted rather than pointed tips. The central incisors converge mesially, but are nevertheless separated by a wide gap at prosthion. They are visible in lateral view, as they are slightly more anteriorly placed than the lateral incisors. The upper canines are tall, trenchant and recurved. There is a lingual pillar from the base of the

Fig. 6. Skull of RMNH 39375: ventral view.

Fig. 7. Skull of RMNH 39375: lateral view.

Fig. 8. Mandible of RMNH 39375: lateral view.

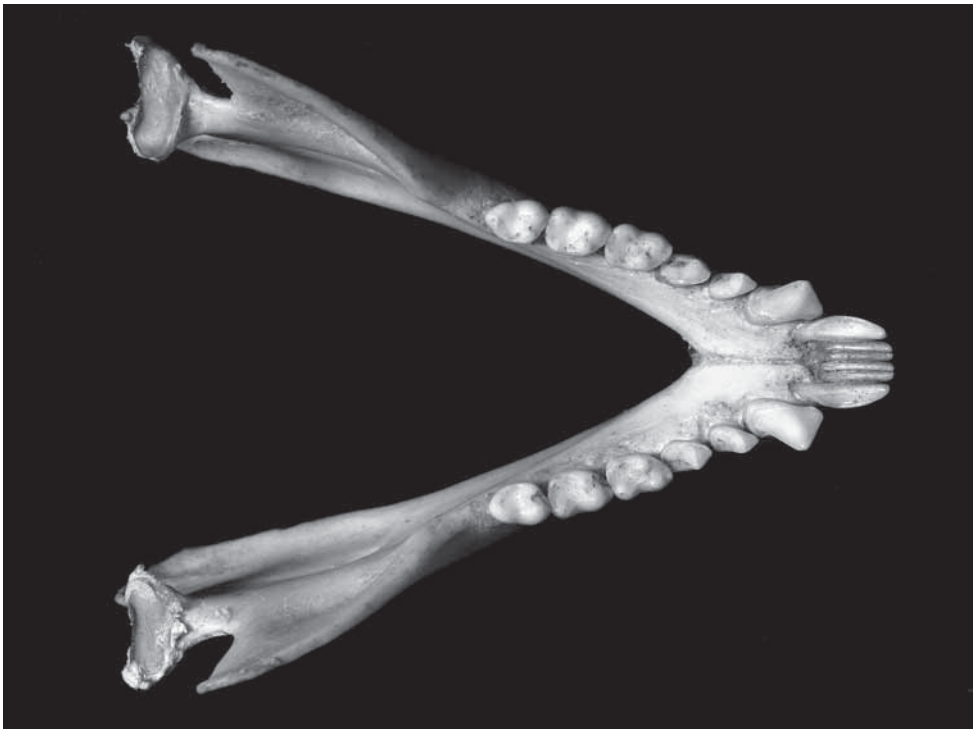


Fig. 9. Mandible of RMNH 39375: occlusal view.

crown to the tip, paralleling the sharp mesial border of the tooth. There is also a small distal heel.

The crowns of all three upper premolars are triangular in buccal outline. The anteriormost premolar, P^2, is taller than P^3 and P^4, but only half the height of the canine. P^2 and P^3 have a single buccal cusp, the paracone, whereas P^4 has both paracone and protocone. The paracone of the anteriormost premolar is located slightly mesial to the middle of the crown, so that the distal buccal margin of the crown is longer than the mesial. In the posterior two premolars, the mesial and distal margins are roughly equal in length. There is no diastema separating P^2 and P^3, as occurs in some other pottos.

The diminutive P^3 is the shortest of the three premolars. It bears a single cusp and a low, faint lingual cingulum. There is a distinct lingual pillar, but no lingual cusp. The crown broadens distally, such that its distal edge is slightly wider than the mesial in occlusal view.

P^4 is taller than P^3, slightly surpassing the height of the buccal cusps of the first molar in lateral view. It bears a distinct lingual protocone along with the prominent paracone located slightly distal to the middle of the crown. There is a faint buccal cingulum, and poorly developed parastyle and metastyle.

M^1 and M^2 have a slight hypocone shelf, and a prominent protocone, paracone and metacone. The molar cusps are not as tall as the paracone of the distalmost premolar. M^3 is relatively small (that is, mesiodistally compressed), but it nevertheless bears three cusps – the protocone, paracone and metacone.

On the lower jaw (Figs 8, 9), there is a toothcomb comprising (on either side) two narrow lower incisors and a wider but nevertheless still incisiform canine. The toothcomb is half the length of the mandibular molar series and moderately procumbent. The anteriormost lower premolar is relatively high-crowned and occludes behind the upper canine.

The crown of P_2 is quite tall in comparison to those of the other premolars; it bears a single cusp and is buccolingually compressed. The mesial border of the crown juts clearly beyond the mesial edge of the root in buccal view; its profile is sharp and straight. The distal border of the crown is longer than the mesial border and slightly concave, ending distally in a distinct heel. There is a stout and smooth-edged lingual pillar and a low lingual cingulum. P_3 is similar in shape to P_2 (buccolingually compressed and mesiodistally elongated), but much shorter in height. Its single cusp is positioned more mesially (resulting in a relatively shorter mesial edge and longer distal edge of the crown). Its heel is more pronounced. P_4 is similar in shape to P_3, but taller and buccolingually compressed. It too, bears a single cusp.

The M_1 trigonid is buccolingually compressed and the talonid basin is buccolingually expanded; the latter is larger than the former. The buccal cusps are displaced mesially relative to the lingual cusps, such that the protoconid is situated mesial to the metaconid and the hypoconid slightly mesial to the entoconid. The mesial margin of the tooth is obliquely oriented; the distal margin much less so. There is a slight paraconid swelling but no hypoconulid.

The trigonid is relatively broader on M_2, but still not as broad as the talonid. The second molar is squarer than the first molar; the protoconid is very slightly mesial to the metaconid, and the entoconid and hypoconid are almost transversely aligned, with the entoconid now mesial to the hypoconid. The M_3 protoconid and metaconid are trans-

versely aligned, and there is a deep transverse groove separating the two mesial from the distal cusps. The distal cusps are closely approximated and situated on the raised distal edge of the tooth, where they merge into a posteriorly emplaced but low hypoconulid. The trigonid of the third molar is wider than the talonid.

Sternum, thorax and vertebral column

There are 8 sternebrae plus the xiphoid process and manubrium. The sternebrae are narrow; the manubrium is large and expanded. There are 7 cervical, 15 thoracic, 7 lumbar, 2 sacral and 20 caudal vertebrae. [Note: These vertebral counts are similar to those reported by Van Campen (1859: 13) for the specimens from Elmina (Ghana). Van Campen reports the same number of cervical, thoracic, and caudal vertebrae, but an additional lumbar and sacral vertebra.]

The spinous process of C2 is short and only mildly bifid; those of the 4^{th}, 5^{th}, and 6^{th} cervical vertebrae are distinctly bifid. The spines of C3 to T3 are moderately elongated (varying from about 8 to 15 mm in length). The more caudal thoracic vertebrae bear relatively thick ribs. The lumbar spinous processes are short and dorsally directed.

Appendicular skeleton

The humerus is slightly longer than the skull, and the femur exceeds skull length by about 20%. There is no entepicondylar foramen on the humerus. The femur sports a strongly medially projecting lesser trochanter; a large, rounded head; a short neck; an anteroposteriorly compressed and mediolaterally expanded shaft; and a short, flat patellar groove. The greater trochanter does not surpass the height of the femoral head. The femoral shaft exhibits a slight anterior concavity in lateral view. The ulna is anteroposteriorly bowed and bears a long styloid process. On the os coxae, the ilium is long and rod-like. There is a rudimentary rectus femoris process, an elongated pubis, short ischium, and large obturator foramen. The acetabulum is large, but not very deep. The cranial aspect of the acetabular lunate articular surface is quite extensive, the dorsal aspect is thin, and the caudal aspect only slightly wider than the dorsal.

The second digit of the hand bears a reduced metacarpal as well as proximal phalanx, and even more reduced middle and distal phalanges. There is a diminutive nail that is wider than it is long. The second digit of the foot is also reduced in length, but with an exceptionally reduced middle phalanx. The terminal phalanx of the second pedal digit is long and narrow, and sports an elongated grooming claw. All three phalanges are present.

4. Taxonomic notes

A number of subspecies of *Perodicticus potto* have been described. Five subspecies were recognized by Hill (1953: 191-194): (1) *P. p. potto* Statius Müller, 1776 [not 1766]; (2) *P. p. juju* Thomas, 1910; (3) *P. p. edwardsi* Bouvier, 1879; (4) *P. p. faustus* Thomas, 1910; and (5) *P. p. ibeanus* Thomas, 1910. Three of these: *P. p. potto*, *P. p. edwardsi*, and *P. p. ibeanus*, are unequivocally accepted, with *juju* generally included in *P. p. potto* and *faustus* in *P. p. edwardsi*. These three forms can be distinguished on the basis of metric characteristics

(Jenkins, 1987: 152; Groves, 2001: 95-96; Stump, 2005; Pimley & Bearder, in press) and may prove distinct species (Stump, 2005; Leon et al., unpubl.). Stump (2005) argues strongly in favour of *juju* being distinct at least subspecifically. The neotype of *P. p. potto* fits within the nominate form, which most clearly differs from the other two recognized subspecies in having weak guard hairs, neck vertebrae with relatively short spinous processes, a relatively long tail, weakly developed orbital rims, weakly developed temporal lines, and more gracile zygomatic arches. In addition, *P. p. potto* differs from *P. p. edwardsi* (and, to a lesser extent, from *P. p. ibeanus*) in having smaller teeth, and from *P. p. ibeanus* in cranial proportions, with *P. p. ibeanus* having a relatively larger interorbital breadth and shorter nasal bones.

Schwartz (1996, 2005) recognizes a second genus and species: *Pseudopotto martini* Schwartz, 1996. The validity of this form remains controversial (Groves, 1997/1998, 2001; Sarmiento, 1997/1998; Leon, 2000; Leon et al., unpubl.). Distinguishing characters are said to include weakly developed temporal lines, a rudimentary, single-cusped M^3, P_2 with an angled mesial projection, tiny P_3, humeri with entepicondylar foramina and strong brachial flanges, and a long tail (Schwartz, 1996).

Dental morphology distinguishes *P. p. potto* from the other subspecies. Most striking is the shape of the anteriormost lower premolar. In *P. p. potto*, this tooth is not conical as in the other subspecies; it is shorter in height and its anterior margin is more angular than in *P. p. edwardsi* or *P. p. ibeanus*. This shape distinction results in a difference in the spacing of the teeth in the upper jaw. There is no diastema behind C^1 in *P. p. potto*, whereas this is often present in the other subspecies. When manifest in the other forms, such a diastema accommodates (in centric occlusion) a very tall and conical P_2. In contrast, when present in *P. p. potto*, diastemata are located between P^2 and P^3 or between P_3 and P_4, and are related to size reduction in the middle premolar. *P. p. potto* is unique in exhibiting extremely reduced third premolars in both upper and lower jaws. P^3 and P_3 are the shortest of all premolars in their respective jaws.

Certain other dental traits vary within and across the three subspecies. These include the size and cusp development of the upper third molar [which is also the tooth most likely to suffer developmental agenesis across primates (Swindler, 2002)]. When present (as is usually the case), it may have one, two or three cusps, and up to three roots. The presence of an entepicondylar foramen in the humerus is also distinctly variable within each of the potto subspecies. There is variation among specimens of *P. p. potto* from the region of Elmina in the expression of this trait, as well as in the degree of flaring of the brachialis flange, and the curvature of the humeral shaft. The neotype has no entepicondylar foramen, slight flaring of the brachialis flange, and relatively little bowing of the humeral shaft, whereas Van Campen's pottos have a well-developed brachialis flange, strong curvature of the humeral shaft, and a large entepicondylar foramen (Van Campen, 1859: 16, pl. I). There is also body size variation within *P. p. potto*, the westernmost populations appearing smaller. Individuals from Elmina and the surrounding region (including the neotype) are slightly larger in overall size than individuals from the westernmost portion of the geographic range of this subspecies.

Coat colour varies within potto subspecies, although there are some subspecific distinctions. For example, the dorsal pelage of *P. p. edwardsi* tends to exhibit black highlights, and the face is a rich chestnut brown, without the lighter colouration and reddish highlights of *P. p. potto*. Universally, younger individuals have thick and dark dorsal

pelage with a silvery frosting throughout. The ventrum is frosty grey. An ontogenetic change to adult colouration proceeds from the head caudally, and can be observed in the Leiden specimens.

In closing, we emphasize that, even at single geographic locations, pottos exhibit a fair amount of variation. Nevertheless, there are consistent morphological differences among populations living in different geographic regions. The question whether the three subspecies recognized at present are to be regarded as different species, as well as the taxonomic validity of *Pseudopotto* as a distinct genus, is outside the scope of this paper. Whereas differences between regional variants have been recognized, the lack of a type specimen has hampered taxonomic interpretations. This manuscript is intended to remedy that situation.

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