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Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae). 1. Type Material Described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum

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ABSTRACT

In this report we identify the original material of the Brazilian erethizontids that Olfers (1818) and Kuhl (1820) described as *Hystrix tortilis*, *H. subspinosa*, *H. insidiosa*, and *H. nycthemera*. Based on our examination of the types and associated archival documents in the Museum für Naturkunde der Humboldt-Universität zu Berlin, many problems concerning the type localities, diagnostic characters, and nomenclature of these species can now be resolved. Among the principal conclusions from our study are the following. (1) The collection of Brazilian mammals donated to the Berlin Zoological Museum by Count von Hoffmannsegg in 1810 is the only known source of specimens of the new erethizontid species described by Olfers (1818). (2) The names *Hystrix tortilis* and *H. subspinosa* are objective synonyms based on the same type material, the lectotype and a paralectotype, both collected at Salvador in the state of Bahia by F. A. Gomes; preserved as skins and skulls in good condition, these specimens exhibit all of the characters hitherto regarded by authors as diagnostic of the species currently known as *Chaetomys subspinosus*. (3) *Hystrix tortilis* and *H. subspinosa* are both available from Olfers (1818); to preserve current usage, we select *subspinosa* as the senior name. (4) The specimen hitherto labeled and cataloged as the type of *Hystrix insidiosa* and reported as such in the literature does not correspond to Olfers' and Kuhl's descriptions and was not part of Hoffmannsegg's original collection; the real holotype, misidentified by Lichtenstein and subsequently cataloged by Peters as *Cercolabes affinis* Brandt, was probably also collected at Salvador by Gomes. (5) We redescribe the characters of *Coendou insidiosus* and comment on its complicated nomenclatural history; in particular, we confirm previous hypotheses that *Coendou pallidus* (Waterhouse) is a junior synonym, and that *Coendou melanurus* (Wagner) is not. (6) A widespread complex of small, long-furred porcupines tentatively referred to *Coendou spinosus* (F. Cuvier) (including *villosus* F. Cuvier, *couiy* Desmarest, *nigricans* Brandt, *sericeus* Cope, and *roberti* Thomas) is diagnosed and contrasted with *Coendou insidiosus*; although these species appear to be distinct based on available museum specimens, unvouchered field identifications should be regarded with caution. (7) *Hystrix nycthemera*, based on a single specimen collected by F. W. Sieber in eastern Amazonia, appears to be the oldest available name for the species currently known as *Coendou koopmani* Handley and Pine. We provide formal synonymies for *Chaetomys subspinosus* (Olfers), *Coendou insidiosus* (Olfers), and *Coendou nycthemera* (Olfers), wherein many additional details of taxonomy and nomenclature are summarized.

RESUMO

Nesse artigo identificamos o material original de eretizontideos brasileiros que Olfers (1818) e Kuhl (1820) descreveram como *Hystrix tortilis*, *H. subspinosa*, *H. insidiosa*, e *H. nycthemera*. Baseado no exame dos tipos e documentos associados a eles presentes nos arquivos do Museum für Naturkunde der Humboldt-Universität zu Berlin, muitos problemas relacionados as localidades tipos, caracteres diagnósticos, e nomeclatura destas espécies podem agora ser resolvidos. As principais conclusões de nosso estudo são: (1) A coleção de mamíferos brasileiros doados ao Museu Zoológico de Berlin pelo Conde von Hoffmannsegg em 1810 contém os unicos espécimes conhecidos das novas espécies de eretizontideos descritos por Olfers (1818). (2) Os nomes *Hystrix tortilis* e *H. subspinosa* são sinônimos objetivos baseados no mesmo material tipo, consistindo do lectótipo e do paralectótipo, ambos coletados em Salvador no estado da Bahia por F. A. Gomes; preservado como peles e crânios em bom estado, estes espécimes exibem todos os caracteres considerados até o presente como diagnósticos de *Chaetomys subspinosus*. (3) *Hystrix tortilis* e *H. subspinosa* ambos estão disponiveis de Olfers (1818); para preservar o uso atual selecionamos *subspinosa* como o nome senior. (4) O espécime catalogado como tipo de *Hystrix insidiosa* e identificado como tal na literatura não corresponde as descrições de Olfers e Kuhl e originalmente não fazia parte da coleção de Hoffmannsegg; o verdadeiro holótipo identificado erroneamente por Lichtenstein e subsequentemente catalogado por Peters como *Cercolabes affinis* Brandt, provavelmente também foi coletado em Salvador por Gomes. (5) Nós redescrevemos os caracteres de *Coendou insidiosus* e comentamos sobre sua complicada história nomemclatural; em particular nós confirmamos as hipóteses de que *Coendou pallidus* (Waterhouse) é um sinônimo junior, e que *Coendou melanurus* (Wagner) não o é. (6) Um complexo amplamente distribuído de pequenos ouriços-cacheiro de pêlo longo tentativamente identificados como *Coendou spinosus* (F. Cuvier) (incluindo *villosus* F. Cuvier, *couiy* Desmarest, *nigricans* Brandt, *sericeus* Cope, e *roberti* Thomas) é diagnosticado e contrastado com *Coendou insidiosus*; enquanto essas espécies

parecem ser distintas baseado em espécimes existentes em museus, identificações de campo sem coleta de um espécime testemunho devem ser vistas com uma certa cautela. (7) *Hystrix nycthemera*, baseado em um único espécime coletado por F. W. Sieber na Amazonia oriental parece ser o nome mais antigo disponível para as espécies no momento conhecidas como *Coendou koopmani* Handley e Pine. Aqui oferecemos a sinonímia formal de *Chaetomys subspinosus* (Olfers), *Coendou insidiosus* (Olfers), e *Coendou nycthemera* (Olfers), além de muitos detalhes adicionais de taxonomia e nomeclatura.

INTRODUCTION

Neotropical erethizontids, variously referred by recent authors to the genera *Chaetomys*, *Coendou*, *Echinoprocta*, and *Sphiggurus*, are morphologically and ecologically distinctive caviomorph rodents that occur in lowland and montane forests from southern Mexico to northern Argentina. Speciose and conspicuously adapted for climbing, they represent one of several independent mammalian radiations in arboreal habitats of the New World tropics. As such, erethizontids are a potentially useful source of comparative data on species endemism and relationships to test biogeographic hypotheses derived from previous and ongoing studies of platyrrhine primates (e.g., Hershkovitz, 1977; Peres et al., 1996), squirrels (M. de Vivo, in prep.), echimyid rodents (da Silva et al., 1993; Lara et al., 1996; L. H. Emmons, in prep.) and other canopy-dwelling groups. The currently confused taxonomy of erethizontids, however, is a major research impediment.

Chief among the difficulties encountered in revising the taxonomy of Central and South American porcupines is the uncertain application of many old names (Tate, 1935; Cabrera, 1961). Some, such as *Hystrix prehensilis* Linnaeus, and *Hystrix mexicana* Kerr, lack type material because they were based on published descriptions by early naturalist-explorers (e.g., Marcgraf, 1648; Hernández, 1651) rather than on examined specimens. Fortunately, most taxonomic ambiguities associated with porcupine names based on bibliographic references have been resolved by appropriate restrictions of the type localities (e.g., by Thomas, 1911).

A more persistent source of confusion is old names based on types that have seldom or never been examined after the original descriptions were published. For example, the usage of Neotropical porcupine binomials attributed to Olfers (1818), Kuhl (1820), Cuvier (1822), Brandt (1835), and other early 19th-century authors has usually been justified only by reference to the literature. Because many early descriptions were brief, and because definite locality information was seldom published, firsthand examination of types and careful evaluation of all evidence relating to their geographic provenance are essential for revisionary research.

Unfortunately, types are sometimes difficult to identify as such after the lapse of many years. Among other problems encountered by modern researchers attempting to identify old types: numerical cataloging was not standard museum practice until the late 19th century (hence early authors could not unambiguously indicate the specimen or specimens they examined), types were usually not segregated from other specimens in old natural history collections, original labels (with their tell-tale handwriting) were sometimes lost or discarded, and specimens originally live-mounted for exhibition were often remade as study skins at a later date (thus altering their appearance from that illustrated in old publications).

This report is the first in a series with the object of resolving key nomenclatural problems in Neotropical porcupine systematics in advance of a comprehensive revision that will necessarily be several years in preparation. Of primary interest in these preliminary notes is the identification and documentation of the type material on which old names of uncertain application were based. Herein we treat the specimens described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. Originally referred to the Linnaean genus *Hystrix*, this material includes the types of

Fig. 1. Detail from a live-mounted specimen of *Coendou insidiosus* showing one of Lichtenstein's printed labels glued to the wooden base. Misidentified as *Cercolabes* (*Sphiggurus*) *affinis* Brandt, this is the only ZMB porcupine that currently remains as originally prepared for exhibition (with the skull inside). Peters' catalog number (1297) is just visible at the bottom of the label, handwritten between the locality ("Brasilien") and the names of the collectors ("Sello[w]. [&] v[on]. Olfers"). The greenish-blue paper on which this information is printed conforms to the geographical color-code for America used in old ZMB exhibition labeling (Lichtenstein, 1816).

species currently known as *Chaetomys subspinosus* and *Coendou insidiosus*; a third species based on type material in Berlin, *Coendou nycthemera*, is currently known by its junior synonym, *C. koopmani*. Below, we explain the history of these specimens and the names associated with them, redescribe their morphological characters, comment on synonyms, and summarize information about geographic distributions.

Background

The nucleus of the mammal and bird collections of the Berlin Zoological Museum (ZMB) at its inception in 1810 was a large series of Brazilian specimens donated by Count (Graf) Johann Centurius von Hoffmannsegg (whose patronymic was also spelled "Hoffmansegg" in contemporaneous publications and manuscripts). Most of Hoffmannsegg's material had been obtained by two collectors working in different parts of the country: (1) Francisco Agostinho Gomes, who resided at the town of Bahia (now Salvador) on the Atlantic coast and sent specimens to Hoffmannsegg from 1801 to 1807; and (2) Friedrich Wilhelm Sieber, who collected in eastern Amazonia from 1803 to 1812.[3] Whereas a correspondent named Beltrão sent the count a few birds from Rio de Janeiro in 1800 (Stresemann, 1950), and João da Silva Feijó sent some insects from Ceará (Papavero, 1971), only Gomes and Sieber are known to have collected specimens of Brazilian mammals for Hoffmannsegg.

According to Stresemann (1950) and Muggelberg (1975, 1976), Hoffmannsegg collaborated with Karl Illiger (director of the ZMB from 1810 to 1813) in sorting, naming, and classifying the mammals and birds collected by Gomes and Sieber, many of which were new species. Although some new mammal names from this material were published by Hoffmannsegg himself (1807) and more appeared (mostly as nomina nuda) in Illiger's "Prodromus" (1811) and in his posthumously printed "Ueberblick" (1815), others remained unpublished on specimen labels and in manuscript lists. After Illiger's death in 1813, Hinrich Lichtenstein was appointed ZMB director, a post that he held until his own death in 1857.

Unfortunately, any original labels that might once have accompanied Hoffmannsegg's mammal collection were lost or discarded, almost certainly as the specimens were being prepared for exhibition between 1811 and 1814; no handwritten labels from the early 19th century are known to survive. By 1814, all of Hoffmannsegg's mammals had been mounted in lifelike poses (with the skull inside) and attached to wooden bases for exhibition in the main building of the Berlin university (on Unter den Linden). Printed paper labels glued to the wooden bases (fig. 1) gave only the Latin binomial, country of origin, and name(s) of the collector(s). Thus, when Wilhelm Peters succeeded Lichtenstein as ZMB director in 1857 and began the current numerical catalog of the mammal collection (Angermann, 1989), only this secondary labeling was available to indicate the provenance and nomenclatural significance of Hoffmannsegg's specimens.

Specimens that Peters believed to be types were in most cases indicated with asterisks in his catalog (fig. 2). Apparently, Peters did not consistently relabel specimens after cataloging them, nor did he remove them from exhibition. Often, his catalog numbers were simply written on Lichtenstein's old printed labels, which remained glued to the wooden bases (fig. 1). The ZMB became part of the Museum für Naturkunde in 1889, at about which time the collections were transferred to the present museum building (on Invalidenstraße). Sometime after this move, Hoffmannsegg's mammals were taken off exhibit and incorporated into the research collection.

During the first half of the present century (between 1938 and 1942 for the specimens concerned in this report), many livemounts were remade as conventional study skins with extracted skulls. Specimen data and catalog numbers were then transcribed to modern skin tags, and the same information was also written directly onto each

[3] According to Urban (1906), Stresemann (1950), and Papavero (1971), Sieber arrived in Brazil to collect for Hoffmannsegg in 1801. However, Sieber's first letter to Hoffmannsegg from Pará (dated 28 September 1803) reported his arrival in Brazil on 16 September 1803 after a 55-day passage from Lisbon.

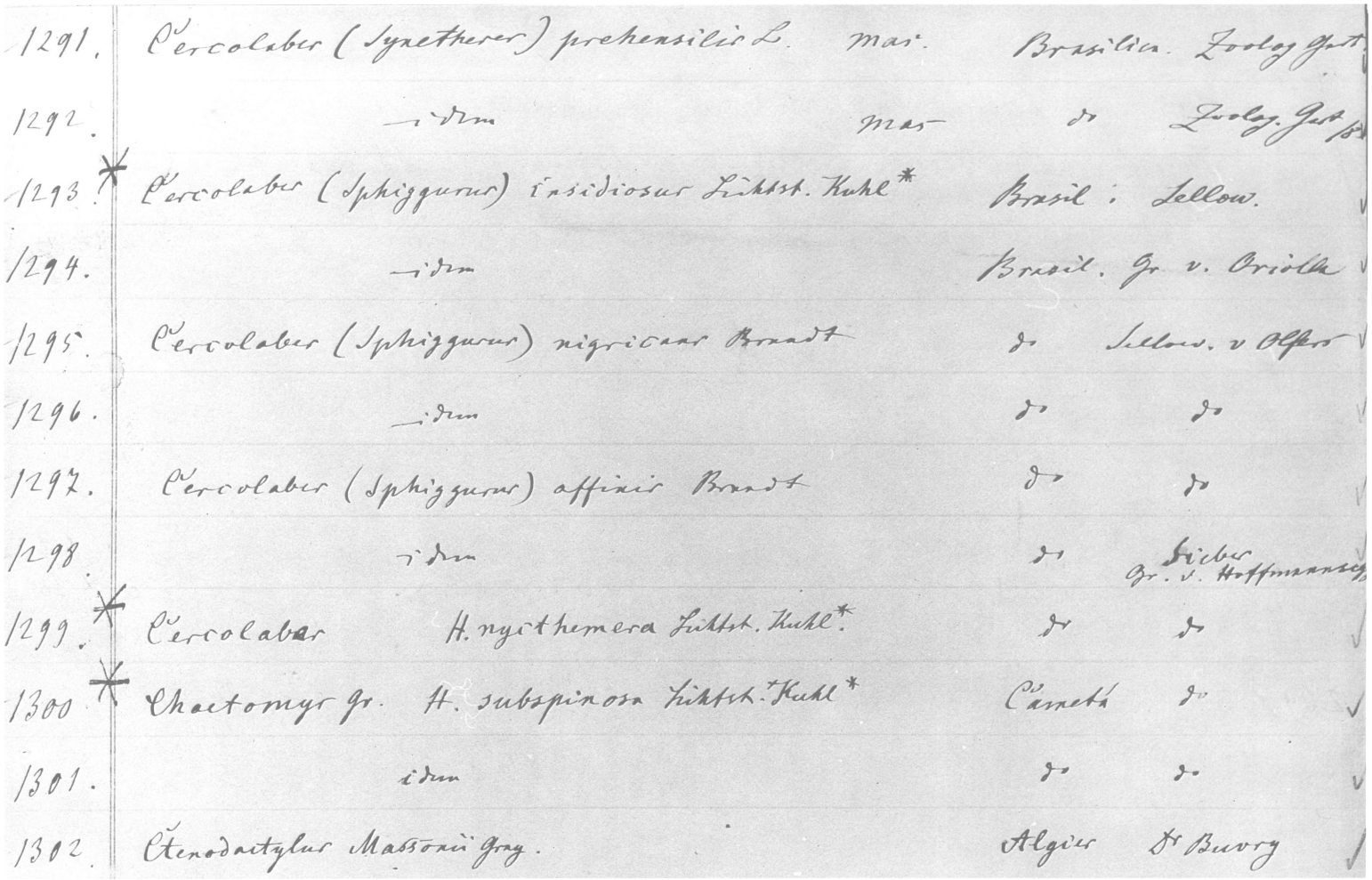

Fig. 2. A page from Peters' catalog of the ZMB mammal collection with the entries for Neotropical porcupine specimens discussed in this report. From left to right, each entry consists of catalog number, scientific name (with notations of authorship), collection locality, and collector(s). Asterisks indicate specimens that Peters believed to be types. Note the almost exact correspondence between Peters' catalog entry for ZMB 1297 and the information printed on Lichtenstein's exhibition label for that specimen (fig. 1).

skull. Although some old exhibition labels were preserved as the specimens were remade, all were subsequently lost.[4]

For many years, authorship of *Hystrix insidiosa*, *H. nycthemera*, and *H. subspinosa* was attributed to Kuhl (1820); for example, by Waterhouse (1848), Tate (1935), and Ellerman (1941). Kuhl himself attributed these names to Lichtenstein, probably as a courtesy to the ZMB director. However, these species had previously been described in Olfers (1818), an obscurely published commentary on Illiger's zoogeographic work (Hershkovitz, 1959).[5] Unfortunately, Olfers stated only that these porcupines were from Brazil, and Kuhl provided no useful geographic data whatever. Neither author mentioned the collectors or how many specimens were examined.

In the absence of original labels, contemporaneous numerical cataloging, and explicit published references to particular specimens, early manuscript records of the ZMB collections are crucial to determine what Neotropical porcupine material was available in Berlin during the first two decades of the 19th century. Of primary importance is a list of the species of mammals and birds represented in the museum at its inception in 1810. Written in sepia ink on folded folio sheets, this document is entitled:

Catalogus
Mammalium
et Avium
Musei Regii
inchoatus
ejusdem Musei fundationis tempore
Ao. 1810[6]

The bottom of the title page is inscribed "Nota Species * insignitas a C[omite]. d[e]. H[offmannseggio]. allatas, reliquas postea vario modo adquisitas."[7] Page two begins the mammal list and includes the following Neotropical porcupines:

* 29. *Hystrix insidiosa* N.
* 30. — *nycthemera* N.
* 31. — *prehensilis*.
* 32. — *subspinosa* N.

Thus, *Hystrix insidiosa*, *H. nycthemera*, and *H. subspinosa* are indicated as new names based on specimens received from Hoffmannsegg. Pencil notations in the left-hand margin (fig. 3) suggest that the museum had one specimen each of *insidiosa* and *nycthemera*, and two specimens each of *prehensilis* and *subspinosa*. Careful handwriting comparisons with contemporaneous manuscripts of known authorship indicate that this list was probably written by Hoffmannsegg himself.

Our examination of both published sources of information about the early history of the ZMB (e.g., Stresemann, 1950; Muggelberg, 1975, 1976; Jahn, 1985) and archival records from the early 19th century (see Appendix) convinces us that all of the Neotropical porcupine specimens present in Berlin prior to 1818 were part of the Brazilian material sent to Hoffmannsegg by Gomes and Sieber. That Olfers (1818) based his descriptions of new mammals, at least in part, on this material is indisputably indicated by his citation of the Berlin museum as a source of named specimens (e.g., fig. 12). Whether or not Olfers' descriptions were also based in part on other specimens collected or observed by himself in Brazil is the question we consider next.

[4] We are indebted to Inge Johnke (née Pasemann), who worked as a secretary and technical assistant in the Säugetier-Abteilung from 1938 to 1942 and from 1945 to 1951, for first-hand information about when and how old live-mounted specimens were remade as study skins and skulls. Hers is the handwriting that appears on the skulls illustrated in this report. Frau Johnke's work was supervised by Hermann Pohle, curator of mammals throughout most of the difficult years of depression, war, and reconstruction from 1926 to 1951 (Angermann, 1989).

[5] Moojen (1952) and Husson (1978) attributed *Hystrix insidiosa* to Lichtenstein (1818a), a guidebook for museum visitors, wherein this species is briefly distinguished from other porcupines displayed in the same cabinet; Hershkovitz (1959) cited Olfers (1818), but not Lichtenstein (1818a). Apparently, neither Moojen, Husson, nor Hershkovitz were aware that the same name was made available in two works with the same date. As first revisers in the sense of the International Code (ICZN, 1985: Article 24), we assign precedence to Olfers' more detailed description.

[6] "Catalog of the mammals and birds of the Royal Museum[,] begun at the time of the founding of the same museum in the year 1810."

[7] "Note[:] Species marked with an asterisk donated by C[ount]. v[on]. H[offmannsegg]., the rest variously acquired later."

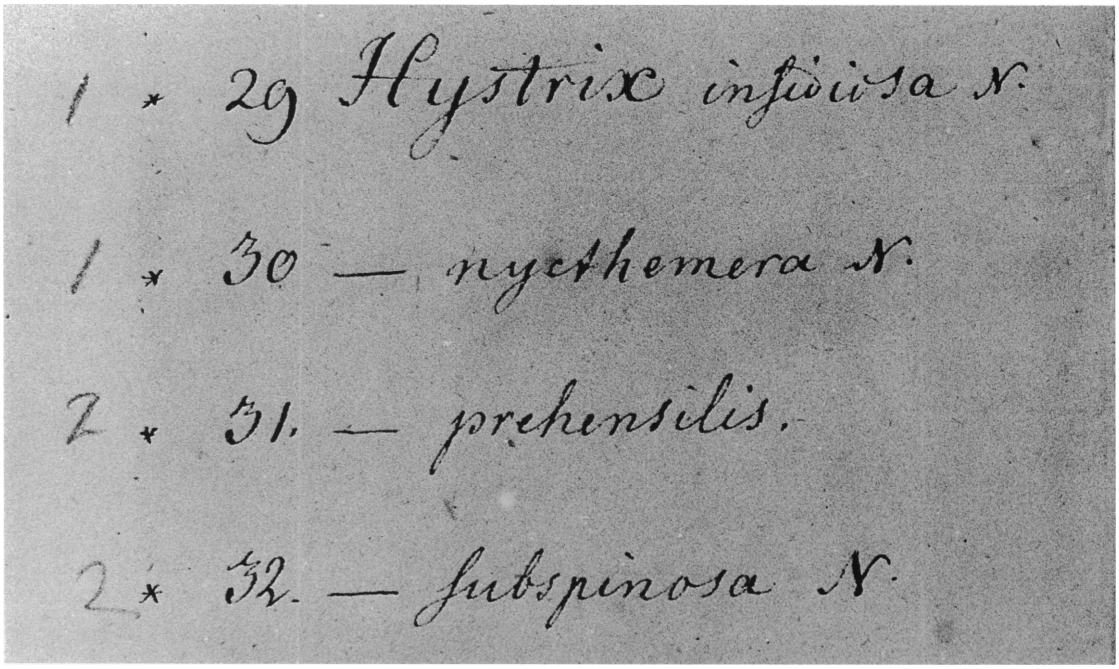

Fig. 3. Detail from page two of the 1810 species list showing the entries for four porcupine species, three of which are indicated as new ("N[ova]."); asterisks identify material donated by Count von Hoffmannsegg (see text). Whereas the original entries are in ink, the numbers to the left of each asterisk, apparently representing a specimen tally, are in pencil.

Ignaz von Olfers (b. 1793) studied foreign languages and natural history at the University of Göttingen from 1812 to 1815 before joining the staff of the Prussian legation to Brazil, which arrived at Rio de Janeiro in the late spring or early summer of 1817 (Stresemann, 1948; Papavero, 1971; Hackethal, 1995).[8] We surmise that Olfers studied the ZMB collections and took extensive notes, probably sometime in 1816, only to prepare himself for his Brazilian travels and not with a view to publishing. In a recently discovered letter to Lichtenstein written from Rio and dated 25 February 1818, however, Olfers explained that he could not refuse a request to contribute to a serial publication about Brazil edited by Baron von Eschwege, the politically influential director of the royal mines in Minas Gerais. Olfers' letter, somewhat exculpatory in tone, goes on to state that his contribution to Eschwege's "Journal von Brasilien" (only two volumes of which were apparently published) was a commentary on Illiger's list of South American mammals, that it had already been written, and that it was not very good.[9] The same letter mentions that he had purchased some local an-

[8] Published references suggest significantly divergent dates for Olfers' arrival at Rio. According to Stresemann (1948: 412), Count von Flemming's diplomatic entourage (including Olfers) arrived "im Frühjahr 1817," whereas Papavero's account (1971: 69) implies that Olfers arrived in 1816. Papavero cannot be correct, however, because a letter written from Paris by Olfers to Lichtenstein is dated 22 April 1817 and states that Olfers was leaving the next day for London. In a subsequent report from Rio dated 15 November 1817, Olfers described the contents of his first shipment to Berlin (consisting of fishes, amphibians, reptiles, insects, and books); the earliest collection date mentioned therein is late July 1817.

[9] "v. ESCHWEGE, dem ich, wie Sie leicht denken können bey seiner hiesigen Lage (als Director der Bergwerke in Minas Geraes) große Verbindlichkeiten habe, gibt unter dem Namen: "Brasilien" eine Zeitschrift heraus, von der das erste Heft bereits erschienen seyn muß; ich könnte es ihm nicht abschlagen, ihm einen Beytrag dazu zu liefern, . . . und habe ihm Bemerkungen zu Illiger's Tafel über die Südamerikanischen Säugthiere geliefert; die Abhandlung ist currente [sic] . . . geschrieben, und nicht viel werth, sie wird aber auch die erste und die letzte seyn" (letter from Olfers to Lichtenstein, Rio de Janeiro 25 February 1818).

imals and was keeping them alive, one of which was a porcupine more-or-less resembling the North American species ("ein Hystrix der dorsata ähnlich").

Thus, it is possible that Olfers' (1818) species accounts included observations on specimens that he obtained himself in Brazil, as suggested by Hershkovitz (1959). The only explicit indications of this in his published text, however, are one reference (op. cit.: 205) to young specimens of "*Didelphys opossum*" (= *Philander opossum*), and another (op. cit.: 227) to a purchased litter of "*Nasua narica*" (= *N. nasua*) His porcupine accounts, by contrast, contain no reference to personal observations made in Brazil, or to any specimens other than those in Berlin. No ZMB porcupine material is now labeled as having been collected by Olfers himself. Although one ZMB specimen label (fig. 1) together with the museum's accessions register (Eingangskatalog) and other archival documents indicate that Olfers collected porcupines in the company of another German naturalist, Friedrich Sellow (or Sello), Olfers and Sellow did not begin collecting together until 10 August 1818 (Urban, 1893; Stresemann, 1948; Papavero, 1971; Hackethal, 1995), five months or more after Olfers had completed his manuscript for Eschwege. An earlier shipment containing a specimen of "*Hystrix insidiosa*" (identified by Lichtenstein) is recorded in the ZMB accessions register as received from Sellow on 25 March 1818, but Sellow sent that shipment on 4 October 1817 from Salvador (Papavero, 1971), where it could not have been seen by Olfers (ca. 1250 km away in Rio).

In summary, the positive evidence from the 1810 species list and the lack of definite evidence for other examined specimens both indicate that Olfers' types are to be sought among the surviving material from Hoffmannsegg's original collection. Although some Hoffmannsegg specimens were apparently sold or exchanged over the years by Lichtenstein (Stresemann, 1950), the types of *Hystrix insidiosa*, *H. nycthemera*, and *H. subspinosa* can be confidently identified from among those remaining in Berlin. Herein we document their rightful status as the primary basis for identifying Olfers' and Kuhl's Neotropical porcupine species.

Materials and Methods

Documents: All of the manuscript documents cited in this report, with the sole exception of Peters' catalog of the mammal collection, are preserved in the archives (Historische Bild- und Schriftgutsammlungen) of the Museum für Naturkunde der Humboldt-Universität zu Berlin (see Appendix). Three rare printed documents that we cite (Lichtenstein, 1816, 1818a, 1818b) are in the museum's library. Peters' catalog of the mammal collection is the first volume ("Catalogus generalis Musei Zoologici Berolinensis Mammalia I") of the Generalkatalog, a bound series of folio ledgers that is still in use in the museum's Säugetier-Abteilung.

Specimens: Catalog numbers prefixed by ZMB in the following species accounts are from the series in continuous use since 1857 in the mammal collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin. We also cite specimens examined from other institutions with the following abbreviations: AMNH, American Museum of Natural History (New York); BMNH, British Museum of Natural History (London); FMNH, Field Museum of Natural History (Chicago); MCZ, Museum of Comparative Zoology at Harvard University (Cambridge, MA); USNM, National Museum of Natural History (Washington, DC); ZINRAS, Zoological Institute of the Russian Academy of Sciences (St. Petersburg).

Measurements: All measurements are in millimeters (mm) and, except as noted, were taken by us. Length of head-and-body and length of tail prefixed by "ca." were measured on dried skins to the nearest 5 mm. Measurements of the hindfoot, recorded to the nearest millimeter, include the claws and were taken from minimally distorted feet that contained the whole pedal skeleton (tarsals, metatarsals, and phalanges). Measurements of the skull and dentition, taken with dial or digital calipers and recorded to the nearest 0.1 mm, are abbreviated and defined as follows (see fig. 4):

CIL Condylo-incisive Length: Measured from the articular surface of one occipital condyle to the greater curvature of the ipsilateral upper incisor.

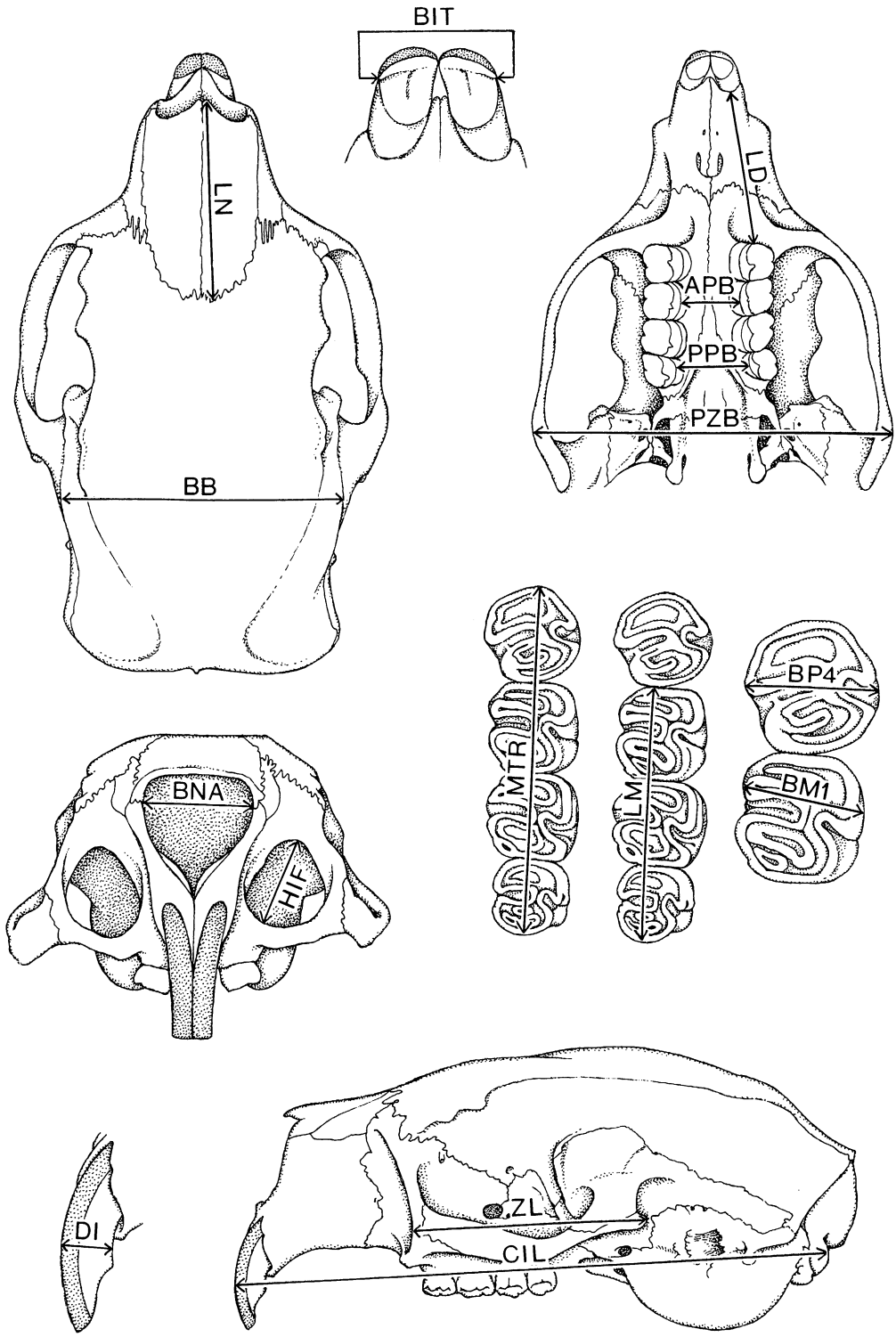

Fig. 4. Limits of 16 craniodental measurements defined in the text.

LD Length of Diastema: Measured from the lesser curvature of an upper incisor at the alveolar margin to the crown of the ipsilateral P4 [or dP4 of subadults].

MTR Maxillary Tooth Row: Greatest crown length from P4 [or dP4 of subadults] to M3.

LM Length of Molars: Greatest crown length of the upper molar series (M1–M3).

BP4 Breadth of P4: Greatest crown breadth of the permanent upper premolar.

BM1 Breadth of M1: Greatest crown breadth of the first upper molar.

APB Anterior Palatal Breadth: Measured between the crowns of the first upper molars.

PPB Posterior Palatal Breadth: Measured between the crowns of the third upper molars.

PZB Posterior Zygomatic Breadth: Greatest breadth across the zygomatic arches behind the orbits.

HIF Height of the Infraorbital Foramen: Measured as the greatest inside diameter, usually at an angle of about 30–40° from the midsaggital plane.

ZL Zygomatic Length: Measured from the posterior margin of the infraorbital foramen to the posterolateral corner of the zygomatic arch.

LN Length of Nasals: Greatest length of one nasal bone (the longest if right and left elements are unequal).

BNA Breadth of Nasal Aperture: Greatest transverse dimension of the nasal orifice, always at or near the nasal/premaxillary sutures.

BB Breadth of Braincase: Transverse dimension of the braincase, measured by placing the caliper jaws just above the squamosal zygomatic root on each side.

DI Depth of Incisor: Distance between the greater and lesser curvatures of an upper tooth.

BIT Breadth of the Incisor Tips: Measured across the enameled tips of both upper teeth.

AGE CLASSIFICATION: We used maxillary tooth eruption, cranial suture closure, and pelage maturation to define a heuristic age classification as follows.

Juveniles—Maxillary toothrow incomplete (three or fewer teeth erupted); all cranial sutures open; pelage often conspicuously immature, including long fur even in species that lack visible fur as adults.

Subadults—Immature maxillary dentition (dP4–M3) completely erupted, or dP4 shed and P4 incompletely erupted; all cranial sutures still visible; pelage always appears mature.

Adults—Permanent maxillary dentition (P4–M3) fully erupted, with light to moderate wear (teeth usually not worn below widest part of crown and almost always with at least some occlusal detail remaining); some cranial sutures usually obliterated.

Old adults—Cheekteeth worn below widest part of crown (and therefore not measurable), with little or no occlusal detail remaining on M1 and M2; only nasal sutures (if any) usually visible.

In assigning specimens to these age classes, primacy was given to dental criteria, but the other ontogenetic markers are useful in judging the age of specimens with missing or precociously worn teeth. Examples of *Chaetomys*, which may retain the milk premolars throughout life, pose special problems for age classification (see the account for *Hystrix subspinosa*, below).

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THE TYPE MATERIAL

Below we identify and redescribe the type material of *Hystrix nycthemera*, *H. subspinosa*, and *H. insidiosa*. We preserve the order in which these species were described by Olfers (1818) for the following accounts because this is also a sequence of increasing complexity for associated nomenclatural problems. Our descriptions are based exclusively on the type material. Comments about synonyms, geographic distribution, and morphological variation among other referred specimens are gathered together under Remarks in each account. Formal synonymies, tracing name changes from Olfers (1818) to the recommended current usage, are provided in a concluding Taxonomic Summary at the end of this report.

Hystrix nycthemera Olfers, 1818

Olfers (1818: 211) described this species as "black changing to white (spines with black tips and white bases) nose scarcely swollen,"[10] gave the length of the body as 11 inches, and the tail length as 11¼ inches. Kuhl (1820: 71) grouped *Hystrix nycthemera* with other long-tailed porcupines lacking visible dorsal fur (e.g., *H. prehensilis* and *H. subspinosa*), from which it was distinguished as "completely black above from the densely crowded spines, which are white basally, the apical third black, very sharp, and slightly larger than those of *H. insidiosa*."[11] Despite the brevity of these two accounts, the animal in question is obviously a small, long-tailed porcupine densely covered above with bicolored spines, the mass effect of which is completely black. Olfers' reference to a scarcely swollen nose makes sense in context, because he described *H. nycthemera* following a reference to *H. prehensilis* Linnaeus, a species in which the muzzle is conspicuously swollen.

TYPE MATERIAL: The holotype (by monotypy), ZMB 1299, consisting of the skin, skull, and mandibles of a subadult of unknown sex (figs. 5–7). According to Peters' catalog and information inked on the skull itself, ZMB 1299 was part of Hoffmannsegg's collection and was obtained in Brazil by Sieber; asterisks in Peters' catalog and another on the skull indicate that this is the type of *Hystrix nycthemera*. We do not challenge these prima facie indications because the morphological characters of ZMB 1299 match Olfers' and Kuhl's descriptions, and because we found no record that other conspecific examples were ever present in Berlin.[12] The skin is mostly intact, but the tail-tip is missing and some pelage has slipped from the crown of the head and from part of the ventrum; scattered holes in the skin have been repaired with cloth patches. The skull is missing part of the left and right parietals and frontals, the left jugal, and both pterygoid processes.

TYPE LOCALITY: Olfers stated only that this species was known from Brazil, which corresponds to the information given in Peters' catalog and on the specimen itself (fig. 6). However, Sieber's collecting activities in Brazil were apparently confined to eastern Amazonia: along the lower Amazon between Óbidos and Pará (now Belém), and on the lower Tocantins at Cametá (Urban, 1906). The known collection localities of other referred specimens of *Coendou nycthemera* (see below) suggests that the type was probably taken somewhere along the south (right) bank of the lower Amazon, or on the lower Tocantins.

DESCRIPTION OF THE HOLOTYPE: *External*—

[10] "... nigro alboque varia (spinis basi albis, apice nigris) naso vix tumido."

[11] "*Supra tota nigra, aculeis confertissimis*; basi albidis, parte tertia apicali nigris, acutissimis, parum majoribus illis H. insidiosae" (italics original).

[12] A pencil notation in the left-hand margin of the 1810 species list (fig. 3) suggests that Hoffmannsegg donated only a single example of this species, and a manuscript specimen list dated 1822 likewise includes only a single entry for *Hystrix nycthemera* (fig. 13). A printed pamphlet describing duplicate specimens offered for sale at auction (Lichtenstein, 1818b) lists *H. insidiosa* and *H. subspinosa*, but not *H. nycthemera*.

Fig. 5. Dorsal view of the skin of ZMB 1299, holotype of *Hystrix nycthemera* Olfers.

The visible dorsal body pelage consists entirely of bicolored quills that are ivory-white basally and blackish distally; the overlapping dark ends, about ⅓ to ½ of each quill, produce the mass effect of a completely blackish porcupine except where quills are missing or parted to reveal the whitish bases. There are no pale-tipped quills anywhere on the head, back, flanks, or rump. The quills are longest middorsally, about 55 mm, but most are substantially shorter, about 30–40 mm over the shoulders, and 25–30 mm on the rump. The ventral surface of the body is covered with bicolored spinous hairs grouped in triads, among which are scattered a few soft and wavy wool hairs.

The dorsal surface of the proximal ⅔ of the tail is covered with bicolored quills like those on the back and rump, but the rest of the tail (excepting the naked prehensile tip) is covered with blackish bristles; the bristles under the base of the tail are much stiffer and denser than those on the lateral and dorsal surfaces. The long mystacial vibrissae extend behind the pinnae when laid back alongside the head; supraorbital, genal, submental, and postcranial vibrissae are also present. The latter are scattered along the forelimb from wrist to elbow, along the hindlimb from ankle to knee, and along the ventral surface between the fore- and hindlimbs.

Skull—The frontal and nasal sinuses are not inflated, resulting in an almost flat dorsal profile from the tips of the nasals to the midparietal region. The nasal bones are long and taper posteriorly to rounded ends that extend well behind the premaxillae. Viewed from above, the zygomatic arches are widest posteriorly and converge toward the rostrum without a secondary widening at the orbits; the jugal is unexpanded. The bony crests and scars associated with the complex origins of M. temporalis on the braincase are not strongly developed.

The incisive foramina are incompletely separated and are recessed in a common fossa that is bordered behind by the maxillary bones. The posterior diastema is distinctly ridged, and the palatal bridge between the cheekteeth is narrowly constricted with a median keel. The anterior margin of the mesopterygoid fossa is /\-shaped (not a rounded arch), and extends between the second molars; the roof of the fossa is completely bony (not perforated by sphenopalatine fenestrae). The auditory bullae are large and elongated posteriorly to contact the paroccipital processes; the roof of the external auditory meatus is smooth, without a distinct dorsal ridge or keel.

Dentition—The upper incisors have deep orange enamel bands and are not strongly procumbent. The cheekteeth essentially resemble those of other erethizontids (except *Chaetomys*) in occlusal morphology. The maxillary toothrows are subparallel. The permanent fourth upper premolar (incompletely erupted in this subadult specimen) is slightly larger than the first upper molar.

Measurements—External and craniodental measurements of the type are provided in table 1 with those of other referred conspecifics for comparison.

REMARKS: *Hystrix nycthemera* is unambiguously referable to *Coendou* Lacépède,[13] and appears to be the oldest available name for the species currently known as *C. koopmani* Handley and Pine (1992). Handley and Pine's description of *koopmani* was based on a series of 61 specimens collected at scattered Amazonian localities from the Rio Madeira eastward to Belém (the type locality); all known collection localities are south of the main channel of the Amazon itself. The characters of *nycthemera* fit within the range of variation described for *koopmani* (op. cit.) in all but one respect. According to Handley and Pine, at least some lateral quills are always pale-tipped in *koopmani*, but pale-tipped quills are so inconspicuous on some of their paratypes from the lower Tocantins (notably AMNH 96317 from Cametá) that only a slight overall darkening would result in the completely blackish appearance of ZMB 1299. The skull of ZMB 1299 is an almost perfect

[13] The specific epithet *nycthemera* has also been combined with *Sphiggurus* F. Cuvier, *Synetheres* F. Cuvier, and *Cercolabes* Brandt, all of which are junior synonyms of *Coendou*. Husson (1978) argued for the retention of *Sphiggurus* as a valid genus, an opinion followed by Woods (1993), but we agree with Handley and Pine (1992) that *Coendou* and *Sphiggurus* cannot be meaningfully diagnosed as separate taxa.

match in measurements and qualitative characters with the skull of AMNH 134208, a subadult male paratype of *koopmani* that we took to Berlin for side-by-side comparison.

Brandt (1835) thought that *Hystrix nycthemera* might be synonymous with his newly described species, *Cercolabes* (*Sphiggurus*) *nigricans*, an opinion apparently endorsed by Wagner (1844), who listed these names as synonyms. Voss's recent examination of Brandt's porcupine specimens in St. Petersburg suggests otherwise, however. The type and only referred specimen of *nigricans*, ZINRAS 30, consists of a mounted skin from which the skull has been extracted and lost. The dorsal body pelage, unlike that of any specimen of *Coendou nycthemera*, includes a sparse coat of long (70–80 mm) blackish fur, the individual hairs of which are tipped with yellow. The underlying quills are conspicuously tricolored (with yellowish bases, blackish middle bands, and reddish tips) over the crown of the head, nape, shoulders, middle back, flanks, thighs, and sides of the tail; the quills of the lower back and rump, however, are bicolored (with yellowish bases and blackish tips). The ventral fur is entirely soft, without any admixture of spinous hairs. Our measurements of the mounted skin suggest a head-and-body length of ca. 390 mm, a tail length of ca. 240 mm, and a hindfoot of 65–70 mm.

Although the skull of ZINRAS 30 is missing, the external characters described above suggest that *nigricans* is a member of the *Coendou spinosus* complex, a possibly conspecific series of populations that extends from Paraguay northeastward along the humid Atlantic coastline of Brazil to Espírito Santo (see Remarks under *Hystrix insidiosa*). Although the published type locality of *nigricans* ("Brazil") is indefinite, Brandt stated that the specimen was sent by "Langsdorff" (= Georg Heinrich von Langsdorff), the Russian General Consul at Rio de Janeiro from 1813 to 1820 (Papavero, 1971). While it is plausible, therefore, that the type came from Rio, Langsdorff traveled widely in Brazil and it is now impossible to be certain where it was really collected.

Handley and Pine (1992) provided excellent morphological comparisons between *Coendou nycthemera* and other congeners with which it has been or might be confused.

Hystrix subspinosa Olfers, 1818

Olfers (1818: 211) described this species as ". . . light brown, with short twisted spines changing to harsh bristles behind the middle of the body, very long at the base of the seminaked tail."[14] He gave the length of the head-and-body as 14¼ inches, and that of the tail as 9 inches. From other long-tailed porcupines lacking visible dorsal fur, Kuhl (1820: 71–72) distinguished *H. subspinosa* as having "undulating spines, resembling seals' whiskers, short and stout on the anterior part of the body, very elongated and slender posteriorly, [where they are] four times larger; fine and straight on the abdomen. Color yellowish-brown, shading to gray."[15]

TYPE MATERIAL: The lectotype, ZMB 1300, consisting of the skin, skull, and mandibles of a subadult of unknown sex (figs. 8–10); and a paralectotype, ZMB 1301, consisting of the skin, skull, and mandibles of a juvenile, also of unknown sex. Peters' catalog and 20th-century museum labels tied to the skin both indicate that ZMB 1300 and 1301 were originally part of the founding Hoffmannsegg collection. Although ZMB 1300 is indicated as the type by asterisks next to its binomial in Peters' catalog (fig. 2), this specimen was apparently first validly designated as the name-bearer by Martin (1994).[16]

The skin of the lectotype, ZMB 1300,

[14] ". . . lucide brunnea[,] spinis brevioribus tortilibus, pone medium corpus abientibus in setas duriusculas, ad basim caudae subnudae longissimas."

[15] "*Aculeis undulatis*, Phocae vibrissis similibus, ad corporis partem anteriorem brevibus, crassis, ad posteriorem longissimis, gracilioribus, quater majoribus; abdominis gracillimis, rectiusculis. Colore bruneo flavicanti, ad cinerascentem vergenti" (italics original).

[16] Martin (1994) referred to ZMB 1300 as the holotype and to ZMB 1301 as the paratype, but both could have served as the basis for Olfers' description; selecting one of two syntypes as the name-bearer makes it the lectotype and the other the paralectotype (ICZN, 1985: Article 74b).

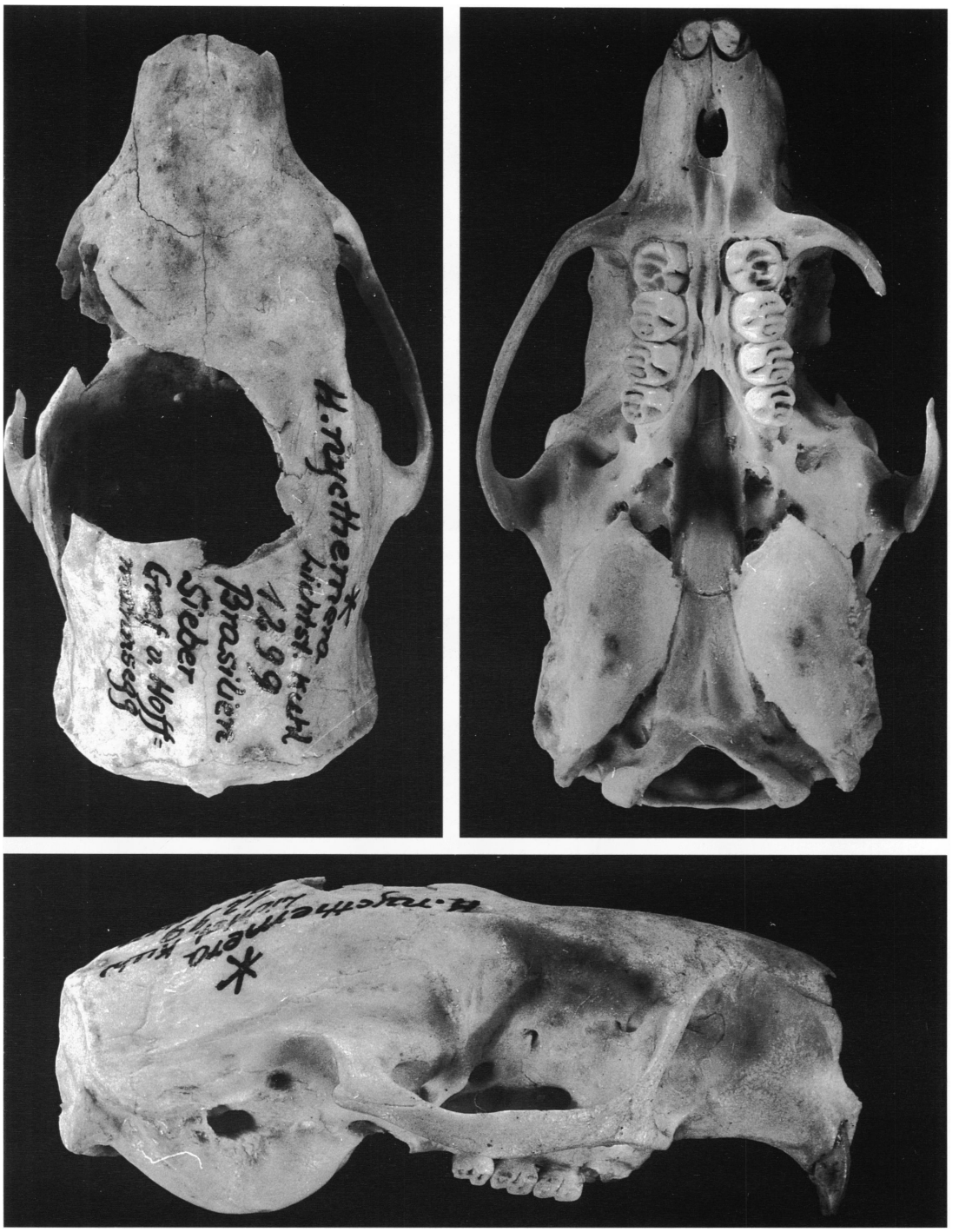


Fig. 6. Dorsal, ventral, and right lateral views of the skull of ZMB 1299, holotype of *Hystrix nycthemera* Olfers.

Fig. 7. Occlusal and left lateral views of the mandibles of ZMB 1299, holotype of *Hystrix nycthemera* Olfers.

lacks pelage on the dorsal surface of the head and neck; a few bare patches of skin are also exposed on the forelegs and ventral surface, and the extreme tip of the tail is missing. Although both upper incisors are broken off at the alveoli, the pterygoid processes are lacking, and a small piece of bone is missing from the occiput, the lectotype skull is otherwise in excellent condition and preserves all of the craniodental characters hitherto regarded by authors as diagnostic of the species. Two mammae surrounded by hairless areolae are visible on the right side of the skin, but because both male and female erethizontids have visible mammae, the sex of the specimen is not certainly indicated by this. The premolars of ZMB 1300 are indistinguishable in size and occlusal morphology from those of the juvenile paralectotype, from which we infer that they represent the milk teeth (dP4/dp4). Because the milk premolars are thought to be retained throughout life in this species (Patterson and Wood, 1982; Martin, 1994), an age classification based, in part, on tooth replacement (see Materials and Methods) is here ambiguous. We judge the lectotype to be a subadult because of its lightly worn third molars and unfused cranial sutures.

The skin of the juvenile paralectotype, ZMB 1301, is completely intact, but the skull is somewhat less well preserved than that of the lectotype. Although the third molars of this specimen are not erupted, the pelage resembles that of the older example, with no soft fur or other sign of immaturity.

TYPE LOCALITY: Olfers gave the type lo-

TABLE 1

External and Craniodental Measurements (mm) of *Coendou nycthemera* from Eastern Amazonia (below Óbidos, including Marajó Island)

	Subadults		
	ZMB 1299[a]	AMNH 134208	Adults[b]
Sex	?	male	9 males, 13 females, 3 unknown
HBL	ca. 280	330	344 ± 22 (290–380) 20
LT	ca. 270	300	313 ± 25 (268–370) 20
HF	ca. 65	55	63 ± 5 (55–75) 22
CIL	68.2	64.9	68.4 ± 3.8 (61.8–77.5) 24
LD	16.0[c]	16.0[c]	17.8 ± 2.0 (13.7–22.4) 24
MTR	16.2[c]	—	15.3 ± 0.5 (14.1–16.3) 25
LM	11.7	—	11.3 ± 0.4 (10.4–12.0) 25
BP4	4.9	4.7	4.6 ± 0.3 (4.2–5.2) 25
BM1	4.4	4.1	4.1 ± 0.2 (3.8–4.7) 25
APB	4.4	4.6	5.2 ± 0.7 (3.7–6.3) 24
PPB	6.4	—	6.8 ± 0.7 (5.3–8.0) 18
PZB	41.5	40.2	40.5 ± 1.7 (38.2–45.0) 23
HIF	8.6	8.5	10.0 ± 0.9 (8.6–12.3) 25
ZL	26.2	25.3	26.1 ± 1.6 (23.2–29.9) 25
LN	19.8	20.4	20.6 ± 1.9 (18.5–24.4) 20
BNA	11.2	11.1	10.8 ± 0.7 (9.4–11.8) 24
BB	31.9	32.6	31.4 ± 1.2 (29.0–33.6) 25
DI	3.0	3.1	3.3 ± 0.2 (2.9–3.6) 24
BIT	4.7	4.5	5.0 ± 0.4 (4.4–5.8) 24

[a] The holotype.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size are provided for the following series of specimens: AMNH 96314, 96320, 96323, 96325–96327, 96329, 134074, 134075, 134187, 134188, 134193–134195, 134199, 134203, 134206, 134207, 134211; MCZ 30551, 30552; USNM 105527, 519689, 519690; ZINRAS 40243.

[c] Estimated values.

cality of *Hystrix subspinosa* as Brazil only, but Wied (1826) stated that the Berlin specimens had been collected by Sieber at Cametá, a locality on the lower Rio Tocantins in the Amazonian state of Pará. This information also appears in Peters' catalog (fig. 2), and on the specimens themselves (e.g., fig. 9). However, because all other known collection localities and sightings of this animal are from the Atlantic coast of southeastern Brazil, Avila-Pires (1967) suggested that Hoffmannsegg's specimens had been mislabeled, probably by Lichtenstein, whose mistake about provenance was then repeated by Wied. The only collector likely to have sent specimens of *H. subspinosa* to Hoffmannsegg was Gomes, who resided in the state of Bahia, where the species is widespread. On this assumption, Avila-Pires (1967) emended the type locality to Ilhéus (a coastal city in Bahia), which is also the emended type locality of *Plectrochoerus moricandi* Pictet, a junior synonym (see Taxonomic Summary, below).

We agree that Gomes obtained ZMB 1300 and 1301 in the state of Bahia, but restricting the type locality to Ilhéus was erroneous. Gomes's correspondence with Hoffmannsegg indicates that he sent three porcupine specimens from Salvador in separate shipments dated 3 February 1801, 20 November 1801, and 24 May 1802 (see Appendix). In a working list of Gomes's material, Illiger tentatively identified the first specimen as "*Hystrix prehensilis* an var?" and gave a brief Latin description that, although omitting many diagnostic traits, unambiguously indicates the species currently known as *Chaetomys sub-*

spinosus.[17] In other contemporaneous notes on Gomes's mammals, wherein the same identification is given and the same description repeated in German, both "*prehensilis* an var" and the description were later crossed out with "*subspinosa* N." substituted, apparently in the same (Illiger's) handwriting (fig. 11). In a letter accompanying the second shipment, Gomes remarked that the enclosed specimen was apparently of the same species as that sent previously, and had been collected on his estate at Salvador.[18] It is therefore clear that Gomes's first two porcupine specimens, both presumably collected at Salvador, were the lectotype and paralectotype of *Hystrix subspinosa*. The third specimen, concerning which nothing was recorded by either Gomes or Illiger about locality, characters, or nomenclature, was probably the holotype of *Hystrix insidiosa* (see below).

DESCRIPTION OF THE LECTOTYPE AND PARALECTOTYPE: *External*—The visible dorsal body pelage consists entirely of wavy spines, which are ivory-white basally with pale brown ends, producing the mass effect of a more-or-less uniform beige or dull buff from head to tail. On the head, these spines are short (10–15 mm in length) and stiff, with hard, sharp points. Posteriorly, the spines increase in length and flexibility, gradually becoming bristle-like (somewhat resembling broomstraws or phocid mystacial vibrissae) and reaching a maximum length of 60–70 mm near the base of the tail, where they have fine, hair-like tips. The ventral pelage is shorter, but otherwise essentially similar to the dorsal pelage in color and morphology, without any sharp line of demarcation between the two.

The dorsal surface of the proximal fourth of the tail is covered with wavy bristle-spines like those on the rump, but the ventral surface of the tail base is densely covered with very stiff, straight (not wavy), orange-yellow bristles; the rest of the tail except the extreme tip is sparsely covered above and below with softer brownish hairs of conventional appearance. The dorsal surface of the tail-tip of the lectotype is bare, but that of the younger paralectotype is sparsely haired like the ventral surface. The cranial and postcranial vibrissae have the same morphology and anatomical distribution as previously described for *Hystrix nycthemera*.

Skull—The cranial sinuses are not inflated. The nasals are conspicuously broader posteriorly than anteriorly, and short, scarcely extending behind the premaxillae. The frontals are very broad, with a large postorbital process on each side that closely approaches a corresponding process of the jugal projecting from below, resulting in an almost complete separation of the orbital and temporal fossae. Viewed from above, the zygomatic arches appear biconvex, with an anterior bulge at the orbits where the jugals are expanded outward. On each side of the skull the attach-

[17] Illiger's early writings, up to and including his 1811 "Prodromus," referred all Neotropical porcupines to *Hystrix prehensilis*, but the notation "an var?" ("or perhaps a variant?") suggests that he had doubts about this usage from the very beginning of his work with Hoffmannsegg's collection. In these notes, Illiger wrote of Gomes's first porcupine, "Mystacis vibrissae nigrae/ nec albae/ aculei pectori[s] et abdominis ab illis dorsi colore vix diversi/ nec nigricantes./ Icon Schreberi colorem rufum exhibet qualis non est." ("The mystacial vibrissae are black and not white; the spines of the chest and abdomen are not very differently colored from those of the back, and are not black. Nor does it resemble the rufous color shown in Schreber's illustration.") The sole diagnostic trait mentioned here is the presence of ventral spines that do not contrast in color with those of the dorsal surface, which fits *Chaetomys subspinosus*, but not *Coendou insidiosus*, the only other erethizontid occurring in coastal Bahia (Santos et al., 1987; Oliver and Santos, 1991): the ventral pelage of *C. insidiosus* consists exclusively of soft fur, not spines.

[18] "Je crois que ce Quadrupède est le même Porc-Épic Co[en]dou que je vous ai dejá envoyé. . . . Cet animal a été attrapé pendant le jour et à la main dans le bois même de mon habitation. Mon Jardinier en allant au Bois l'[a] trouvé sur an Arbre, marchant par un[e] de ces branches, tout de suite il a fait couper ce[tte] branche ou il se tennoit et pendant qu'on le cupoit, cet animal ne cessoit pas de marcher et de s'assurer avec la queue, les mains et les jambes de tout sa force et de frapper les dents [les] un[e]s dans les autres avec tant de violence qui se faisoit entendre. Lorsqu'il a vu que l[a] branche alloit tomber s'élance par lui même en bas ou il a été pris facilement à la main, mais pour le prendre il faut mètre la main sur le dos de manière qu'il ne puisse [pas] toucher avec les dents. Ce fait me force à penser que cet animal ne dort [pas] pendant le jour. Se je ne puis pas encore avancer si sa chair est bonne à mange[r], seulement je vous assure que les nègres la trouvent bonne" (letter from Gomes to Hoffmannsegg, Bahia 20 November 1801).

Fig. 8. Dorsal view of the skin of ZMB 1300, lectotype of *Hystrix subspinosa* Olfers.

ments of M. temporalis are marked by a horizontal bony ridge, continuous with the postorbital process of the frontal, along the dorsolateral contour of the braincase; and another crest, vertically oriented, near the frontosquamosal suture in the rear of the orbit. The dorsal surface of the frontals and parietals between the temporal ridges is conspicuously rugose on the subadult lectotype, but not on the juvenile paralectotype.

The incisive foramina, completely enclosed in the premaxillae, are separated by a robust median septum, and are not recessed together in a common fossa. The lateral diastemal ridges are strongly marked; passing on each side from the incisor alveoli around the incisive foramina, they converge to within a few millimeters just in front of the cheekteeth. The median diastemal ridge, less well developed than the lateral ridges, is continuous with an inconspicuous median ridge between the toothrows. The palatal bridge is narrow and perforated only by inconspicuous nutrient foramina. In the lectotype, the anterior margin of the mesopterygoid fossa is a flattened, straight-sided arch that extends only between the third molars; the roof of the fossa is perforated by narrow slits flanking the presphenoid-basisphenoid suture, but lacks large sphenopalatine fenestrae. The auditory bullae are elongated, extending to the paroccipital process on each side; the margins of the external auditory canals are produced as irregular bony tubes; and the dorsal roof of the meatus lacks a well developed ridge or keel.

Dentition—The upper incisors are small, with yellow-orange enamel bands, and apparently opisthodont (these teeth are broken off at the alveoli on both skulls). The cheekteeth are longer than wide, hypsodont, and unlike those of other erethizontids in occlusal morphology; the maxillary rows are subparallel. The premolars, presumably the deciduous teeth in both specimens, are smaller than the first molars.

Measurements—Measurement data from the lectotype (ZMB 1300), the only nonjuvenile specimen we examined, are incomplete because of the broken incisors: HBL, ca. 360; LT, ca. 260; HF, 67; CIL, 74.6; LD, 24.0 [to dP4]; MTR, 19.3 [dP4–M3]; LM, 14.5; Breadth of dP4, 3.8; BM1, 3.7; APB, 4.1; PPB, 5.7; PZB, 42.3; HIF, 10.9; ZL, 30.3; LN, 24.8; BNA, 10.1; BB, 31.3.

REMARKS: Olfers (1818) named this species *Hystrix tortilis*, attributing the epithet to Illiger, who had previously published it as a nomen nudum in his 1815 "Ueberblick" (see Nomina Nuda and Dubia, below). Hershkovitz (1959: 349), however, stated that ". . . Olfers used Illiger's *nomen nudum* for the sole purpose of identifying it with the description of the specimen for which the new name *H. subspinosa* is proposed." This interpretation is clearly erroneous. The format of Olfers' account (fig. 12) unambiguously associates *tortilis* with the description and consigns *subspinosa* to synonymy. Examination of other species accounts in the same publication lends no support to Hershkovitz's argument that Olfers intended to replace Illiger's name with another. Fortunately, it is not necessary to change the taxonomic usage of well over a century and a half, during which the taxon in question has been known consistently as *subspinosa* by almost all mammalogists.

According to the International Code of Zoological Nomenclature (ICZN, 1985: Article 11e),

> A name first published as a junior synonym is not thereby made available unless prior to 1961 it has been treated as an available name and either adopted as the name of a taxon or treated as a senior homonym; such a name dates from its first publication as a synonym (for type species if a genus-group name see Article 67l; for type series if a species-group name see Article 72b (iii); for authorship, see Article 50g).

Therefore, even though Hershkovitz (1959) wrongly interpreted Olfers' intention, his treatment of *Hystrix subspinosa* as an available name and his adoption of it for the taxon in question made the name available from 1818. Article 50g of the code assigns authorship to Olfers, so *H. subspinosa* and *H. tortilis* are both available with the same author and date of publication. Having already identified the type material of *H. subspinosa* in accordance with Article 72b (iii), we hereby designate ZMB 1300 as the lectotype also of *H. tortilis*. Of these two coeval objective synonyms, we select *H. subspinosa* as senior to preserve current usage.

The genus *Chaetomys*, with *Hystrix sub-*

Fig. 9. Dorsal, ventral, and left lateral views of the skull of ZMB 1300, lectotype of *Hystrix subspinosa* Olfers.

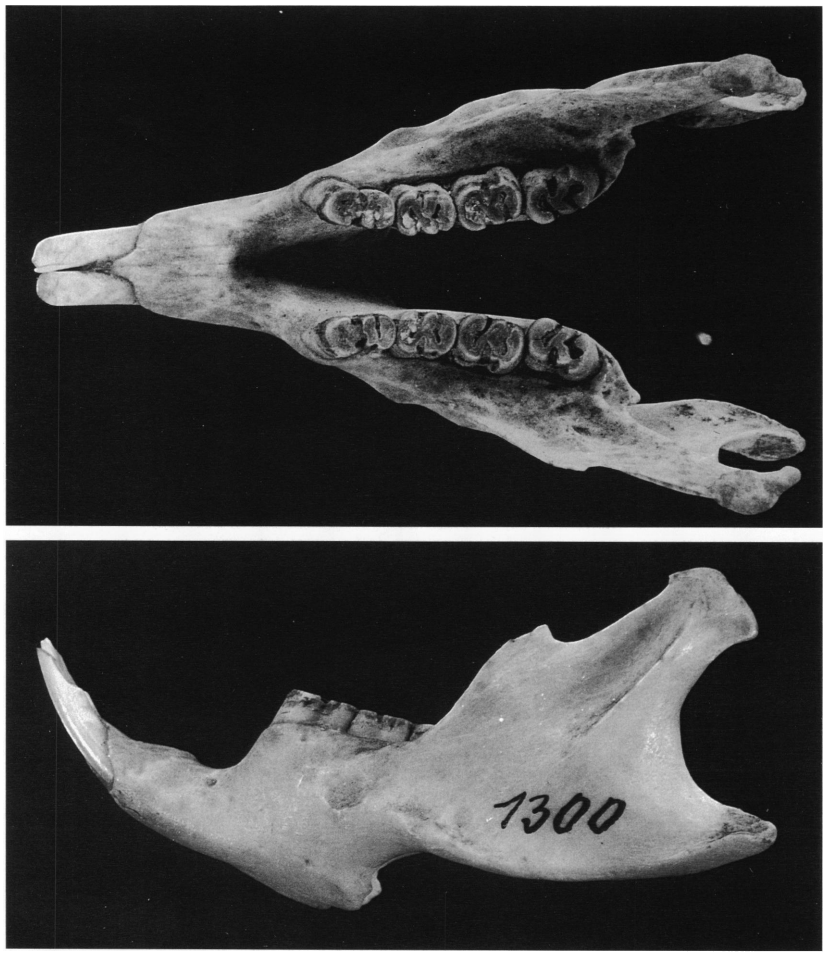


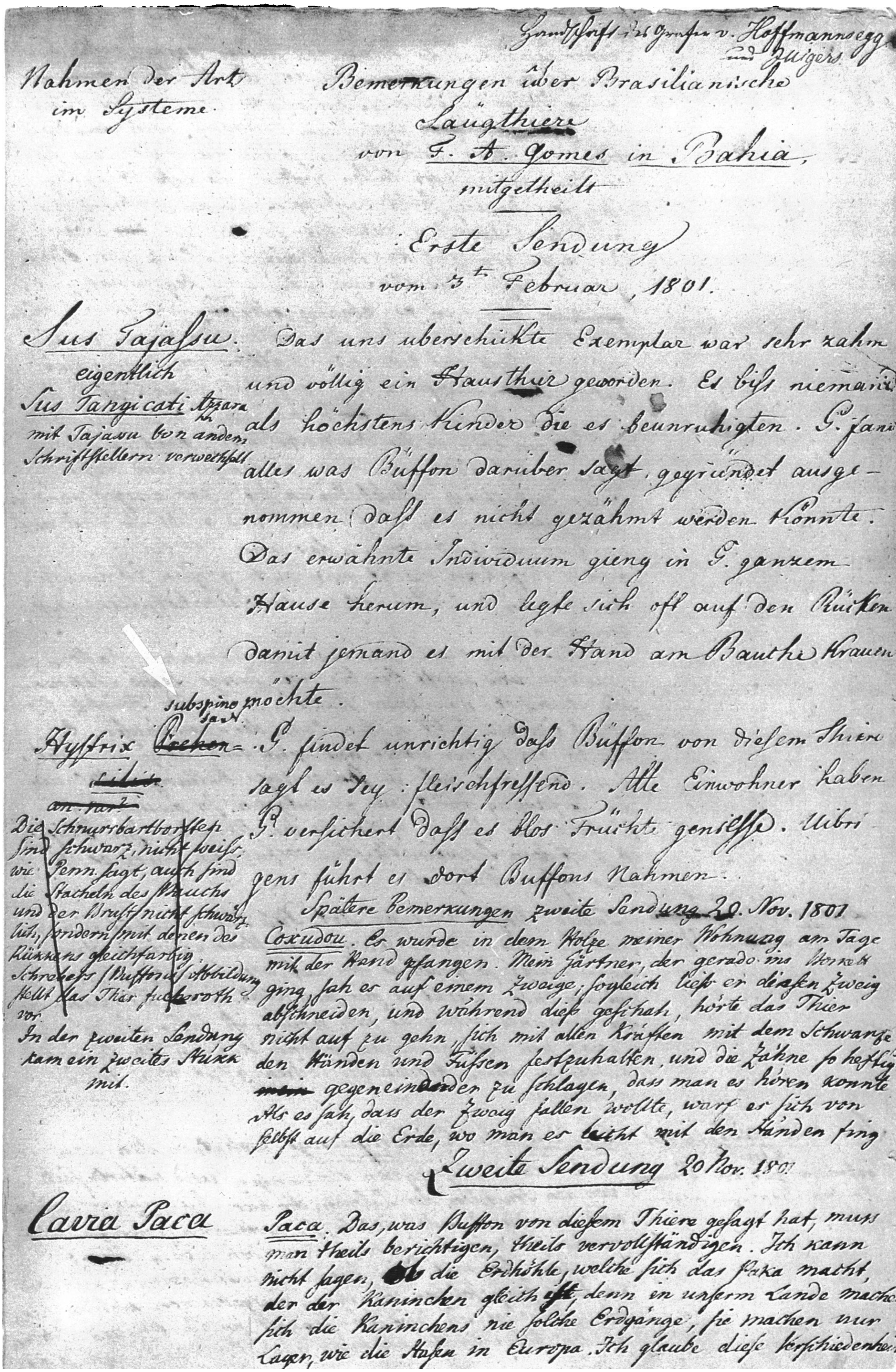
Fig. 10. Occlusal and left lateral views of the mandibles of ZMB 1300, lectotype of *Hystrix subspinosa* Olfers.

spinosa as the type and only referred species, was erected by Gray (1843) to emphasize the conspicuous differences in pelage, cranial, and dental characters between this animal and other erethizontids. Some authors (e.g., Miller and Gidley, 1918; Stehlin and Schaub, 1951; Patterson and Wood, 1982; Woods, 1993) have referred *Chaetomys* to the Echimyidae, but Martin (1994) persuasively argued that *Chaetomys* is not an echimyid and recommended that it be classified in the monotypic erethizontid subfamily Chaetomyinae as originally proposed by Thomas (1897). We agree that *Chaetomys* is an erethizontid, but we defer further discussion of its affinities to a later publication wherein relevant character data can be summarized in the context of a phylogenetic analysis.

Pictet's (1843) description of *Plectrochoerus moricandi*, also based on a specimen from Salvador (see Taxonomic Summary, below), is consistent with Waterhouse's (1848) suggestion that this taxon is a junior synonym of *Chaetomys subspinosus*, but we have not examined Pictet's type in Geneva.

Hystrix insidiosa Olfers, 1818

Olfers (1818: 211) described this species as ". . . hairy, spines short, sparsely scattered and intermingled with the fur, with yellow


Handschrift des Grafen v. Hoffmannsegg und Illigers.

Nahmen der Art im Systeme

Bemerkungen über Brasilianische Säugthiere von F. A. Gomes in Bahia mitgetheilt

Erste Sendung vom 3ten Februar, 1801.

Sus Tajassu. eigentlich Sus Tangicati Azzara mit Tajassu von andern Schriftstellern verwechselt

Das uns überschickte Exemplar war sehr zahm und völlig ein Hausthier geworden. Es biss niemand als höchstens Kinder die es beunruhigten. G. fand alles was Buffon darüber sagt, gegründet ausgenommen, dass es nicht gezähmt werden könnte. Das erwähnte Individuum gieng in G. ganzem Hause herum, und legte sich oft auf den Rücken damit jemand es mit der Hand am Bauche krauen möchte.

Hystrix subspinosa

Die Schnurrbartborsten sind schwarz, nicht weiss, wie Penn. sagt, auch sind die Stacheln des Bauchs und der Brust nicht schwärzlich, sondern mit denen des Rückens gleichfarbig. Schrebers (Buffons) Abbildung stellt das Thier zu roth vor. In der zweiten Sendung kam ein zweites Stück mit.

G. findet unrichtig dass Buffon von diesem Thiere sagt es sey fleischfressend. Alle Einwohner haben G. versichert dass es blos Früchte geniesse. Übrigens führt es dort Buffons Nahmen.

Spätere Bemerkungen zweite Sendung 20. Nov. 1801

Coxudou. Es wurde in dem Holze meiner Wohnung am Tage mit der Hand gefangen. Mein Gärtner, der gerade ins Gehölz ging, sah es auf einem Zweige, sogleich liess er diesen Zweig abschneiden, und während dies geschah, hörte das Thier nicht auf zu gehn, sich mit allen Kräften mit dem Schwanze den Händen und Füssen festzuhalten, und die Zähne so heftig gegeneinander zu schlagen, dass man es hören konnte. Als es sah, dass der Zweig fallen wollte, warf es sich von selbst auf die Erde, wo man es leicht mit den Händen fing.

Zweite Sendung 20 Nov. 1801

Cavia Paca

Paca. Das, was Buffon von diesem Thiere gesagt hat, muss man theils berichtigen, theils vervollständigen. Ich kann nicht sagen, ob die Erdhöhle, welche sich das Paka macht, der der Kaninchen gleich ist, denn in unserm Lande machen sich die Kaninchens nie solche Erdgänge, sie machen nur Lager, wie die Hasen in Europa. Ich glaube diese Verschiedenheit

bases and brown tips, tail thick."[19] He gave the length of the head-and-body as 12 inches, and that of the tail as 17½ inches; the latter measurement must be a printer's lapsus, however, because no porcupine has a tail so much longer than the head-and-body (the correct value was probably 7½ inches). Kuhl (1820: 71) separated *H. insidiosa* from other long-tailed porcupines under the heading "dorsum covered with spines and fur" (as opposed to spines only), and then described it as, "The size of *Arctomys marmota* [= *Marmota marmota*]. Spines sparsely distributed, with straw-colored bases and brown tips, very sharp, less than an inch long, crowded more closely together at the base of the tail, neck, and above the eyes. Fur shaggy, long, pale ash-colored, concealing the spines. Tail covered with bristles."[20]

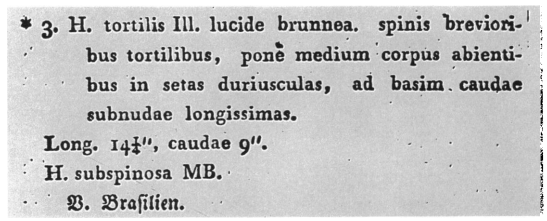
Two ZMB specimens are identified as "*Cercolabes* (*Sphiggurus*) *insidiosus* Licht. Kuhl" in Peters' catalog (fig. 2) and on 20th-century labels tied to the skins. One of these, ZMB 1293, is cataloged and labeled as the type, collected in Brazil by "Sellow." The other, ZMB 1294, is cataloged and labeled as collected in Brazil by "Graf v[on]. Oriolla."

Husson (1978) stated that ZMB 1293 was the holotype of *Hystrix insidiosa*, citing a 1975 letter from Angermann, who based her inference on the asterisks in Peters' catalog entry. The specimen itself could not be located in 1975. Subsequent recuration efforts in Berlin unearthed both ZMB 1293 and 1294, together with the additional Neotropical porcupine material described below.

Neither ZMB 1293 nor 1294 can possibly be the type of *Hystrix insidiosa*. Whereas Olfers and Kuhl both described *insidiosa* as having bicolored spines (yellowish basally with brown tips), the quills of ZMB 1293 and 1294 are conspicuously tricolored (yellowish basally, with a blackish middle band, and orange or reddish tips) over the head, forequarters, upper back, and flanks. Also, Kuhl described the fur of *insidiosa* as pale

[19] ". . . villosa, spinis brevioribus, sparsim vellere immixtis, basi flavis, apice brunneis, cauda crassa."

[20] "Magnitudine Arctomyis marmotae. *Aculeis sparsis*, basi stramineis, apice bruneis, acutissimis, *pollice minoribus*, ad caudae basin, collum et supra oculos magis confertis. Pilis villosis longis, pallide cinereis, spinas obtegentibus. Cauda setosa" (italics original).



* 3. H. tortilis Ill. lucide brunnea. spinis brevioribus tortilibus, ponè medium corpus abientibus in setas duriusculas, ad basim caudae subnudae longissimas.
Long. 14¼", caudae 9".
H. subspinosa MB.
B. Braſilien.

Fig. 12. Olfers' (1818: 211) species account for *Hystrix tortilis*. Throughout his text, Olfers placed numbers next to the name of each species he treated as valid; synonyms (if any) were consistently listed following the description (if provided). The abbreviation "MB" indicates that the source of *H. subspinosa* was material so labeled in the "Museo Berolinensi" (= Berlin Zoological Museum).

←

Fig. 11. The first page of detailed notes prepared by Hoffmannsegg and Illiger on the mammals that Gomes sent from Bahia. Entitled "Bemerkungen über Brasilianische/ Säugthiere/ von F. A. Gomes in Bahia/ mitgetheilt" ("Remarks on Brazilian mammals communicated by F. A. Gomes in Bahia"), these notes are organized in two columns. The right-hand column contains excerpts (in German) from Gomes's letters (which were written in French); these are arranged by dated shipments, beginning with the first ("Erste Sendung") of 3 February 1801. The left-hand column gives the identification of the specimens to which the corresponding excerpts from Gomes's letters refer. Gomes's remarks on his first porcupine specimen, excerpted in the second paragraph of the right-hand column, concerned Buffon's erroneous statement that the prehensile-tailed porcupines of the New World are carnivorous ("G. findet unrichtig daß Buffon von diesem Thier sagt es sey fleischfressend . . ."). Opposite this passage is a preliminary identification of the accompanying specimen as "*Hystrix Prehensilis* an var?" and a German version of the Latin description that we translate in footnote 17. Both "*Prehensilis* an var" and the description were later crossed out, with "subspinosa N" (arrow) written above. The third paragraph in the right-hand column (entitled "Spätere Bemerkungen zweite Sendung 20 Nov. 1801") is an excerpt from Gomes's remarks on the second specimen he sent, a passage that we reproduce in footnote 18.

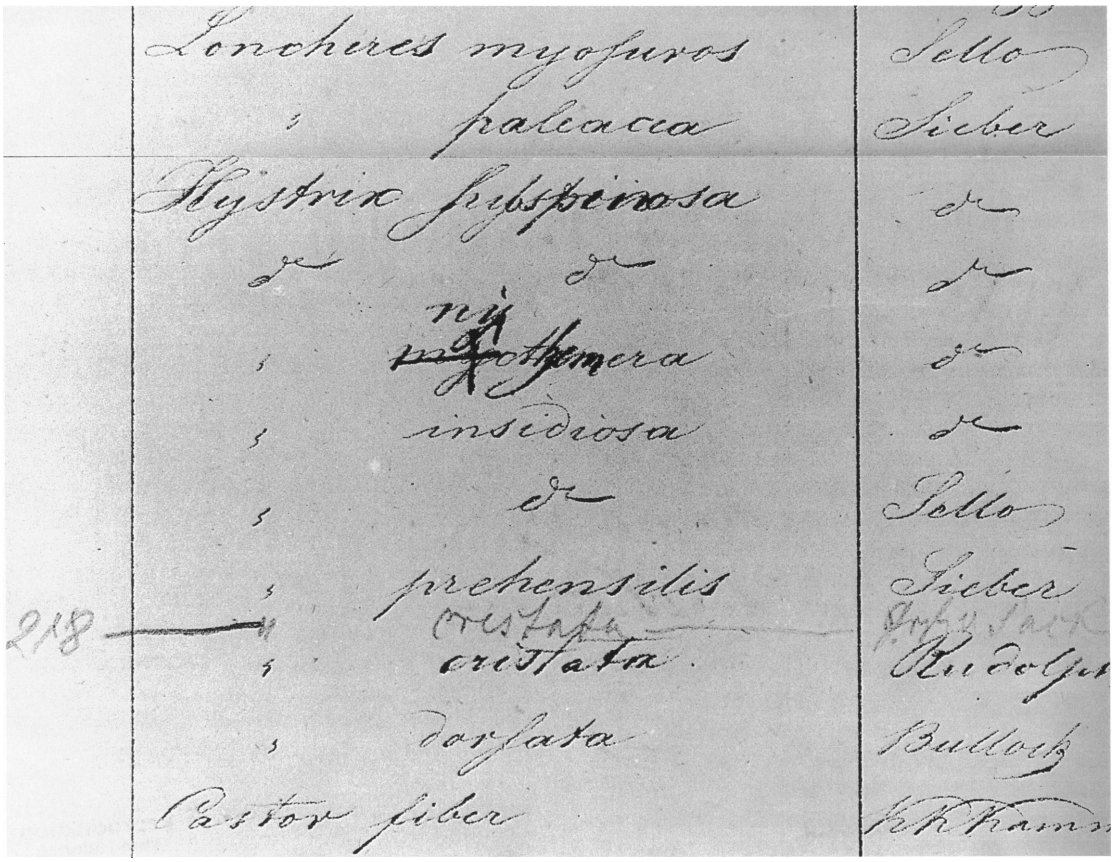


Fig. 13. Detail from a manuscript specimen list of ZMB mammals dated 1822 ("Nachweisung über den Zuwachs des Königl. zoologischen Museums . . . 1822") showing entries for two specimens identified as *Hystrix insidiosa*, one collected by "Sieber" (presumably ZMB 1298) and the other by "Sello[w]" (presumably ZMB 1297). Apparently, both specimens were subsequently misidentified as *Cercolabes* (*Sphiggurus*) *affinis* (see text).

ash-color, but ZMB 1293 and 1294 have blackish fur tipped with yellow. Finally, neither specimen is from Hoffmannsegg's original collection, the only possible source of Olfers' types.

By contrast, two other ZMB specimens correspond exactly to Olfers' and Kuhl's descriptions of *Hystrix insidiosa*. One of these, ZMB 1297, is a skin (with glass eyes and with the skull inside) mounted in a lifelike pose on a wooden base (fig. 1). Glued to the wooden base is a printed label on greenish-blue paper that reads "*Cercolabes/affinis* Brandt./Brasilien. Sello[w] [&] v[on]. Olfers." Such unnumbered exhibition labels were only used for ZMB material prior to Peters' numerical catalog, and this fact, together with the publication date of Brandt's specific epithet *affinis*, brackets the manufacture between 1835 and 1857, during Lichtenstein's tenure as museum director. The second specimen, ZMB 1298, was also once mounted for exhibition on a platform (the soles of the hands and feet are still perforated by wires), but was later remade as a conventional study skin with extracted skull. Although the skin tag identifies this specimen only as "*Cercolabes*," Peters' catalog entry for ZMB 1298 (like that for 1297 on the line above it; fig. 2) gives the identification as "*Cercolabes* (*Sphiggurus*) *affinis* Brandt." The provenance of ZMB 1298 is recorded as "Sieber/Gr[af]. v[on]. Hoffmannsegg" in Peters' catalog and (with minor differences in

abbreviation and punctuation) on the skin tag and skull. That these specimens were originally identified as *H. insidiosa* is suggested by an 1822 manuscript specimen list of ZMB mammals (fig. 13) which includes one example of that species collected by "Sieber" (presumably ZMB 1298), and another collected by "Sello[w]" (presumably ZMB 1297).

How did two specimens of *Hystrix insidiosa* come to be labeled and cataloged as *Cercolabes* (*Sphiggurus*) *affinis*, and how did two specimens of a different species come to be misidentified as *C.* (*S.*) *insidiosus*? The simplest explanation is that Lichtenstein, unencumbered by modern notions of nomenclatural priority, may have relabeled ZMB specimens to conform with the taxonomy in Brandt's (1835) influential monograph on porcupine classification. Using the descriptions and nomenclature in Brandt (1835), ZMB 1293 and 1294 are unambiguously referable to *Cercolabes* (*Sphiggurus*) *insidiosus*, whereas ZMB 1297 and 1298 could plausibly be identified as *C.* (*S.*) *affinis*. Brandt, however, was mistaken in his usage of *insidiosus*, and Lichtenstein apparently compounded Brandt's error with one of his own.[21] The misidentifications in Peters' catalog were undoubtedly copied directly from Lichtenstein's exhibition labels.

TYPE MATERIAL: The holotype (by monotypy), ZMB 1298, consisting of the skin and skull of a young adult of unknown sex (figs. 14–16). The skin, made up around a wooden dowel projecting from the mouth, is in reasonably good condition, but it is slightly torn in a few places, the toes of the left hindfoot are broken, and the tail-tip is partially detached. The skull lacks the right upper incisor (broken off at the alveolus) and both occipital condyles; the left zygoma is broken and repaired.

We identify ZMB 1298 as the holotype because, as part of the founding Hoffmannsegg collection, it is the only extant specimen of *Hystrix insidiosa* that could have served as the basis for Olfers' description. Additionally, several lines of evidence suggest that Hoffmannsegg had only a single example of this species. First, we have seen that Gomes (the only known collector who could have provided Hoffmannsegg with specimens of *H. insidiosa*, see below) sent him just three porcupines, two of which were the lectotype and paralectotype of *H. subspinosa*. Second, pencil notations in the margin of the 1810 species list (fig. 3) suggest that only one specimen of *H. insidiosa* was present when Hoffmannsegg's mammals were donated to the ZMB. Third, a pre-1818 specimen list in Lichtenstein's handwriting[22] likewise indicates that the ZMB had only a single example of *H. insidiosa* prior to Sellow's first shipment from Bahia. Thus, although Lichtenstein (1818b) listed *H. insidiosa* among the duplicate specimens offered for sale at auction, no Hoffmannsegg material of this species was apparently sold.

TYPE LOCALITY: Olfers (1818) gave the type locality only as Brazil, which Husson (1978) restricted to the vicinity of Salvador in the state of Bahia. Although Husson's restriction was based on the mistaken assumption that the type was collected by Sellow, he was almost certainly correct about the type locality. Despite the information in Peters' catalog and on the labeling of the specimen itself, ZMB 1298 cannot have been obtained by Sieber, whose collecting itinerary was restricted to Amazonia (Urban, 1906). Of Hoffmannsegg's two mammal collectors, only Gomes (residing at Salvador) worked within the known range of *Coendou insidiosus* in the Atlantic rainforest region. It is probably not coincidental that the types of both *Hystrix subspinosa* and *H. insidiosa*, each of which must have been sent to Hoff-

[21] Voss recently examined Brandt's erethizontid material in the Zoological Institute of the Russian Academy of Sciences in St. Petersburg. ZINRAS 32, the only surviving specimen of the two that Brandt (1835) described as *Cercolabes* (*Sphiggurus*) *insidiosus*, is an example of *Coendou spinosus* (F. Cuvier), not *Coendou insidiosus* (Olfers). The type and only referred specimen of Brandt's *Cercolabes* (*Sphiggurus*) *affinis*, ZINRAS 31, although similar to *Coendou insidiosus* (Olfers) in some respects, is conspicuously different in other characters that we describe under Remarks (below).

[22] Although the original entries in this list ("Säugetierkatalog vor 1818"), including those for *Hystrix* spp. on page 96, are undated, subsequent additions in a different ink are dated 1818; hence, the porcupine entries were presumably made in the interval 1813–1817.

Fig. 14. Dorsal view of the skin of ZMB 1298, holotype of *Hystrix insidiosa* Olfers.

mannsegg by Gomes, were mislabeled as collected by Sieber. We speculate that Lichtenstein might not have been familiar with the sources of Hoffmannsegg's collection, and in preparing exhibition labels after Illiger's death assumed that all of the count's specimens came from Sieber. We note that other Hoffmannsegg specimens from the Atlantic rainforest region (e.g., the type of *Bradypus torquatus*) have also been impossibly attributed to Sieber (e.g., by Wied, 1826), so the problem is not limited to these porcupines.

DESCRIPTION OF THE HOLOTYPE: *External*—The dorsal pelage consists of short bicolored quills that are almost completely concealed by a dense coat of long fur. The fur, about 50–60 mm long middorsally, is soft to the touch and consists only of fine, wavy wool hairs that are pale yellowish-gray for most of their length but tipped with brown, producing the mass effect of a darker wash over a predominantly pale coat. The underlying quills, reaching a maximum length of only about 35 mm over the shoulders and upper back, are yellowish basally and brownish distally. Over the forequarters, the quills are gently curved, pale brown at midlength, but darkening to blackish-brown at the tips. By contrast, the shorter rump quills are straight and lack any transitional coloration between the yellowish base and the blackish-brown ends. None of the quills anywhere on the body is pale-tipped. The uniformly blond ventral pelage is composed entirely of soft fur (wavy wool hairs mixed with straighter and somewhat stiffer hairs of approximately the same length and color); there are no conspicuously thickened spinous hairs grouped in triads or other recognizable patterns in the ventral pelage.

The dorsal surface of the proximal half of the tail is covered with the same mixture of pale fur and bicolored quills as on the back and rump, but the underside of the base of the tail is densely covered with stiff blackish-brown bristles; dark (brownish) bristles also extend along the sides of the tail and onto the dorsal caudal surface between the fur-and-quill covered base and the naked prehensile tip. The cranial and postcranial vibrissae, uniformly dark brown (without pale tips), have the same morphology and anatomical distribution as previously described for *Hystrix nycthemera*.

Skull—The cranial sinuses are uninflated, resulting in a dorsal profile that is essentially flat from the nasal tips to the midparietal region. The nasals are long and tapering, with rounded posterior margins that extend well behind the premaxillae. The bony relief associated with the origins of M. temporalis on the braincase is not strongly developed. Viewed from above, the zygomatic arches are widest across the squamosal roots and converge anteriorly with only a slight secondary widening at the orbits; the jugal is unexpanded.

The incisive foramina, surrounded by the premaxillae, are recessed in a common fossa. Diastemal ridges are only developed posteriorly, where the palate just in front of the toothrows is shallowly trisulcate. The palatal bridge (between the toothrows) is broad and smooth, without a well-developed median keel. The mesopterygoid fossa extends to the posterior margins of the second molars; its anterior margin is a straight-sided arch with a bluntly rounded apex. The roof of the mesopterygoid fossa is completely bony, lacking conspicuous fenestrae, but with tiny perforations flanking the presphenoid-basisphenoid suture (which is already fused in this young adult). The bullae are small, rounded ovoids that are not closely adpressed to the paroccipital processes. The dorsal roof of the external auditory meatus is smooth, without any bony ridge or keel.

Dentition—The upper incisors, much deeper than wide and strongly procumbent, have pale yellow-orange enamel bands. The small cheekteeth, in subparallel rows, resemble those of other erethizontids (except *Chaetomys*) in occlusal morphology. The fourth upper premolar is slightly smaller than M1.

Measurements—Measurements of the type and of other referred specimens are given in table 2.

REMARKS: *Hystrix insidiosa* has usually been placed in the genus *Sphiggurus* F. Cuvier (most recently by Woods, 1993), but we agree with Handley and Pine (1992) that *Sphiggurus* cannot be meaningfully diagnosed as a taxon distinct from *Coendou* Lacépède. *Coendou insidiosus* has an extraor-

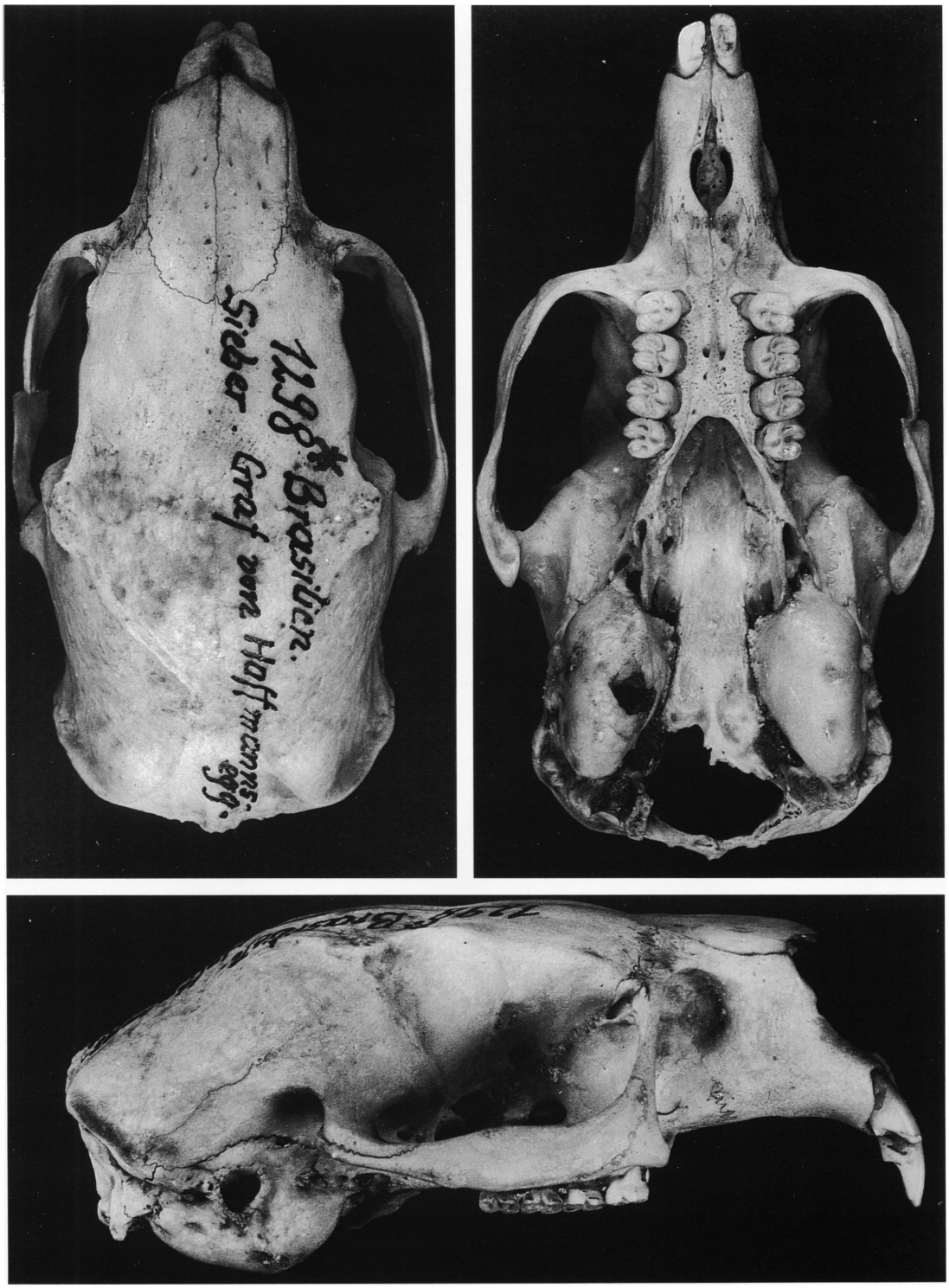


Fig. 15. Dorsal, ventral, and right lateral views of the skull of ZMB 1298, holotype of *Hystrix insidiosa* Olfers.

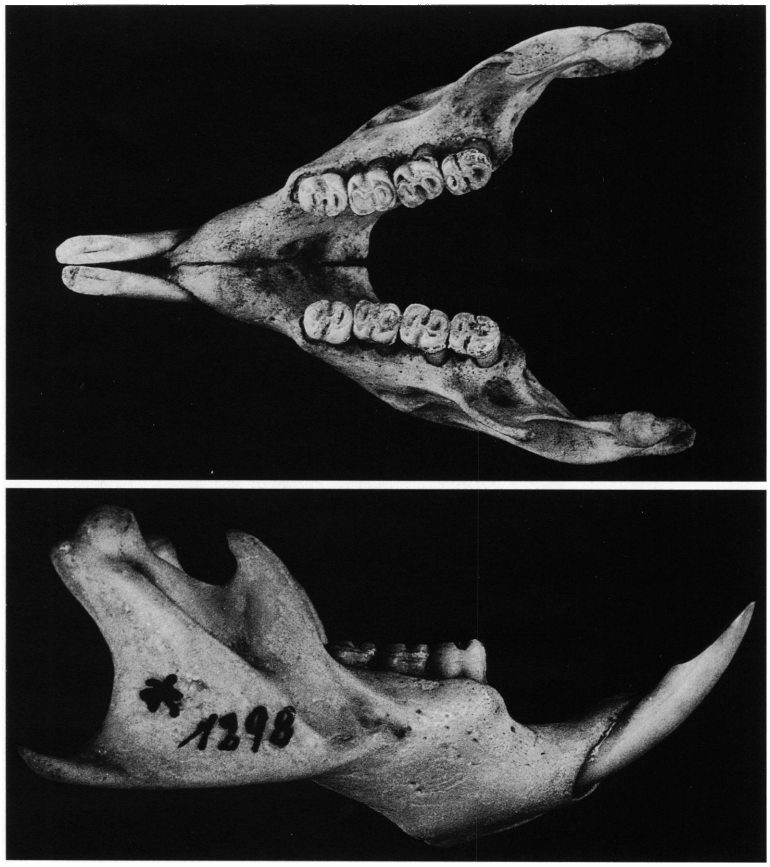


Fig. 16. Occlusal and right lateral views of the mandibles of ZMB 1298, holotype of *Hystrix insidiosa* Olfers.

dinarily complex nomenclatural history (see Taxonomic Summary, below), including several important questions of synonymy that we discuss below. Unfortunately, only a few specimens of *C. insidiosus* are currently available to assess intraspecific character variation.

Among the specimens we refer to *Coendou insidiosus* (see Taxonomic Summary, below, for museum catalog numbers of the material examined) are some with darker (brownish) fur than the holotype and others with conspicuously paler (whitish) fur. Oliver and Santos (1991) likewise noted significant pelage color variation among the animals they observed in a field study of this species: nonalbino white-furred examples were found as well as those with "... the more typically coloured pelage in which the hair is grey ..." A color photograph of a "... normal coloured adult from the vicinity of Itabuna, southern Bahia, Brazil" (op. cit.: pl. 2) clearly shows the pale grayish fur to be washed with brown as described above for the holotype. The single individual with whitish fur that we examined (FMNH 52411, a zoo specimen of uncertain geographic origin) is clearly not an albino because the quill tips, vibrissae, caudal bristles, and claws are brown. Superficially, the mass-effect color of the darkest skin at hand (AMNH 76838) is a somber brownish-gray, but the parted fur is conspicuously pale for about two-thirds of its length.

Intraspecific cranial variation is likewise present, some of which is doubtless individual, some ontogenetic, and some perhaps reflects population divergence. However, as most specimens lack precise locality data, geographic variation cannot be identified as

TABLE 2
External and Craniodental Measurements (mm) of *Coendou insidiosus*

	Brazil			Zoo specimens	
	ZMB 1298[a]	ZMB 1297[b]	AMNH 76838[c]	AMNH 90119	FMNH 52411
Age	adult	adult?	adult	adult	old adult
Sex	?	?	?	?	?
HBL	ca. 310	ca. 320	350	ca. 345	ca. 340
LT	ca. 220	ca. 200	180	ca. 240	ca. 260
HF	58[d]	59	57[d]	—	65
CIL	66.1	—	64.9	61.3	71.0
LD	18.6	—	18.8	15.6	20.4
MTR	13.6	—	13.9	14.0	14.3[d]
LM	10.2	—	10.5	10.3	10.4[d]
BP4	3.8	—	4.2	3.8	4.3
BM1	3.9	—	4.2	4.0	4.0[d]
APB	5.8	—	4.9	3.7	6.2
PPB	7.5	—	6.6	6.5	8.4
PZB	39.2[d]	—	37.6	40.0	43.8
HIF	9.3	—	9.1	9.0	9.5
ZL	25.9	—	26.7	26.9	27.6
LN	19.0	—	20.8[d]	21.4	—
BNA	10.0	—	—	9.3	11.0
BB	29.7	—	29.6	30.5	31.1
DI	3.3	—	3.1	3.1	3.6
BIT	4.1[d]	—	4.0	4.3	4.7

[a] The holotype, probably collected at Salvador, Bahia state.
[b] Skin only examined (skull inside), possibly also from Salvador.
[c] From "Itirussu" (= Itiruçu), Bahia state.
[d] Estimated values.

such in our very small sample. Instead of describing all of the details in which other referred material diverges from the holotype, we abstract the features common to all the specimens we are calling *Coendou insidiosus* to give a provisional diagnosis.

We recognize *Coendou insidiosus* as a small porcupine with short bicolored quills (not exceeding 35 mm in any of the specimens examined) that are almost completely concealed (except on the head) by long, soft, pale-based or all-pale fur. The woolly dorsal fur lacks any distinctively longer, stiffer, or contrastingly colored guard hairs, and the ventral pelage is composed exclusively of fur of conventional appearance that never includes thickened spinous hairs grouped in triads or other obvious clusters. The vibrissae and caudal bristles are uniformly dark (brown or blackish brown, without conspicuously paler tips) even when the fur is completely whitish. The tail is apparently about one-half to three-quarters the length of head-and-body (only one of the specimens we examined is accompanied by measurements made in the flesh).

None of the skulls of *Coendou insidiosus* that we examined has grossly inflated dorsal sinuses. The zygomatic arches, widest near the squamosal roots, taper anteriorly with only a slight secondary widening (if any) at the orbits; the jugal is not grossly expanded. Even in old adults, the bony ridges associated with M. temporalis are not conspicuously developed. The anterior margin of the mesopterygoid fossa is apparently never /\-shaped nor a smoothly rounded arch, but converges with straight sides to a blunt apex near the point of contact between the second and third molars. The auditory bullae are small ovoids, and the dorsal roof of the external auditory meatus is smooth (not ridged or keeled). The cheekteeth are very small in all of the specimens we measured (MTR =

13.6–14.3 mm, LM = 10.2–10.5 mm; table 2).

Cercolabes pallidus Waterhouse (1848) is a junior synonym of *Coendou insidiosus* as previously suggested by Handley and Pine (1992). Waterhouse based his description on "... two specimens of this pale-coloured Tree-Porcupine, one of which is said to be from the West Indies; they are both immature animals, the largest ... having but three molars on each side of the jaw. Possibly this may be the *H. insidiosa* of Lichtenstein, but I think that Kuhl, who described that animal, would scarcely have omitted to notice the black hue of the undersurface of the tail, which forms a strong contrast with the pale tint of the other parts" (op. cit.: 435).

We examined Waterhouse's original material of *Cercolabes pallidus*, which consists of the stuffed skin of the lectotype (BMNH 46.1.9.14; designated by Thomas, 1927), its separately cataloged skull (BMNH 46.3.2.13), and a paralectotype (BMNH 42.10.7.15, a skin only). Although the skins are now faded and soiled, and the specimens are both juveniles, the characters of this small series perfectly match those of *Coendou insidiosus* as diagnosed above. The BMNH mammal catalog entry for 46.1.9.14 gives the original identification of the lectotype as "*Cercolabes insidiosus*" and the provenance as "Brazil[,] Purchased of Brandt." The type locality of *pallidus* is therefore Brazil, not the West Indies.[23]

Schinz (1824) believed that *Hystrix insidiosa* was the same species as "Le Couiy," a small, long-furred Paraguayan porcupine described but not formally named by Azara (1801). This opinion was subsequently endorsed, inter alia, by Wied (1826), Rengger (1830), Schinz (1845), Burmeister (1854), and Hershkovitz (1987). Azara's couiy, however, appears to be a distinct species that we provisionally identify as *Coendou spinosus* (F. Cuvier) (included as synonyms are *villosus* F. Cuvier, *couiy* Desmarest, *nigricans* Brandt, *sericeus* Cope, and *roberti* Thomas).[24]

Although considerable geographic variation is evident within what we are calling *Coendou spinosus*, all of the specimens referable to this species resemble one another and differ from *C. insidiosus* by having (1) longer quills (40–80 mm middorsally) that are tricolored (tipped with red, orange, yellow, or ivory-white) over the head, shoulders, middle back, flanks, thighs, and sides of the tail (versus all quills shorter and bicolored in *insidiosus*); (2) dark-based fur that is tipped with orange, yellow, or gray (versus pale-based or all-pale fur in *insidiosus*); (3) conspicuously bicolored mystacial vibrissae and ventral caudal bristles, both of which have dark bases and pale tips (versus all-dark vibrissae and caudal bristles in *insidiosus*); and (4) larger cheekteeth (MTR = 15.1–17.1 mm, LM = 10.9–12.7 mm; see table 2 for corresponding measurements of *insidiosus*).

The specimen from Espírito Santo state that Emmons (1990: 200) identified as a possible intergrade between *C. insidiosus* and *C. villosus* (= *C. spinosus* in our usage) is BMNH 3.9.4.87, a subadult female skin and skull collected by Alphonse Robert at Engenheiro Reeve (= Rive at 20°46′S, 41°28′W; Paynter and Traylor, 1991). Although superficially pale gray, not unlike some specimens of *C. insidiosus*, BMNH 3.9.4.87 has the longer (to 40–45 mm) tricolored quills, dark-based fur, bicolored vibrissae and caudal bristles, and larger cheekteeth (LM = 11.7 mm) that characterize *C. spinosus*. We therefore refer BMNH 3.9.4.87 to the latter species and note that unvouchered field identifications of *Coendou* from this part of the Atlantic rainforest region

[23] A cardboard tag tied to BMNH 42.10.7.15, the paralectotype, has the pencil notation "W. Indies," but as the rest of the label is written in ink it seems doubtful that this datum is original.

[24] Only two names are unambiguously based on Azara's (1801) description of "Le Couiy," of which *paragayensis* Oken (1816), recently resurrected by Emmons (1990), is the older. However, Oken (1816) is a non-Linnaean work (Hershkovitz, 1949), so *paragayensis* is unavailable. The other name based on Azara's description is *couiy* Desmarest (1822), which is available in the event that the small hairy Paraguayan porcupine is judged to be taxonomically distinct from Brazilian populations. Cuvier's (1822) description of *Coendou spinosus* was based on a specimen in the Paris museum (Waterhouse, 1848: 420), not on Azara's text (contra Tate [1935: 298] and Cabrera [1961: 602]).

should be regarded with caution (e.g., the sight records of *C. insidiosus* mapped by Oliver and Santos, 1991). The possibility that the Rio Doce delimits the ranges of *insidiosus* and *spinosus* in southern Espírito Santo merits future testing by museum and field researchers.

The type and only referred specimen of *Cercolabes* (*Sphiggurus*) *affinis* Brandt consists of a mounted skin (ZINRAS 31) from which the skull has been extracted and lost. Although similar to *Coendou insidiosus* in having mostly bicolored quills that are more-or-less concealed beneath a coat of long fur, ZINRAS 31 differs in other characters: (1) tricolored quills (with yellowish bases, dark brown middle bands, and buffy tips) are scattered over the head, nape, and shoulders; (2) the quills are generally longer (to about 43 mm middorsally) and stouter than those of any specimens of *insidiosus* we examined; (3) the coarse, woolly fur is uniformly brownish from root to tip; (4) the caudal bristles under the base of the tail are distinctly bicolored (blackish brown basally with yellow tips); and (5) our measurements of the mounted skin (HBL = ca. 340 mm, LT = ca. 270 mm, HF = 65–70 mm) together with those given by Brandt (1835: 414) suggest an absolutely larger animal with a relatively longer tail. Thus, although *insidiosus* more closely resembles *affinis* than it does any other porcupine described by Brandt (1835), these taxa appear to be distinct based on the scant material at hand. Unfortunately, the type locality of *affinis* is known only as "Brazil" (op. cit.: 414).

Another species of small hairy porcupine, *Coendou melanurus*, was apparently first misidentified as *insidiosus* by Cabanis (1848), an error subsequently propagated by Cabrera (1961) and Husson (1978), both of whom regarded *insidiosus* and *melanurus* as conspecific. To evaluate this hypothesis, we examined the type series of *Cercolabes melanurus* Wagner, as well as the type of *Sphiggurus melanurus* Gray (a junior synonym) and 15 other specimens in North American and European museums. Based on this material, we are able to unambiguously diagnose *melanurus* from *insidiosus* by several chromatic and morphological characters. As previously suggested by Emmons (1990) and by Handley and Pine (1992), these are clearly distinct species that occupy widely separated ranges: *melanurus* in the Guiana subregion of Amazonia, *insidiosus* in the northern part of the Atlantic rainforest region (see Voss and Emmons, 1996, for definitions of these areas).

Although both *Coendou melanurus* and *C. insidiosus* have short bicolored quills concealed beneath a dense coat of long, pale-based fur, the species are otherwise dissimilar in external appearance. In addition to being larger in all external dimensions than *insidiosus*, *melanurus* has a relatively much longer tail, about equal to the combined length of head and body (compare measurements of Surinamese specimens of *melanurus* [misidentified as *insidiosus*] in Husson, 1978, with those in our table 2). The unparted pelage of *melanurus* is blackish thickly streaked with yellow or ivory-white, a striking mass effect caused by the admixture of predominantly blackish wool hairs with much longer, coarser, pale-tipped guard hairs. By contrast, the fur of *insidiosus* appears uniformly whitish, grayish, or dull brownish-gray, and contains only wool hairs. Whereas the caudal bristles are pitch black in *melanurus*, those of *insidiosus* are distinctly brownish.

Coendou melanurus is much larger in all craniodental dimensions than *C. insidiosus*, a contrast that is perhaps best reflected in length of the molar toothrow (MTR = 15.7–19.4 mm in *melanurus*, 13.6–14.3 mm in *insidiosus*). In visual comparisons of skulls, the rostrum is proportionately much broader and deeper in *melanurus* than in *insidiosus*, the dorsal cranial sinuses are more inflated, the jugal more expanded below the orbit, and the auditory bullae more elongated. Additionally, the roof of the external auditory meatus has a conspicuous bony keel in *melanurus*, whereas the roof of the meatus is smooth in *insidiosus*.

NOMINA NUDA AND DUBIA

Of the seven species of Neotropical porcupines listed on page 108 of Illiger's (1815) posthumously published "Ueberblick der Säugethiere nach ihrer Vertheilung über die Welttheile," only *Hystrix prehensilis* Linnae-

us (1758) and *H. mexicana* Kerr (1792) had previously been described. The remaining five names were new: *H. volubilis*, *H. rutila*, *H. pollicaris*, *H. tortilis*, and *H. insidiosa*. Unfortunately, Illiger did not describe them. Apart from the list on page 108, the only other mention of Neotropical porcupines in his "Ueberblick" is a discussion of generic nomenclature on page 113, which may be freely translated as follows.

> Of the porcupines, *Hystrix*, recent naturalists have treated those South American species that have a prehensile tail under the ill-chosen name *Coëndus* [sic]. The gradual transition of this organ found among the numerous recently discovered species, [however], argues against this separation.

No other known work by Illiger, whether published before or after his death in 1813, contained descriptions of his new Neotropical porcupine species. Unaccompanied by diagnoses or descriptions, these five names (*volubilis*, *rutila*, *pollicaris*, *tortilis*, and *insidiosa*) were nomina nuda when they first appeared in print in 1815, and remained so for several years thereafter.

Olfers (1818) provided descriptions himself, or indicated the bibliographic sources of descriptions, for most of the new names of South American mammals that appeared as nomina nuda in Illiger's "Ueberblick." Some of Illiger's nomina nuda, however, were apparently based on specimens or bibliographic sources unknown to Olfers. Mysteriously, some new names published by Olfers were not listed in Illiger's "Ueberblick" (for example, *Hystrix nycthemera* and *H. subspinosa*) even though they appeared in earlier documents handwritten by Hoffmannsegg and Illiger (e.g., figs. 3, 11). Possibly, Illiger thought that some of the names that he and Hoffmannsegg had previously used in manuscript were bad Latin or were descriptively inadequate, and decided to use others for publication.

The notation "*H. pollicaris* Ill.?" was included without comment under Olfers' (1818: 211) account for *Hystrix nycthemera*. We presume that Olfers was uncertain about Illiger's intended usage because the name no longer appeared on specimen labels in the ZMB. Since it was not definitely associated with any published description, Illiger's *pollicaris* remains a nomen nudum.

Hystrix volubilis likewise remains undescribed, although Olfers (1818: 212) speculated that it was probably based on an anomalous ("abweichenden") specimen of *H. tortilis* (= *H. subspinosa*, see above). Hershkovitz (1959) and Cabrera (1961) accordingly listed *H. volubilis* in their synonymies for *Chaetomys subspinosus*. We do not do so in ours (see Taxonomic Summary, below) because Illiger's *volubilis* is both unavailable and of dubious application.

By contrast, Olfers clearly had a specimen identified as *Hystrix rutila* in hand. He described it (op. cit.: 211) as having "Very reddish fur that conceals minute black spines with white bases."[25] He gave the length of the body as 6–7 inches, the length of the tail as 4–5 inches, noted (in German) that the specimen was "Probably a juvenile of some as yet unknown species," and stated that it came from "Para."

No extant ZMB material fits Olfers' description of *H. rutila*, which, as he inferred, was probably based on an immature specimen. All *Coendou* have long fur as neonates, even those species that lack visible fur as adults. The measurements and the reference to minute black spines with white bases suggest a juvenile of a small-bodied, long-tailed species with bicolored quills. Although it seems probable that Olfers' type of *H. rutila* was a young example of *Coendou nycthemera*, which has reddish juvenile fur (Handley and Pine, 1992) and occurs in the vicinity of Pará (now Belém), no positive identification is possible in the absence of the specimen itself. Certainly, however, there is no good reason (contra Hershkovitz, 1959, and Cabrera, 1961) to list *H. rutila* in the synonymy of *Chaetomys subspinosus*, a species that lacks distinctly bicolored spines.

TAXONOMIC SUMMARY

Below we summarize the nomenclatural history of *Chaetomys subspinosus*, *Coendou insidiosus*, and *Coendou nycthemera* based on our research with the types and other museum specimens. These are not complete synonymies because we have not attempted

[25] "Vellere longo rutilo, spinas minutas nigras, basi albas occultante."

to determine whether every usage of these names in the literature has been correct or not. Instead, we list only synonyms and significant new name combinations, providing comments where appropriate to justify the recommended current usage.

The names of Brazilian states are indicated by italics in the lists of Specimens Examined.

Chaetomys subspinosus (Olfers, 1818)

Hystrix tortilis Illiger, 1815: 108. Nomen nudum.

H[ystrix]. tortilis Olfers, 1818: 211. Original description, based on unspecified material from Brazil in the Berlin Zoological Museum.

H[ystrix]. subspinosa Olfers, 1818: 211. A manuscript name cited as a synonym of *H. tortilis*. However, Hershkovitz's (1959) adoption of *subspinosa* Olfers as the valid name for the bristle-spined porcupine of southeastern Brazil made this epithet available from 1818 under Article 11e of the International Code (ICZN, 1985), and we have chosen *subspinosa* to have precedence over *tortilis* to preserve current usage. We redescribe the lectotype and a paralectotype in this report.

H[ystrix]. subspinosa Kuhl, 1820: 71. A junior synonym based on the same ZMB material previously described by Olfers.

Chaetomys subspinosus: Gray, 1843: 21. New genus with *subspinosus* as the type and only referred species.

Plectrochoerus moricandi Pictet, 1843: 227. New genus and species based on a specimen sent from "Bahia" to the Geneva museum; a junior synonym according to Waterhouse (1848). We have not seen the type, but we agree that Pictet's description of *moricandi* fits the characters of *subspinosus*. Moojen (1952) restricted the type locality to the coastal town of Ilhéus, but this restriction was unnecessary because it did not solve any taxonomic problem; furthermore, Pictet's "Bahia" was certainly a reference to the town of Bahia (now Salvador), not to the state.

C[ercolabes]. subspinosus: Wagner, 1844: 35. New name combination. In referring *subspinosus* to *Cercolabes* Brandt, Wagner was unaware of Gray's and Pictet's new generic names. Schinz (1845), however, apparently used *Cercolabes* for this species because he rejected *Chaetomys* and *Plectrochoerus* as valid genera.

Chaetomys tortilis: Moojen, 1952: 100. New name combination.

TYPE MATERIAL: The lectotype, ZMB 1300, and a paralectotype, ZMB 1301, each represented by skin, skull, and mandibles in the Museum für Naturkunde der Humboldt-Universität zu Berlin.

TYPE LOCALITY: Brazil by original designation; incorrectly stated by Wied (1826) to be Cametá in the Amazonian state of Pará; emended by Avila-Pires (1967) to the town of Ilhéus in southeastern Bahia state. However, previously unreported documents cited herein indicate that the type material was collected at Salvador in northern Bahia.

KNOWN GEOGRAPHIC RANGE: Moist forests of the Atlantic coastal region of southeastern Brazil, from southern Sergipe state to northern Rio de Janeiro (roughly between 11° and 22° S latitude), including easternmost Minas Gerais (Santos et al., 1987; Oliver and Santos, 1991).

MORPHOLOGICAL DESCRIPTIONS: Olfers (1818), Kuhl (1820), Gray (1843, 1844), Pictet (1843), Waterhouse (1848), Ellerman (1941), Moojen (1952), Martin (1994), and this report.

SPECIMENS EXAMINED: *Bahia*, Ilhéus (USNM 304578), Salvador (ZMB 1300, 1301).

Coendou insidiosus (Olfers, 1818)

Hystrix insidiosa Illiger, 1815: 108. Nomen nudum.

H[ystrix]. insidiosa Olfers, 1818: 211. Original description based on unspecified material from Brazil in the Berlin Zoological Museum. We identify and redescribe the holotype in this report.

H[ystrix]. insidiosa Lichtenstein, 1818a: 19. Secondary description in a pamphlet for visitors to the Berlin Zoological Museum. The complete text of Lichtenstein's very brief description is given by Husson (1978: 488). Lichtenstein had certainly seen the same Hoffmannsegg specimen named by Olfers, but he might also have received additional material from Friedrich Sellow by the time he wrote his guide.

H[ystrix]. insidiosa Kuhl, 1820: 71. Another secondary description, probably based on the same Hoffmannsegg specimen named by Olfers and perhaps other material sent to Berlin by Sellow.

Cercolabes (*Sphiggurus*) *insidiosus*: Brandt, 1835: 407. New name combination based on misidentified material collected in "Brazil" and sent to the Imperial Academy of Sciences in St. Petersburg by Georg Heinrich Langsdorff. The sole surviving specimen of the two that Brandt described as *C.* (*S.*) *insidiosus*, ZINRAS 32, is an example of *Coendou spinosus* (F. Cuvier).

S[ynoetheres]. insidiosa: Lund, 1841: 99. New name combination for material collected at or near Lagoa Santa, Minas Gerais, Brazil. We have not examined Lund's specimens (at the Universitets Zoologisk Museum, Copenhagen) to determine if they were correctly identified.

C[ercolabes]. insidiosa: Cabanis, 1848: 779. New usage, based on unspecified but obviously misidentified specimens or observations from British Guiana (Guyana). The animal in question was certainly *Coendou melanurus* (Wagner), the only species of small hairy porcupine known from the Guianas.

Cercolabes pallidus Waterhouse, 1848: 434. A junior synonym based on two specimens in the British Museum of Natural History. The lectotype (BMNH 46.1.9.14), designated by Thomas (1927), is from Brazil, not the West Indies (as implied by Hall (1981: 854) and other authors.

Synetheres (Sphiggurus) insidiosus: Trouessart, 1881: 184. New name combination implied by the nomenclaturally indefensible synonymy given for *S. (S.) villosus* (F. Cuvier).

Sphingurus insidiosus: Winge, 1887: 61. New name combination, using Alston's (1876) incorrect subsequent spelling of *Sphiggurus* F. Cuvier. Winge applied this binomial to material in the Copenhagen museum collected by Lund and other Danish zoologists working at or near Lagoa Santa. We do not know if Winge's material was correctly identified.

Coendu insidiosus: Trouessart, 1897: 623. New name combination, using an incorrect subsequent spelling of *Coendou* Lacépède.

Coendou (Sphiggurus) insidiosus: Tate, 1935: 307. New name combination.

Coendou (Sphiggurus) insidiosus insidiosus: Cabrera, 1961: 600. New usage, based on the mistaken idea that *melanurus* Wagner is only subspecifically distinct from *insidiosus*. The type material of *Coendou melanurus* (two syntypes in the Naturhistorisches Museum Wien, collected by Johann Natterer at Manaus, Brazil) and other referred specimens we examined represent a distinct species as previously suggested by Emmons (1990) and Handley and Pine (1992). Cabrera did not explain why he thought that *insidiosus* and *melanurus* were conspecific, but he might have been influenced by Cabanis's (1848) misidentification of Guyanese material (see above).

Sphiggurus insidiosus: Husson, 1978: 484. New usage, implying lack of even subspecific distinction between *insidiosus* and *melanurus* (see above). Husson was confused about the characters of Atlantic rainforest porcupines, having no example of true *insidiosus* on hand to compare with Surinamese examples of *melanurus* in the Leiden museum.

TYPE MATERIAL: The holotype (by monotypy), ZMB 1298, consisting of a skin, skull, and mandibles in the Museum für Naturkunde der Humboldt-Universität zu Berlin.

TYPE LOCALITY: Brazil by original designation; restricted by Husson (1978) to the vicinity of Salvador in the state of Bahia. Although Husson's restriction was based on a false assumption (that the type was collected by Friedrich Sellow), his choice of Salvador is almost certainly correct for other reasons explained herein.

KNOWN DISTRIBUTION: According to Santos et al. (1987) and Oliver and Santos (1991), almost the same as that of *Chaetomys subspinosus*, i.e., moist forests of the Atlantic coastal region of southeastern Brazil, from southern Sergipe state to northern Rio de Janeiro (roughly between 11° and 22° S latitude). However, unvouchered sight records of small *Coendou* species may be unreliable from the southern portion of this range.

MORPHOLOGICAL DESCRIPTIONS: Most published descriptions alleged to be of this species were actually based on misidentified material. To the best of our knowledge, only Olfers (1818), Kuhl (1820), and Waterhouse (1848 [in his account of *pallidus*]) described specimens of true *insidiosus*. Color and black-and-white photographs of living examples were published by Oliver and Santos (1991).

SPECIMENS EXAMINED: "Brazil" (BMNH 46.1.9.14/46.3.2.13 [skin and skull of same individual cataloged separately]; ZMB 1297); *Bahia*, Itirussú 3000 ft (AMNH 76838), Salvador? (ZMB 1298). "West Indies" (BMNH 42.10.7.15). Zoo specimens of unknown origin (AMNH 90119, FMNH 52411).

Coendou nycthemera (Olfers, 1818)

H[ystrix]. nycthemera Olfers, 1818: 211. Original description based on unspecified material from Brazil in the Berlin Zoological Museum. We identify and redescribe the holotype in this report.

H[ystrix]. nycthemera Kuhl, 1820: 71. Secondary description, based on the same ZMB specimen named by Olfers.

Cercolabes nycthemera: Waterhouse, 1848: 417.

New name combination. Waterhouse incorrectly included *bicolor* Tschudi, a distinct species, as a junior synonym.

Synetheres (*Synetheres*) *nycthemera*: Trouessart, 1881: 183. New name combination.

Coendu nycthemera: Trouessart, 1897: 622. New name combination, using an incorrect subsequent spelling of *Coendou* Lacépède.

Coendou (*Sphiggurus*) *nycthemera*: Tate, 1935: 307. New name combination.

Coendou (*Coendou*) *nycthemera*: Ellerman, 1941: 187. New name combination.

Coendou koopmani Handley and Pine, 1992: 238. A junior synonym based on 61 specimens from scattered Amazonian localities south of the main river itself. The type (USNM 519689) was collected at Belém.

TYPE MATERIAL: The holotype (by monotypy), ZMB 1299, consisting of a skin, skull, and mandibles in the Museum für Naturkunde der Humboldt-Universität zu Berlin.

TYPE LOCALITY: Brazil by original designation, herein restricted to eastern Amazonia (below Óbidos) south of the main channel of the Rio Amazonas.

KNOWN DISTRIBUTION: Amazonian lowlands east of the Rio Madeira and south of the Rio Amazonas, including at least part of Marajó Island (Handley and Pine, 1992).

MORPHOLOGICAL DESCRIPTIONS: Olfers (1818), Kuhl (1820), Handley and Pine (1992), this report.

SPECIMENS EXAMINED: *Amazonas*, Auará Igarapé (AMNH 91726), Villa Bella Imperatriz (AMNH 92898); *Pará*, Belém (USNM 394733, 519689), Cametá (AMNH 96316, 96317; MCZ 30551–30555), Curralinho (AMNH 134074, 134075, 134078, 134080, 134187, 134188, 134191, 134193–134196, 134199, 134203, 134205—134208, 134211), Ilha do Taiuna (AMNH 96314, 96319–96329; ZINRAS 40243), Marajó (USNM 519690–519693), Mocajuba (AMNH 96330), Muaná (USNM 105527), "Rio Tocantins" (AMNH 97277).

REFERENCES

Alston, E. R.
1876. On the classification of the order Glires. Proc. Zool. Soc. London 1876: 61–98 + pl. IV.

Angermann, R.
1989. Die Säugetierkollektion des Museums für Naturkunde der Humboldt-Universität zu Berlin. Säugetierkd. Inf. 3(13): 47–68.

Avila-Pires, F. D. de
1967. The type locality of *Chaetomys subspinosus* (Olfers, 1818) (Rodentia, Caviomorpha). Rev. Bras. Biol. 27: 177–179.

Azara, F. de
1801. Essais sur l'histoire naturelle des quadrupèdes de la Province du Paraguay, 2 vols. Paris: Charles Pougens.

Brandt, J. F.
1835. Mammalium rodentium exoticorum novorum vel minus rite cognitorum musei academici zoologici descriptiones et icones. Mem. Acad. Imp. Sci. St.-Petersbourg, ser. 6 (tome III), pt. 2. (tome I): 358–442 + 17 pls.

Burmeister, H.
1854. Systematishe Uebersicht der Thiere Brasiliens, welche während einer Reise durch die Provinzen von Rio de Janeiro und Minas geraës gesammelt oder beobachtet wurden. Erster Theil: Säugethiere (Mammalia). Berlin: Georg Reimer.

Cabanis, J.
1848. Saeugethiere. *In* R. Schomburgk (ed.), Reisen in Britisch-Guiana in den Jahren 1840–1844, Dritter Theil [vol. 3], Versuch einer Fauna und Flora von Britisch-Guiana: 766–786. Leipzig: J. J. Weber.

Cabrera, A.
1961. Catálogo de los mamíferos de América del Sur. Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia" 4(2): xxii + 309–732.

Cuvier, F.
1822. Examen des espèces du genre porc-épic. Mem. Mus. d'Hist. Nat. 9: 413–437.

Desmarest, M. A. G.
1822. Mammalogie ou description des espèces de mammifères. Seconde partie, contenant les ordres des rongeurs, des édentés, des pachydermes, des ruminans, et des cétacés. Paris: Chez Mme. Veuve Agasse.

Ellerman, J. R.
1941. The families and genera of living rodents, 2 vols. London: British Museum (Natural History).

Emmons, L. H.
1990. Neotropical rainforest mammals, a field guide. Chicago: Univ. Chicago Press.
Gray, J. E.
1843. [Description of *Chaetomys*, n. gen.] Proc. Zool. Soc. London 1843: 21–22.
1844. Mammalia. *In* R. B. Hinds (ed.), The zoology of the voyage of H.M.S. Sulphur, under the command of Captain Sir Edward Belcher [etc], vol. 1: 7–36 + pls. I–XVI. London: Smith, Elder and Co.
Hackethal, S.
1995. Friedrich Sellow (1789–1831). Skizzen einer unvollendeten Reise durch Südamerika. Fauna Flora Rheinland-Pfalz 17: 215–228.
Hall, E. R.
1981. The mammals of North America, 2 vols. New York: Wiley.
Handley, C. O., Jr., and R. H. Pine
1992. A new species of prehensile-tailed porcupine, genus *Coendou* Lacépède, from Brazil. Mammalia 56: 237–244.
Hernández, F.
1651. Nova plantarum, animalium, et mineralium mexicanorum historia. Roma: B. Deuersini & Z. Masotti, typis V. Masacardi. [Not seen.]
Hershkovitz, P.
1949. Status of names credited to Oken, 1816. J. Mammal. 30: 289—301.
1959. Nomenclature and taxonomy of the Neotropical mammals described by Olfers, 1818. J. Mammal. 40: 337–353.
1977. Living New World monkeys (Platyrrhini) with an introduction to primates, vol. 1. Chicago: Univ. Chicago Press.
1987. A history of the Recent mammalogy of the Neotropical region from 1492 to 1850. Fieldiana Zool. (n. ser.) 39: 11–98.
Hoffmannsegg, G. von
1807. Beschreibung vier affenartiger Thiere aus Brasilien. Mag. Ges. Naturforsch. Fr. Berlin 1: 83–104.
Husson, A. M.
1978. The mammals of Suriname. (Zool. Monogr. Rijksmus. Nat. Hist. 2). Leiden: E. J. Brill.
ICZN
1985. International code of zoological nomenclature, 3rd. ed. Berkeley: Univ. California Press.
Illiger, K.
1811. Prodromus systematis mammalium et avium. Berolini [Berlin]: C. Salfeld
1815. Ueberblick der Säugethiere nach ihrer Vertheilung über die Welttheile. Abh. K. Akad. Wiss. Berlin 1804–1811: 39–159.
Jahn, I.
1985. Zur Vertretung der Zoologie und zur Entwicklung ihrer institutionellen Grundlagen an der Berliner Universität von ihrer Gründung bis 1920. Wiss. Z. Humboldt-Univ. Berlin Math.-Naturwiss. Reihe. 34(3/4): 260–280.
Kerr, R.
1792. The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus; Class I. Mammalia: containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the Systema Naturae as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, etc. London: J. Murray and R. Faulder.
Kuhl, H.
1820. Beiträge zur Zoologie und vergleichenden Anatomie. Frankfurt am Main: Verlag der Hermannschen Buchhandlung.
Lara, M. C., J. L. Patton, and M. N. F. da Silva
1996. The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. Mol. Phylogenet. Evol. 5: 403–413.
Lichtenstein, H.
1816. Das zoologische Museum der Universität zu Berlin [1st ed]. Berlin: In Commission bei Ferdinand Dümmler.
1818a. Das zoologische Museum der Universität zu Berlin, Zweite Ausg. [2nd ed.]. Berlin: publisher unknown.
1818b. Verzeichniß von ausgestopften Säugethieren und Vögeln welche am 12ten October 1818 u. folg. Tage im zoologischen Museum der Königl. Universität zu Berlin durch den Königl. Auctionscommissarius Bratring dem Meistbietenden öffentlich verkauft werden sollen. Berlin: publisher unknown.
Linnaeus, C.
1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae: Laurentii Salvii.

Lund, P. W.
1841. Blik paa Brasiliens Dyreverden för sidste Jordomvaeltning. Anden Afhandling: Pattedyrene. Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Matematiske Afhandlinger 8: 61–144 + 12 pls.

Marcgraf ("Marcgravius"), G.
1648. Historiae rerum naturalium Brasiliae, etc. [Not seen. For the very lengthy complete bibliographic citation of this historical work see Hershkovitz, 1987.]

Martin, T.
1994. On the systematic position of *Chaetomys subspinosus* (Rodentia: Caviomorpha) based on evidence from the incisor enamel microstructure. J. Mamm. Evol. 2: 117–131.

Mayr, E., E. G. Linsley, and R. L. Usinger
1953. Methods and principles of systematic zoology. New York: McGraw-Hill.

Miller, G. S., Jr., and J. W. Gidley
1918. Synopsis of the supergeneric groups of rodents. J. Washington Acad. Sci. 8: 431–448.

Moojen, J.
1952. Os roedores do Brasil. Rio de Janeiro: Instituto Nacional do Livro.

Muggelberg, H.
1975. Leben und Wirken Johann Karl Wilhelm Illigers (1775–1813) als Entomologe, Wirbeltierforscher und Gründer des Zoologischen Museums der Humboldt-Universität zu Berlin. Mitt. Zool. Mus. Berlin 51: 257–303
1976. [Continued] Mitt. Zool. Mus. Berlin 52: 137–174, 331–355.

Oken, [L. von]
1816. Lehrbuch der Naturgeschichte. Dritter Theil, Zoologie. Zweite Abtheilung, Fleischthiere. Jena: August Schmid.

Olfers, I. [F. J. M.] von
1818. Bemerkungen zu Illiger's Ueberblick der Säugthiere nach ihrer Vertheilung über die Welttheile, rücksichtlich der Südamericanischen Arten (Species). *In* W. L. von Eschwege, Journal von Brasilien, oder Vermischte nachrichten aus Brasilien, auf wissenschaftlichen Reisen gesammelt, Abhandlung [chapter] 10: 192–237. Weimar: Im Verlage des Gr. H. S. priv. Landes-Industries-Comptoirs. [Eschwege's book is sometimes cited as volume 15 (Heft 2) of the "Neue Bibliothek der wichtigsten Reisebeschreibungen zur Erweiterung der Erd- und Völkerkunde" edited by F. J. Bertuch.]

Oliver, W. L. R., and I. B. Santos
1991. Threatened endemic mammals of the Atlantic forest region of south-east Brazil. Wildl. Preserv. Trust Spec. Sci. Rep. 4: 125 pp.

Papavero, N.
1971. Essays on Neotropical dipterology, with special reference to collectors (1750–1905), 2 vols. São Paulo: Mus. Zool. Univ. São Paulo.

Patterson, B., and A. E. Wood
1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. Bull. Mus. Comp. Zool. 149: 371–543.

Paynter, R. A., Jr., and M. A. Traylor, Jr.
1991. Ornithological gazetteer of Brazil, 2 vols. Cambridge, MA: Mus. Comp. Zool., Harvard Univ.

Peres, C. A., J. L. Patton, and M. N. F. da Silva
1996. Riverine barriers and gene flow in Amazonian saddle-back tamarins. Folia Primatol. 67: 113–124.

Pictet, F.-J.
1843. Description d'un nouveau genre de rongeurs de la familie des Histricins. Rev. Zool. 6: 225–227.

Rengger, J. R.
1830. Naturgeschichte der Saeugethiere von Paraguay. Basel: Schweighauserschen Buchhandlung.

Santos, I. B., W. L. R. Oliver, and A. B. Rylands
1987. Distribution and status of two species of tree porcupines, *Chaetomys subspinosus* and *Sphiggurus insidiosus*, in south-east Brazil. Dodo, J. Jersey Wildl. Preserv. Trust 24: 43–60.

Schinz, H. R.
1824. Naturgeschichte und Abbildungen der Säugethiere. Zürich: Brodimanns lithographischer Kunstanstalt.
1845. Systematisches Verzeichniß aller bis jezt bekannten Säugethiere oder Synopsis Mammalium nach dem Cuvier'schen System, 2 vols. Solothurn: Druck von J. Gassmann, Sohn.

Silva, M. N. F. da, and J. L. Patton
1993. Amazonian phylogeography: mtDNA sequence variation in arboreal echimyid rodents (Caviomorpha). Mol. Phylogenet. Evol. 2: 243–255.

Stehlin, H. G., and S. Schaub
1951. Die Trigonodontie der simplicidentaten Nager. Basel: Verlag Birkhäuser AG.

Stresemann, E.
1948. Der Naturforscher Friedrich Sellow (†1831) und sein Beitrag zur Kenntnis Brasiliens. Zool. Jahrb. 77: 403–425.

1950. Die brasilianischen Vogelsammlungen des Grafen von Hoffmannsegg aus den Jahren 1800–1812. Bonn. Zool. Beitr. 1: 43–51, 126–143.

Tate, G. H. H.

1935. The taxonomy of the genera of Neotropical hystricoid rodents. Bull. Am. Mus. Nat. Hist. 68: 295–447.

Thomas, O.

1897. On the genera of rodents: an attempt to bring up to date the current arrangement of the order. Proc. Zool. Soc. London 1896: 1012–1028.

1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. Proc. Zool. Soc. London 1911: 120–158.

1927. A selection of lectotypes of American rodents in the collection of the British Museum. Ann. Mag. Nat. Hist. 9(19): 545–554.

Trouessart, E.-L.

1881 ["1880"]. Catalogue des mammifères vivants et fossiles [part 2], ordre des rongeurs. Bull. Soc. d'Etudes Sci. D'Angers 1880: 58–212.

1897. Catalogus mammalium tam viventium quam fossilium, nov. ed., fascic. III. Rodentia II (Myomorpha, Hystricomorpha, Lagomorpha). Berolini [Berlin]: R. Friedländer & Sohn.

Tschudi, J. J. von

1844–1846. Untersuchungen über die Fauna Peruana. St. Gallen: Druck und Verlag von Scheitlin und Zollikofer.

Urban, I.

1893. Biographische Skizzen 1. Friedrich Sellow (1789–1831). Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr. 17: 177–198.

1906. Vitae itineraque collectorum botanicorum. *In* C. F. Ph. von Martius, A. G. Eichler, and I. Urban (eds.), Flora Brasiliensis, vol. 1 (pt. 1): 2–154. Monachii [Munich]: Apud R. Oldenbourg. [Reprinted by J. Cramer in Weinheim, 1965.]

Voss, R. S., and L. H. Emmons

1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bull. Am. Mus. Nat. Hist. 230: 115 pp.

Wagner, J. A.

1844. Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber, Supplementband, Vierte Abtheilung. [Part four of Wagner's supplement to Schreber's multivolume work.] Erlangen: in der Expedition des Schreber'schen Säugthier[e] und des Esper'schen Schmetterlingswerkes, etc.

Waterhouse, G. R.

1848. A natural history of the Mammalia, vol. 2. Containing the Rodentia, or gnawing Mammalia. London: Hippolyte Baillière.

Wied, M., Prinz zu

1826. Beiträge zur Naturgeschichte von Brasilien, Band II (Abtheilung II, Mammalia). Weimar: Verlage des Gr. H. S. priv. Landes-Industrie-Comptoirs.

Winge, H.

1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii 1(3): 200 pp. + 8 pls.

Woods, C. A.

1993. Suborder Hystricognathi. *In* D. E. Wilson and D. M. Reeder (eds.), Mammal species of the world, 2nd. ed.: 771–806. Washington, DC: Smithson. Inst. Press.

APPENDIX

Unpublished Sources

Below we list the principal unpublished sources we consulted in the Historische Bild- und Schriftgutsammlungen of the Museum für Naturkunde der Humboldt-Universität zu Berlin. Archival materials relating to the zoological collections (Bestand: "Zool. Mus.") are filed by their official catalog designation (Signatur), which is prefixed by "SI" (= Schriftgut I) for all the early 19th century manuscripts relevant to this project; page (Blatt) numbers are used to distinguish separate documents with the same Signatur. Sieber's correspondence with Hoffmannsegg, however, is preserved among the papers of the Gesellschaft Naturforschender Freunde zu Berlin (Bestand: "G.N.F.").

Bestand: Zool. Mus.

SI Frühe Kataloge Säugetiere Bd. I

Blätter 1–13 "Catalogus Mammalium et Avium Musei Regii . . . Ao. 1810." (The 1810 species list; title page is Bl. 1, porcupine entries are on Bl. 2a.)

Blätter 17–25 "Nachweisung über den Zuwachs des Königl. zoologischen Museums . . . 1822" (The 1822 specimen list; reproduced porcupine entries are on Bl. 24a.)

Blätter 71–115 "Säugetierkatalog vor 1818" (Porcupine entries are on Bl. 96.)

SI Frühe Kataloge Säugetiere Bd. II

Blätter 1–9 "Inventarium der Säugetiere ca. 1822/1823" (Listing of "*Hystrix*" on Bl. 6a–7 identical with that on Bl. 24a of "Nachweisung . . ."; the relevant species are here listed as numbers 212–216)

SI Eingangskatalog 1811–1857

(Entry for "*Hystrix insidiosa*" in Sellow's shipment of 25 March 1818 is on Bl. 12; entry for "*Hystrix insidiosa*" in Olfers and Sellow's shipment of 8 September 1820 is on Bl. 33a. According to a specimen list in SI OLFERS III, Olfers and Sellow's "*H. insidiosa*" was a skin only, and therefore cannot be ZMB 1297, a mounted skin with the skull inside. As no other porcupine identified as *H. insidiosa* was apparently received from these collectors, it is possible that ZMB 1297 was mislabeled, and that this is really the specimen sent by Sellow from Bahia in 1818. The contents of Olfers' first and second shipments from Brazil are not registered in the Eingangskatalog, probably because they mostly contained fluid-preserved material destined for the anatomical collections, not the zoological museum. See notes on SI OLFERS I and III, below.)

SI OLFERS I "Acta enthaltend: die Correspondenz mit Dr. Ignatz v. Olfers zu Rio de Janeiro . . ."

Blatt 3 (Letter, Olfers to Lichtenstein, Paris 22 April 1817)

Blätter 4–13 (Untitled report by Olfers describing his first shipment [no mammals], Rio de Janeiro 15 November 1817)

Blätter 14–19 (Letter, Olfers to Lichtenstein, Rio de Janeiro 25 February 1818)

Blätter 20–26 (Untitled report by Olfers describing his second shipment [including some mammals but no *Hystrix*], Rio de Janeiro 5 July 1818)

SI OLFERS III "Acta enthaltend: die Eingangs-Verzeichnisse der Naturaliensendungen von Dr. von Olfers und F. Sellow aus Brasilien . . ." (Bl. 1, 1a, and 2 concern Sellow's first shipment; Bl. 6 and 8 concern Olfers' second shipment; this file also contains lists of specimens in Sellow and Olfers' joint shipments, not all of which were registered in the "Eingangskatalog.")

SI Akte GOMES, F.A.

Blätter 14–19 (Letter from Gomes to Hoffmannsegg, Bahia 17 September 1801; reference to first porcupine is on Bl. 18a–19)

Blätter 20–25 (Ditto, 20 November 1801; quoted reference to second porcupine on Bl. 21–21a)

Blätter 30–37 (Ditto, 24 May 1802; reference to third porcupine on Bl. 32a)

Blätter 82–116 "Verzeichnisse der Sendungen" (Reproduced first page of Hoffmannsegg's and Illiger's excerpts on mammals is Bl. 83; page with quoted Latin diagnosis of "*Hystrix prehensilis* an var" is Bl. 95a; "Envoy de la Caisse Nr. 7 du 24 May 1802" with mention of third porcupine is on Bl. 108)

Bestand: G.N.F.

S Akte HOFFMANNSEGG (This file includes Sieber's letters to the count from Lisbon and Brazil, 3 May 1802 to 30 April 1806.)

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://nimidi.amnh.org. Or address mail orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

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