FIELDIANA

Zoology

Published by Field Museum of Natural History

New Series, No. 11

NEOTROPICAL DEER (CERVIDAE)
PART I. PUDUS, GENUS *PUDU* GRAY

PHILIP HERSHKOVITZ

RECEIVED

MAR 1982

FIELD MUSEUM LIBRARY

March 22, 1982

Publication 1330

NEOTROPICAL DEER (CERVIDAE)
PART I. PUDUS, GENUS *PUDU* GRAY

FIELDIANA

Zoology

Published by Field Museum of Natural History

New Series, No. 11

NEOTROPICAL DEER (CERVIDAE) PART I. PUDUS, GENUS *PUDU* GRAY

PHILIP HERSHKOVITZ

*Curator Emeritus
Division of Mammals
Department of Zoology
Field Museum of Natural History*

Accepted for publication May 22, 1980

March 22, 1982

Publication 1330

Library of Congress Catalog Card No.: 81-67141

ISSN 0015-0754

PRINTED IN THE UNITED STATES OF AMERICA

CONTENTS

I.	Introduction	1
	Material	2
	Abbreviations	2
	Measurements	2
	Review of Cervid Classification with Particular Reference to South	
	American Genera	2
	Odocoileine Origins and Radiation	8
	Cheiridia	9
	Limb Proportions	11
II.	Genus <i>Pudu</i> Gray	13
	Synonymic History	13
	Conservation	14
	Taxonomy	15
	Generic Characters	15
	Generic Comparisons	22
	Fawnal Spotting Pattern	23
	Ancestral Characters and Relationships	24
	Origin, Dispersal, Speciation	25
III.	The Species of <i>Pudus</i> , Genus <i>Pudu</i> Gray	43
	Key to the Species	43
IV.	<i>Pudu mephistophiles</i> de Winton	44
	Synonymic History	44
	Distribution	45
	Conservation	48
	Vernacular Names	50
	Taxonomy	51
	Characters	51
	Comparisons	57
	Specimens Examined	58
V.	Biology of <i>Pudu mephistophiles</i>	58
	Habitat	58
	Habits	58
	Maintenance in Captivity	59
	Ungulate Associations	59
	Reproduction	59
VI.	<i>Pudu puda</i> Molina	60
	Synonymic History	60
	Distribution	62
	Conservation	62
	Taxonomy	64
	Characters	65
	Karyotypes	70
	Comparisons	70
	Specimens Examined	70
VII.	Biology of <i>Pudu puda</i>	71
	Habitat	71
	Maintenance in Captivity	71
	Ungulate Associations	73

	Numbers and Aggregations	73
	Migrations	73
	Locomotion, Play	74
	Enemies	74
	Diseases and Parasites	74
	Food and Water	74
	Earthquake Sensitivity	75
	Temperature Regulation	75
	Reproduction, Growth, Development	75
	Longevity	79
VIII.	Summary	79
IX.	Acknowledgments	79
X.	Gazetteer and Explanation of Maps	80
XI.	Literature Cited	83

LIST OF ILLUSTRATIONS

1. Dispersal and speciation of pudus	2
2. Left forefeet and hind feet of brocket, <i>Mazama rufina</i> , and muntjac, <i>Muntiacus reevesi</i>	6
3. Nares in Odocoileinae and Cervinae	7
4. Artiodactyl hind feet showing gradient of metatarsal bone reduction	10
5. Size relationship and body form of six South American deer	16
6. Body form of four South American deer	17
7. Facial color pattern of Odocoileinae	18
8. Head characters of smallest South American deer	19
9. Facial markings of five South American deer	20
10. Front and hind feet with outline of interdigital glands	21
11. Skulls, left side of adult female pudus and brockets	26
12. Skulls, dorsal surface of adult female pudus and brockets	27
13. Skulls, palatal surface of adult female pudus and brockets	28
14. Skulls, left side of adult male pudus and brockets	29
15. Skulls, dorsal surface of adult male pudus and brockets	30
16. Skulls, palatal surface of adult male pudus and brockets; inset, deciduous-like pm ³	31
17. Mandibles of pudus and brockets, lateral surface of left rami	32
18. Upper cheek teeth of adult pudus and brockets, and juvenal cheek teeth of <i>Mazama chunyi</i>	33
19. Lower cheek teeth of adult pudus and brockets, and juvenal cheek teeth of <i>Mazama chunyi</i>	34
20. Lower front teeth of pudus and brockets, labial surface	35
21. Lower front teeth of pudus and brockets, lingual surface	36
22. Permanent and deciduous incisor-canine series in pudus and brockets	37
23. Upper right and lower left second and third molars of pudus	38
24. Forefeet and hind feet of pudus with vestiges of metacarpal bones II and V (telemetacarpalia)	40
25. One-week-old southern pudu	41
26. One-week-old gray brocket	41
27. Red brocket doe with fawn	42
28. Northern pudus, adult male and female	43
29. Northern pudu, adult female	43
30. Geographic distribution of <i>Pudu mephistophiles</i>	46
31. Pelage and hair types of <i>Pudu mephistophiles</i>	53
32. Sectioned hair from <i>Pudu mephistophiles</i>	54
33. Saturation in mammalian tegumentary color	55
34. Color of hairs of <i>Pudu mephistophiles</i> and <i>P. puda</i>	56
35. Geographic distribution of <i>Pudu puda</i>	63
36. Southern pudus in Cologne zoo	67
37. Southern pudus in Berlin zoo	67

LIST OF TABLES

1. Homologies of artiodactyl carpal and tarsal bones	11
2. Artiodactyl limb proportions	12
3. External and cranial measurements of adult <i>Pudu mephistophiles</i>	52
4. External and cranial measurements of adult <i>Pudu puda</i>	68
5. Antler cycle in <i>Pudu puda</i>	69
6. Birth records of <i>Pudu puda</i>	72
7. Growth and development of a male <i>Pudu puda</i> in the Cologne zoo	76
8. Chronology of weight increment in <i>Pudu puda</i>	77
9. Three oldest longevity records for <i>Pudu puda</i>	78
10. Composition of milk produced by <i>Pudu puda</i>	79

I. INTRODUCTION

The diminutive, spike-antlered deer of the genus *Pudu* are smallest of living true deer and smallest of New World ungulates. Of the two known species, the northern occurs in the high, equatorial Andes from southern Colombia to central Peru between latitudes 5°N and 12°S, and the southern is found in the southern half of Chile and in bordering parts of Argentina between latitudes 35°S and 53°S (fig. 1).

This report is the first of a proposed series on the genera of neotropical Cervidae and part of a monograph begun more than three decades ago with the intent of completing a unified work. My preliminary publications in ensuing years include attempts to clarify the nomenclature and taxonomic status of some neotropical deer (1948, 1958a, 1958b), descriptions of a new subspecies and species of brockets of the genus *Mazama* (1959a, 1959b), and comments on South American cervid origin and distribution (1958c, 1966, 1972). Work on the monograph itself, which had already become a sizable manuscript, suffered delays and lengthy interruptions and seemed interminable as a single work.

The present plan is to update and complete each generic review as a separate publication, with particular attention paid to taxonomy, zoogeography, and life history of the included species. In this report, the issues of origin, evolution, and supergeneric classification are touched upon mainly for orientation and reference. Full discussion of these topics necessarily awaits completion of studies of both living and fossil forms. Detailed descriptions of more specific subjects, such as dental anatomy, hoofs, antlers, glands, genitalia, and other soft parts, will be presented in those reports where most appropriate or demanding. For example, because simple antlers of pudus and brockets are similar, the attention in this account focuses on other characters, such as limb bones, which distinguish pudus from all other deer. On the other hand, distinction of brockets (*Mazama* spp.) from their nearest relative, the white-tailed deer (*Odocoileus virginianus*), is based largely on antler size and shape. It is proper, therefore, to reserve both description of the morphology and discussion of the evolution of branched antlers from the simple, spike-like form for reports on those particular deer. The final number of the proposed series will include a synthesis.

The study of neotropical deer, particularly in the field, has been largely neglected. The 11 or so extant species exceed the combined number of species of the Odocoileinae and tribe Cervini native to other comparable zoogeographic regions.

Man's persecution of deer is persistent and practically uncontrolled. Most of the species have already vanished from large areas of their former range. Under present conditions of mock conservation, some species may disappear completely before the end of the century.

FIG. 1. Dispersal and speciation of pudus. Dashed line at northeastern base of Andes indicates presumed temperate zone habitat of ancestral species during a glacial period. With onset of the postglacial period, pudus presumably moved with their natural temperate zone habitat to higher altitudes in the north (arrows) and to higher latitudes in the south (triangles) in the wake of retreating glaciers. The widely separated populations then differentiated into *Pudu mephistophiles* in the north, and the more evolved *P. puda* in the south. Character for character, the southern species can be derived from the northern. Actual geographic range of *P. mephistophiles*, if not continuous, probably is—or was—less fragmented than indicated on the basis of available data.

MATERIAL

Specimens examined in the preparation of this report include skins, skulls, and postcranial skeletons representing 57 pudus, as well as an uncounted number of representatives of all other forms of neotropical deer preserved in the institutions listed under the "Abbreviations" section. In addition, reference was made, as occasion required, to other artiodactyls in the Field Museum collections.

Photographs of skulls and dentition are based on "normal" specimens in good condition selected from material at hand. In some cases, it was necessary to substitute mandibles or teeth of specimens other than those used for illustrating the main parts of the skull.

ABBREVIATIONS

AMNH—American Museum of Natural History

ANSP—Academy of Natural Sciences, Philadelphia

BM—British Museum (Natural History)

FMNH—Field Museum of Natural History

MCZ—Museum of Comparative Zoology, Harvard University

USNM—National Museum of Natural History, Smithsonian Institution

I take this opportunity to thank the authorities of the sister institutions mentioned here for permission to study the material in their charge.

MEASUREMENTS

Standard external and cranial measurements are used here. Limb bone measurements are of greatest length, irrespective of the points. Width of metapodials, however, is measured between widest points across the distal epiphyseal union. Combined length of the articulated thoracic and lumbar vertebrae is equated with trunk length (TL, table 2), and used as principal reference for proportional lengths of limb bones. In most cases, articulations were made manually and the vertebrae measured in sections. Carpal, tarsal, and phalangeal dimensions are omitted here.

In comparisons of pudu postcranial skeletal bones with those of other artiodactyls (table 2), ratios instead of actual measurements are given to eliminate or minimize actual size differences between species, sexes, age classes, and individuals.

REVIEW OF CERVID CLASSIFICATION

WITH PARTICULAR REFERENCE TO SOUTH AMERICAN GENERA

The first comprehensive and soundly documented arrangement of deer, including the South American forms, is that by Brooke (1878, p. 889). His scheme, less a classification than a dichotomous key to the genera or generic groups, is abstracted as follows:

- I. Plesiometacarpi (proximal ends of lateral metacarpals persistent, fig. 2).
 - A. Posterior portion of nasal cavity not divided into two chambers by vomer (fig. 3). Genera: *Cervulus* (= *Muntiacus*), *Elaphodus*, *Cervus* (subgenera, *Cervus*, *Rusa*, *Rucervus*, *Elaphurus*, *Axis*, *Pseudaxis*, *Dama*).
- II. Telemetarpi (distal ends of lateral metacarpals persistent, fig. 2).

- A. Posterior portion of nasal cavity not divided into two chambers by vomer (fig. 3). Genera: *Alces*, *Hydropotes*, *Capreolus*.
- B. Posterior portion of nasal cavity divided into two chambers by vomer (fig. 3). Genera: *Cariacus* (= *Odocoileus*, with subgenera *Odocoileus*, *Blastocerus* [includes *Ozotoceros* = *Blastoceros*], *Furcifer* [= *Hippocamelus*], *Coas-sus* [= *Mazama*]), *Pudua* (= *Pudu*), *Rangifer*.

The subfamilies Cervinae and Capreolinae, recognized by Pocock (1911, p. 971) in his arrangement of cervids, are equivalent to Brooke's Plesiometacarpal and Telemetacarpal. In 1923, Pocock (p. 206) elevated each well-marked genus or generic group of telemetacarpalid deer to subfamily rank without indication of interrelationships, except through the following artificial key (abstracted):

- A. Telemetacarpalia (fig. 2).
 - 1. Vomer dividing posterior nares (fig. 3).
 - a. Cuboideonavicular and external cuneiform bones united (Pudinae, figs. 4, 24).
 - b. Cuboideonavicular and external cuneiform bones separated (fig. 2).
 - (1). Antlers present in males only (Odocoileinae).
 - (2). Antlers present in both sexes (Rangiferinae).
 - 2. Vomer not dividing posterior nares (fig. 3).
 - a. Antlers absent; upper canine hypertrophied in males (Hydropotinae).
 - b. Antlers present; upper canine minute or absent in either sex.
 - (1). Muzzle short, not swollen (Capreolinae).
 - (2). Muzzle very long, much swollen (Alceinae).
- B. Plesiometacarpalia (fig. 2).
 - 1. Cuboideonavicular and external middle cuneiform bones fused (Muntiacinae = Cervulinae, fig. 2).
 - 2. Cuboideonavicular and cuneiform bones discrete (Cervinae).

Lydekker (1915, p. vii) grouped all deer in the family Cervidae (Section Pecora). The family, in turn, was divided into subfamilies Moschinae and Cervinae, the latter with genera *Muntiacus*, *Elaphodus*, *Dama*, *Cervus*, *Elaphurus*, *Odocoileus*, *Blastocerus*, *Hippocamelus*, *Mazama*, *Pudu* (*Pudella*, a subgenus), *Capreolus*, *Rangifer*, and *Hydropotes*.

Living and fossil South American deer are central to the classification of the Cervidae presented by Carleton (1922, p. 442). In the following, the two subfamilies and attributed characters are abstracted, cervine generic names omitted:

- A. Cervinae (Eurasian).
 - 1. Vomer incompletely ossified, the vertical plate not extending to posterior portion of nasal cavity.
 - 2. Plesiometacarpalid or telemetacarpalid.
 - 3. Metatarsal tuft, when present, on proximal half of metatarsus.
 - 4. Upper canine tusk-like to absent.
 - 5. Premaxillary and nasal bones usually articulating.
 - 6. Antlers simple, dichotomous, branched, or absent.
- B. Neocervinae (New World).
 - 1. Vomer completely ossified, vertical plate extending to posterior portion of nasal cavity.
 - 2. Telemetacarpalid.
 - 3. Metatarsal tuft, when present, on distal half of metatarsus.

4. Upper canine small or absent.
5. Premaxillary and nasal bones usually not articulating.
6. Antlers.
 - a. Absent (*†Blastomeryx*, North American Miocene).
 - b. Simple (*Mazama*, *Pudu*).
 - c. Bifurcate (*Hippocamelus*).
 - d. Dichotomous (*Blastocerus*).
 - e. Branched (*Odocoileus*, *Rangifer*).

Included within the "Neocervinae" are the extinct, branch-antlered *Antifer*, *Paraceros*, *Morenelaphus*, *Pampaecervus*, and *Epieuryceros*. "Neocervinae," the group name erected by Carrette, is not derived from a generic name and has no status.

Kraglievich (1932, pp. 425–429) dismissed Carrette's concept of "Neocervinae" as contrived and composite. His own arrangement, based primarily on antler form, is:

- a. Mazaminae (*Mazama*, *Pudu*).
- b. Odocoileinae (*Odocoileus*, *Blastocerus*, *Hippocamelus*).
- c. *†Antiferinae* (*†Antifer*).
- d. Alcinae (*Alces*).
- e. Cervinae (*Cervus*, *Rangifer*, *†Paraceros*, *†Morenelaphus* [*†Pampaecervus*, a subgenus]).
- f. *Incertae sedis* (*†Epieuryceros*).

Living and fossil genera of North American deer (Cervidae) are classified in key form by Frick (1937, pp. 32, 34, 205) primarily on the basis of teeth and antlers. South American genera are included only "tentatively, for comparison—unstudied," in "Division C.-Cervini. Pleistocene—Recent," with the following subfamilies and their respective genera:

Subfamily 7. Cervinae (*Procoileus*, *Cervus*).

Subfamily 8. Odocoilenae (*Odocoileus*, *Eucervus*).

Subfamilies 8 and 9a. Alcenae-Rangiferinae (*Cervalces*, *Alces*, *Rangifer*)

Subfamilies 8 and 9a (continued). Odocoilenae and (?)Rangiferinae (*Pudu*, *Hippocamelus*, *Blastocerus*, *Mazama*, *Ozotoceros*, *†Palaeodocoileus*, *†Paraceros*, *†Morenelaphus*, *†Antifer*).

Simpson's (1945, p. 152) Cervoidea, with the single family Cervidae, contains the following subfamilies, with extant American tribes and genera included where pertinent:

†Palaeomerycinae

Moschinae

†Dromomerycinae

Muntiacinae

Cervinae

Odocoileinae

Odocoileini (*†Antifer*, *†Epieuryceros*, *†Morenelaphus*, *Odocoileus*, *Mazama*, *Hippocamelus*, *Blastocerus*, *Ozotoceros*, *Pudu*)

Alcini (*†Cervalces*, *Alce*)

Rangiferini (*Rangifer*)

Hydropotini (*Hydropotes*)

Capreolini (*†Procapreolus*, *Capreolus*)

FRONT LIMB

Mazama rufina
70563

Muntiacus reevesi
15575

HIND LIMB

FIG. 2. Left forefoot and hind foot of brocket, *Mazama rufina*, with vestiges of metacarpal bones II and V distal in position (telemetacarpalia), and of muntjac, *Muntiacus reevesi*, with vestiges of the same metacarpal bones proximal in position (plesiommetacarpalia). Front digital bones of *Mazama rufina* lacking.

FIG. 3. Nares are divided posteriorly by bony extension of vertical plate of vomer (arrow) in Odocoileinae, as in *Mazama americana*, but are undivided posteriorly in Cervinae, as in *Capreolus capreolus*.

Simpson (1945, p. 267) discarded the prior subfamily group name Capreolinae for Odocoileinae, "because *Odocoileus* makes a better type."

Flerov (1952) criticized Simpson's concept of cervoid relationships and rearranged the Cervoidea as follows:

Moschidae

Cervidae

†Palaeomerycinae

†Dromomerycinae

Cervulinae (=Muntiacinae)

Cervinae (*Capreolus*, *Cervus*, *Elaphurus*, *Alces*, †*Pliocervus*, †*Procapreolus*, †*Cervavitus*, †*Eucladocerus*, †*Pseudalces*, †*Megaloceros*, †*Cervalces*)

Neocervini (*Mazama*, *Pudu*, *Odocoileus* [with subgenera *Odocoileus*, *Blastocerus*, *Hippocamelus*, *Rangifer*, †*Antifer*, †*Epieuryceros*, †*Pampaecocervus*, †*Morenelaphus*]).

According to Churcher (1966), †*Epieuryceros* and †*Antifer* (in the preceding rearrangement) probably are congeneric with *Blastocerus*.

Cabrera (1961, pp. x, 324), in his *Catálogo de los mamíferos de America del Sur*, recognizes the extant South American genera of Cervidae in the following order: *Odocoileus*, *Blastocerus*, *Ozotoceros*, *Hippocamelus*, *Mazama*, *Pudu* (with subgenus *Pudella*).

For convenience of a single reference, a provisional classification of currently recognized genera and living species of South American cervids is provided herewith:

Cervidae Gray 1821

Odocoileinae Pocock 1923 (New World deer)

Pudini (new rank=Pudinae Pocock 1923)

Pudu Gray 1850 (Pudus)

P. mephistophiles de Winton 1896

P. puda Molina 1782

Odocoileini Simpson 1945

Mazama Rafinesque 1817 (Brockets)

M. americana Erxleben 1777

M. chunyi Hershkovitz 1959

M. gouazoubira Fischer 1814

M. rufina Pucheran 1851

†*Charitoceros* Hoffstetter 1963

Hippocamelus Leuckart 1816 (Huemuls)

H. antisensis D'Orbigny 1834

H. bisulcus Molina 1782

Blastoceros Fitzinger 1860 (= *Ozotoceros* Ameghino 1891 [Pampas deer])

B. bezoarticus Linnaeus 1758

Blastocerus Gray 1850 (?synonyms: †*Antifer* Ameghino 1889, †*Paraceros* Ameghino 1889, †*Epieuryceros* Ameghino 1889 [Swamp deer])

B. dichotomus Illiger 1815

Odocoileus Rafinesque 1832 (synonyms: †*Paleodocoileus* Spillmann 1931, †*Protomazama* Spillmann 1931 [White-tailed deer])

O. virginianus Zimmermann 1780

†*Agalmaceros* Hoffstetter 1952

†*Rohnia* Castellanos 1957

†*Morenelaphus* Carette 1922 (?synonyms: †*Pampaeocervus* Carette 1922,

†*Habromeryx* Cabrera 1929)

Representatives of all listed genera have been recorded from the Pleistocene of South America. In addition, deer fragments from the Uquian or the Pliocene-Pleistocene boundary in Argentina have been identified with *Blastoceros* (= *Ozotoceros*), *Antifer*, and *Habromeryx* (Pascual et al, 1966, p. 21).

ODOCOILEINE ORIGINS AND RADIATION

It has been suggested by Matthew (1908; Flerov, 1952) that the Miocene *Blastomeryx* Cope 1877 from South Dakota, Wyoming, and Colorado is a primitive generic model from which New World deer can be derived. *Blastomeryx*, in turn, he declared, appeared to be derived from the Oligocene *Leptomeryx*. Judged by descriptions, skeletal parts of the known species of *Leptomeryx* are indeed comparatively primitive, and antlers are lacking. However, the large body size, comparable to that of the larger species of *Mazama*, and, above all, the lanian or

traguline-like upper canine remove *Blastomeryx* from the line leading to modern Odocoileinae, or, for that matter, to the Cervidae.

Whatever the ancestral stock, it is no less likely that the Odocoileinae originated in South America as in North America. The principal theater of radiation, however, almost certainly was South America. Pudus, tribe Pudini, with their mosaic of primitive, highly specialized and unique characters, appear to represent a very early offshoot of the ancestral stock. Brockets and branch-antlered deer represent a second offshoot, if not the main stem itself. They have retained most of the basic ancestral characters and their evolution has been directed, in the main, toward increasing body mass and social complexity.

Among the branch-antlered deer now living in South America, *Odocoileus* alone may have originated in Middle America, although its ancestral home may have been elsewhere. From Middle America, *Odocoileus* must have spread into South and boreal America with major radiation taking place in the latter. Circumpolar caribou or reindeer, genus *Rangifer*, are the northernmost odocoileines. They could have diverged from the same stock that gave rise to modern *Odocoileus*. The extinct Argentine *Morenelaphus* with caribou-type antlers may represent a third group, or, perhaps, a subgroup of the second.

CHEIRIDIA

The artiodactyl manus and pes evolved for support of the limbs on enlarged third and fourth ungual digits. The modification, doubtless beginning at a preancestral stage, involved loss of metapodial I and digit 1, disappearance of a discrete, carpal central bone, and, usually, the trapezium, reduction of digits 2 and 5 together with the corresponding metapodial bones, and elongation and coalescence of metapodials III and IV into a single, functional element—the cannon bone. Fusion of the middle metapodial bones progresses from midshaft toward both ends, with union of the distal portions lagging behind the proximal. A graded series of metapodials III and IV from separate to entirely fused, excepting the distal articular facets, can be formed with species of suborder Suina, followed by the tragulid *Hyemoschus* and selected forms of camelids, bovids, and cervids in the order named (fig. 4). Locomotorially, the front limb is specialized mainly for pulling, the hind limb mainly for pushing.

As already noted, in nearly all living Old World cervids, only the proximal ends of the disappearing lateral metacarpals persist (plesiometa carpalid, fig. 2). In all living cervids of New World origin, the distal ends persist (telemeta carpalid, fig. 2). The latter condition may be more primitive because the metacarpal vestiges occur at the digital or functional end. However, functional difference between the two limb types is not apparent. Carpal bones, on the other hand, remained fairly constant throughout the order Artiodactyla.

Individual forelimb and hind limb bones are serially homologous (table 1), but evolution of the homologues does not always proceed at the same rate or in the same direction. Metatarsi III and IV and corresponding digits do resemble their forelimb homologues. In contrast, metatarsi II and V have disappeared except sometimes for vestiges, particularly in pudus, without consistent orientation proximally or distally. The corresponding digits do not articulate with the rest of the skeleton, thus resembling the condition in plesiometa carpalid deer. The tarsal central or navicular bone, unlike the carpal central bone, is present and well developed. In Pecora and Tragulina, it is integrated with the cuboid to form

HIND LIMB

FIG. 4. A morphological gradient of artiodactyl hind feet showing reduction from four free metatarsal bones, as in *Sus* (Suina) and *Hyemoschus* (Tragulina), to a single bone by fusion of metatarsals III and IV and loss of II and V, as in *Mazama*, *Pudu*, and *Muntiacus*. Also, navicular, cuneiform (fused tarsals 2 and 3), and cuboid (fused tarsals 4 and 5) are separate in *Sus*, but completely fused in *Hyemoschus*, *Muntiacus*, and *Pudu*. In *Mazama* and remaining odocoileines, however, only navicular and cuboid bones are fused.

TABLE 1. Homologies of artiodactyl carpal and tarsal bones are shown horizontally. Names in columns marked "1" are used in comparative anatomy, those in columns marked "2" are the customary English names employed in this work. Names connected by a brace are of bones fused in all artiodactyls except as noted; those followed by a slash (/) are further fused with the next listed bone in suborders Tragulina and Pecora. Sesamoid bones, except the pisiform, are not named. Names and homologizations are adopted from Flower (1885, pp. 281-311; 339-360).

Carpalia		Tarsalia	
1	2	1	2
Radiale	=Scaphoid	Tibiale	} =Astragalus or Talus
Intermedium	=Lunar ¹	Intermedium	
Ulnare	=Triquetrum or cuneiform	Fibulare	=Calcaneum
Carpale 1	=Trapezium ²	Tarsale 1	=Internal cuneiform
Carpale 2/	=Trapezoid/	Tarsale 2	} =Middle cuneiform
Carpale 3	=Magnum	Tarsale 3	
Carpale 4 }	=Unciform	Tarsale 4 }	} =External cuneiform
Carpale 5 }		Tarsale 5 }	
Centrale	=Central ¹	Centrale	=Cuboid/
			=Cuboideonavicular ³
			=Navicular

¹Lunar and central fused in Artiodactyla. ²Presumed lost in Artiodactyla except in *Hippopotamus*. ³Cuneiform and cuboideonavicular bones always fused in Tragulina, giraffid *Okapia*, and cervids *Muntiacus* and *Pudu*; middle and external cuneiforms (tarsales 2, 3) are distinct in Suina.

the cuboideonavicular bone. External and middle cuneiform bones (cuneiforms 2 and 3) of the tarsus are fused, except in Suina, and the internal cuneiform is small but discrete in all artiodactyls. In *Pudu* and *Cervulus* (= *Muntiacus*), the cuboideonavicular bone is further united with outer and middle cuneiform bones into a single element, as in the chevrotains *Tragulus* and *Hyemoschus* (Tragulidae, Tragulina, Artiodactyla), and giraffids.¹

Fusion of cuboid, navicular, and outer and middle cuneiform bones into a single unit obviously evolved independently in the four disparate artiodactyl groups just cited. Functional difference between simplified and primitive artiodactyl tarsi is questionable, particularly in *Giraffa*, where both types may occur in the same animal. Seemingly, the tragulid and pecorid tarsus operates as a unit irrespective of articular relationships between its components.

Tarsal similarities among the four groups in question do not imply metatarsal similarities. Limb proportions differ widely among them. The tragulid metatarsus is most primitive in retention of complete, albeit slender and elongate, metatarsal bones II and V; whereas the same bones are absent in giraffids, muntjacs, and deer, except pudus and possibly a few other species in which they may persist as vestiges. Furthermore, pudu metapodials, as represented by the cannon bone (III + IV), are relatively shorter and broader than those of other artiodactyls, and thus nearer the primitive condition still exhibited by living members of the suborder Suina.

LIMB PROPORTIONS

Forelimb length, based on combined length of humerus, radius, and metacarpus (H + R + MC, table 2) in pudus and the great majority of quadrupedal

¹Consistently in *Okapia* (FMNH 26066, 104733, 108987) and variably in *Giraffa* (fused in both tarsi of FMNH 34930, fused in left, separate in right of FMNH 34424); all zoo animals.

TABLE 2. Artiodactyl limb proportions: Cervidae (Odocoileinae: *Pudu*, *Mazama*, *Odocoileus*, *Blastoceros*; Cervinae: *Capreolus*; Cervulinae: *Cervulus* [Muntiacini]); Bovidae (*Oreotragus*, *Strepsiceros*, *Gazella*, *Bison*); Tragulidae (*Hyemoschus*).

[illegible]

* All figures are proportions of greatest length of limb bones compared. F = femur, H = humerus, MC = united metacarpal bones III + IV, MT = united metatarsal bones III + IV, R = radius, T = tibia, TL = combined length of thoracic and lumbar vertebrae. See "Measurements" (pp. 52, 68) for additional information.

mammals, is less than hind limb length, based on combined length of femur, tibia, and metatarsus ($F + T + MT$). As shown in Table 2, length of forelimb ($H + R + MC$) to trunk length (TL), based on combined length of articulated thoracic and lumbar vertebrae, ranges from about 73% (*Pudu*) to about 104% (*Mazama*) in adult artiodactyls sampled. The average length of hind limb to trunk (TL) ranges from about 89% (*Bison*, followed by about 105% in *Pudu* and *Oreotragus*) to about 139% (*Mazama gouazoubira*). Individual variation is considerable, and present ratios based on the sum of straight-line lengths of long limb bones are greater than—but probably directly proportional to—standing shoulder and rump heights in which limb bones articulate at angles.

The cervid humerus is usually the longest thoracic limb bone. In pudus, it is relatively longer than in all other cervids and bovids measured. The humerus, however, contributes least to standing shoulder height. The cervid radius may be nearly as long as the humerus, sometimes slightly longer. The metacarpus is the shortest of the long thoracic limb bones, but nearly all its length enters into standing shoulder height. In most Bovidae, the radius is the longest forelimb bone, but in others, notably gazelles, the metacarpus is longest. In both cervid and bovid hind limbs, the tibia is usually the longest bone, the metatarsus being shortest of the three long bones. As in the forelimb, almost the entire length of the metatarsus enters into total standing rump height.

Metapodials of pudus are not only relatively shortest among cervids, but also broadest. Ratio of metapodial width to length of the small Andean brockets, *Mazama rufina* and *M. chunyi*, appears to be nearly the same when greatest width is measured across the distal epiphysis. However, metapodial shafts of all brockets, particularly those of the metacarpus, are relatively narrower than those of pudus.

II. GENUS *Pudu* GRAY

SYNONYMIC HISTORY

- Pudu* Gray, 1850, Gleanings Knowlsely Menagerie, p. 69—subgenus of *Coassus* Gray. Gray, 1852, Proc. Zool. Soc. London, 1850: 242—subgenus of *Coassus* Gray. Gray, 1852, Cat. Mamm. Brit. Mus., Ungulata, p. 240—genus. Sclater, 1870, Proc. Zool. Soc. London, 1870: 116—classification. Lydekker, 1915, Cat. Ungulate Mammals Brit. Mus., 4: 214—characters. Knottnerus-Meyer, 1907, Arch. Naturg., (73) 1: 15, 16, 97, 108—cranial characters. Carrette, 1922, Rev. Mus. La Plata, 26: 412, 420, 422, 425, 428, 445—history; characters; classification. Pocock, 1923, Proc. Zool. Soc. London, 1923: 181, 207—characters; classification (genus of subfamily Pudinae). Kraglievich, 1932, Anal. Mus. Hist. Nat., Montevideo, (3) 2: 265—characters; phylogeny. Pocock, 1932, Proc. Zool. Soc. London, 1932: 395—antlers; comparisons. Flerov, 1952, Fauna U.S.S.R., n.s. no. 56, Mammals, 1, (2): 218—description. Hershkovitz, 1958, Fieldiana, Zool., 36(6): 619—distribution; *Pudella* a synonym. Cabrera, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia," 4(2): 343—subgenus of *Pudu* Gray; included species: *P. pudu* Molina. Haltenorth, 1963, Handb. Zool., 8(32): 4, 9, 42, 47, 48—subgenus of *Mazama*; characters; classification; *Pudella* Thomas a synonym. Hershkovitz, 1972, in Keast, Erk, and Glass (eds.), *Evolution, mammals and southern continents*, State U. of New York Press (Albany), pp. 362, 371, 392—history, distribution, ecology, adaptation. Whitehead, 1972, *Deer of the world*, Viking Press, New York, pp. 64, 112, 169—species, *P. pudu*, *P. mephistophiles*; classification.
- Pudua* Garrod, 1877, Proc. Zool. Soc. London, 1877: 18—emendation of *Pudu* Gray; species, *Pudua humilis* Bennett. Brooke, 1878, Proc. Zool. Soc. London, 1878: 926—characters. De Winton, 1896, Proc. Zool. Soc. London, 1896: 508—characters. Lydekker, 1898, *Deer of all lands*, p. 307—characters.

- Pudella* Thomas, 1913, Ann. and Mag. Nat. Hist., (8)11: 588—type, *Pudua mephistophiles* de Winton. Lydekker, 1915, Cat. Ungulate Mammals Brit. Mus., 4: 217—subgenus of *Pudu* Molina. Pocock, 1923, Proc. Zool. Soc. London, 1923: 207—genus of subfamily Pudinae. Cabrera, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia," 4(2): 344—subgenus of *Pudu* Molina. Brokx, 1972, J. Mammal., 53(2): 260—may be *Mazama*. *Mazama*, Flerov (part, not Rafinesque), 1952—Fauna U.S.S.R., n.s. no. 56, Mammals, 1, (2): 218—part, *M. mephistopheles* [sic] de Winton only. Haltenorth, 1963, Handb. Zool., 8(32): 47, 48—part, *Pudu* Gray, a subgenus.
- Mezama* [sic] Cabrera, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia," 4(2): 344—misprint for *Mazama* in synonymy of subgenus *Pudu*.
- Coessus* [sic], Cabrera, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia," 4(2): 344—misprint for *Coassus* in synonymy of subgenus *Pudu*.

Type species.—*Coassus pudu* [= *Capra puda* Molina], by virtual tautonymy.

Included species.—*Pudu mephistophiles* de Winton, *P. puda* Molina.

Distribution (fig. 1).—Temperate zone forests and fringing grasslands of southern Colombia, Ecuador, north central Peru, southern Chile, and adjoining parts of Argentina. Altitudinal range from sea level to about 1,000 m above in Chile and Argentina, and between 2,000 and 4,000 m in Colombia, Ecuador, and Peru.

CONSERVATION

A program for the study and management of deer threatened with extinction throughout the world was launched by the International Union for Conservation of Nature and Natural Resources (IUCN). The first of three reports presented by Cowan & Holloway (1973; 1974; 1975) lists 25 threatened forms, including the South American pampas deer (*Blastoceros bezoarticus*), marsh deer (*Blastocerus dichotomus*), and the northern and southern huemuls (*Hippocamelus antisensis* and *H. bisulcus*). Certainly, the objectives and rationale of this conservation program apply no less to pudus than to any other deer species threatened with extinction.

The geographic distribution of pudus given here (figs. 1, 30, 35), based on museum specimens and published records, does not reflect the present status of the animal in nature. In the years intervening since 1782, when the first pudu was made known to science, there has been enormous shrinkage in the peripheral and internal ranges of the genus. Hunting by man is a much greater menace to the survival of pudus than is habitat destruction. Pudus readily adapt as individuals to the marginal and even seemingly improbable habitats to which they are being driven. It is unlikely, however, that the species can remain viable for long under such circumstances. Present conservation measures, based on establishment of national parks and nature reserves, are inadequate, because in virtually all cases, the legally protected animals are defended by nothing more potent than the mere letter of the law.

As yet, Peru has no national park or nature reserve where pudus are definitely known to exist. Colombia has three parks that certainly harbor the northern pudu and three that probably do. Ecuador has one. Chile has four or five parks, and possibly more, where the southern pudu still may occur. Argentina can boast of at least three national parks where the southern pudu may still be found, if only as a vanishing species, unless a successful program for breeding the animal in semicaptivity is put into effect immediately.

Information regarding past and recent status of each of the two kinds of pudus in the wild is included under various headings in the species accounts.

TAXONOMY

The name *Pudu* was proposed to contain *Capra puda* Molina (*Cervus humilis* Bennett, a synonym) by Gray (1850; 1852a [1850], p. 242), as a subgenus of *Coassus* Gray 1843 [= *Mazama Rafinesque* 1817]. Soon after, Gray (1852b, pp. x, 240) raised *Pudu* to full generic rank. Characterization of the genus, however, was never adequate until Brooke (1874, p. 36; 1878, p. 926) pointed to the fused cuboideonavicular and outer and middle cuneiform bones of the tarsus.

Pudua, introduced by Garrod (1877, p. 18), is merely an invalid emendation or Latinization of the original barbaric name.

Pudella, erected by Thomas (1913, p. 588) for generic distinction of *Pudu mephistophiles* de Winton from *P. puda* Molina, was predicated on absence of preorbital glands, shallow lacrimal bone, contact between premaxillary and nasal bones, crown length of first incisor three to four times that of i_2 , narrower, more pointed hoofs, and rhinarium larger and projecting back in midline. Some of the foregoing characters are equivocal, and the others are usually evaluated as of specific grade in related genera. For example, in *P. mephistophiles*, the preorbital glands with facial opening are present, not absent as claimed, but are little developed, the lacrimal fossa shallow. In *P. puda*, the glands are large, the external opening conspicuous, the lacrimal fossa correspondingly deep. These characters parallel those distinguishing most brockets from *Mazama rufina*, or *Odocoileus virginianus* from *O. hemionus*. The premaxilla does indeed contact the nasals in *P. mephistophiles*, but may or may not in *P. puda*. Middle lower incisors are not significantly different between these species; hoofs are nearly as long and narrow, but average deeper in *P. puda*, and therefore appear to be more blunt.

Lydekker (1915, p. 217), citing only the facial glands, lacrimal bones, and lower middle incisor crown length as diagnostic characters, reduced *Pudella* to subgeneric rank. Pocock (1923, p. 207), however, regarded *Pudella* and *Pudu* as distinct genera of his subfamily Pudinae. Flerov (1952, p. 200) referred only to the *Mazama* skull mismatched with the type skin of *Pudu mephistophiles* for sinking *Pudella* in the synonymy of *Mazama*. Evidently, he overlooked the fact that *P. mephistophiles* was typified by the skin only with associated leg bones, and *Pudella* was based on the holotype skin plus two topotype skins and skulls of *P. mephistophiles*. In any event, *Pudu* and *Mazama*, with *P. mephistophiles* included, were recognized as distinct genera, but other South American genera are listed by Flerov as subgenera of *Odocoileus*. Haltenorth (1963, p. 48) compromised by relegating *Pudella* to the synonymy of *Pudu* and reducing the latter to a subgenus of *Mazama*. Otherwise, his arrangement of remaining groups of South American deer agrees with that of Flerov.

GENERIC CHARACTERS

External.—Smallest of Cervidae (figs. 5, 6), legs short, body low slung, rump little or not raised above withers, ears more or less rounded; combined head and body length less than 85 cm; height at shoulder less than 50 cm; tail obsolescent, less than 8% of combined head and body length and concealed in rump; weight less than 15 kg. General body color dominantly agouti with crown and extremities more or less saturate and contrasting with trunk; ears without white edging; lateral narial area and chin rufous to blackish, never marked with white,

FIG. 5. Size relationship and body form of six South American deer, from smallest (*Pudu*) to largest (*Blastocerus*); the numbers refer to approximate average shoulder height (cm).

FIG. 6. Body form of four South American deer, not to scale; compare dorsal contour, rump height, limb proportions, neck, muzzle, ears. From top, left to right, northern pudu (photograph by F. Kleinschmidt, courtesy Berlin zoo); southern pudu (photograph by H. Frädriich, courtesy Berlin zoo); northern huemul (photograph courtesy Berlin zoo); red brocket (photograph courtesy San Diego zoo).

the pale, lateral rostral band absent (figs. 7, 8); buttocks without sharply contrasting patch or band. Pelage of back harsh, basal portions of hairs pithy and brittle; hairs of crown whorled; paired frontal tufts present and unspotted in females; nuchal hairs always directed back. Frontal glands not evident in females; external opening of preorbital (lacrimal) gland small or large (figs. 8, 9); forefoot and hind foot pedal glands contained in shallow interdigital trough or small pouch (fig. 10); specialized tarsal and metatarsal tufts weakly developed or absent, corresponding glands not defined in dry skin. Fore and hind hoofs slender, length twice or more greatest width; fore and hind dew claws longer than wide; soles between outer and middle digits thickly clothed with hair (fig. 10).

Cranial (figs. 11–17).—Rostrum short, the diastema shorter than alveolar length of upper cheek teeth (pm^2-m^3); length of nasals less than length of frontals at midline; superior border of orbit depressed below frontal suture at same plane; greatest supraorbital breadth of frontals less than width of brain case; upper portion of supraoccipital moderately inflated, its median protuberance

FIG. 7. Facial color pattern of *Odocoileinae*, a composite of all species.

a. nares patch	j. posterior auricular border
b. dark lateral rostral band	k. inner auricular surface
c. pale lateral rostral band	l. outer auricular surface
d. rostral band	m. mental patch
e. inferior orbital band	n. mandibular band
f. superior orbital band or
superciliary band	o. buccal patch
g. anterobasal auricular patch	p. gular patch
h. posterobasal auricular patch	q. opening of preorbital pouch
i. anterior auricular border	r. frontal spot or tuft (marks
frontal gland in female)

projecting beyond lambdoidal crest in lateral view; ascending ramus of pre-maxillary extending to, or widely separated from, lateral border of nasals; malar articulating with one-half or less inferior suture of facial plate of lacrimal and hardly or not at all entering into composition of inferior surface of lacrimal fossa; transverse diameter of orbit greater than inferior margin of facial plate of lacrimal; auditory bullae little or not inflated.

Pudu mephistophiles *Pudu puda* *Mazama chunyi* *Mazama rufina*

FIG. 8. Stylized heads of smallest South American deer showing individual color pattern, ear form, preorbital pouch opening, and dorsal outline of rhinarium.

Dental (figs. 18–23).—Greatest mesiodistal crown length of permanent i_1 equal to or less than combined crown length of permanent i_{2-3} (fig. 22), all permanent incisors not in place before eruption of last molar; lower deciduous front teeth like replacements, but di_1 relatively broader, di_{2-3} and dc narrower, more pointed, the entire series of front teeth approaching those of adult *Mazama* (fig. 22); deciduous upper canine usually present in *Pudu mephistophiles*, never persistent, but often succeeded by the permanent canine; dc absent in *P. puda* or, if present, shed after eruption of m^1 and rarely, if ever, replaced (figs. 11, 13, 14, 16).

FIG. 9. Heads of five South American deer; compare facial markings, muzzle length, preorbital gland, ear shape; antlers of *P. mephistophiles* partially rubbed, of *M. rufina* and *H. antisensis* in velvet. (Photograph of *Pudu puda* courtesy Cologne zoo; remaining photographs courtesy Berlin zoo.)

FIG. 10. Front and hind feet (left lateral and ventral surface) of pudus, brocket, and Virginia deer. Pouch of interdigital gland is indicated by dashed line.

On the basis of upper molars of a specimen of *Mazama americana* ("M. tema") and one of *Odocoileus virginianus*, Frechkop (1965) concluded that all *Odocoileinae* (his *Capreolinae*) were characterized by a short crista or crochet, springing from the inner distal enamel border of the hypocone, labeled "x" in his illustrations (Frechkop, 1965, p. 4, figs. 1, 2, 3). In a spot check of Field Museum specimens, this crista (fig. 23, XI) appears to be absent or incipient in *Pudu mephistophiles* and *Blastoceros bezoarticus*, and rudimentary to moderately developed in unworn molars of *P. puda*, usually present in *Mazama americana* and *M. rufina*, present or absent in *Mazama gouazoubira*, *Blastoceros dichotomus*, *Odocoileus hemionus*, and *O. virginianus*. In two specimens at hand of *Mazama chunyi*, the character is present in m^{1-2} of the type, a juvenile with unerupted m^3 , and undeterminable in the considerably worn molars of an old female (fig. 18).

Crest XI size is variable in all species. Where it appears to be absent in moderately worn teeth of a given species, it may be found in one or more unerupted molars, mainly m^1 , of some individuals of the same species. In some cases, a crest equivalent to crista XI springs from the medial border (V) of the hypocone. The comprehensive account of cervid dental morphology is reserved for a future article of this series.

Dental succession.—Sequence of eruption of permanent teeth determined from inadequate material in the Field Museum and extrapolations therefrom, is:

$m1-m2-m3-pm4-pm3-pm2-c$ (*P. mephistophiles*)

$m1-m2-(i1 \text{ or } m3)-pm4-pm3-pm2-i2, (i3-c)$.

Antlers.—Spike-like, usually less than 10 cm measured from burr and directed straight back in line with dorsal plane of frontal bone. Pedicles develop during eruption of m^2 , burr and antlers form during eruption of m^3 , well-developed antlers present in all 17 males examined with complete dentition.

Antler casting is not evident in present material. Published and secondary data indicate, however, that new antlers grow during spring to early summer, mature during summer to early fall, drop in winter. Antler cycle of southern hemisphere pudus acclimatized in northern hemisphere zoos adjusts to northern seasons.

Vertebral formula.—Seven cervicals, 12–13 thoracic, 6–7 lumbar, 4–5 sacral, 8 caudal; total, 38–39 vertebrae. Generally, form and relative size are the same as those of other cervids.

Limb bones and proportions (fig. 24, table 2).—Metapodials extremely short and broad; cuboid, navicular and external and middle cuneiform bones fused into a single tarsal element; length of metacarpal splints II and V from approximately one-half to two-thirds length of metacarpals III and IV; central portions of metatarsal bones II and V frequently persistent as splints, each ankylosed to the adjacent metatarsal bone.

Male genitalia.—In reference to *Pudu puda*, Brambell & Mathews (1977, p. 27) note, "The testes are subcutaneous, but not scrotal. The penis is not long but lies on the abdominal wall." Presumably, the same condition obtains in *P. mephistophiles*.

GENERIC COMPARISONS

Pudus, like other strictly New World deer, are characterized by retention of the distal portion of the obsolescent metacarpals II and V (telemetacarpalid) and

by division of the posterior nares into two chambers by the vertical plate of the vomer (figs. 2, 3, 24). In exclusively Old World Cervinae, vestiges of the lateral metacarpals are proximal (plesiometacarpalid) and the posterior nares are undivided.²

Pudus are most readily distinguished from all other deer by their small size (fig. 5). Only the dwarf brocket, *Mazama chunyi* Hershkovitz, is similarly small. Pudus are further distinguished from other cervids by the low-slung body without highly raised rump; short, thick legs, comparatively small, more or less rounded ears, small eyes, thick rhinarium with rounded nostrils, muzzle without white narial and mental patches or spots (figs. 6, 8, 9), tail completely hidden by rump hairs; mandibular symphysis usually more angular in horizontal plane than in related deer, alignment of incisors and canines of each side more nearly oblique than transverse. Caudal vertebrae number only 8 in *Pudu*, 11 in *Mazama*, and 10 or more in other cervids. The shallow interdigital depression or pocket containing the pedal glands in *Pudu* is primitive compared with the well-developed interdigital pouch of the hind feet, at least, of other New World deer (fig. 10).

The key osteological character separating *Pudu* from other true deer, i.e., Cervinae and Odocoileinae, is the consistent union of the cuboideonavicular and external and middle cuneiform tarsal bones into a single bone (figs. 2, 4, 24). Other living cervids with similarly fused tarsal bones are the Asiatic plesiometacarpalid tufted deer (*Elaphodus*) and muntjac (*Cervulus* Blainville, the valid name currently replaced by the erstwhile nomen nudum *Muntiacus* Rafinesque [Int. Comm. Zool. Nomencl. 1957, Opinion 460]). It is a curious coincidence, as shown by Pocock (1911, p. 952, figs. 134b-c), that the interdigital integumentary folds containing fore and hind pedal glands are about as simple in muntjacs and tufted deer as in pudus. The extremely short, broad metapodials of *Pudu*, with metacarpals proportionately wider than metatarsals, are a bovine-like character unmatched in other cervids (table 2).

Dental peculiarities are absent in *Pudu* (figs. 18-23). The form of their lower incisors accords with the less specialized deer type characterized by the rectangular or moderately spatulate crown of i_1 . The more specialized crown of i_1 in *Mazama* and a number of other New and Old World deer is broadly spatulate or cuneate. In the deciduous teeth of most pudus, however, a comparatively expanded crown of i_1 , and attenuate i_{2-3} , c_1 adumbrate the more specialized front teeth of brockets (figs. 20, 22). The upper canine persists in many adult *P. mephistophiles*, whereas only the deciduous upper canine appears occasionally in immature *P. puda*.

FAUNAL SPOTTING PATTERN

The juvenal coat of *Pudu puda* is spotted, whereas that of *P. mephistophiles* is not. Inasmuch as adult *P. mephistophiles* is more primitive than *P. puda* in every respect, including coat color, it is logical to infer that the unspotted juvenal coat

²Among circumboreal cervids, the American moose or Palearctic elk (*Alces*) and caribou or reindeer (*Rangifer*) are telemetacarpalid, with the nares undivided in *Alces* and divided in *Rangifer*. The wapiti or deer (*Cervus*) is plesiometacarpalid, the nares undivided. Old World roebuck (*Capreolus*), Chinese water deer (*Hydropotes*), and musk deer (*Moschus*) also are telemetacarpalid.

color is also more primitive. Fawns of the Andean taruga, *Hippocamelus antisensis*, and the marsh deer, *Blastocerus dichotomus*, are also unspotted. Those of remaining neotropical deer are spotted (cf., figs. 25–27). Judged on its own merits, an unspotted, unmarked, or unpatterned coat characterized by agouti pelage is most primitive. Conversely, any coat color pattern that departs from the primitive agouti as a result of pigmentary dilution or loss is derived. In the case of white or whitish fawnal spotting, the pigmentary loss appears in the fetal pelage or lanugo. The juvenal character adumbrates the adult spotting that appears on some axis deer (*Axis*), fallow deer (*Dama*), and some Sika deer (*Cervus*). In these forms, the overall trend is toward paler coloration approaching albinism.

The whitish spotting pattern similar to that of fawns, or a more advanced whitish spot and stripe, or entirely striped pattern appears in many mammalian lines. This characterizes the juvenal coat of swine and tapirs, and the adult coat of many rodents, e.g., ground squirrels (*Spermophilus*), paca (*Agouti*), and the white stripe pattern of zebras. A blackish spotting coat pattern, noted in most felids and many other groups, is also common, whether in the juvenal or adult stages, or both. In these, however, the blackish spots may be reminders of a more primitive blackish coat. On the other hand, whitish spotting, which entails loss of melanin, is derived.

ANCESTRAL CHARACTERS AND RELATIONSHIPS

Pudus sometimes are referred to as dwarf or pygmy deer, and it has been suggested (von Lehmann, 1960, p. 50) that these and all other spike-antlered deer are literally dwarfed. The ancestral pudu is unknown and it cannot be ascertained whether it was larger or smaller than its descendants. Nevertheless, of the two living kinds, the smaller *Pudu mephistophiles* is evidently more primitive than the larger *P. puda*. Brockets, genus *Mazama*, are also small, ranging in size from *Mazama chunyi*, which is equal to the larger species of *Pudu*, and *M. americana*, which grades into the smaller forms of the otherwise much larger, white-tailed deer, *Odocoileus virginianus*. Thus, it can be asserted that the overall trend is toward greater body size and increasing antler size and complication. No doubt, dwarfed populations and races of deer develop from time to time, but probably most, if not all, are ecological rather than genetic demes or races.

Small size and rudimentary antlers restricted to the male are primitive deer characters. Also, the smaller the deer, the smaller and more simple its antlers, irrespective of the age of the individual or grade of specialization of any or all other of its parts. Conversely, the larger the individual, the larger the antlers tend to grow, and the larger the race or species within a given phyletic line, the more complex the antlers tend to become. Thus, the extremely small body and simple antlers of *Pudu*, although primitive, do not in themselves imply an ancestral condition or denote a close relationship to the small-bodied, spike-antlered *Mazama*.

The affinities of *Pudu*, morphologically as well as historically, are with other neotropical cervids. However, the comparatively short muzzle, obsolescent tail, fused cuboideonavicular and external and middle cuneiform bones, and short, broad metapodials remove *Pudu* from all other deer and from consideration as an ancestral model. At the same time, primitive cervid characters of *Pudu mephistophiles* from which those of *Mazama* and other New World deer can be derived

include the relatively large and well-developed lateral metacarpals, vertically inclined antorbital vacuity, shape of lower incisors, the more than sporadic persistence of upper canines, the comparatively simple interdigital tegumentary fold for containment of pedal glands, absence of specialized tarsal and metatarsal tufts and glands, comparatively short, rounded ears and small eyes, slightly raised rump, dominantly agouti pelage, and unspotted fawn.

The remote, possibly Miocene-Pliocene, nearest common ancestor postulated here must have been sylvan, smaller than living pudus, body low slung, rump unraised, antlers simple or rudimentary and directed back parallel to the frontal plane. The tail must have been comparatively well developed, middle digits, including hoofs, long and mobile, facial or lacrimal glands small but not rudimentary, tarsal, metatarsal, and frontal glands and tufts rudimentary or absent, ears small, rounded, nuchal hairs directed back, coronal crests or whorls absent, adult pelage coarse but not pithy, general coloration agouti without special markings, fawn unspotted, metapodials broad, lateral metacarpals nearly or virtually complete, the corresponding digits or dew claws well developed, cuboideonavicular and cuneiform bones discrete, premaxillary and nasal bones in contact, antorbital vacuity small, its long axis vertical, crowns of lower incisors more nearly square than spatulate, upper canines small and persistent, vertebral formula 7C, 13T, 7L, 5S, 11C. More characters can be added, but with those mentioned, the others fall into place.

ORIGIN, DISPERSAL, SPECIATION

The origin of *Pudu* in terms of time and place is unknown. The ancestral stock of the genus, and the Odocoileinae in general, is likewise unknown. As noted earlier (p. 8), the Palaeomerycinae, including *Blastomeryx*, the imputed ancestral root, is a specialized traguline-like or moschine-like group that disappeared without known issue in the New World. In any event, it seems likely that *Pudu* and *Mazama* represent divergent lines of the tiny ancestral odocoileine, which must have lived during the early Pliocene or late Miocene in boreal America, Middle America, or South America. The genus *Pudu* itself must be regarded as South American, likely since Pliocene. The distribution and interrelationship of its two living species are clear, and their evolutionary history can be reconstructed from available morphologic and geographic data as well as from what is known of Pleistocene climates (Van der Hammen, 1974).

It is believed that the immediate ancestor of modern pudus differed little from *Pudu mephistophiles*. During what possibly was a last glacial period, the former must have occupied the temperate zone forest fringe at the eastern base of the Cordillera Oriental, in what now is Colombia, Ecuador, Peru, and, perhaps, northern Bolivia. When the Andean glaciers retreated, the temperate zone forest with its fauna followed in its wake. In the case of the pudu, some populations moved into higher altitudes at the same latitudes, clinging to the forest fringes forming on the shores of large rivers, such as the Putumayo, Pastaza, Huallaga, and Ucayali. Other populations moved southward along the base of the eastern Andes into higher latitudes as far as the Strait of Magellan and westward through forested passes into Chile. Evidently, no relic pudu populations persisted where the climate of the original temperate lowland habitat became tropical or subtropical (fig. 1).

Complete geographic isolation of northern and southern pudus is reflected in

FIG. 11. Adult female pudu and brocket skulls, left side.

FIG. 12. Adult female pudu and brocket skulls, dorsal surface.

FIG. 13. Adult female pudu and brocket skulls, palatal surface.

FIG. 14. Adult male pudu and brocket skulls, left side.

FIG. 15. Adult male pudu and brocket skulls, dorsal surface.

FIG. 16. Adult male pudu and brocket skulls, palatal surface; inset, enlargement of premolars 2-4 with deciduous-like pm^3 .

FIG. 17. Mandibles of pudus and brockets, lateral surface of left rami.

FIG. 18. Upper cheek teeth (pm^2-m^3) of adult pudus and brockets, and dpm^{2-4} , m^{1-2} of juvenal *Mazama chunyi* (type, AMNH).

FIG. 19. Lower cheek teeth (pm_2 - m_3) of adult pudus and brockets, and dpm_2 - 4 , m_1 - 2 of juvenal *Mazama chunyi* (type).

FIG. 20. Lower front teeth (i_{1-3} , c) of pudus and brockets, labial surface; left i_1 erupting in *Pudu puda* (FMNH 49934).

FIG. 21. Lower front teeth (i_{1-3} , c), lingual surface, of same specimens shown in Figure 20.

FIG. 22. Permanent and deciduous incisor-canine series (i₁₋₃, c) in pudus and brockets; *Mazama chunyi* juv. 73098, type, AMNH.

FIG. 23. Upper right and lower left second and third molars of *Pudu*, the top m^3 unerupted of type, AMNH 73098. For explanation of symbols, see facing page; system of symbols and homologies based on Hershkovitz (1977, pp. 298-301).

EXPLANATION OF SYMBOLS USED IN FIGURE 23.

1	eocone (paracone)	1	eoconid (protoconid)
2	protocone	2	metaconid
		3	[paraconid, absent]
4	metacone	4	hypoconid
5	hypocone	5	entoconid
<i>a</i>	mesostyle (parastyle)	<i>a</i>	mesiostylid (parastylid)
<i>b</i>	distostyle (metastyle)	<i>b</i>	distostylid (hypoconulid)
<i>d</i>	plagioconule (metaconule)	<i>d</i>	plagioconulid
<i>e</i>	postentoconule	<i>e</i>	postentoconulid
		<i>h</i>	entostylid- <i>h</i>
<i>j</i>	ectostyle- <i>j</i> (stylocone)	<i>k</i>	ectostylid- <i>k</i> *
<i>k</i>	ectostyle- <i>k</i>	<i>l</i>	ectostylid- <i>l</i> (mesostylid)
<i>l</i>	ectostyle- <i>l</i> (mesostyle)	<i>m</i>	ectostylid- <i>m</i>
<i>m</i>	ectostyle- <i>m</i>	<i>l</i>	ecocristid
<i>l</i>	ecocrista	<i>ll</i>	epicristid
<i>ll</i>	epicrista (crest labeled "++" by Frechkop, 1965, figs. 1,2)	<i>III</i>	protolophid
<i>III</i>	protoloph (protocrista)	<i>IV</i>	plagiocristid
<i>IV</i>	plagiocrista (metoloph)		
	IV' medial		
	IV'' median		
<i>V</i>	entocrista	<i>VI</i>	distocristid
<i>VI</i>	distocrista (from postero- lingual cingulum C)	<i>VIII</i>	postentocristid
<i>XI</i>	crista-XI (individually variable in cervids)		
<i>XII</i>	crista-XII (individually variable in cervids; charac- teristic of notoungulates)	<i>ε</i>	"trigonid" basin or fossa
<i>ε</i>	pretrigon basin or fossa	<i>α</i>	talonid basin or fossa
<i>α</i>	trigon basin or fossa	<i>β</i>	talonid basin or fossid
<i>β</i>	talon basin or fossa		δ posttalonid basin or fossid
		<i>en</i>	entoflexus
		<i>ex</i>	ectoflexus
		<i>nex</i>	neoectoflexus

* Present in lower first molars only of individual figured.

FRONT LIMB

Pudumephistophiles

86846

Pudupuda

24363

HIND LIMB

FIG. 24. Left forefeet and hind feet of pudus with vestiges of metacarpal bones II and V distal in position (telemetacarpalia). Digits are missing in *Pudumephistophiles*.

FIG. 25. One-week-old southern pudu fawn (photograph by H. Frädriich, courtesy Berlin zoo).

FIG. 26. One-week-old gray brocket fawn (photograph by J. Frädriich, courtesy Berlin zoo).

FIG. 27. Red brocket doe with fawn (photograph courtesy Gladys Porter Zoo, Brownsville, Texas).

the wide morphologic differences between them. The southern species, with its much greater distance from the hypothetical ancestral home, departs most from the postulated ancestral form. *Hippocamelus*, with its two species, the northern *H. antisensis* and the southern *H. bisulcus*, appears to have had a parallel history of dispersal and speciation.

Most populations of the northern *P. mephistophiles* are still confined to the heads of the same Amazonian streams that defined their presumed habitats lower down. A few have spread across divides into watersheds draining into the Caribbean or Pacific Oceans. Apparent absence of significant differences between extant populations of northern Colombia, Ecuador, and Peru suggests that gene flow has been maintained between them throughout the major climatic event that shifted without notably altering the pudu habitat. Alternatively, the habitat shift was accomplished so swiftly or recently, with the actual linear distances covered so short, that no significant differentiation occurred in any population, geographically isolated as it may appear to be now or may have been then.

III. THE SPECIES OF PUDUS, GENUS *Pudu* GRAY

KEY TO THE SPECIES

- Size smaller; face, outer surface of ears, chin, forefeet and hind feet dark brown or blackish; preorbital gland small, external opening inconspicuous; lacrimal fossa shallow or dish-shaped; long axis of antorbital vacuity nearly or quite vertical; fawns unspotted; (Colombia, Ecuador, Peru) *Pudu mephistophiles* (figs. 5, 6, 8, 9, 28, 29; p. 44).
- Size larger; face reddish buffy or brown; ears, narial patch, chin, forefeet and hind feet reddish; preorbital gland large, external opening large, conspicuous; lacrimal fossa deep or bowl-shaped; long axis of antorbital vacuity diagonal to nearly horizontal to basal plane of skull; fawns spotted; (Chile, Argentina)
Pudu puda (figs. 5, 6, 8, 9, 36, 37; p. 60).

Pudu mephistophiles

FIG. 28. Northern pudus, adult male and female (photograph by H. Frädriich, courtesy Berlin zoo).

Pudu mephistophiles

FIG. 29. Northern pudu, adult female, same individual shown in Figure 28. Note frontal tuft (photograph by H. Frädriich, courtesy Berlin zoo).

IV. *Pudu mephistophiles* de WINTON

NORTHERN PUDU (figs. 28, 29)

SYNONYMIC HISTORY

- Pudua mephistophiles* de Winton, 1896, Proc. Zool. Soc. London, 1896(2): 508, pl. 19 (animal)—part, not skulls shown in figs. 2, 4 [= *Mazama*]. Lydekker, 1898, *Deer of all lands*. Rowland Ward, London, p. 308, pl. 24, fig. 1 (animal)—characters. Lydekker, 1901, *Great and small game of Europe, western Asia and America*. Rowland Ward, London, p. 374—characters.
- [*Pudella*] *mephistophiles*, Thomas, 1913, Ann. Mag. Nat. Hist., ser. 8, 11: 588—classification.
- Pudu* (*Pudella*) *mephistophiles*, Lydekker, 1915, Cat. Ungulate Mammals Brit. Mus., 4: 217; ECUADOR: *Pichincha* (Páramo de Papallacta); characters; type history. G. M. Allen, 1942, *Extinct and vanishing mammals of the western hemisphere*, p. 412—ECUADOR; characters; type history; endangered species. Avila Pires, 1974, Publ. Biol. Inst. Invest. Cient., U.A.N.L., México, 1:161—distribution; conservation.
- P[udu]. mephistophiles*, Hoffstetter, 1952, Mem. Soc. Geol. France, 31(66): 369—ECUADOR: *Mazama fusca* Spillmann, a synonym.
- Pudu mephistophiles*, Hershkovitz, 1958, Mammalia, 22(4): 545—metatarsal glands and tufts not defined. Hershkovitz, 1959, Proc. Biol. Soc. Washington, 72: 48–49, pls. 3C, 4D (skull), pl. 5B (front teeth)—comparisons. Cabrera, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia," 4(2): 344—distribution; *P. m. wetmorei* Lehmann, a synonym. Crandall, 1964, *Management of wild animals in captivity*. U. of Chicago Press, pp. 557, 560, 594–5—characters; no record of captivity. Grimwood, 1969, Spec. Publ. no. 21, American Comm. Int. Wild Life Protection and New York Zool. Soc., p. 78 (map), 79—PERU: *Huánuco* (Pamachucho [sic]; Carpathian summit on Huánuco-Tingo María road; upper Río Hualлага valley, above Huánuco; near Chaglla; Yanacocha, Río Quero, 25 km NW Huánuco; between Huánuco and Ambo, 2700–3300 m; Quivilla road, 40 km from Huánuco); *Junin* (above San Ramón, 200–300 m; Río Huasahuasi valley; upper Río Paucartambo, 10°50' S, 70°00' W); conservation; local names *sacha cabra*, *antagallo*. Dansie and Winice, 1971, *Deer of the world*. Hitchings and Mason, Ltd., Plymouth, England, pp. 21, 23, fig. (map, distribution)—ECUADOR; PERU. Schauenberg, 1973, Mus. Genève, 14(134): 12—figs. pp. 13, 14 (animal), fig. p. 15 (habitat), fig. p. 16 (head)—ECUADOR; COLOMBIA; history; conservation; distribution; occurrence in Peru questioned.
- P[udu]. mephistophiles mephistophiles*, Mochi and Carter, 1953, *Hoofed mammals of the world*, Scribner's and Sons, Ltd., London, pl. VIII, text only.
- Pudu m[ephistophiles]. mephistophiles*, Lehmann, 1960, Nov. Colombianas, Univ. Cauca, Popayán, 1(5): 282—ECUADOR; antler form.
- Pudu mephistophiles mephistophiles*, Whitehead, 1972, *Deer of the world*, Viking Press, New York, pp. 29, 64, 165, map 9 (distribution)—distribution; classification.
- Pudua mephistopheles* [sic], Thomas, 1908, Ann. Mag. Nat. Hist., ser. 8, 1: 350—cranial characters: skull originally figured as corresponding to type skin = *Mazama*. Lönnberg, 1913, Ark. Zool., Stockholm, 8 (16): 33—ECUADOR: *Pichincha* (Papallacta, 12,000 ft).
- Pudu mephistopheles* [sic], Soukup, 1961, Biota, 3 (28): 331—PERU. Frädriich, 1975, Zool. Gart., 45(1): 67, 72, figs. 5, 6, 7 (animal), fig. 9 (skull)—ECUADOR: *Cotopaxi* (W of Salcedo); maintenance in Berlin zoo. Brambell and Mathews, 1977, Proc. Symposium 1, Ass. Br. Wild Animal Keepers, p. 25—characters.
- P[udu]. mephistopheles* [sic], Brokx, 1972, J. Mammal., 52(2): 360—upper canine present in specimen examined.
- Pudu* (*Pudella*) *mephistopheles* [sic], Lehmann, 1945, Rev. Univ. Cauca, Popayán (Colombia), Zool., no. 6: 76—comparisons.
- Pudella mephistophelis* [sic], Cabrera and Yepes, 1940, *Mamíferos Sud-Americanos*. Hist. Nat. Ediar (Buenos Aires), p. 278—ECUADOR; PERU.
- M[azama]. mephistopheles* [sic], Flerov, 1952, Fauna U.S.S.R., n.s. no. 56, 1(2): 218 (in text), 220 (in text)—probably a juvenal of *M. rufina* Pucheran. Haltenorth, 1963, Handb. Zool., 8(32): 48—ECUADOR; PERU; characters.
- M[azama]. m[ephistopheles]. mephistopheles* [sic], Haltenorth, 1963, Handb. Zool., 8(32): 48—classification.
- Mazama fusca* Spillmann, 1931, Die Säugethiere Ecuadors im Wandel der Zeit. Univ. Central, Quito, 1: 37, 41 (measurements)—ECUADOR: *Pichincha* (type locality, Mt. Antisana near snow line); holotype, adult male, skull only, perhaps preserved in the Escuela

- Politécnica, Quito. Hoffstetter, 1952, *Mém. Soc. Géol., France*, 31(66): 369, regarded as a synonym of *P. mephistophiles*.
- Pudu* (*Pudella*) *mephistophiles wetmorei* Lehmann, 1945, *Rev. Univ. Cauca*, Popayán, (Colombia), *Zool.* no. 6: 76, figs. p. 78, 80 (animal; skull)—COLOMBIA: *Cauca* (type locality, Páramo de San Rafael, Puracé, ESE Popayán, western slope of the Cordillera Central, 3400 m); holotype, adult male, skin and skull, Museo de Historia Natural, Universidad del Cauca, Popayán, no. 3801, collected 1 February 1945 by F. C. Lehmann. Cabrera, 1961, *Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia,"* 4(2): 344—a synonym of *P. mephistophiles* de Winton.
- P[udu]. mephistophiles wetmorei* [sic], Hoffstetter, 1952, *Mém. Soc. Géol. France*, 31(66): 369—COLOMBIA.
- P[udu]. m[ephistophiles]. wetmorei*, Mochi and Carter, 1953, *Hoofed mammals of the world*, Scribner's and Sons, Ltd., London, pl. VIII, text only.
- Pudu mephistophiles wetmorei*, Lehmann, 1959, *Nov. Colombianas*, 1(4): 202, fig. (animal), fig. 3 (antlered skull)—COLOMBIA: *Cauca* (Páramo de Guanacas, partial albino; Páramo de las Delicias, albinos); *Valle* (Páramos de Barragán, east of Tuluá); description; skull; hunting; conservation. Whitehead, 1972, *Deer of the world*, Viking Press, New York, pp. 29, 64, 169, map 9 (distribution)—classification; distribution.
- P[udu]. mephistophelis* [sic] *wetmorei* [sic] Hoffstetter, 1952, *Mém. Soc. Géol. France*, 31(66): 369—COLOMBIA.
- Pudu mephistophelis* [sic] *wetmorei* [sic], Keirans, 1973, *J. Med. Entomol.*, 10(3): 254—COLOMBIA: *Cauca* (Pusna, 2800 m); tick parasite (*Ixodes montoyanus*).
- M[azama]. m[ephistopheles].* [sic] *wetmorei*, Haltenorth, 1963, *Handb. Zool.*, 8(32): 48—COLOMBIA.
- Pudu* sp. Keirans, 1973, *J. Med. Entomol.*, 10(3): 254—COLOMBIA: *Cauca* (Malvasá, 3500 m, 3000 m); tick parasite (*Ixodes montoyanus*).

Type.—Originally described from the skin and attached leg bones of an immature female, and a mismatched skull of *Mazama rufina*, both presented in 1896 to the British Museum (Natural History), by Ludovic Söderström. The mismatch was discovered by Thomas (1908, p. 350) and the type was restricted to the skin BM 96.1.28.5, by Lydekker (1915, p. 217).

Type locality.—Said to be the Páramo de Papallacta, but probably taken in temperate zone forests below páramo zone, southeast of Quito, eastern slope of the Cordillera Oriental, Pichincha, Ecuador. The altitude is said to be between 3,600–3,700 m above sea level, but probably should be estimated at 200 or 300 m lower.

DISTRIBUTION

(fig. 30)

Restricted to the temperate zone forests and fringing grasslands or páramos above treeline in the Cordillera Central of southern Colombia, from the departments of Valle and Tolima southward through the Cordillera Oriental of Ecuador and Peru into the department of Junín. The parts of the Andean chains actually occupied are poorly known, and distributional gaps between locality records in northern Ecuador and central Peru are unresolved.

According to Lehmann (1945, p. 76), the Colombian pudu is known to occur in the Cordillera Central, from the Páramo and Valle de las Papas and probably the Páramo del Lebrero, northeast of the Valle de las Papas; northward through the páramos of Sotará, Puracé, Las Delicias, Guanacas, and Moras, in the department of Cauca, to those of Las Hermosas in the department of Valle. The pudu has also been reported by Lehmann (1959, p. 203) to the north in the region of the Páramos de Barragán east of Tuluá, department of Valle. In Lehmann's opinion, the range never extended farther north because of a deep depression in

FIG. 30. Distribution of *Pudu mephistophiles* de Winton, based on museum specimens and published 19th and 20th century locality records (dots). For locality names, see corresponding numbers in "Gazetteer" (p. 80).

the Andes that acts as a climatic barrier. Altitudinal range is given as between 3,000 and 4,000 m.

Dr. Hernando Chiriví Gallego, head of the Laboratorio de Fauna of INDERENA (Instituto de Desarrollo de los Recursos Naturales Renovables), Ministerio de Agricultura, Bogotá, informs me (*in litt.*, 23 April 1979) that the range of *Pudu mephistophiles* may extend as far north as Mt. Quindío (4°42'N, 75°25'W). He adds that a skull of a pudu from the Páramo de Moras is in the INDERENA collection, and that pudus are well known by the name *venado chonta* in the páramos of Azufral, Cumbal, and Chiles in the department of Nariño.

The parts of páramos presumably inhabited by pudus are actually subpáramos, mostly—if not entirely—secondary in origin and characterized by low, thin, fire-resistant forest growths or matorrales, usually dominated by *Polylepis*. The steep, eastern slope of the Cordillera Central in the upper Río Magdalena valley, below the Páramo de las Papas in the department of Huila, where I found signs and remains of pudus, ranges from 2,700 to 4,000 m above sea level and is thickly forested.

The seeming absence of pudus from the Colombian Cordillera Oriental, which joins with the Cordillera Central at the Páramo de las Papas, is perplexing. The head of the Río Magdalena, which marks the dichotomy between the eastern and western chains, is narrow and shallow enough at altitudes above 2,000 m for a pudu to jump, walk, or step across, and no doubt pudus do as occasions require. Farther down and eastward, the crest of the Cordillera Oriental loses altitude, and, passing the point (Picos de Fragua) where it turns sharply north-eastward, it forms a deep saddle at the divide between the Río Suaza (Magdalena) and Río Orteguzaza (Caquetá). Here the climate is comparatively dry, upper tropical to subtropical, and acts as a barrier to northern spread of many temperate zone mammals, including pudus, but serves (or served) as a pass for tropical zone Amazonian mammals. The Colombian Cordillera Occidental, except for a few isolated peaks and subpáramos, is too low to provide suitable habitat for pudus.

The pudu has not been recorded from Carchi and Imbabura, the two Andean provinces of northern Ecuador, but is known there by the name *sacha cabra*. One was captured with hunting dogs in the virgin forests northeast of San Gabriel, Carchi, during my explorations there in 1934.

Dr. Fernando Ortiz Crespo of the Pontifica Universidad Católica del Ecuador in Quito, informs me (*in litt.*, 6 March 1979) that he heard rumors of pudus being sighted around Volcán Chiles in the western Andes at the Ecuadorian-Colombian border. Dr. Ortiz mentions that the scarcity of the species may be due to competition with *Mazama* in forests between 2,500–3,200 m altitude, and to the absence of suitable habitat higher up. He observes, however, that the animal is rarely encountered because of its nocturnal or, at least, crepuscular habits and the difficulty of access to its extremely accidented habitat where it can be hunted only with dogs. He particularly notes that pudus are not confined to the isolated patches of *Polylepis* forest found in páramo and that these animals, including the holotype recorded from the Páramo de Papallacta, may have originated in forests well below the páramo zone.

The occurrence of pudus in the southern half of Ecuador, south of the Río Pastaza, and northern Peru, north of Huánuco department, is not on record. However, Dr. Antonio Brack Egg, a distinguished naturalist, formerly of the Dirección General Forestal y de Fauna, Lima, believes (*in litt.*) that pudus may be present in the páramos of Huancabamba at the headwaters of the Ríos Quiroz,

Chinchipe, and Huancabamba, in the departments of Piura and Amazonas on the Peruvian-Ecuadorian border. Grimwood (1969, p. 79) provides the following details on the occurrence of pudus in central Peru:

The occurrence of this genus within Peruvian limits does not appear to have been previously recorded. There is, however, a misidentified mounted specimen of *Pudu mephistophiles* (De Winton) in the museum of the Colegio "Leoncio Prado" at Huanuco, which was shot some years ago at Pamacucho, 4 kms. from that town; and in 1965 I obtained the skin and skull of a male of that species which had been killed near Carpish summit on the Huanuco-Tingo Maria Road. Subsequently, I have seen the animal alive in that region and have been shown skins or photographs of other animals killed there and in a number of localities in the upper Huallaga valley above the town of Huanuco.

The distribution of this species appears to be very limited. At Carpish it is quite common in the forests on both sides of the divide, from the summit at approximately 3,000m. down to about 2,300m. on the eastern side and down to where forest gives way to cultivation at about 2,000m. on the western side. It is also known from similar country near Chaglla, 30 kms. further south.

In the upper Huallaga basin the species occurs in a much drier habitat, and has been shot at Yanacocha, on the Río Quere [sic=Quero], 25 kms. northwest [sic=SW] of Huanuco; at Pamacucho; and in a number of small patches of woodland between Huanuco and Ambo which lie at 2,700 to 3,300m., are no more than a few square kilometers in size, and are separated from each other by many miles of arid hillside. It is also reported to occur in an isolated patch of forest at 3,300m., 40 kms. from Huanuco on the Quivilla road.

I believe *Pudu mephistophiles* also to occur in parts of the Department of Junín, although I have seen no specimen from that region. Local hunters, however, have unhesitatingly identified my Carpish specimen as the same animal as one known locally as "Antaglo" which is reported to be very plentiful at elevations of from 2,000 to 3,000m. on the forested heights above San Ramon and also in the valley of the Río Hausanhausi [sic], to the north. The antaglo is only doubtfully known in the Oxapampa area, but is reliably reported from the upper Río Paucartambo at approximately 76.00'W, 10.50'S.

The Peruvian population of *Pudu mephistophiles* appears to be entirely isolated from the nearest known population in Ecuador, since no small deer of any kind is known in any area north of Huanuco where I have made enquiries.

The specimen from Carpish mentioned above was shipped to the Field Museum but never arrived (Grimwood 1969, p. 80). To date, the only preserved specimen of a Peruvian pudu known to me is the pelt from Bosque Zapatogocha, Huánuco, presented to the Field Museum by Peter Hocking.

Early reports of the occurrence of pudus in southern Peru and Bolivia prove to have been based on pelts or bones of the dwarf brocket, *M. chunyi* (Herschkovitz, 1959a).

CONSERVATION

The late Professor Lehmann warned in 1960 (p. 282) that the pudu was being hunted almost daily in the Colombian highlands by campesinos and often by villagers who sometimes killed as many as six or seven deer in a single organized hunt. At this rate of attrition, he argued, the pudu's extinction was foreseeable in the near future. Lehmann added that account must be taken of the limited range of the species (as known then) and of the increasingly large portions that man was converting to his own use. This alone, he declared, is enough to doom the pudu unless the government provides the vigilance and control needed to

ensure survival of the natural fauna and flora by establishment of appropriate nature reserves.

The Colombian government has since (1968) founded the Puracé National Park and others. Pudus of the Puracé region, the first known from Colombia, served Lehmann for the original description of his *Pudu mephistophiles wetmorei*. Oddly, Hunsaker (1972, p. 445) mentions the mountain tapir (*Tapirus pinchaque*) but overlooks the pudu among the protected species of this park.

Present status of *P. mephistophiles* in Colombian National Parks has been summarized by Dr. Hernando Chiriví Gallego (see above, p. 47). The information is abstracted below with some comments. For location of parks listed, see "Gazetteer" (p. 80) and map (fig. 30, p. 46). Additional information on Colombian national parks is provided by Hunsaker (1972) and Harroy (1972).

LOS NEVADOS, Cordillera Central, astride boundaries between departments of Caldas, Resaralda, Quindío, and Tolima; 4°45'N, 75°20'W; 50,000 ha (200 sq miles); established 1977. Not plotted on map, Figure 30.

"Local informants distinguish a small reddish deer whose description agrees with that of *Mazama rufina*, and a smaller dark one like *Pudu mephistophiles*" (Chiriví).

This park lies within the range of *Mazama rufina*, but well north of the northernmost authenticated locality recorded for the northern pudu.

LAS HERMOSAS, Cordillera Central, departments of Valle and Tolima, established 1977.

"A mounted specimen of *Pudu mephistophiles* is in the Hunters Club of Ibagué, Tolima. It was taken in the páramo above Roncesvalles, Tolima" (Chiriví).

Lehmann (1945, p. 76) also recorded the pudu from the Valle side of the Páramo de las Hermosas.

NEVADO DEL HUILA, departments of Huila, Tolima, and Cauca.

"There is no information but in all probability the pudu is present" (Chiriví).

PURACÉ, Cordillera Central, Cauca; 80,000 ha (293 sq miles), 2,500–4,700 m; established 1968.

"A specimen (skin and skull) from Laguna de Cusiaco near the headwaters of Río Magdalena, is preserved in the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá" (Chiriví).

MUNCHIQUE, Cordillera Central, Cauca.

"Dr. Heliodoro Sánchez, Chief, Division of National Parks, INDERENA, observed a pudu from a distance of a few meters on the western slope of Cerro de Munchique, between 2,500–2,600 m" (Chiriví).

CUEVA DE LOS GUÁCHAROS, Cordillera Oriental, Huila, 15,000 ha (61 sq miles), 1,700–4,000 m.

"There are vague rumors of the existence of pudus in the highest mountains surrounding the Park" (Chiriví).

Pudu hunting in Colombia, Dr. Chiriví informs me, has been prohibited since 1969. However, without the necessary vigilance in the mostly unsupervised parks, survival of the species, where presently known to occur, is dubious.

In Ecuador, the Parque Nacional de Cotopaxi harbors pudus. The pair captured west of Salcedo and exhibited in the Berlin zoo (fig. 28) must have originated in this park. There may be more havens. Dr. Fernando Ortiz Crespo informs me (see above, p. 47) that the Ecuadorian Ministerio de Agricultura and Ganadería plans to establish nature reserves that include pudu habitats. Among areas under consideration are the slopes of Mt. Cotacachi, Imbabura Province; the eastern flanks of Mt. Tungurahua, Tungurahua Province; Mts. Altar and Sangay in Morona-Santiago; and the eastern slope of the Cordillera Oriental at

the latitude of Mt. Cayambe, Napo, which would incorporate the type locality of *Pudu mephistophiles*. Dr. Ortiz adds that conservationists can speed up the establishment of such reserves by exerting pressure on the highest governmental levels.

I.R. Grimwood, Technical Adviser on Wild Life for the British Ministry of Overseas Development, on assignment to the Peruvian Servicio Forestal y de Caza, is equally urgent in his assessment of the situation in Peru. He (1969, p. 80) gave this observation:

It is improbable that this species will survive for much longer in the isolated forest patches in which it occurs in the upper Huallaga basin, where it is relentlessly hunted with dogs and guns. It has, however, outlasted the white-tailed deer in many of them because it does not break cover, as does that species. . . . The species is also hunted in the Carpiish, Chaglla and San Ramon areas, but in these regions destruction of habitat for settlement is likely to present a greater threat. Control of hunting is, however, necessary.

Pudu mephistophiles does not occur in any existing or projected national park or reserve [cf., Dourojeanni, 1968]. The creation of a special sanctuary, for which the high ground above the San Ramon gorge is suggested, is therefore desirable.

In a personal communication dated 1 April 1979, Dr. Antonio Brack expresses doubt that the pudu ever occurred in the San Ramón region. In any event, he adds, the original environment has been destroyed and the region now is unsuited for a reserve. Brack further states that the only area where pudus are known to occur in abundance is in the Cordillera de Carpiish, department of Huánuco, where the government plans to establish a reserve when funds and national conditions permit. In Brack's opinion, *Pudu mephistophiles* in Peru is not seriously threatened, as long as good habitat over an extensive zone of the eastern slope of the Andes remains closed to highways.

A national park worth mention because it may shelter pudus in an area where never recorded is that of San Andrés de Cutervo (6°13'S, 78°42'W), Cajamarca, altitude, 2,200–3,000 m. It is the smallest of Peru's national parks (2,500 ha). Harroy (1972, p. 77) describes it as ". . . totally protected: no occupation, no exploitation; lumbering is now forbidden almost everywhere. Staff headquarters at the town of San Andrés de Cutervo, 3 km from the Park."

VERNACULAR NAMES

The Colombian pudu, according to Lehmann (1945), is called *venado conejo* (rabbit deer). Those with antlers in velvet may be distinguished as *caciques* (chiefs). Melanic individuals of the Valle de las Papas, Cauca, are recognized as a distinct variety called *venado chonta* (chonta is a species of palm with dark trunk). On the eastern slope of the Páramo de las Papas, Huila, where I worked, *venado chonta* is the name applied to the small, red mountain brocket, *Mazama rufina*; whereas the sympatric pudu is called *venado churucu* (or *churucu*, also used for the blackish, woolly monkey, *Lagothrix lagothricha lugens*).

The most widely used name for the pudu in Ecuador and Peru is *sacha cabra* (wild goat). The notation "local name *ollique*" appears on the collector's tag of a specimen from Cayambe, Ecuador, preserved in the British Museum (Natural History). Grimwood (1969) includes *antagallo* as the name used in Junín, Peru.

The Chilean name "pudu" now is universal for both recognized species of the genus *Pudu*. I follow Haltenorth (1963, p. 48) in distinguishing the two as "northern pudu" and "southern pudu."

TAXONOMY

The original description of *Pudu mephistophiles* de Winton is based on a skin with foot bones intact, and the skull of a subadult brocket, apparently *Mazama rufina* Pucheran. The skin and mismatched skull were received from Mr. Ludovic Söderström, British consul in Quito, Ecuador. De Winton (1896, p. 511) examined the foot bones still in the skin and observed that "Osteologically they agree with *P. humulis* [= *Pudu puda*], the ectocuneiform and navicular-cuboid bones being all in one."

The erroneous association of the type skin and foot bones with a *Mazama* skull was discovered by Thomas (1908) when he received two additional specimens from Mr. Söderström, both with properly matched skins and skulls.

The three known skins of *P. mephistophiles* from the type region in northern Ecuador average slightly more saturate in general body color than southern Colombian representatives of *wetmorei*, and one of them agrees with the holotype of *wetmorei* as described. A skin from the Cordillera de los Llanganates, south of the type region of *mephistophiles*, with a buffy or olivaceous-appearing coat is absolutely indistinguishable from the majority of Colombian specimens I examined, including four topotypes of *wetmorei*. An adult male and female, also from Llanganates, reported by Frädrieh (1975, p. 75) are said to "differ insignificantly from the more northern *wetmorei*." In the absence of any notable difference in color or any other character including antler shape, which varies even more widely, there appear to be no grounds for recognition of *wetmorei* as a race of *P. mephistophiles*.

CHARACTERS

Size.—Smallest of living deer; measurements are given in Table 3.

Coloration and pelage (figs. 31–34).—General body color buffy agouti (olivaceous) to reddish brown agouti, the middorsum dominantly dark brown, pelage stiff, adpressed, the hairs pithy; cover hairs of middorsum about 35 mm long, guard hairs like cover hairs, but about 5 mm longer, basal half of both types pale brown or grayish brown, terminal half dark brown (eumelanin) with buffy to reddish (pheomelanin) subterminal band 0.5 mm wide; fine brown curly wool hairs thinly spread and completely hidden to view by cover hairs. Head, including muzzle, chin, outer surface of ears, contrastingly colored dark brown or blackish (eumelanin), the hairs generally unbanded, specialized markings absent; inner surface of ears sharply defined whitish, grayish, or pale buff; rostral hairs banded, usually with a single, narrow pheomelanic ring; orbital ring or stripe absent; neck, including nape, dominantly buffy, the individual hairs with broad pheomelanic bands. Belly, inner sides of thighs and arms buffy to rufous, the hairs unbanded; forefeet and hind feet dark brown contrasting with buffy to reddish agouti of flanks; hoofs extremely long and narrow.

Fawns unspotted, pelage coarse, less hispid, more relaxed, color pattern more uniform, without markedly contrasting dark head and legs.

Color variation.—General body color of the holotype is reddish brown; back of head, nape, and shoulders more or less like back, rump more saturate than middle of back. Of two juvenals in the British Museum (Natural History), one, a topotype from Papallacta, is slightly more saturate throughout than the holotype; the other, from Mt. Cayambe in type region, is slightly paler.

TABLE 3. External and cranial measurements (in mm) of adult *Pudu mephistophiles* de Winton

Locality	Sex	Head and body	Tail	Hind foot*	Ear*	Height at withers	Skull greatest length	Zygomatic breadth	Greatest supraorbital breadth	Brain-case width	Nasals	Diastema	Cheek teeth	Antlers right/left
COLOMBIA														
Puracé**	♂	620	30	-	70	320†	132‡	68	-	-	32‡	-	40	56/45‡
Puracé§	♀	665	45	-	-	405	-	-	-	-	-	-	-	-
Puracé	♀	-	-	-	-	-	135	67.6	34	44.3	33.4	36.5	43.3	-
Puracé	♀	-	-	-	-	-	142	67.5	37	43.1	34.1	36.8	43.4	-
Puracé	♂	710	-	-	-	-	135	68.0	38	45	29.6	35.7	40.9	-
La Vega	♂	-	-	-	-	-	129	66.0	34	44.8	31.5	33.3	42.4	51/-
Malvasá	♂	720	-	180	-	-	135	72.4	37	47.7	35.0	36.3	41.5	25/21
Malvasá	♂	-	-	-	-	-	132	68.7	39	45.2	36.4	36.4	41.4	82/81
Malvasá	♂	-	-	145	65	-	131	65.1	37	43.1	35.1	34.4	41.6	50/52
Malvasá	♂	-	-	-	-	-	130	64.1	35	44.4	33.5	35.0	42.1	60/65
Malvasá	♂	-	-	176	81	-	129	-	35	43.8	35.3	32.0	39.8	16/21
Malvasá	♀	-	-	174	79	-	127	67.2	36	43.4	33.6	34.4	43.5	-
Malvasá	♀	740	-	178	82	-	136	65.8	36	43.9	29.9	37.5	40.3	25/26
Malvasá	♀	-	-	-	-	-	134	67.3	34	45.5	34.6	36.6	40.6	-
Malvasá	♀	-	-	180	73	-	133	65.9	33	44.5	31.2	35.4	42.6	-
Malvasá	♀	-	-	-	-	-	127	65.4	32	43.0	27.8	34.0	41.1	-
ECUADOR														
ECUADOR [¶]	♀ [¶]	650	-	160	-	250	131	62	-	32	-	-	40	-
ECUADOR [¶]	♀	600	-	160	-	290	127	65	-	35	-	-	40	-
ECUADOR [¶]	♂	600	-	160	-	280	130	67	-	38	-	-	41	-

* Measurements not comparable inter se. ** Holotype of *P. m. wetmorei* from Lehmann (1945, p. 77; 1960, p. 281). † "Without hoofs." ‡ As corrected by Lehmann (1960, p. 281). § Topotype of *P. m. wetmorei* from Lehmann (1945, p. 77); skull said to be slightly larger than that of holotype. ¶ Measurements from Frädrich (1975, p. 73); animals died in Berlin zoo, said to be adult. ¶ Weight 5.8 kg.

PELAGE

FIG. 31. Pelage and hair types plucked from middorsum of *Pudu mephistophiles*.

The 23 southern Colombian specimens examined, all from type region of *Pudu mephistophiles wetmorei* Lehmann, vary from reddish brown to olivaceous buff or ochraceous in general body color; coats of individuals taken in May, June, September through February appear new or slightly worn.

In his description of *P. mephistophiles wetmorei* from southern Colombia, Lehmann (1945, p. 78) noted that bright reddish, as well as nearly black, individuals had been observed in the savannas of Paletará, and that he had seen a half dozen or so pudus as dark as the holotype. A female from the Páramo de Guanacas, described and figured by Lehmann, is a partial albino with whitish head, throat, nape, and shoulder bands, and a sprinkling of whitish hairs over the remainder of the otherwise uniformly brownish body. Lehmann (1959) also mentioned that completely albino pudus and albino Andean brockets, *Mazama rufina*, had been taken in the same region and in contiguous Páramo de las Delicias to the north.

FIG. 32. Longitudinal section of hair from *Pudu mephistophiles*, midback; scanning electron microscopic views at magnifications given. Hair structure is not discussed in Part I. A, cuticle showing irregular crenate pattern of overlapping scales; $\times 1,000$. B, same as A, $\times 2,000$. C, cuticle and air pockets of cortex, $\times 700$. D, cortex, $\times 700$.

The single Peruvian specimen at hand, from 10,000 ft in Bosque Zapatogocha, Carpish Divide, Huánuco, is juvenal or subadult. Head and body length of 790 mm (tail 50, hind foot 260, ear 60), recorded on the field label indicates an adult, but the same measured on the tanned skin is not more than 700 mm. The comparatively long and lax pelage agrees most nearly with that of a juvenal from Malvasá, Colombia, with head and body length about 640 mm measured on the tanned skin. However, the Peruvian specimen differs from the Malvasá sample and all other FMNH specimens from Colombia, plus one ANSP skin from Ecuador, by its generally saturate brown color and lack of contrast between its

SATURATION PROCESS

FIG. 33. Saturation, the evolutionary pathway by which mammals have diverged in coloration from a hypothetically common, dominantly agouti-colored ancestor. This process terminates in either uniformly eumelanin (blackish) hairs, as in *Pudu mephistophiles*, or pheomelanin (reddish) hairs, as in *Pudu puda*. For source of figures and evolutionary account of mammalian tegumentary color patterns, see Hershkovitz, 1977, p. 92.

dark brown back, rump, and outer sides of forelegs and hind legs. This recently accessioned individual has not been compared with the dark pudus from Ecuador now in the British Museum, or with those recorded by Lehmann from southern Colombia. The Peruvian specimen may represent a dark race separable from the typical Ecuadorian form.

Rhinarium.—Somewhat bulbous, with posterodorsal border projecting backward along midline.

Tegumentary glands (figs. 10, 11, 14).—Preorbital gland in preserved or tanned skin is represented by an inconspicuous pouch opening about $\frac{1}{2}$ cm in diameter. Forefeet and hind feet pedal glands are contained within shallow, interdigital, trough-like skin fold; tarsal and metatarsal glands, if present, are not evident on dry or tanned skin.

Hoofs and toes (fig. 10).—Hoofs are comparatively long and narrow, greatest length being about three to five times the width measured on plantar surface. Front toes, including hoofs, are comparatively widespread, as seen in dry skin and noted in the living animal (Frädrich, 1975, p. 72) and presumably are endowed with unusual power of abduction.

FIG. 34. Randomly selected hairs plucked from 11 chromogenetic fields of preserved skins of *Pudu puda* and *P. mephistophiles*.

Skull (figs. 11–17).—Lacrimal fossa shallow or dish-shaped without fenestrations, its ventral border hardly or not at all encroaching on malar and maxillary bones; superior border of ascending ramus of premaxillary expanded, contacting lateral margin of nasals; anterodorsal border of lacrimal flat; long axis of antorbital vacuity nearly or quite vertical; plane area of vacuity generally much less than one-half, rarely slightly more than plane area of facial plate of lacrimal; perforations on upper surface of zygomatic process of squamosal, if present, usually less than 1 mm in diameter each; angle of mandible produced well beyond posterior plane of condyle as an expanded subrectangular process; lunar notch between angle and condyle, deeply excised, concavity between base of angle and ramus well defined.

Cranial measurements are given in Table 3.

Dentition.—Upper permanent canine persistent in eight of 15 skulls with complete permanent dentition; deciduous canine present in two of three young with only first molars erupted, and in two of three with second molars erupted; metaloph and metaconule present, postentoconule absent in fully erupted molars (fig. 23).

The form of left pm^3 in FMNH 24362 (fig. 16) is that of a deciduous tooth. In size and wear, however, it agrees with the upper third premolar of the right side and of other pudus. There is no sign of a replacement tooth. Ostensibly, the deciduous-like premolar is the permanent tooth.

Antlers.—Adult male skulls examined were collected October through February and one in July in the department of Cauca, Colombia. All support polished antlers, the longest of which exceeds 90 mm (table 3). Antlers of the holotype of *Pudu mephistophiles wetmorei*, collected February 1945, are also polished (Lehmann, 1960, p. 283). The adult male of a pair of Ecuadorean pudus that arrived in the Berlin zoo during April rubbed the velvet from its antlers in June (Frädrich 1975, p. 76).

The foregoing suggest that antlers of adult male pudus in southern Colombia and northern Ecuador may be shed from February into March, are in velvet from March into June and possibly July, and are polished from June or July until cast.

I find no information on antlers of Peruvian representatives of the species.

A skull of a three-horned pudu from Páramo de Guanacas, Cauca, Colombia, without date of collection, is figured by Lehmann (1959, p. 204). The antlers, still in velvet, are said to be fully developed and completely separated. Two antlers occupy normal positions and in the photograph appear to be more or less symmetrical. The third antler, slightly shorter than the others, arises directly to the right of the normal right antler.

Vertebral formula.—In a male (FMNH 86846) from Malvasá, Cauca, Colombia: 7 cervical, 13 thoracic, 6 lumbar, 4 sacral, 8 caudal.

COMPARISONS

Pudu mephistophiles is distinguished from *P. puda*, its only congener, by characters already mentioned under generic headings (p. 15), key to the species (p. 43), and in the description of the species (above and pp. 65, 70). The only other deer with which the northern pudu need be compared is the smallest known brocket, *Mazama chunyi*.

Using greatest skull length as most reliable indicator of overall body size in present material, that of one fully adult *Mazama chunyi* (all available) is 146 mm, whereas mean and extremes of 14 adult *Pudu mephistophiles* are 132.5 mm (127–142). Externally, as represented by four skins, including holotype, *M. chunyi* more nearly resembles pale Colombian representatives of *P. mephistophiles* than the saturate Peruvian individual at hand. The brocket is separable by its white narial (trimmed away in holotype) and mental patches, tail distinct from rump, the underside sharply defined white, ears probably similarly short and rounded but edges white, their outer surface brownish like muzzle and crown, not blackish, coronal hairs not whorled, body color dominantly pheomelanin, not eumelanin or agouti, lower portion of legs not markedly different in color from upper legs or flanks, and fawn spotted.

In *Mazama chunyi*, as in all brockets, external cuneiform bone is present as a discrete tarsal bone, and crown of first permanent incisor is broadly spatulate, its greatest length more than combined length of i_{2-3} . For additional characters, see comparison between *Pudu* and *Mazama* (p. 22).

SPECIMENS EXAMINED

Total 29. COLOMBIA. *Cauca*: Páramo de Puracé, 4 (USNM, 1; FMNH, 1; AMNH, 2); Malvasá, 15 (FMNH); Quintana, 1 (FMNH); La Vega, 1 (FMNH); Paletará, 2 (AMNH); Coconuco, 1 (AMNH). ECUADOR. *Pichincha*: Páramo de Papallacta, 2 including holotype (BM); Mt. Cayambe, 1 (BM); *Tungurahua*: Cordillera de los Llanganates, 1 (ANSP). PERU. *Huánuco*: Bosque de Zapatogocha above Acomayo, 1 (FMNH).

V. BIOLOGY OF *Pudu mephistophiles*

HABITAT

In tracking the northern pudu, I found the animal confined to the central Andean forests in southern Colombia and the eastern Andean forests in northern Ecuador, at altitudes between 2,700 and 4,000 m. The severely accidented terrain where the animal still may be found probably is its last retreat rather than the predilect abode of this persistently persecuted little animal.

The southern Colombian habitat is described by Lehmann (1945, p. 78) as the dense brush or matorrales of the páramos and the sedge and *frailejón* (*Espeletia*) covered swamps of the Andean summits. I have never seen signs of pudus where grasses or *frailejón* dominate. However, Lehmann points out that pudus sometimes attempt to escape pursuing dogs by climbing trunks of trees inclined over streams or bluffs, which occur only in the temperate zone forests below true páramo. In any event, pudus may invade borders of interdigitating grasslands or páramo to eat the succulent herbs and shoots that appear with the first rains after the dry season burnings.

The following is Grimwood's comparison (1969, pp. 77) of the habitat of *Pudu mephistophiles* in central Peru with that of the very similar-appearing pygmy brocket, *Mazama chunyi* of southern Peru:

The two species occupy the same type of habitat, avoiding the cold and damp of the highest woods and of the thickets above tree line, and [are] found on the eastern [Andean] slopes only from about 3,200 m downwards, in regions where [the alder] *Alnus jorulensis* is often the dominant tree. Both species are also known from a rather different, drier habitat, in isolated patches of forest or woodland in the high valleys immediately to the west of the main eastern watershed.

HABITS

Little is known of the behavior of the northern pudu in the wild beyond what can be inferred from its habitat (see preceding section) and gross morphology. Grimwood (1969, p. 77) compared the pudu with the very similar *Mazama chunyi* and noted that, "Both are very small nocturnal deer, found only singly or in pairs, which emerge in clearings or fields at dusk. Both are much given to whistling and both are said often to be dazed if disturbed by day, so that they can sometimes be caught by hand."

Lehmann (1945, p. 78) observed that, when pursued by dogs, the pudu runs in a weaving pattern. Grimwood also noticed that, in flight, the animal does not

break cover, but circles in the thickets and among the cliffs. Its long, fine, widespread hoofs facilitate climbing, and, as previously noted (Lehmann, 1945, p. 76), the pudu sometimes escapes dogs by running or climbing up inclined trees. Grimwood believes, on the basis of information received from hunters, that the little deer is as nimble on rocks as the African klipspringer (*Oreotragus*).

MAINTENANCE IN CAPTIVITY

Northern pudus are frequently captured alive, but, according to Lehmann (1945, p. 78), they do not survive long in captivity. One pudu in Lehmann's possession in Cali, Colombia, became very tame and particularly fond of milk, but died in two months. Lehmann adds that a friend, Guillermo Valencia, confessed his inability to keep captured pudus alive for more than a few weeks despite all efforts, including maintenance in a natural environment.

The first northern pudu received in a European zoo were two females from Ecuador that arrived dead or dying 23 November 1968, at the Berlin zoological garden. This report, by Frädrieh (1975, p. 73), includes a notice without particulars of the later accession in 1970 of a northern pudu by the same zoo. Subsequently, Frädrieh continues, a pair captured in Ecuador, west of Salcedo between Mt. Cotopaxi and the Cordillera de los Llanganates, arrived at the Berlin zoo in good condition 12 April 1972. After the usual quarantine, the pair was placed on public view and fed a standard brocket diet (Frädrieh, 1974). The male died 6 August 1972. The autopsy showed pasteurellosis, tracheobronchitis, and fibrinous pneumonia. The female died of food poisoning 11 October 1972.

I find no other published records of *Pudu mephistophiles* in zoological gardens.

UNGULATE ASSOCIATIONS

Cervids occurring within parts of the range of *Pudu mephistophiles* are the brockets, *Mazama rufina* and *M. americana*, white-tailed deer, *Odocoileus virginianus*, and taruga, *Hippocamelus antisensis* (fig. 5). The latter, known from the Andes of Ecuador, Peru, Bolivia, and northern Argentina is nearly, if not already, extinct in Ecuador and Peru. The pinchaque or woolly or mountain tapir, *Tapirus pinchaque*, associates with the pudu in Colombia and Ecuador; its numbers are dwindling.

The dwarf deer, *Mazama chunyi*, is common in the southern Peruvian departments of Cuzco, Puno, and Madre de Dios in habitats appropriate for *Pudu mephistophiles*, but the latter is unknown south of the department of Junín. Information on the distribution of small deer in southern Peru is meager, and identifications often have been equivocal or based on hearsay. The pudu, common as it appears to be in central Peru, was not reliably reported from that country until 1969 (Grimwood, p. 79), and the first museum-preserved specimen is recorded here. *M. chunyi*, long confused with *P. mephistophiles*, was not recognized as a distinct species until 1959. The two little deer may yet prove to be sympatric.

REPRODUCTION

A female from Ecuador that arrived at the Berlin zoo 12 April 1972 died 11 October 1972 carrying a fully developed female fetus (Frädrieh, 1975, p. 76). Grimwood (1969, p. 80) reports that, in central Peru, nearly full-term fetuses were taken from pudus killed in April and November.

The meager data indicate that, in *Pudu mephistophiles*, a gestation period of seven months is followed by a postpartum estrus as in *Pudu puda*.

VI. *Pudu puda* MOLINA SOUTHERN PUDU (figs. 36, 37)

SYNONYMIC HISTORY

- Capra puda* Molina, 1782, *Saggia storia Nat. Chile*, libr., 4: 308, 343.
- Capra puda*, Anonymous ("An American Gentleman"), 1808, *The geographical, natural and civil history of Chile*, 1: 217, 240—"Translation from the original Italian of Abbe don J. Ignatius Molina, Saggia . . ." Printed for J. Riley, Middletown, Conn.
- [*Ovis*] *Pudu* [sic], Gmelin, 1788, *Linnaeus Syst. Nat.*, ed. 13, 1: 201—classification.
- Ovis Pudu*, Shaw, 1800, *Gen. Zool.*, 2(2): 392.
- [*Aries*] *pudu*, Fischer, 1814, *Zoognosia Tab. Syn.*, 3: xvi, 406.
- [*Antelope*]. *Pudu*, Blainville, 1816, *Bull. Soc. Philomatique*, pp. 76, 80—classification.
- M[azama]. pudu*, Rafinesque, 1817, *American Monthly Mag.*, 1: 437—regarded as a goat antelope.
- Mazama pudu*, Vanoli, 1967, *Säugetierk. Mitteil.*, 15(2): 155, figs 1–10 (adults, young)—CHILE: Osorno-Llanquihué; habits, habitat, reproduction; food; growth; development; antlers; enemies; disease; conservation.
- Mazama* [(*Oreamnos*)] *puda*, Rafinesque, 1817, *American Monthly Mag.*, 2: 44—classification.
- M[azama (Pudu)]. pudu*, Haltenorth, 1963, *Handb. Zool.*, 8(32): 48—classification.
- Antilocapra pudu*, Lesson, 1842, *Nouv. Tabl. Reg. Animal, Mamm.*, p. 182—classification.
- Cervus pudu*, Gay and Gervais, 1846, *Ann. Sci. Nat.*, (3)5: 88—CHILE: classification; description; measurements; *Cervus humilis* Bennett, a synonym. Gay, 1847, *Hist. Chile, Zool.*, 1: 158, Atlas, pl. 9 (animal), pl. 1 (skull)—CHILE: from *Cauquenes* to *Chiloé*; Indian name, *pudu* or *puudu*. Pucheran, 1852, *Arch. Mus. Hist. Nat. Paris*, 6: 482—characters; measurements; history. Slater, 1866, *Proc. Zool. Soc. London*, 1866: 104, fig. (animal)—menagerie specimen. Slater, 1871, *Proc. Zool. Soc. London*, 1871: 238, pl. 17 (animal)—menagerie specimen; antler shedding. Garrod, 1877, *Proc. Zool. Soc. London*, 1877: 4, 13, 14—alimentary tract; penis; cranial characters; classification. Huet, 1890, *Bull. Soc. Nat. Acclim. France*, 1888/1889, p. 86—coloration.
- C[*ervus*]. *pudu*, Wagner, 1855, *Schreber's Säugth.*, Suppl., 5: 390, pl. 26 (animal)—characters; *humilis* Bennett a synonym.
- Coassus* [(*Pudu*)] *Pudu* Gray, 1850, *Gleanings Knowlsely Menag.*, p. 69—characters. Gray, 1852, *Proc. Zool. Soc. London*, 1850: 242—CHILE: *Concepción*; *Chiloé*; classification; characters; part synonymy: *Capra pudu* Molina, *Cervus pudu* Gervais, *Cervus humilis* Bennett.
- Pudu pudu*, Slater, 1870, *Proc. Zool. Soc. London*, 1870: 116—classification. Wolffsohn and Porter, 1908, *Rev. Chilena Hist. Nat.*, 12: 74—CHILE: *Valdivia*; local names, *venado*, *venadito*, *pudu* (Araucano). Pocock, 1911, *Proc. Zool. Soc. London*, 1910: 967, 978—interdigital gland. Lydekker, 1915, *Cat. Ungulate Mammals Brit. Mus.*, 4: 215—characters; synonymy; CHILE: *Maule*; *Constitución*; *Concepción* (Concepción); *Cautín* (Temuco). Synonyms, *humilis* Bennett, *chilensis* Gray. Pocock, 1923, *Proc. Zool. Soc. London*, 1923: 201, fig. 13 (foot gland), fig. 14b (rhinarium), fig. 15 (ear)—external characters. Wolffsohn, 1923, *Rev. Chilena Hist. Nat.*, 27: 160—CHILE: *Concepción* (Pedro Valdivia); *Maule* (Constitución); measurements. Yepes, 1929, *Rev. Chilena Hist. Nat.*, 33: 472—CHILE: *Maule* (Constitución) to *Magallanes*; ARGENTINA: western *Neuquén* to western *Santa Cruz*. Junge, 1932, *Zool. Garten*, 5: 249—sensitivity to heat. Cabrera and Yepes, 1940, *Mamíferos Sud-Americanos. Hist. Nat. Ediar* (Buenos Aires), p. 278, pl. 88 (animal); characters; distribution. Yepes, 1943, *Rev. Argentina Zoogeogr.*, 3: 75—ARGENTINA: *Neuquén* (Cordillera del Trompul, San Martín de Los Andes; Brazo Correntoso, south of Cordillera del Trompul; La Lolog, San Martín de Los Andes); local name, *corzuelo*. Osgood, 1943, *Field Mus. Nat. Hist.*, Zool. Ser., 30: 228—CHILE: *Magallanes* (Isla Riesco; Río Baker); *Llanquihué* (Cayetúe [sic], Lago Todos Santos; Petrohué, Lago Todos Santos); *Chiloé*; *Cautín* (Pitrufuén); *Concepción* (San Pedro); *Arauco* (Santa Juana; Vega Blanca, Sierra Nahuelbuta); *Valdivia* (Valdivia); characters; variation;

- habits. Schmidt, 1944, *Argentinische Säugetiere*. (Buenos Aires); pp. 170, 237, 5 figs. (adults and young), 1 fig. (skull)—ARGENTINA: Río Negro (Lago Mascardí); *Neuquén* (Río Quillén). Flerov, 1952, *Fauna U.S.S.R.*, n.s., no. 56, Mammals, 1(2): 220 (in text)—listed. Junge, 1954, *Bol. Jardín Zool.*, Concepción (Chile), 1: 3, fig. (animal)—two females in captivity. Hershkovitz, 1958, *Mammalia*, 22(4): 545—metatarsal glands and tuft not defined. Mochi and Carter, 1953. *Hoofed mammals of the world*, Scribner's and Sons, Ltd., London, pl. VIII, fig. 16 (animal)—characters. Hershkovitz, 1959, *Proc. Biol. Soc. Washington*, 72: 45, pls. 3D, 4B (skull)—comparisons. Walker, 1964, *Mammals of the world*, Johns Hopkins Press, Baltimore, 2:1399, fig. (animal)—CHILE; "BOLIVIA." Crandall, 1964, *The management of wild animals in captivity*. U. of Chicago Press, pp. 557, 560, 594—characters; exhibition in zoos. Greer, 1965, *Publ. Mus. Michigan St. U. Biol. Ser.*, 3(2): 146—CHILE: *Malleco* (Laguna Malleco; Galvarino, 10 km W, 61 m); *Angol* (Cordillera de Nahuelbuta); measurements. Junge, 1966, *Int. Zoo Yearb.* 6: 263—CHILE: *Angol*; *Malleco*; *Valdivia* (Mariquina); habits in captivity. Windecker, 1967, *Fr. Kölner Zoo*, 10(2): 58, 4 figs. incl. 2 col. (animals)—Cologne zoo; characters of adult and young; gestation; antler shedding; diet in captivity; hunting in wild. Pefaur, Hermosilla, Di Castri, González and Salinas, 1968, *Rev. Soc. Med. Vet. (Chile)*, 18(1-4): 4, 5, 6, 7, 8, 11, 14—CHILE: *Curico* (?); *Nuble*; *Concepción*; *Arauco*; *Bio-Bio*; *Malleco*; *Cautín*; *Valdivia*; *Osorno*; *Llanquihué*; *Chiloé*; *Aysén*; *Magallanes*; distribution; disease (hoof-and-mouth); endangered species. Hick, 1968, *Fr. Kölner Zoo*, 4(10): 111, 16 photographs, 2 in color (female and young)—gestation, birth and chronology of growth and behavior in Cologne zoo. Hick, 1969, *Int. Zoo Yearb.*, 9: 110—CHILE: *Llanquihué* (Lago Llanquihué)—mating; antler growth and shedding; molt; birth, growth, behavior of young in Cologne zoo. Kohls, 1969, *J. Med. Entomol.*, 6(3): 280—CHILE: *Valdivia* (Santo Domingo, 10 km SE Valdivia; Callumapu, 15 km W. Valdivia); ticks (Acarina): *Ixodes taglei*, *I. stilesi*. Hick, 1979, *Fr. Kölner Zoo*, 4(10): 113, fig. (week old young)—birth in Cologne zoo. Hick, 1971, *Z. Kölner Zoo*, 14(2); fig. p. 83 (mother with F2 young ♂)—breeding in Cologne zoo. Dansie and Wince, 1971, *Deer of the world*. Hitchings and Mason, Ltd., Plymouth, England, pp. 21, 23, fig. (animal), fig. (map, distribution)—CHILE. Wetterberg, 1972, *Oryx* 11(5): 347, fig. (animal) fig. (map, Parque Nacional Vicente Pérez Rosales)—CHILE: *Llanquihué* (Parque Nacional Vicente Pérez Rosales); ARGENTINA: *Neuquén* (Parque Nahuel Huapi); habitat; conservation; food; habits; predators. Koulischer, Tyskens and Mortelmans, 1972, *Acta Ool. Path. Antwerp*, 56: 25, 28, fig. 2 (karyotype)—karyotype ($2n=70$; $FM=74$). Whitehead, 1972, *Deer of the world*, Viking Press, New York, pp. 29, 64, 65, 169, map 9 (distribution), figs. 24a, b (animal)—characters; distribution. Avila Pires, 1974, *Publ. Biol. Inst. Invest. Cient. U.A.N.L.*, México, 1: 61—distribution; conservation. Spotorno and Fernández-Donoso, 1975, *Mamm. Chrom. Newsl.*, 16(1): 17, fig. 10 (karyotypes)—CHILE: *Llanquihué* (Llanquihué); karyotype ($2n=70$, $FM=74$); weights. Frädriich, 1975, *Zool. Gart.*, 45(1): 67, figs. 1, 2 (animal), fig. 3 (mother with fawn), fig. 4 (fawn), fig. 8 (skull)—characters; maintenance in Berlin zoo; antlers; breeding. Czernay, 1977, *Zool. Gart.*, 47(3/4): 226, figs. 2, 3 (growth graph), fig. 4 (male), figs. 5, 6 (mating), fig. 7 (fawn), figs. 8, 9, 10, 11 (mother and young), figs. 12, 13 (family group), fig. 4 (antlers in velvet). Brambell and Mathews, 1977, *Proc. Symp.* 1, Assoc. Brit. Wild Animal Keepers, p. 25—characters, reproduction, management in captivity.
- P[udu]. pudu*, Wolffsohn, 1927, *Rev. Universitaria*, Univ. Católica Chile, p. 240—CHILE: hunting, domestication. Schneider, 1946, *Bol. Soc. Biol. Concepción*, 21: 78—CHILE: *Concepción* (Nahuelbuta); *Cayumanque*; *Manquimávida*; habits. Hoffstetter, 1952, *Mém. Soc. Géol. France*, 31(66): 369—CHILE.
- Pudu puda*, Flower, 1929, *List of vertebrated animals Zool. Soc. London 1828-1927*, p. 325—listed.
- P[udu]. puda*, Zuckerman, 1952, *Proc. Zool. Soc. London*, 122: 901—births in London zoo, 23 May 1932 to 29 May 1933.
- P[uda]. pudua* [sic], Carrette, 1922, *Rev. Mus. la Plata*, 26: 445—characters.
- Pudu pudua*, Castellanos, 1940, *Rev. Chilena Hist. Nat.*, 44: 159—ARGENTINA: southern Andes near Chilean border.
- Pudua pudu*, Lydekker, 1898, *Deer of all lands*, p. 307—characters; distribution. Matschie, 1899, *Sitz.-Bericht Gesellsch. Naturf. Berlin*, p. 130—distribution. Lydekker, 1901, *Great and small game of Europe, western and northern Asia and America*. Rowland Ward, London, p. 373—characters.

- Nanelaphus Pudu*, Fitzinger, 1873, Sitzb. Akad. Wiss. Wien (1873), 68(1): 361—classification.
- Ovis dubia* Afzelius, 1815, N. Act. Reg. Soc. Sci., Upsalla, 7: 217—new name for *Capra pudu* Molina; work not seen.
- Cervus humilis* Bennett, 1831, Proc. Zool. Soc. London, 1831: 27—CHILE: precise locality unknown; type female, skin originally in the collection of the London Zoological Society, now in the British Museum (Natural History) no. 55.12.24.248. Gay and Gervais, 1846, Ann. Sci. Nat., Paris, ser. 3, 5: 90—a synonym of *Cervus pudu* [sic] Molina. Fraser, 1849, Zoologica typica, pl. 14 and text—CHILE: Concepción; Chiloé.
- C[ervus]. humilis*, Sundevall, 1846, K. Svenska Vet. Akad. Handl., 1844: 183—part, CHILE: specimen seen in Paris museum.
- Cervus* [(*Capreolus*)] *humilis*, Lesson, 1842, Nouv. Tabl. Reg. Anim., p. 172—classification.
- Pudu humilis*, Gray, 1852, Cat. Mamm. Brit. Mus., Ungulata, p. 240, pl. 36, fig. 1 (skull captioned *Pudu chilensis*)—CHILE: characters; part synonymy. Gray, 1872, Cat. ruminant Mamm. Brit. Mus., p. 93. Gray, 1873, Handlist ruminant animals Brit. Mus., p. 163—type history; CHILE. Jentink, 1887, Cat. Osteol. Mus. Pays-Bas, 9: 153—CHILE. Jentink, 1892, Cat. Syst. Mamm. Mus. Pays-Bas, 11: 183—CHILE.
- Pudua humilis*, Garrod, 1877, Proc. Zool. Soc. London, 1877: 18—classification. Sclater, 1877, List Vertebrated Animals Zool. Soc. London, p. 139, fig. 18 (animal)—male exhibited live. Brooke, 1879, Proc. Zool. Soc. London, 1878: 927—CHILE. Sclater, 1883, List Vertebrated Animals Zool. Soc. London, p. 174, fig. 28 (animal)—2 males, 1 female exhibited live. Sclater, 1896, List Vertebrated Animals Zool. Soc. London, p. 185—1 male, 2 females exhibited live. De Winton, 1896, Proc. Zool. Soc. London, 1896: 507, figs. 1, 3 (skull); characters; comparisons. Kidd, 1900, Proc. Zool. Soc. London, 1900: 686—hair pattern. Reiche, 1903, Anal. Mus. Nac. Chile, p. 46—CHILE: Arauco (Isla de la Mocha, extirpated).
- Coassus humilis*, Rütimeyer, 1881, Abh. Schweiz. Paläont. Gesellsch., 8: 31, 93—cranial characters; relationships; distribution.
- Pudu chilensis* Gray, 1852, Cat. Mamm. Brit. Mus., Ungulata, pl. 36, fig. 1 (skull)—CHILE: (no precise locality); name in caption for figured skull or same specimen denominated *Pudu humilis* in text (p. 240). Gray, 1873, Hand-list of edentate, thick-skinned and ruminant mammals in the British Museum, p. 163—adult female, skull nos. 972 and 50.11.29.6 (same figured 1852), skin of type skull received from Zoological Society of London.
- "Chevreuil," Poeppig, 1829, Férussac, Bull. Sci. Nat. Géol., Paris, 19: 96—CHILE: high altitudes; size.
- "pudu," Poeppig, 1835, Reise in Chile, Peru und Amazonstr., 1: 450—CHILE: Bio Bio (Antuco). Ulmer, 1959, America's First Zoo, 11(1): 7—exhibited 1877 in Philadelphia Zoological Garden.
- Type*.—None in existence; name based on native accounts of the animal.
- Type locality*.—Southern provinces of Chile.

DISTRIBUTION

(fig. 35)

Forests of southern Chile and some adjacent parts of southwestern Argentina; in Chile, from the province of Maule, southward nearly or quite to the Strait of Magellan; in Argentina, from southwestern Neuquén, southward along the Andean foothills and mountain passes into southwestern Santa Cruz province; altitudinal range from sea level to nearly 1,000 m above.

CONSERVATION

Pudus are still hunted in Chile, among other areas, as a cheap source of protein or as an expensive form of sport and their habitat is rapidly being destroyed, except possibly in the following national parks:

NAHUEL BUTA, Arauco-Malleco, 1,000–1,500 m altitude, 5,414 ha (20 sq miles). Pudus

FIG. 35. Distribution of *Pudu puda* Molina, based on museum specimens and published 19th and 20th century records (dots). For locality names, see corresponding numbers in "Gazetteer" (p. 80).

have been recorded from the Cordillera de Nahuelbuta, but no information is at hand regarding the present status of the native mammals of this park.

TOLHUECA, Malleco, 1,500–2,000 m, 3,000 ha (12 sq miles). Although this park is within the geographic range of and provides a suitable habitat for pudu, it hardly is large enough to support more than a small population.

VICENTE PÉREZ ROSALES, Llanquihué, 135,175 ha (522 sq miles). According to Chilean authorities surveyed by Harroy (1971, p. 168), hunting is permitted in the park. However, Wetterberg (1972, p. 348) reports pudu abundant and generally unmolested in the area.

VILLARICA, Cautín, 13,780 ha (53.1 sq miles); "... inaccessible and has few inhabitants," according to Harroy (1971, p. 168), and incorporates good pudu habitat.

TORRES DEL PAINE, Magallanes, 10,000–20,000 ha.

Three additional parks are located within the geographic range of *Pudu pudu*, namely:

LAGO SAN RAFAEL, Aisén (590,000 ha); PUYEHUÉ, Valdivia (75,000 ha); and PIRIHUEICO, Valdivia (13,950 ha). These are not regarded as conservation areas, due to the high number of human habitations and excessive exploitation, such as unrestricted or uncontrolled hunting, fishing, lumbering, stock grazing, and rapid destruction of forest.

The future of the pudu in Argentina is clouded. Dennler de la Tour (1957, p. 159) observes, "Among the animals most in need of protection in Argentina are the Andean deer 'huemul,' *Hippocamelus bisulcus*, and the dwarf deer 'pudu,' *Pudua pudu*. These are threatened not only by 'development' and poaching, but by the introduction of the European red and fallow deer in the park areas." A decade later, Nottebohm (1967, p. 117) warned that disappearance of the huemul and pudu from Argentine territory is imminent. The following is a list of Argentine national parks, from north to south, where pudus (and huemuls) live now or lived in the past:

LOS COPAHUES, northwestern Neuquén, 80,000 ha (310 sq miles). The pudu is not known to occur in northern Neuquén at present, if it ever did before.

LAGUNA BLANCA, central Neuquén, 1,000–2,000 m, 11,250 ha (40 sq miles); doubtful if the pudu occurred in the area surrounding the lake.

LANÍN, southwestern Neuquén, 600–3,776 m, 395,000 ha (1,500 sq miles). This area adjoins Nahuel Huapi National Park and has the same fauna, including pudu and huemul.

NAHUEL HUAPÍ, southwestern Neuquén, 720–3,554 m, 785,000 ha (3,000 sq miles) of which only 60,000 ha (260 sq miles) is nature reserve, the remainder being private lumbering, farming, and grazing property. According to Dennler de la Tour (1957, p. 160), "The huemul and the pudu have been almost eradicated by poaching, by the dogs of sheepbreeders and by the introduction of European deer."

LOS ALERCES and ANEXO PUELO, western Chubut, 400–2,280 m, 280,000 ha (1,100 sq miles). Although the pudu has not been recorded here, the park lies within its probable geographic range and has a suitable habitat.

PERITO FRANCISCO P. MORENO, west central Santa Cruz, 800–2,770 m, 115,000 ha (400 sq miles). Dennler de la Tour (1957, p. 163) includes the huemul and guanaco in the local fauna, but does not mention the pudu, which may occur nearby if not inside the park.

LOS GLACIERES, southwestern Santa Cruz, 300–2,441 m, 670,000 ha (2,600 sq miles). Dennler de la Tour (1957, p. 162) reports that the "huemul and pudu are present, though reduced in numbers."

TAXONOMY

Molina (1782, p. 308–309) described the "pudu (*Capra pudu*) as a kind of wild goat about the size of a six-month-old kid, brown in color, the male with small horns. The animal is called *venado* or roebuck by the Spaniards but improperly as

it has all the characters of a goat except for lack of a beard and in that its horns are smooth, rounded and divergent."

Gmelin (1788, p. 201) referred the pudu to the genus *Ovis*, but rendered the original specific name "*pudu*," a misspelling used by nearly all subsequent authors.

Rafinesque (1817a, p. 437) thought the pudu was akin to goat antelopes when he referred it to his newly described genus *Mazama*, together with *Mazama ovina* (*Oreamnos americanus americanus* Blainville). Later he (1817b, p. 44) included *Mazama puda*, *Mazama dorsata* (= *O. americanus americanus*), and *Mazama sericea* (= *O. americanus americanus*) in "a particular subgenus (or perhaps genus) which I shall call *Oreamnos*, distinguished by the horns slightly curved backwards or outwards, often rough or annulated, and long hair, besides living in mountains: if the horns should prove hollow, it will have much affinity with the genus *Rupricapa* [sic]." This judgment was made earlier by Blainville (1816, p. 76).

The true nature of *Capra puda* Molina remained equivocal until 1846 when Gay & Gervais (p. 88) demonstrated the cervid characters of two pudu skins and one skull that Gay brought to the Paris museum. They also showed that *Cervus humilis* Bennett, described in 1831 on the basis of a female that had lived in the gardens of the London Zoological Society in 1830, represented the same species.

The name *Pudu chilensis* Gray appears first as the caption for the figure of a skull in Gray's *Catalogue of the Specimens of Mammalia in the Collection of the British Museum* (1852b, pl. 36, fig. 1). This name is valid, although it almost certainly is a *lapsus* for, and definitely a synonym of, *P. humilis* Bennett, the only species Gray (1852b, p. 240) actually described in the text.

The preceding synonymy includes a complete bibliographical history of *Pudu puda* Molina.

CHARACTERS

Size.—Average larger than *Pudu mephistophiles*, smaller than *Mazama chunyi*.

Coloration and pelage.—General body color buffy agouti with middorsum usually contrastingly colored reddish brown agouti; pelage stiff, adpressed, the hairs pithy; dorsal cover hairs about 30 mm long, guard hairs like cover hairs about 5 mm longer, basal half of both types grayish, of terminal half brownish (eumelanin) with subterminal pheomelanin band on back, flank, rostrum, cheek, and neck; crown, outer surface of ears, supraorbital stripe or circumorbital band, narial and mandibular patches ochraceous to rufous, terminal portions of hairs uniformly pheomelanin, inner surface of ears, chin, throat like preceding but paler, the uniformly reddish parts contrasting with surrounding buffy or reddish agouti areas, including rostrum, cheeks, nape, neck, shoulders, flanks; chest, belly, inner sides of upper parts of front and hind limbs reddish, lower parts of limbs entirely reddish, hairs unbanded.

Fawns spotted, pelage less hispid than that of adults.

Color variation.—The dominant pheomelanin ranges in coloration from buffy to reddish or reddish brown. Of four adult males from Chiloé taken in January, one is in new buffy pelage, another is in new reddish pelage, and two are in old reddish pelage. The remaining adults and unspotted subadults at hand with known dates of capture are in unworn pelage, all from Chile, as follows:

February—buffy ♂, Chiloé.

April—reddish ♀, Puerto Montt; rufous ♀, Temuco.

April—buffy ♀, Cautín.

July—buffy ♂, Angol.

September—buffy ♀, Angol.

October—buffy ♀, Valdivia.

November—buffy ♂, Petrohué.

One female (without collection date) from San Pedro, Concepción, is in worn, faded, buffy pelage. The condition of the fur in this example, however, may be the result of exposure to sunlight and wear after the specimen was prepared as a round study skin. Two undated males, one from Arauco, are in unworn, buffy pelage.

Worn pelage appears to be associated with the reddish color, but not certainly with the buffy. New pelage, however, may be buffy or reddish. There is no indication in present material that an animal may molt from one dominant color to the other.

Molt.—Winter molt begins in fall, summer molt in spring. Starting with birth-date, fawns begin to shed the juvenal spotted coat during the sixth week and lose it completely by end of the second month (Vanoli 1967, for Chilean pudu; Hick, 1967/1968, and Frädrieh, 1975, for German zoo pudus).

Rhinarium.—Not notably swollen or bulbous, posterodorsal border slightly convex or forming a straight line between nostrils.

Tegumentary glands.—Preorbital gland large, the opening wide, conspicuously displayed; interdigital glands of forefoot contained in deep trough or pocket of hind foot in well-defined pouch; tarsal and metatarsal glands not evident in available material.

External genitalia.—According to Garrod (1877, p. 9, fig. 16), the glans penis is similar to that of *Odocoileus* and *Blastoceros* (*Ozotoceros*).

Skull.—Lacrimal fossa large, bowl-shaped and often fenestrated, the maxillary bone contributing to ventral border, malar bone excluded; anterodorsal border of facial plate of lacrimal bone slightly to moderately convex or convoluted; superior border of ascending ramus of premaxillary bone not expanded, and either contacting or widely separated from lateral margin of nasal bone; long axis of antorbital vacuity diagonal to nearly horizontal, plane area of vacuity from approximately one-half to nearly as large as plane area of facial plate of lacrimal; perforations present on upper surface of root of zygomatic process of squamosal bone, the diameter of posteriormost usually more than 1 mm; angle of mandible subcircular, produced little beyond posterior plane of condyle; lunar notch between condyle and angle little excised, concavity between base of angle and ramus more or less defined.

Cranial measurements are given in Table 4.

Dentition.—Upper deciduous canine, present in some fawns, shed without replacement after eruption of first molar; metaloph absent in fully erupted molars, postentoconulid and corresponding crista rudimentary in unerupted, absent in fully erupted molars.

Antlers (table 5).—Growth completed and spikes polished during summer, shed in winter same day new growth begins. In high, southern hemisphere latitudes, mature antlers are rubbed clean of velvet in December and dropped in July (Vanoli, 1967). Antlers of pudus introduced into northern European zoos maintain southern periodicity until cast. During the next one or two years, antler development and other vital processes adjust to reversed seasons. Antlers attain

FIG. 36. Southern pudus, females, in Cologne zoo (photograph courtesy Cologne zoo).

FIG. 37. Southern pudus in Berlin zoo. *Left*, breeding male; *center*, male in velvet; *rear*, five-month-old male; *right*, female. [Photograph by J. Frädriich, courtesy Berlin zoo; caption from H. Frädriich (1975, p. 69).]

TABLE 4. External and cranial measurements (in mm) of adult *Pudu puda* Molina.

Locality	Sex	Head and body	Tail	Hind foot	Ear from crown (c) and notch (n)	Height at withers	Weight* (kg)	Skull greatest length	Zygomatic breadth	Greatest supraorbital breadth	Brain-case width	Nasals	Diastema	Cheek teeth	Antlers right/left
CHILE															
San Pedro	♀	—	—	—	—	—	—	134	65.3	38	47.8	33.2	35.8	44.7	—
La Mocha	♀	696	32	165	—	—	13.4	139	—	44	51.0	—	—	51.0	74/50+
Angol	♂	752	43	205	72 n	—	—	141	64.3	36	47.3	31.0	37.5	45.4	—
Petrohué	♂	795	35	—	88 c	385	—	155	—	37	47.4	38.0	37.0	46.4	65/67
Chiloé	♂	820	40	196	72 n/78 c	405	9.5	155	70.8	42	47.9	44.5	40.5	52.0	73/68
Chiloé	♂	767	31	200	72 n/90 c	425	—	150	70.0	40	46.9	43.6	43.3	47.4	—
Chiloé	♂	825	42	205	—	430	—	150	71.9	42	49.4	49.4	42.0	47.4	72/65
Chiloé	♂	747	38	173	72 n/78 c	410	10.9	150	—	41	48.7	43.0	38.0	50.0	67/68
Chiloé	♂	—	—	—	—	388	—	148	67.0	37	48.8	39.1	39.7	47.0	62/59
Chiloé	♂	—	—	—	—	—	—	142	65.3	41	47.3	36.7	36.0	45.3	41/36
Chiloé	♂	—	—	—	—	—	—	148	69.0	43	48	42	39	47	cast
Chiloé	♀	—	—	—	—	—	—	145	66.0	38	48	37	38	46	—

* Male and female captured live in Llanquihué weighed 10 kg and 8.3 kg, respectively (Sportorno & Fernández-Donoso, 1975:17).

TABLE 5. Antler cycle in *Pudu pudu* in European zoos.

Antlers						
Date animal introduced	Date mature L/R*	Date shed L/R*	Length (mm)	Weight (gm)	Zoo locality	Source
— 1864	—	Annually	—	—	London	Slater (1871:238)
— 1864	—	Nov. 1869	63.5	—	London	Slater (1871:238)
— 1864	—	Dec. 1870	74	—	London	Slater (1871:238)
July 1967	— end Nov. 1967	20/21 July 1967 7/8 April 1968	80	6.5	Cologne Cologne	Hick (1967/1968:111) Hick in Frädrich (1975:69)
19 Oct. 1969	—	3/5 March 1970	—	—	Berlin	Frädrich (1975:69)
14 Oct. 1969	—	16/16 March 1970	—	—	Berlin	Frädrich (1975:70)
	18/19 June 1970	18/18 Dec. 1970	—	—	Berlin	Frädrich (1975:70)
	1 May 1971	24/26 Dec. 1971	—	—	Berlin	Frädrich (1975:70)
9 Nov. 1966	(?) 11–16 July 1967**	19/21 March 1967 7/6 Jan. 1968	—	—	Berlin	Frädrich (1975:70)
		2/2 Jan. 1969	—	—	Berlin	Frädrich (1975:70)
	7/8 June 1969	15/15 Jan. 1970	—	—	Berlin	Frädrich (1975:70)
	5/7 June 1970	15/14 Jan. 1971	—	—	Berlin	Frädrich (1975:70)
	5 June 1971	18/12 Jan. 1972	—	—	Berlin	Frädrich (1975:70)
	9 June 1972	13/28 Jan. 1973	—	—	Berlin	Frädrich (1975:70)
	17 June 1973	23/25 Dec. —	80	—	Berlin	Frädrich (1975:70)
	22 May 1974		—	—	Berlin	Frädrich (1975:70)
19 Oct. 1971 (23 May 1973)	— May 1974	3/5 March 1972	—	—	Erfurt	Czernay (1977:229)
		—	25	—	Erfurt	Czernay (1977:230)

* Left/right, "mature," in this context, means date velvet completely lost. ** This date is given by Frädrich (1975, p. 70) for the March 1967 antler shedding, but it fits only the January 1968 shedding.

polished maturity from end of May to mid-July, are shed between mid-December and end of January (table 5). Yearling antlers are little more than buds. Second-year spikes grow to about 30 mm. Recorded lengths of third- to eighth year antlers range from 63 mm to 90 mm (Vanoli 1967, p. 162).

Vertebral formula.—In a male (FMNH 24363) from Quellón, Isla de Chiloé: 7 cervical, 12 thoracic, 7 lumbar, 5 sacral, 8 caudal. In two specimens (MCZ 5022; 6029) from Chile, precise locality unknown: 7, 7; 13, 13; 6, 7; 4, 4; 8, 5(+?).

KARYOTYPES

The chromosomes of a male pudu studied by Koulischer et al (1972) have a diploid number of 70, with fundamental number of 74. Sixty-six autosomes are acrocentric or telocentric and one pair is metacentric. The X chromosome, a metacentric, is the largest of the complement; the Y chromosome, also metacentric, is the smallest. A few satellites are seen attached to the largest autosome pair.

Spotorno & Fernández-Donoso (1975) found virtually identical karyotypes in a male and female pudu captured alive in Llanquihué. Satellites attached to the largest autosome pair are evident in the illustration of the karyotype, and the metacentric X chromosomes are by far the largest of all.

The pudu karyotype is grossly similar to that of *Odocoileus*. The only other neotropical deer for which karyotypic data are available is the red brocket, *Mazama americana*, with formulae, as cited by Taylor et al (1969, p. 349), " $2n=68$ and $NF=74$ (Taylor et al [Taylor, Hungerford, and Snyder, unpublished] 1968)." According to the authors cited, an extra pair of metacentric autosomes in the brocket accounts for the lower diploid number of chromosomes. It is curious, however, that Benirschke (1977, p. 52, pl. 9) found 50 chromosomes in father and son and 49 in the mother of a family group of *Mazama americana*.

COMPARISONS

All distinctive characters of *Pudu pudu* can be derived from an ancestral form, such as *P. mephistophiles*. Average size is larger, general body form less squat, more brocketlike, with slightly longer muzzle, less-rounded, more elongate ears, and larger eyes; tegumentary glands, most notably lacrimal and pedal, more developed; general body coloration of adult less agouti, the monochromal hairs pheomelanin; fawn with characteristic cervid spotted pattern; cranial parts more advanced, the lacrimal pit large, more deeply excavated, antorbital vacuity larger, its long axis more nearly horizontal; permanent upper canines almost entirely lost. The same relationship holds for all other specific characters described elsewhere. In virtually every case the differences are quantitative. It remains to be tested whether or not complete reproductive isolation between the species has been achieved.

SPECIMENS EXAMINED

Total 31. CHILE. *Concepción*: San Pedro, 1 (FMNH); *Arauco*: Santa Juana, 1 (FMNH); *Sierra Nahuelbuta*, 1 (FMNH); *Isla Mocha*, 1 (AMNH); *Malleco*: Angol, 3 (AMNH); *Cautín*: Maquehua, 1 (AMNH); *Pitrufquén*, 2 (FMNH); *Toltén*, 2 (FMNH); *Valdivia*: Valdivia, 1 (FMNH); *Llanquihué*: Petrohué, 1 (FMNH); *Puerto Montt*, 1 (AMNH); *Chiloé*: Isla Chiloé, 8(5 FMNH; 1 USNM; 2 MCZ); *Lago Cucao*, 1 (AMNH); *Quellón*, 6 (FMNH); *Río Inio*, mouth, 1 (FMNH).

VII. BIOLOGY OF *Pudu pudu*

HABITAT

The Chilean habitat of *Pudu pudu* is the humid forest or Valdivian biotic district, which lies south of the Santiago. As described by Osgood (1943, p. 30), the Valdivian

... extends along the coast and through the mountains to the vicinity of the Gulf of Penas, about lat. 47°S. There is some interdigitation at the northern boundary where humidity increases with altitude, but the change is fairly abrupt from a region [the Santiago] of moderate rainfall and relatively light vegetation to one of great humidity and dense forest. [Footnote: "... rainfall at Valparaiso 20-40 inches; at Valdivia, 80-200 inches."] In the heart of this district, vegetation is widely varied and highly exuberant. Heavy forest growth is combined with dense undergrowth and the numerous cryptograms that go with an atmosphere constantly charged with moisture.

According to Wetterberg (1972, p. 348):

... The most favorable pudu habitat in the [Vicente Pérez Rosales National] Park is ... classified as the Valdivian Forest Type, and the Coigue [Coihue] Forest Type. In the lower altitudes, pudu are often found in the understory thickets consisting of small trees of tiaca (*Caldcluvia paniculata*), avellano (*Guevina avellano*), luma (*Amonyrtus luma*), arrayan (*Myceugenella apiculata*) and huedhued (*Pernettya furians*). I never saw tracks at elevations above 1200 m. nor have sightings been reported by others. At these higher ranges, the understory is often quila (*Chusquea quilla*) and colihue (*C. colue*).

Greer (1965, p. 146) notes that pudus have been seen regularly in the Laguna Malleco area, which "... is heavily forested with coihue (*Nothofagus dombeii*), rauli (*N. alpina*) and roble (*N. obliqua*) along with dense patches of cane [*Chusquea* sp.]."

The habitat in adjacent parts of Argentina is similar to the Chilean.

MAINTENANCE IN CAPTIVITY

In sharp contrast to its northern congener, the southern pudu adjusts readily to captivity, whether as household pet in its native lands, or as resident in zoological gardens in Argentina, Chile, Belgium, England, Germany, Holland, and the United States. Doubtless, it can survive in any temperate zone climate where deer are kept. The female sent to the London zoo in 1830, which served as type of *Cervus humilis* Bennett (= *Pudu pudu*), may have been the first pudu shown in a European zoo. Since then, according to the *International Zoo Yearbook*, published since 1960 by the London Zoological Society, the animal has been kept and successfully bred in the Berlin, Cologne, Erfurt, Hellenthal, Wuppertal, Rotterdam, and London zoos. Birth records, for which dates are available, are listed in Table 6.

A pudu breeding farm, that began with a pair captured in the wild, was established in 1938 in Neuquén, Argentina, by Otto Neumeyer (in Schmidt, 1944, p. 239). A total of eight individuals, including third-generation young, was reported in 1944.

In 1976, according to the *International Zoo Yearbook* for 1978, only 12 animals were living in zoos, as follows: Antwerp 5, West Berlin 1, Cologne 1, Erfurt 1, Wuppertal 3, and Chillán (Chile) 1.

The official studbook keeper, as of 1978, is J. P. Guillermo Staudt, Director, Wildfreigehege Hellenthal, 5374 Hellenthal-Eifel, West Germany, acting under supervision of Carlos Junge, Director, Jardín Zoológico de Chillán Viejo, Chillán, Chile.

TABLE 6. Birth records of *Pudu puda*.

Locality	Mated	Birth	Sex	Birth weight	Shoulder height	Gestation days	Source
Argentina	July 193—	15 Nov. 1939	♂	—	—	—	Neumeayer in Schmidt (1944)
Argentina	—	Nov. 1943–Jan. 1944 (3)	♀♀	—	—	—	Neumeayer in Schmidt (1944)
Chile	—	6 Dec. —	♀	37 oz	15 cm	207	Vanoli (1967)
Chile	—	— Nov. —	♂	35 oz	—	223	Vanoli (1967)
Chile	13 July 1966	31 Jan. 1967	♂	—	—	202	Hick (1967:68:111)
(Chile)	—	5 Nov. —	o	—	—	—	Frädrich (1975:70)
Berlin*	—	—	—	—	—	—	Frädrich (1975:70)
(Chile)	—	13 Nov. —	o	—	—	—	Frädrich (1975:70)
Berlin**	—	—	—	—	—	—	—
(Chile)	—	—	—	—	—	—	—
Cologne	24 April 1967	13 Nov. 1967	♂	—	25 cm (?)	204	Hick (1967:68:112)
Cologne	—	2 Aug. 1968	♀	—	—	—	Windecker (1969:8)
Cologne	—	6 June 1969	♀	—	—	—	Anon. (1969:72)
Cologne	—	8 Jan. 1970	♀	—	—	—	Windecker (1971:6)
Cologne	—	28 July 1970	♂	—	—	—	Anon. (1970:67)
Cologne	—	22 May 1971	♀	—	—	—	Hick (1971:84)
Cologne	—	29 May 1971	♂	—	—	—	Hick (1971:84)
Cologne	—	4 June 1971	♀	—	—	—	Hick (1971:83)
Cologne	—	11 May 1972	♂	—	—	—	Anon. (1972:57)
Cologne	—	27 April 1973	♀	—	—	—	Anon. (1973:75)
Cologne	—	6 May 1974	♀	—	—	—	Anon. (1974:103)
Cologne	—	25 May 1975	♀	—	—	—	Kullmann (1976:36,39)
Cologne	—	10 May 1977	♂	—	—	—	Anon. (1977:101)
Cologne	—	8 June 1977	♂	—	—	—	Anon. (1977:101)
London	—	23 May 1932	o	—	—	—	Zuckerman (1952:901)
London	—	29 May 1933	o	—	—	—	Zuckerman (1952:901)
London	—	— 1975	o	—	—	—	Brambell & Mathews (1977:27)
Erfurt	—	23 May 1973	♂	—	—	218	Czernay (1977:230)
Erfurt	—	3 Sept. 1974	♂	—	—	—	Czernay (1977:230)
Erfurt	—	2 May 1975	♀	—	—	—	Czernay (1977:230)

* Pregnant when imported 26 August. ** Pregnant when imported 8 July.

UNGULATE ASSOCIATIONS

The huemul, *Hippocamelus bisulcus*, is the only other native cervid in Chile, and the only one that might occur within the Argentine portion of the range of *Pudu pudu*. Historically, the range of the grassland vicugna (*Vicugna vicugna*) and guanaco (*Lama guanicoe*) may have contacted that of the pudu in Chile and Argentina, but probably without sympatry.

NUMBERS AND AGGREGATIONS

The Abbé Molina (1782, p. 308) notes that, with onset of winter in the mountains, pudus descended in flocks ("a truppe") to the warm coastal plains of the southern provinces. Gay (1847, p. 159) says they lived in small flocks in the central valley between the cordilleras. However, accounts of modern authors indicate that the pudu, an inhabitant of forest thickets, is a sedentary and solitary animal except during the fall rut when it pairs and in spring when the single young accompanies its mother. Housse (1953, *ex* Wetterberg, 1972, p. 349) allows that pudus may have occurred in small herds before the last half of the 19th century, when the animals abounded, but "now that they have decreased, these groups of two or three are not a herd in formation but rather families not yet dispersed." Natives of the Nahuelbuta region informed Greer (1965, p. 146) that "pudus do not change places of habitation and are in the area in equal numbers in all seasons."

Osgood (1943, p. 230) spoke of the animal living in very dense forest, and of only once catching a glimpse of one. Those collected on his two Chilean expeditions evidently were solitary animals driven from cover by dogs. Schneider (1946, p. 78) encountered the pudu singly or in pairs in the heavily forested parts of the Cordillera de Nahuelbuta, the Cayumanque, and Manquimávida. The semidomesticated pudus that Vanoli (1967) observed in gardens or small preserves were loners, pairs, or family groups consisting of parents with their young of the season.

The largest known concentration of pudus lives on the privately owned Margarita Island, Lake Todos Los Santos, Llanquihué, within the Vicente Pérez Rosales National Park. At this island, Wetterberg (1972, p. 348) reported "a herd of 10-15 with no natural predators or dogs to disturb them, and no interference apart from an occasional stick thrown at them when they wander too close to the vegetable garden. Some of these pudus were brought to the island by colonists on the mainland whose dogs had chased them into lakes or streams where they might have drowned." Wetterberg himself saw only two captive pudus in the town of Peulla, and a pair "casually walking down the road near the hotel at La Ensenada in the early evening."

MIGRATIONS

It has been said (Molina, 1782, p. 309) that herds of pudus come down from the cordillera at the beginning of winter to feed on the plains of the southern provinces of Chile. Yepes (1943, p. 75) states that the deer entered Argentina from Chile through numerous passes in the humid, forested zones of the Andes. He records pudus from elevations as high as 900 m (Lago Lolog) above sea level, but most of the mountain passes to which Yepes alludes are much higher. The pudu does not descend the Argentine slope of the Andes to the Patagonian scrublands.

Occurrence of seasonal migrations has not been verified. According to Osgood (1943, p. 229), "In early accounts and many later ones based on them, [the pudu] is usually spoken of as an animal of the cordillera, but this appears not to be the case since it is actually recorded only from heavily forested regions either near sea level or at very moderate elevations."

Present information indicates that the pudu is a sedentary, cryptic animal, its movements localized and likely limited to the narrowly circumscribed territory of the individual or family group, or to the quest of new territory by the matured young of the year.

LOCOMOTION, PLAY

Information on pudu locomotion consists of a few observations of wild or captive animals in flight or play. Vanoli (1967, p. 155) compares the low, crouching, zigzagging flight of the short-legged pudu with movements of a young boar. Playful, developing young bound and gambol like kids (Hick, 1967/1968). Adults often engage in playful flight in early morning or evening, running and doubling until they pant with tongue hanging out (Vanoli, 1967). Junge (1966, p. 264) describes the female of the pair in the Chillán (Chile) zoo as "sometimes very playful toward evening and early in the morning. She runs about the enclosure like a puppy, zig-zagging, skipping and jumping on the spot till she is so exhausted that the foam shows on her muzzle. Sometimes the more sedate male joins in these games for a moment but he soon gives up or gives his high-spirited mate a rather firm dig in the ribs with his horns. The female then quickly ceases her playfulness and retires to the hut."

ENEMIES

Principal natural enemies of *Pudu pudu* include the native foxes (*Dusicyon* spp.), puma (*Felis concolor*), spotted cats (*F. guigna*, *F. colocolo*), and possibly the eagle owl (*Bubo*). The introduced enemies—man and domestic dogs—have exterminated the pudu throughout most of its range and greatly reduced its numbers in the remainder.

DISEASES AND PARASITES

Hoof-and-mouth disease among free-living pudus was reported by Vanoli (1967, p. 162). He also mentioned infestation with ticks. Two kinds of parasites have since been identified as *Ixodes taglei* and *I. stilesi* by Kohls (1969, p. 280).

FOOD AND WATER

Free-living pudus in Chile, according to Vanoli (1967, pp. 156–157) and others, feed on many kinds of native and introduced trees, shrubs, and vines. They browse mainly on foliage, but also eat bark, twigs, buds, blossoms, fruits, berries, acorns and other nuts, vegetables, and ferns. Branches of the Rosaceae, including roses, raspberries, and blackberries, are preferred above all (Junge, 1966, p. 264). Grass is seldom eaten, but plantain (*Plantago*), clover, other weeds, and cereals are. Salt is taken eagerly. Pudus thrive on the regular vegetarian zoo fare, including commercial food pellets (Czernay, 1977; Hick, 1967/68). Caged young also eat insects (Hick, 1969, p. 115). Perhaps many kinds of invertebrates are consumed in the wild by pudus of all ages. Vanoli (1967) observes that,

among the pudus in reserves and gardens of the Osorno-Llanquihué district, females are fastidious eaters, nibbling a leaf here and another there, seldom eating large quantities of any one kind, except roses, which they especially appreciate. In contrast, males, particularly old bucks, satisfy themselves with basic foods.

The free-living, semidomesticated pudus that Vanoli (1967, p. 162) observed in Chile drank water in summer and winter, even when available food was not dry.

EARTHQUAKE SENSITIVITY

The semidomesticated, free-living pudus of the Osorno-Llanquihué region observed by Vanoli (1967, p. 159) panicked with the onset of the 1960 earthquake in southern Chile. Their lacrimal glands were everted as they fled from one hiding place to another. The subsequent eruption of volcanic ash caused them to cower in their retreats for long periods, with infrequent sallies for foraging.

Unusual behavior of animals prior to earthquakes has attracted man's attention through the ages. For detailed discussions of the subject, see Evernden (1976).

TEMPERATURE REGULATION

Pudus normally live in cool, shaded forests. With regard to those in the Concepción (Chile) zoo, Junge (1932, p. 241) noted, "Should the animal be exposed to the full glare of the sun for 1 or 2 hours it would die the evening of the same day." According to Junge (1966, pp. 263-264), pudus at the Chillán Viejo (Chile) zoo breathed with their mouths open when the temperature rose to 32° C (= 90° F). "Cooling the enclosure by spraying," he writes, "was not a success as the animals were more troubled by a damp heat than by a dry one. On very hot days they withdrew completely into the darkness of their huts to rest or ruminate." In winter, however, as shown by Vanoli (1967, p. 162, fig. 10), free-living pudus emerge into clearings to bask in the warmth of the high sun.

REPRODUCTION, GROWTH, DEVELOPMENT (Tables 7-9)

The female is sexually mature when about six months old (Vanoli, 1967, p. 160; Hick, 1967/68, p. 111). Males may become sexually mature at about the same age, according to Hick (1967/68, p. 111; 1969, p. 110), who has the word of a Chilean resident that a six-month-old female pudu "was covered by a male of the same age" and gave birth about seven months later. The successful mating of a nine-month-old Erfurt zoo male was reported by Czernay (1977, p. 230). Although Vanoli (1967, p. 157) mentions a fertile mating by a one-year-old male, he (1967, p. 163) sets the age of male sexual maturity at 1½ years.

The rut occurs in the fall. Competition or battles between males for possession of the female is unknown. Vanoli (1967) summarizes the mating behavior of a pair of free-living, semidomesticated Chilean animals as follows. The buck is drawn by pheromones to the estrous female living within or near his home range. On meeting, they engage in bouts of butting, the blows usually directed to flanks and groin. This courtship intensifies to a point at which both animals hurl themselves against each other. The buffeting is followed by mutual grooming, with the female carefully licking the male from top to bottom and the buck reciprocating less diligently and thoroughly. The rut lasts several days, and,

TABLE 7. Growth and development of a male *Pudu puda* in the Cologne zoo, Germany.*

Day	Remarks
1	Born 13 November 1967 before 8:00 A.M.; bleats; mother eats fetal membranes; fawn rises, walks to distant corner of cage, lies down; suckles standing up whilst being groomed by mother; weight "about 1000 g" shoulder height "about 25 cm" (=15 cm?). [Weight at birth 370 g, shoulder height 15 cm "after a few hours ran about and hid in a tree in the bush grass," (V). Born London Zoo, 1975, in usual sleeping area; father present; mother active but returns to feed young, licking fawn's anal region while suckling; first suckling attempt at about 10 hr (B).]
2	Changes resting place repeatedly; bleats to call mother; utters alarm cry when frightened. [Definite suckling at 27 hr; suckles for about 5 min at 2-4 hr intervals; gains about 80 g daily (B).]
3	Rests hidden under straw; gambols; nibbles on lettuce and straw but does not swallow; suckles at intervals during day; preorbital glands everted when frightened; goes to mother for nursing. [Fed only in early morning, noon, and evening (V). Runs playfully (B).]
4	Suckles regularly at 10:00, 12:00, 16:00, and 18:00 hours; eats dirt; cowers when frightened. [Ingests dirt and gravel (V).]
5	Enjoys standing in water tank.
8	Tests food eaten by mother but spits it out.
9	[Tests solid food (B).]
12	Eats leaves.
14	Eats lettuce; stands in water trough for longer periods. [Height, 20 cm; eats tender leaves; runs along with adults (V).]
15	Straw covering cage floor replaced by sand and cinders; prefers to sit on cinders; rises on cage bars.
16	Cage movements follow regular pattern; changes resting place.
17	No longer hides; rests in center of cage.
19	Lowers head and butts mother.
22	Butts mother and observer (Hick); eats bananas and commercial food pellets for first time.
24	Following fright attempts to climb onto mother's back.
26	Takes to cover more readily when frightened; groomed less often by mother; alternates running with butting.
28	Eats hay; takes grasshopper from observer's hand; fawn and mother often rest near each other.
30	[Last seen suckling (B).]
33	Leaps over mother's back in play.
37	Licks salt stone.
38	Caught and ate cockroaches.
39	Mother goes to resting young for nursing.
40	Young nearly resembles mother in size, spotted coat disappearing; both use same place for defecation and urination.
52	Spot pattern virtually gone.
60	Weaned; rejected by mother when attempts to suckle. [Nearly as large as mother; shoulder height about 30 cm, spotted pelage gone (V). Faunal stripes disappear (B).]
62	Eats adult fare.
65	Accustomed to solid food; no longer attempts to suckle.
90	[Faunal spots gone (B).]
180	♂ young sexually mature. [♀ young sexually mature (V).]
270	[First antlers appear in ♂ (V), ♂ sexually mature (Czernay, 1977, p. 230).]

* Source: Hick (1967/68; 1969), with interpolations in brackets from Vanoli, 1967 (V), free living, Chile; Brambell & Mathews, 1977 (B), London zoo; and Czernay, 1977, Erfurt Zoo.

TABLE 8. Chronology of weight increment, actual and proportional, in a male and female *Pudu puda* born in the Thüringer zoo, Erfurt, Germany, from day 1 to day 98 for both, to sexual maturity (182 days) and beyond (205 days) for female only.

Day	♀ *	Daily average increment	♂ **	Daily average increment
1	0.78	11.5%	—	—
2	0.87	—	.70	—
2–3	—	9.2%	—	14.3%
4	1.03	—	.90	—
4.5	—	3.4%	—	7.8%
6	1.10	—	1.04	—
6–7	—	8.2%	—	8.2%
8	1.28	—	1.21	—
8–11	—	2.7%	—	5.4%
12	1.42	—	1.47	—
12–15	—	3.9%	—	3.7%
16	1.64	—	1.69	—
16–17	—	3.4%	—	2.1%
18	1.75	—	1.76	—
18–20	—	3.8%	—	3.3%
21	1.95	—	2.04	—
21–24	—	2.1%	—	2.3%
25	2.11	—	2.23	—
25–29	—	2.7%	—	2.1%
30	2.40	—	2.46	—
30–33	—	1.0%	—	1.3%
34	2.50	—	2.69	—
34–37	—	1.6%	—	0.4%
38	2.66	—	2.73	—
38–42	—	1.4%	—	1.5%
43	2.85	—	2.94	—
43–47	—	1.8%	—	1.6%
48	3.10	—	3.17	—
48–55	—	0.8%	—	1.1%
56	3.30	—	3.44	—
56–62	—	1.7%	—	1.0%
63	3.70	—	3.67	—
67	3.85	—	3.80	—
63–70	—	0.7%	—	0.8%
71	3.90	—	3.90	—
71–80	—	0.4%	—	0.3%
81	4.05	—	4.0	—
81–98	—	0.6%	—	0.6%
99†	4.60	—	4.40	—
112	4.80	—	—	—
118	5.03	—	—	—
146	5.45	—	—	—
160	5.77	—	—	—
170	6.05	—	—	—
182	6.25	—	—	—
195	6.20	—	—	—
205	6.25	—	—	—

Source: Czernay (1977, pp. 238, 239).

* Born 2 May 1975 in Erfurt zoo. ** Born 3 September 1974 in Erfurt zoo. † After 99 days, male resisted too vigorously for accurate weighing.

TABLE 9. Three oldest longevity records for *Pudu puda*.

Earliest recorded date	Age	Last recorded date	Interval	Zoo locality	Reference
10 July 1909	Adult ♀	1 Jan. 1917	7 yr, 6 mo	Berlin	Frädrich (1975:71)
9 Nov. 1966	Adult ♂	10 June 1974 (living)	8 yr, 7 mo	Berlin	Frädrich (1975:71)
14 Feb. 1866	Newborn	17 Feb. 1875	9 yr, 5 days	London	Jones, in Crandall (1964:595)*

* The information was contained in an unpublished mimeographed manuscript dated 1958. I find no reference to this pudu in publications of the Zoological Society of London.

during a three-day peak the buck mounts the doe repeatedly. He thrusts without panting or other signs of effort, but the female reacts to each thrust with a bleat.

During the rut of the following year, Vanoli reports, the male served the same female, as well as a six-month-old, sexually mature virgin. No courtship preceded his repeated mountings of the younger animal. On the approach of the buck, she arched her back, then stooped and pressed against the ground in response to the male's probings. She was silent throughout the act. However, the older doe responded with bleats to the thrusting of the male, as she had the year before.

Newborn pudus are dropped in the spring of northern or southern hemispheres after a gestation of about seven months (202 to 223 days). Neumeyer (in Schmidt, 1944) reports six births in Neuquén, Argentina, from November through January, four occurring in November alone. Two births in the Osorno-Llanquihué region recorded by Vanoli (1967) occurred in November and December. A late January birth in an unspecified Chilean locality was mentioned by Hick (1969, p. 110), and two pregnant females that arrived in the Berlin zoo produced in November of the same year according to Frädrich (1975). Eighteen other parturitions occurred in western European zoos during the following months; the details are given in Table 6.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1	0	0	1	11	1	1	1	1	0	1	0

The 13 (72%) spring (April, May, June) and summer (July, August, September) births were produced by captive does that had borne young the preceding year in the same zoos. A wild, captured female that arrived pregnant in the Cologne zoo was responsible for the single November birth. The history of the lone January birth, also in the Cologne zoo, is not given.

Fifteen births in the Berlin, Erfurt, Cologne, and Wuppertal zoos from 1967 to the end of 1973, compiled by Frädrich (1975, p. 70), are distributed by months as follows, with the January birth in the Cologne zoo excluded:

April	May	June	July	August
1	4	6	3	1

Sex of 22 young born in the same four German zoos is 11 males and 11 females. Newborn listed in Table 6 include 10 males, eight females, and five with no sex recorded. Twins have not been recorded.

Composition of milk is shown in Table 10.

TABLE 10. Composition of milk produced on 32nd lactation day (4 June 1975) by wild-caught pudu (*Pudu pudu*) maintained in Erfurt zoo since August 1971, compared with other ungulates and *Homo*.

Component	Pudu	Mule deer	Roebuck	Goat	Cow	Human
a. Fat	3-4	10.5	6.7	4.07	2.8-3.5	3.5
b. Albumin	2.03	9.56	8.8	3.76	3.5	1.2-1.5
c. Lactose	7-8	3.91	3.9	4.44	4.7	7
d. Potassium	81	-	-	-	150	53
e. Calcium	37	-	-	-	130	31
f. Phosphorous	46	-	-	-	97	15
g. Sodium	110	-	-	-	53	15
h. Chlorine	22	-	-	-	100	36

Values: a—c = g/100 ml; d—h = mg/100 ml after electrolysis.

Source: Czernay (1977, p. 235).

LONGEVITY

The three oldest longevity records for zoo-kept *Pudu pudu* are listed in Table 9. Age at accession of each of the first two animals listed probably is more than one year.

VIII. SUMMARY

The South American deer of the genus *Pudu*, comprised of two of the smallest living species, is characterized and compared with other artiodactyls, particularly with respect to limb proportions and metapodial morphology. A hypothetical reconstruction of pudu history is presented, and the genus is arranged systematically as representative of tribe Pudini, subfamily Odocoileinae, family Cervidae. The northern Andean species, *P. mephistophiles* de Winton, is shown to be primitive, and the southern Chilean-Argentine species, *P. pudu* Molina, derived. Both species are described, characterized, and compared: their geographic ranges are plotted, and their life history notes are summarized. The status of wildlife conservation of the pudu also is discussed.

IX. ACKNOWLEDGMENTS

Thanks are expressed to the authorities of the institutions listed in the "Abbreviations" section for permission to study the material in their charge. Most of the pen drawings were prepared by Marion Pahl, former Field Museum staff artist; others were contributed by Zorica Dabich of the present staff. Most photographs of skulls were taken by Curtis Bean, a work-study student, later a volunteer, the remainder by staff photographer Ron Testa, who also processed the prints. Sarah Derr Bruner typed the manuscript, and technical assistant Barbara Brown helped with research and preparation of the manuscript for publication.

I am indebted to the following persons and their institutions for providing photographs of living pudus and brockets used in the comparisons and descriptions of external characters:

Dr. Don D. Farst, Director, and Violet K. Springman, Information Coordinator, Gladys Porter Zoo, Brownsville, Texas.

Dr. Hans Frädrich, Assistant Director, Zoologischer Garten, Berlin.

Uta Hick, Scientific Assistant, Zoologischer Garten, Köln (Cologne).

Dr. Clyde A. Hill, San Diego Zoological Society.

X. GAZETTEER AND EXPLANATION OF MAPS

(figs. 30, 35)

Localities mentioned in the text are listed from north to south by country, province, or department, and by nearest town, subdivision, or topographic feature where *Pudu* were captured, observed, or reported as probably present. Documentation for specimens I examined is included with their respective localities. Documentation for other recorded localities is contained in the literature cited in text, including the annotated synonymies for each of the two species. The numbers identify the localities plotted in Figures 30 and 35.

COLOMBIA—*Pudu mephistophiles*

Valle (Valle del Cauca)

1. Barragán, 4°01'N, 75°52'W.
2. Las Hermosas (Páramo), 3°48'N, 75°56'W.
2. Las Hermosas.

Cauca

3. Moras (Páramo), 2°50'N, 76°12'W.
4. Delicias (Páramo), 2°38'N, 76°14'W.
4. Malvasá, 2°34'N, 76°04'W; 3,000–3,500 m.
K. von Sneider, November–December 1956; January 1957, September 1957, October 1957, December 1957; January–February 1958, 15 (FMNH).
5. Munchique (Cerro), 2°32'N, 76°57'W.
6. Pusna. See Pusha.
6. Pusha (Cerro), Totoró, 2°30'N, 76°24'W; 2,800 m.
6. Guanacas (Páramo), 2°27'N, 76°15'W.
6. Quintana, 2°24'N, 76°25'W.
K. von Sneider, November 1945, 1 (FMNH).
6. San Rafael (Páramo), 3,400 m.
Adjacent to Páramo de Puracé (q.v.).
6. Puracé (Páramo), 2°21'N, 76°23'W; 2,800 m, 3,480 m, 3,500 m.
F. Lehmann, July 1945, 1 (USNM), February, May 1953, 2 (AMNH); 1 (FMNH).
6. Coconuco, Paletará, 2°16'N, 76°22'W; 3,200 m.
H. Van Deusen, 1 (AMNH).
7. Sotará (Páramo), 2°12'N, 76°31'W.
7. Paletará, 2°10'N, 76°26'W.
H. Van Deusen, 2 (AMNH).
8. La Vega, 2°05'N, 76°50'W; 3,500 m.
K. von Sneider, November 1956, 1 (FMNH).
9. Las Papas (Páramo), 1°55'N, 76°36'W; 4,000 m.
9. Cusiyaco (Laguna), 1°55'N, 76°36'W.
9. Lebrero (Páramo), NE Páramo de las Papas (q.v.).
9. Valle de las Papas, 1°52'N, 76°40'W.

Tolima

10. Los Nevados.
11. Roncesvalles, 4°01'N, 75°32'W.

Huila

12. Nevado del Huila.
13. San Antonio, upper Río Magdalena, 1°57'N, 76°29'W; 2,700–4,000 m.
P. Hershkovitz, August–September 1951 (observation).
14. Cueva de Los Guácharos, ca. 1°35'N, 76°00'W.

Nariño

15. Azufral (Páramo), 1°05'N, 77°43'W.
16. Cumbal (Páramo), 0°57'N, 77°52'W.
17. Chiles (Páramo), 0°48'N, 77°57'W.

ECUADOR—*Pudu mephistophiles*

Carchi

18. Atal, Hacienda El Vínculo, 0°35'N, 77°44'W. Cordillera Pimanpiro, W slope Cor-

dillera Oriental.

P. Hershkovitz, October 1934 (report).

Pichincha

19. Cayambe (Mt.), 0°2'N, 77°59'W.

L. Söderström, May 1898, 1 (BM).

20. Deleted.

21. Papallacta, 0°22'S, 78°08'W.

L. Söderström 1896, 1 (BM), May 1897, 1 (BM).

21. Papallacta (Páramo), 3,600–3,700 m. See Papallacta.

22. Antisana (Mt.), 0°30'S, 78°08'W.

Cotopaxi

23. Parque Nacional de Cotopaxi. See Salcedo.

23. Salcedo, W of, 1°02'S, 78°34'W; 3,500 m.

Tungurahua

24. Llanganates (Cordillera), 1°13'S, 78°15'W.

Andes-Amazon Expedition 1935–1936, 1 (ANSP).

PERU—*Pudu mephistophiles*

Huánuco

25. Quivilla road (Quivilla=9°32'S, 76°41'W); 3,300 m.
40 km NW Huánuco (q.v.).

26. Carpath (summit), 9°42'S, 76°09'W; 2,000–3,000 m.
On Huánuco-Tingo María Road.

26. Zapatogocha (Bosque), Acomayo, 9°43'S, 76°04'W; 3,100 m.
P. Hocking, November 1972, 1 (FMNH).

26. Chaglla, 9°50'S, 75°54'W.

27. Yanacocha, Río Quero, 9°48'S, 76°25'W.

27. Huánuco, above, 9°55'S, 76°14'W.

27. Pamacucho, 4 km from Huánuco (Grimwood, 1969, p. 79).

27–28. Huánuco and Ambo, between, 9°55'S, 76°14'W—10°07'S, 76°10'W; 2,700–3,300 m.

28. Ambo, 10°07'S, 76°10'W. See Huánuco and Ambo, between.

Junín

29. Paucartambo (Río), 10°57'S, 75°16'W.

29. San Ramón, above, 11°08'S, 75°20'W; 2,000–3,000 m.

30. Huasahuasi (Río), 11°15'S, 75°37'W.

CHILE—*Pudu puda*

Maule

1. Constitución, 35°20'S, 72°25'W; 1 m.

2. Cauquenes, 35°58'S, 72°21'W; 143 m.

Concepción

— Pedro Valdivia, not located

3. Concepción, 36°50'S, 73°03'W; 13 m.

4. San Pedro, 36°51'S, 73°02'W; 17 m.
Carlos S. Reed, 1 (FMNH).

5. Manquimávida, 36°57'S, 73°01'W.

5. Cayumanque, 36°40'S, 72°33'W.

Bío Bío

6. Antuco, 37°20'S, 71°41'W; 602 m.

Arauco

7. Santa Juana, 37°11'S, 72°52'W; 75 m.

W. H. Osgood, 1 (FMNH).

8. Cordillera de Nahuelbuta. See Sierra Nahuelbuta.

8. Sierra Nahuelbuta, 37°48'S, 73°02'W; highest point, 1,440 m.
W. H. Osgood, November 1939, 1 (FMNH).

8. Vega Blanca. See Sierra Nahuelbuta.

9. Isla de la Mocha. See Isla Mocha.

9. Isla Mocha, 38°22'S, 73°56'W.

D. S. Bullock, December 1932, 1 (AMNH).

Malleco

10. Angol, 37°48'S, 72°43'W; 150 m.
D. S. Bullock, September 1929, 2 (AMNH), July 1932, 1 (AMNH).
11. Laguna Malleco, 38°13'S, 71°49'W.
12. Galvarino, 38°24'S, 72°47'W; 61 m.

Cautín

13. Temuco, 38°44'S, 72°36'W; 113 m.
13. Maquehue, Temuco. See Maquehua.
13. Maquehua, Temuco, 38°46'S, 72°39'W.
D. S. Bullock, April 1910, 1 (AMNH).
14. Pitruquén, 38°59'S, 72°39'W; 93 m.
Carlos S. Reed, June 1926, 1 (FMNH), November 1955, 1 (FMNH).
15. Toltén, 39°13'S, 73°13'W.
Carlos S. Reed, March, May 1926, 2 (FMNH).

Valdivia

16. Callumapu, 39°36'S, 72°13'W.
17. Valdivia, 39°48'S, 73°14'W; 7 m.
Carlos S. Reed, October 1936, 1 (FMNH).
17. Santo Domingo, 39°53'S, 73°12'W.
18. Mariquina, 40°08'S, 72°20'W.

Llanquihué

19. Vicente Pérez Rosales, Parque Nacional, 41°00'S, 72°15'W.
19. Petrohué, Lago Todos Santos, 41°08'S, 72°25'W.
W. H. Osgood, November 1939, 1 (FMNH).
19. Cayetúe. See Cayutúe.
19. Cayutúe, Lago Todos Santos, 41°14'S, 72°17'W; 221 m.
20. Lago Llanquihué, 41°08'S, 72°48'W; 51 m.
21. Llanquihué, 41°15'S, 73°01'W; 54 m.
22. Puerto Montt, 41°28'S, 72°57'W; 1 m.
F. M. Chapinar, April 1920, 1 (AMNH).

Chiloé

- Isla Chiloé.
Carlos S. Reed, December 1925, 2 (FMNH), February 1933, 1 (FMNH); B. Dean, 1 (USNM); Gerrard, 2 (MCZ); no data, 2 (FMNH).
23. Lago Cucao, Isla Chiloé, 42°38'S, 74°07'W.
Junius Bird, 1936, 1 (AMNH).
 24. Quellón, Isla Chiloé, 43°08'S, 73°40'W.
W. H. Osgood, January 1923, 6 (FMNH).
 25. Río Inio, mouth, Isla Chiloé, 43°21'S, 74°07'W.
W. H. Osgood, January 1923, 1 (FMNH).

Aisén

26. Río Baker, 47°30'S, 73°37'W.

Magallanes

27. Isla Riesco, 53°00'S, 73°37'W.

ARGENTINA—*Pudu puda**Neuquén*

28. Quillén (Río), 39°23'S, 70°56'W.
29. Lago Lolog, San Martín de los Andes, 40°05'S, 71°20'W.
30. Cordillera del Trompul, San Martín de los Andes, 40°08'S, 71°26'W.
30. Lago Lacar, 40°11'S, 71°30'W.
30. Brazo Correntoso, San Martín de los Andes, south of Cordillera del Trompul.
31. Lanín Parque Nacional, 39°30'S, 71°30'W; 600–3,776 m.
32. Nahuel Huapí Parque Nacional, 41°00'S, 71°30'W.

Río Negro

33. Lago Mascaridí, 41°21'S, 71°52'W; 798 m.

Chubut

34. Los Alerces Parque Nacional, 42°50'S, 71°50'W.

Santa Cruz

35. Perito Francisco P. Moreno Parque Nacional, 47°50'S, 72°15'W; 800–2,770 m.
36. Los Glaciers Parque Nacional, 50°00'S, 73°30'W.

XI. LITERATURE CITED

- ANONYMOUS. 1969. Tiergeburten im Kölner Zoo. Fr. Köln. Zoo, **12**(2): 71–72.
- . 1970. Tiergeburten im Kölner Zoo. Fr. Köln. Zoo, **13**(2): 67.
- . 1972. Säugetiere und Vogel die im Kölner Zoo geboren und grossgezogen wurden. Z. Köln. Zoo, **15**(2): 57.
- . 1973. Säugetiere und Vogel, die im Kölner Zoo geboren wurden. Z. Köln. Zoo, **16**(2): 75.
- . 1974. Säugetiere und Vogel, die im Kölner Zoo geboren wurden. Z. Köln. Zoo, **17**(3): 103.
- . 1977. Säugetiere und Vogel, die seit dem Erscheinen der Letzten Zoo-Zeitschrift im Kölner Zoo geboren wurden. Z. Köln. Zoo, **20**(3): 101.
- . 1978. Säugetiere und Vogel, die seit dem Erscheinen der Letzten Zoo-Zeitschrift im Kölner Zoo geboren wurden. Z. Köln. Zoo, **21**(1): 27.
- BENIRSCHKE, K. 1977. Genetic management. Int. Zoo. Yearb., **17**: 50–60, pl. 9.
- BLAINVILLE, H. H. DE. 1816. Sur plusieurs espèces d'animaux mammifères, de l'ordre des ruminans. Bull. Sci. Soc. Philomat. Paris, **1816**: 73–82.
- BRAMBELL, M. R., AND S. J. MATHEWS. 1977. Criteria for the management of pudu in captivity. Proc. Symp. 1, Assoc. Brit. Wild Animal Keepers, pp. 25–28.
- BROOKE, V. 1874. On Slater's muntjac and other species of the genus *Cervulus*. Proc. Zool. Soc. London, **1874**: 33–42, pls. 8, 9.
- . 1878. On the classification of the Cervidae, with a synopsis of the existing species. Proc. Zool. Soc. London, **1878**(2): 883–998, pl. 55.
- CABRERA, A. 1961 (1958–1961). Catálogo de los mamíferos de America del sur. Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia," **4**(2): 309–732.
- CARETTE, E. 1922. Cérvidos actuales y fósiles de Sud America. Rev. Mus. de la Plata, **26**: 393–472.
- CHURCHER, C. S. 1966. Observaciones sobre el status taxonómico de *Epieuryceros* Ameghino 1889 y sus especies *S. truncus* y *E. proximus*. Ameghiniana, **4**(10): 351–362, 13 figs.
- COWAN, I. M., AND C. W. HOLLOWAY. 1973. Threatened deer of the world: Conservation status. Biol. Conserv., **5**(4): 243–250, 1 fig.
- . 1974. Threatened deer of the world: Research programmes for conservation. Biol. Conserv., **6**(2): 112–117, 1 fig.
- . 1975. Geographical location and conservation of the threatened deer of the world. Proc. Working Meeting IUCN Survival Service Comm. Deer Specialist Group. Longview, Washington, IUCN (Morges), pp. 11–22.
- CZERNAY, S. 1977. Zur Haltung und Zucht von Südpudus (*Pudu pudu* Molina 1782) im Thüringer Zoopark Erfurt. Zool Gart (n.f.), **47**(3/4): 226–240, 14 figs.
- DENNLER DE LA TOUR, G. 1957. The national parks and reserves of Argentina. Oryx, **4**(3): 159–167, 3 figs.
- DOUROJEANNI, M. J. 1968. Estado actual de la conservación de la flora y de la fauna en el Peru. Ciencia Interamericana, **9**(1–6): 1–12, 8 figs.
- EVERNDEN, J. F. (ED.). 1976. Abnormal behavior prior to earthquakes, I. Office of Earthquake Studies. U.S. Geol. Surv., Menlo Park. California, 429 pp.
- FLOWER, W. H. 1885. An Introduction to the Osteology of the Mammalia. Macmillan and Co., London, ed. 3, pp. i–ix, 1–383, 134 figs.
- FLEROV, K. K. 1952. Musk deer and deer. Fauna of U.S.S.R. Mammals. (Moscow) **1**(2): 1–257, 78 figs. (English translation published 1960 for the National Science Foundation, Washington, D.C., and the Smithsonian Institution by the Israel Program for Scientific Translations.)
- FRÄDRICH, H. 1974. Notizen über seltener gehaltene Cerviden. Teil I. Zool. Gart. (n.f.), **44**(4): 189–200, 10 figs.
- . 1975. Notizen über seltener gehaltene Cerviden. Teil II. Zool. Gart., **45**(1): 67–77, 9 figs.

- FRECHKOP, S. 1965. Notes sur les mammifères. LII.-Au sujet d'un caractère dentaire des cervidés. Bull. Inst. Roy. Sci. Nat. Belgique, **41**(25): 1-10, 8 figs.
- FRICK, C. 1937. Horned ruminants of North America. Bull. Amer. Mus. Nat. Hist., **49**: i-xxviii, 1-669, 68 figs.
- GARROD, A. H. 1877. Notes on the visceral anatomy and osteology of the ruminants, with a suggestion regarding a method of expressing the relation of species by means of formulae. Proc. Zool. Soc. London, **1877**: 2-18.
- GAY, C. 1847. Historia física y política de Chile. Mus. Hist. Nat. Chile Santiago, **1**: 1-496.
- GAY, C., and P. GERVAIS. 1846. Sur le *Capra pudu* et l'*Equus bisulcus* de Molina. Ann. Sci. Nat. Zool. Paris, ser. 3, **5**: 87-94.
- GMELIN, J. F. 1788. Caroli Linne Systema Naturae per regna tria naturae . . . Leipzig, ed. 13, **1**: [12], 1-500.
- GRAY, J. E. 1850. Gleanings from the menagerie and aviary at Knowsley Hall. Hoofed quadrupeds. Knowsley [4], 1-76, 62 pls.
- . 1852a. Synopsis of the species of deer (Cervina), with the description of a new species in the gardens of the society. Proc. Zool. Soc. London, **1850**: 222-244, pls. 22-28.
- . 1852b. Catalogue of the specimens of Mammalia in the collection of the British Museum. Part III. Ungulata Furcipedata. London. pp. i-xvi, 1-286, 2 figs., 37 pls.
- GREER, J. K. 1965. Mammals of Malleco Province Chile. Publ. Mus. Michigan St. U., Biol. Sci., **3**(2): 49-152, 8 pls, 5 figs.
- GRIMWOOD, I. R. 1969. Notes on the distribution and status of some Peruvian mammals, 1968. Special Publ. no. 21. American Committee for International Wild Life Protection and New York Zoological Society. vi + 1-86 pp., illus.
- HALTENORTH, T. 1963. Klassifikation des Säugetiere: Artiodactyla. I. Handb. Zool., Berlin, **8**(32/1): 1-167, 16 pls.
- HARROY, J. P. 1971. United Nations list of national parks and equivalent reserves. Hayez, Brussels, ed. 2, 601 pp., illus.
- . 1972. Addendum-Corrigendum to the second edition of the United Nations list of national parks and equivalent reserves. Hayez, Brussels, 107 pp.
- HERSHKOVITZ, P. 1948. The technical name of the Virginia deer with a list of the South American forms. Proc. Biol. Soc. Washington, **61**: 41-48.
- . 1958a. The technical names of the South American marsh deer and pampas deer. Proc. Biol. Soc. Washington, **71**: 13-16.
- . 1958b. The metatarsal glands in white-tailed deer and related forms of the neotropical region. Mammalia, **22**(4): 537-546.
- . 1958c. A geographic classification of neotropical mammals. Fieldiana: Zool., **36**(6): 583-620.
- . 1959a. A new species of South American brocket, genus *Mazama* (Cervidae). Proc. Biol. Soc. Washington, **72**: 45-54, 4 pls.
- . 1959b. A new race of red brocket deer (*Mazama americana*) from Colombia. Proc. Biol. Soc. Washington, **72**: 93-96.
- . 1966. Mice, land bridges and Latin American faunal interchange. In Wenzel, R. L. and V. V. Tipton, (eds.). *Ectoparasites of Panama*. Field Museum of Natural History, Chicago, pp. 725-751, figs. 151-154.
- . 1972. The recent mammals of the neotropical region: A zoogeographic and ecological review. In Keast, A., Erk, F. G., and Glass, B. (eds.). *Evolution, Mammals and Southern Continents*. State U. of New York Press, Albany, N.Y., pp. 311-431, 16 figs.
- . 1977. Living New World monkeys (Platyrrhini) with an introduction to Primates. Vol. 1. U. of Chicago Press, Chicago, 1,117 pp., 520 figs., 7 col. pls.
- HICK, U. 1967/68. Geglückte Aufsucht eines Pudus (*Pudu pudu* Mol.) im Kölner Zoo. Fr. Köln. Zoo, **10**(4): 111-117, 15 figs.
- . 1969. Successful raising of a pudu, *Pudu pudu*, at Cologne Zoo. Int. Zoo. Yearb., **9**: 110-112.
- . 1971. Säugetiere und Vogel, die in Kölner Zoo geboren und grossgezogen wurden. Z. Köln. Zoo, **14**(2): 83-84.

- . 1975. In Frädrich H., Notizen über seltener gehaltene Cerviden. Teil II. Zool. Gart. (n.f.), 45: 1–69.
- HOUSSE, P. R. 1953. Animales salvajes de Chile en su clasificación moderna. Universidad de Chile (Santiago). (Work not seen, cited from Wetterberg, G. B. 1972. Pudu in a Chilean national park. *Oryx*, 11(5): 349.)
- HUNSAKER II, D. 1972. National parks in Colombia. *Oryx*, 11(6): 441–448, 4 figs.
- JONES, M. L. 1964. In Crandall, L.S., The Management of Wild Mammals in Captivity. U. of Chicago Press, Chicago, p. 595.
- JUNGE, C. 1932. Pduhirsche sind sehr hitzeempfindlich. Zool. Gart. (n.f.), 5: 241.
- . 1966. Pudu (*Pudu pudu*) at Chillan Viejo Zoo. Int. Zoo. Yearb. 6: 263–264.
- KOHL, G. M. 1969. *Ixodes taglei* n. sp. (Acarina: Ixodidae) a parasite of the deer, *Pudu pudu* (Mol.), in Chile. J. Med. Entomol., 6(3): 280–283.
- KOULISCHER, L., J. TYSKENS, AND J. MORTLEMANS. 1972. Mammalian cytogenetics. VII. The chromosomes of *Cervus canadensis*, *Elaphurus davidianus*, *Cervus nippon* (Temminck) and *Pudu pudu*. Acta Zool. Path. Antwerp., no. 56: 25–30, 3 figs.
- KRAGLIEVICH, L. 1932. Contribución al conocimiento de los ciervos fósiles del Uruguay. An. Mus. Hist. Nat. Montevideo, ser. 2(3): 355–439, pls. 60–67.
- KULLMANN, E. 1976. Jahresbericht 1975 der Aktiengesellschaft zoologischer Garten Köln. Z. Köln. Zoo, 19(2): 31–41.
- LEHMANN, E. VON. 1960. Das Problem der Grössenabnahme (Deminutions-Tendenz) beim Reh., Z. Jagdwissensch. 6(2): 41–51, 1 fig.
- LEHMANN, F. C. 1945. Un venado del subgénero *Pudella* nuevo para la Ciencia. Rev. Univ. Cauca (Popayán, Colombia) Zool. no. 6: 76–79, 2 figs.
- . 1959. *Pudu mephistophiles wetmorei* Lehmann—Venado Conejo. Nov. Colombianas. Contrib. Cient. Mus. Hist. Nat. Univ. Cauca (Popayán, Colombia), 1(4): 202–204, 3 figs.
- . 1960. Notas adicionales sobre *Pudu mephistophiles wetmorei* Lehmann. Nov. Colombianas. Contrib. Cient. Mus. Hist. Nat. Univ. Cauca (Popayán, Colombia), 1(4): 280–283, 1 fig.
- LYDEKKER, R. 1915. Catalogue of the Ungulate Mammals in the British Museum (Natural History). Vol. IV. Artiodactyla, families Cervidae (deer), Tragulidae (chevrotains), Camelidae (camels and llamas), Suidae (pigs and peccaries), and Hippopotamidae (hippopotamuses). British Museum, London, xxi + 1–438.
- MATTHEW, W. D. 1908. Osteology of *Blastomeryx* and phylogeny of the American Cervidae. Bull. Amer. Mus. Nat. Hist., 24: 535–562.
- MOLINA, G. I. 1782. Saggio sulla storia naturale del Chili. Tommaso d'Aquino Press, Bologna, Italy, 368 pp.
- NOTTEBOHN, F. 1967. Argentine fauna: Time of decision. Anim. Kingd. 70: 112–118, 9 figs.
- OSGOOD, W. H. 1943. The mammals of Chile. Field Museum Zool. Ser., 30(542): 1–268, 33 figs.
- PASCUAL, R., E. ORTEGA AND E. TONNI. 1966. Las edades del Cenozoico mamalífero de la Provincia de Buenos Aires. In Borrello, A.V., Paleontografía bonaerense. Com. Inv. Cient. Prov. Buenos Aires. (La Plata), fasc. 4 (Vertebrata): 3–27.
- PEFAUR, J. 1969. Consideraciones sobre el problema de la conservación de los mamíferos silvestres Chilenos. Bol. Informativo Santiago, no. 93/94: 4–10.
- POCOCK, R. I. 1911. On the specialised cutaneous glands of ruminants. Proc. Zool. Soc. London, 1910: 840–986, 142 figs.
- . 1923. On the external characters of *Elaphurus*, *Hydropotes*, *Pudu*, and other Cervidae. Proc. Zool. Soc. London, 1923: 181–207, figs. 2–17.
- RAFINESQUE, C. S. 1817a. Museum of natural sciences. Dissertation on water snakes, sea snakes and sea serpents. American Monthly Mag., 1: 431–437.
- . 1817b. Descriptions of seven new genera of North American quadrupeds. American Monthly Mag., 2: 44–46.
- SCHMIDT, H. 1944. Argentinische Säugetiere. Imprenta Mercier, Buenos Aires, 258 pp., 117 figs., 2 col. pls.

- SCHNEIDER, C. O. 1946. Catálogo de los mamíferos de la Provincia de Concepción. Bol. Soc. Biol. Concepción, **21**: 67-83.
- SCLATER, P. L. 1871. Notes on rare or little known animals now or lately living in the Society's Gardens. Proc. Zool. Soc. London, **1871**: 221-240, pls. 14-17.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85**: i-xvi, 1-350.
- SPOTORNO, O., AND R. FERNANDEZ-DONOSO. 1975. The chromosomes of the Chilean dwarf-deer "pudu," *Pudu pudu* (Molina). Mamm. Chromosome Newsl., **16**(1): 17-18, fig. 10.
- TAYLOR, K. M., D. A. HUNGERFORD, AND R. L. SNYDER. 1969. Artiodactyl mammals: Their chromosome cytology in relation to patterns of evolution. In Benirschke, K., (ed.). Comparative Mammalian Cytogenetics. Springer Verlag, New York, pp. 346-356.
- THOMAS, O. 1908. A new deer of the brocket group from Venezuela. Ann. and Mag. Nat. Hist., ser. 8, **1**: 349-350.
- . 1913. On certain of the smaller S.-American Cervidae. Ann. and Mag. Nat. Hist., ser. 8, **11**: 585-589.
- VAN DER HAMMEN, T. 1974. The Pleistocene change of vegetation and climate in tropical South America. J. Biogeogr., **1**: 3-26.
- VANOLI, T. 1967. Beobachtungen an pudus, *Mazama pudu* (Molina 1782). Säugetierk. Mitt., **15**(2): 155-163, 10 figs.
- WETTERBERG, G. B. 1972. Pudu in a Chilean national park. Oryx, **11**(5): 347-351. 4 figs.
- WINDECKER, W. 1969. Jahresbericht des Zoologischen Gartens Köln 1968. Fr. Köln. Zoo, **13**(1): 3-12.
- . 1971. Jahresbericht des Zoologischen Gartens Köln 1970. Zeitschr. Köln. Zoo, **14**(1): 3-12.
- WINTON, W. E. DE. 1896. On some mammals from Ecuador. Proc. Zool. Soc. London, **1896**: 507-513, pls. 19, 20.
- YEPES, J. 1943. Localidades argentinas para el pudu chileno. Rev. Argentina Zoogeogr., **3**(1-2): 75-76.
- ZUCKERMAN, S. 1952. The breeding season of mammals in captivity. Proc. Zool. Soc. London, **122**: 827-950.

Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496
Telephone: (312) 922-9410