

THE GENUS MARTES (MUSTELIDAE) IN NORTH AMERICA:
ITS DISTRIBUTION, VARIATION, CLASSIFICATION, PHYLOGENY
AND RELATIONSHIP TO OLD WORLD FORMS

by

Edwin M. Hagmeier

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National Museum of Canada

ABSTRACT

The Genus *Martes* (Mustelidae) in North America: its Distribution, Variation, Classification, Phylogeny and Relationship to Old World Forms

Three subgenera of the genus *Martes* exist in the world today. The first, *Martes*, consists of the following species: *M. americana*, *M. foina*, *M. martes*, *M. melampus* and *M. zibellina*; the second, *Pekania*, of only one, *M. pennanti*; and the third, *Charronia*, of one, *M. flavigula*, with sometimes a second, *M. guatkinsi*.

Within the subgenus *Martes*, *M. americana*, *M. martes*, *M. zibellina* and possibly *M. melampus* are so closely related morphologically that there appears good reason to believe that they all belong to one species.

Two species occur in North America, namely *M. americana* and *M. pennanti*. Until recently *M. americana* was considered to consist of two species, *M. americana* and *M. caurina*, and thirteen or so subspecies. The recent work of P. L. Wright indicates that while the two "species" are distinctive morphologically, they intergrade at the point where their ranges meet and must be considered a single species. *Martes pennanti* has been considered one species, consisting of three subspecies.

The concept of the subspecies proves in many respects to be unsatisfactory. It lacks reality, it involves the arbitrary partitioning of continua, it possesses no lower limit, and it is determined deductively. This, together with the clinal nature of variation in marten and fisher leads to the conclusion that marten of the New World should be considered as represented by only two subspecies (*M. a. americana* and *M. a. caurina*), the fisher by one species, and no named subspecies.

The distribution of marten and fisher corresponds closely to the distribution of the northern evergreen forests. The distribution is less precise in fisher than in marten.

Fossils referable to the genus *Martes* are first recorded from the Miocene of both the Old and New Worlds. Twenty-eight fossil species are known (when synonyms are disposed of), of which five are still living, two of them in North America. It appears that modern martens and fishers arrived in the New World (or evolved there) late in the Pliocene or early in the Pleistocene.

During the Pleistocene marten found habitable environments in the forest refugia of south eastern United States, the Rocky Mountains south of the ice sheet, the Coast and Cascade Mountains south of the ice sheet, and Alaska and Yukon. Fisher presumably occurred in all of these refugia except the Alaska-Yukon one. With post-glacial climatic amelioration they migrated to the regions of their present occurrence.

GRADUATE STUDIES

Field of Study: Zoology

Vertebrate Zoology — I. McT. Cowan

Invertebrate Zoology — W. A. Clémens

Other Studies:

Vertebrate Palaeontology — J. T. Gregory

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INTRODUCTION

The genus Martes constitutes the fishers and martens. Seven or eight species are considered to occur in the world today, including the pine and stone marten, the sable, yellow bellied and Japanese marten in the old world, and the American marten and fisher in the new. No revisionary work has been done on the new world forms in half a century, and it is the purpose of this paper to fill the need. Yeager (1941) points out that of the fur bearing mammals he considered, only badger, otter and raccoon have received less attention in the literature than the wolverine, fisher and marten together, so that it is apparent that much future work is needed before these animals can be considered relatively well understood.

Myers (1952) suggests that systematic papers should make the problems being solved clear, hence the following statement of the problem. This is an attempt to define the limits of the genus concerned, to study its geographic variation in North America, to devise a useable classification from this, to determine the relationship of the new world species to those of the old world, and to devise a plausible phylogeny for the whole genus, with emphasis here on the American forms.

This study is unusual in that it attempts to bridge two points of view concerning marten classification which necessitates the use of certain arbitrary standards of usage, with which the reader must be familiar to understand what follows.

The older classification considers North American marten and fisher to be made up of three species containing between them sixteen subspecies, whereas I attempt to advance the view that a truer conception of reality is to recognize only two species, and two subspecies. These two ideas are not by any means self-exclusive, but merely a different interpretation of the same thing. Classification is always arbitrary and since whatever view accepted is a matter of opinion, I am bound to present both views, the older scheme and my own. In the following, as a means by which the reader may recognize what classification is referred to at any given place in the text, the term species, subspecies (or form or race) and the trinomial or its components are always, when referred to in the older sense, placed in inverted commas. The use of inverted commas for the older scheme is not meant to imply derogatory treatment of it. The scheme could have been reversed. Since, however, I am championing the new plan, it seems logical to employ the above method.

To orientate the reader then, the old scheme of classification is as follows:

"Martes americana"

"M. a. americana"

"M. a. atrata"

"M. a. brumalis"

"M. a. abieticola"

"M. a. actiosa"

"M. a. kenaiensis"

"M. a. abietinoides"

"Martes caurina"

"M. c. caurina"

"M. c. origenes"

"M. c. sierrae"

"M. c. humboldtensis"

"M. c. vancouverensis"

"M. c. nesophila"

"Martes pennanti"

"M. p. pennanti"

"M. p. columbiana"

"M. p. pacifica"

The new scheme I offer, a simplification of the above, is as follows:

Martes americana

M. a. americana

M. a. caurina

Martes pennanti

This study is based upon the examination of 3301 marten and fisher skulls of which measurements were taken on 1698. The specific distribution of these is as follows:

<u>Martes americana americana:</u>	1803 examined,	1044 measured
<u>M. a. caurina:</u>	936 examined,	390 measured
<u>M. pennanti:</u>	352 examined,	206 measured
<u>M. flavigula</u> and <u>guatkinsi:</u>	32 examined,	2 measured
<u>M. foina:</u>	81 examined,	19 measured
<u>M. martes ;</u>	12 examined,	7 measured
<u>M. zibellina:</u>	77 examined,	20 measured
<u>M. melampus:</u>	8 examined,	3 measured

Besides these a representative number of skins of each were examined. The specimens examined are in the collections of the following: University of British Columbia, British Columbia Provincial Museum, National Museum of Canada, Royal Ontario Museum of Zoology, University of Michigan, Carnegie Museum, Museum of Vertebrate Zoology in Berkeley, American Museum of Natural History, United States National Museum, United States Biological Survey, University of Utah, Museum of Comparative Zoology in Cambridge, and Peabody Museum, Yale University. Besides these, I have been allowed to examine specimens belonging to Messrs R. Y. Edwards, W. Cottle, R. Webb, J. Bryant, K. Racey and Doctors P. L. Wright and L. E. Yeager. Mr. D. Flook and Mr. C. Lensinck have donated specimens of their own to me, and Mr. E. McEwen provided me with measurements of specimens in his possession.

It is pleasant to name the individuals who have provided assistance during the course of the study. They include the custodians of the above named collections, especially Drs. D. Johnson, and H. Tate, and Miss Viola Schantz. Dr. Johnson also loaned specimens and transcribed portions of his rare copy of Kerr's Animal Kingdom for my use. Dr. P. L. Wright, besides allowing me to examine his specimens, sent me a manuscript copy of his paper on marten conspecificity a year before its publication. Mr. K. Racey provided valuable advice on western martens. Dr. L. Yeager cleaned a large series of skulls so that I might examine them. Mr. Calvin Lensinck and Mr. Donald Flook both made gifts of marten skulls from Alaska and Mackenzie. Mr. Lensinck also provided material on marten distribution. Dr. G. G. Simpson

provided information on nomenclature.

Dr. I. McT. Cowan is directly responsible for the instigation of this study in that he first suggested the problem to me, and has guided me throughout, though he must not be held responsible for its errors. Both he and Dr. W. Clemens have been a source of ready information and encouragement; I am obliged to both too, for having assisted in obtaining funds to assist me in the work. These funds were provided by the British Columbia Sugar Refining Company and the British Columbia Research Council.

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CLASSIFICATION

A. THE GENUS MARTES

HISTORY OF CLASSIFICATION

The post-Linnaean synonymy of the generic term Martes as applied to martens and fishers, follows:

- 1758, Mustela Linnaeus, vol. 1, p. 45.
- 1758, Zibelline Buffon and D'Aubenton, vol. 7, p. 309.
- 1765, Pekan Buffon and D'Aubenton, vol. 1, p. 304 and pl. 42.
- 1765, Fouine Buffon and D'Aubenton, vol. 13, p. 161.
- 1771, Fisher Pennant, p.
- 1774, Pekan Charlevoix, vol. 3, p. 134.
- 1775, Martes Frisch, p. 11.
- 1777, Mustella Scopoli, p. 491.
- 1792, Martes, Pinel, vol. 1, p. 55. Type Martes domestica
Pinel = Martes foina Erxleben.
- 1800, Viverra Shaw, vol. 1, p. 414.
- 1816, Tayra Oken, p. 1001.
- 1820, Martes, Nilsson, vol. 1, p. 38.
- 1829, Zibellina Kaup, vol. 1, p. 31.
- 1843, Galadicitis Smith, W. Jardines Nat. Library, vol. 35, pt.1,
p. 167.
- 1847, Putorius Boitard, vol. 8, p. 12 (Dict. Univ. Hist. Nat. 8:).
- 1865, Charronia Gray, p. 108.
- 1865, Foina Gray, p. 108.
- 1865, Pekania Gray, p. 107.
- 1865, Gulo "H. Smith", according to Gray 1865: 108.
- 1873, Aelurodon Cope, p. 1.

1904, Palaeogale Trouessart, p. 201.

1907, Pustella Millard, p. 1040 (Journ. Bombay Nat. Hist. Soc. 17:).

1911, Martes, Thomas, p. 139.

1924, Plionictis Matthew, vol. 21, p. 135.

1928, Lamprogale Ognev, p. 26.

1937, Charionia Thom, p. 317 (Journ. Bombay Nat. Hist. Soc. 39).

Ray, in 1693 was the first to use the name Martes in a generic sense, according to Trouessart (1897). Linnaeus, however, used the term Mustela for the genus including with it the weasels. For this reason it took a long while for agreement to be reached as to the proper designation for the genus of martens in the strict sense. During the 18th and 19th centuries, Mustela was held to be the proper generic term, the weasels being named Putorius, but since the first decade of the 20th century, Martes has been used, Mustela being reserved for the weasels, minks and ermines, and Putorius as genus or subgenus for the black-footed ferret Mustela (Putorius) nigreipes.

Alston, in 1879, was the first to interest himself in the problem. He wrote that most writers used the term Mustela for the martens on the ground that Cuvier (1817) had done so. Alston concluded that the term was used not as Linnaean genus, but rather as "sous-genres" and hence was inapplicable. The first proper naming of martens was done by Nilsson in 1820, who used the term Martes. Thus, concludes Alston, the proper term

should be Martes Nilsson 1820. He adds that certain authors have used the term Martes in the past, not after Nilsson, but from Cuvier in 1797. This is incorrect, he states, since the word used was merely the plural form of the French Martre. Flower and Lydekker in 1891 state that while Cuvier (1817) used the term Mustela as a sub-genus for the martens, usual practice allows them consideration as a full generic term. They conclude that martens should be named Mustela Cuvier 1817.

Trouessart (1898-99) followed Alston in refuting Mustela Linnaeus as the proper term, and retaining Martes Nilsson. Allen in 1902 (a) gave consideration of Oken's (1816) use of Tayra for the genus name, and while considering him scarcely Linnaean, nowhere completely condemned him. Sherborn in 1902-1933 gave authority for Martes to Pinel (1792).

In 1904, Palmer, in his Index Generum, attributed the name Martes to Frisch (1775). Thomas and Miller in 1905 condemned Palmer's usage of Frisch's term. They state that while Frisch appears superficially binomial, he is not, and often used phrases for his generic terms, and that his terminology was thus unacceptable.

Thomas, in 1911, reviewing the conflicting claims of the terms Mustela and Martes as applying to the martens, concluded that only Martes was valid. He said that Linnaeus chose many of his terms from Gesner (1606 and 1617-1621) and that by going to Gesner one could determine what "type" Linnaeus was thinking of in his application of names. Concerning the genus Mustela (Systema Natura 10, p. 45), the type, he concluded, is

by tautonymy Mustela erminea ("Mustela" Gesner, misquoted as Mustela vulgaris). In this instance alone of the Gesner quotations in the Systema, he said, is a second name attached to the primary one, for which tautonymy is claimed. This proved to be a misquotation by Linnaeus, for while Linnaeus wrote "Mustela vulgaris" Gesner, Gesner actually wrote only "Mustela" in the German edition quoted by Linnaeus, while in the Latin edition he wrote "Mustela proprie sic dicta" in contradistinction to his "Mustelis diversis", which included the marten and the polecat; Thomas concluded that the Mustela referred to by both Gesner and Linnaeus was clearly the ermine, and that it must be considered the type species. Almost all writers since Thomas have used Martes, under various authorities, for the martens, restricting Mustela to the weasels and ermines.

Heider, Kuhlitz, Hesse, Schulze and Kukenthal (1926-35) assert that a reference to Martes was made by Brisson in 1762, but assert that neither he nor Pinel can be considered legitimate authorities. Wagler's (1830) usage of the term was used for Herpestes (a viverrid) and concluded that Nilsson (1820) must be considered the proper authority. Ognev in 1931 credited the term to Pinel, as did Neave (1930-1940).

Brongersma, in 1941, reviewed the problem of the use of the term Mustela and concluded that four different species were involved as types. De Blainville (1841), he asserts, employed Mustela foina as an anatomical type, even though it was not mentioned by Linnaeus (see above). Chenu and Desmarest (date uncertain, but probably 1852 or 1853, p. 263) named M. martes as

type, although not in a nomenclatural sense. Coues in 1877 (p. 60) named Mustela martes. This type was also used by Cuvier (1817, pp. 142-149), Miller and Rehn (1901, p. 226), Palmer (1904, p. 436) and Elliot (1905b, p. 419). Elliot in 1901 (p. 33) mentioned Mustela lutra as the type, but this apparently was a lapsus, since on page 352 he mentioned Mustela lutra as the type of the genus Lutra Erxleben. Thomas in 1911, as pointed out above, named Mustela erminea Linnaeus the type of the genus.

Brongersma concluded that if the International Regulations were to be closely followed, Coues' designation (M. martes) would have to be maintained over that of Thomas (M. erminea). Since, however, Thomas' usage had been employed by most workers for thirty years, much confusion would be created by a change and the author expressed the hope that the Commission would pass an opinion making Mustela erminea the type of the genus Mustela, so that the martens might retain the name Martes. Brongersma believed the authority for the latter term should be attributed to Pinel.

In 1945, Simpson in his Classification of Mammals reverted to Palmer's usage of Frisch as the authority for Martes. In a letter dated 1951 he writes: "I took Martes Frisch 1775 from Palmer.... Since Frisch is doubtfully or not binomial, the more usual and probable reference is Martes Pinel.... There is, however, also some question as to Pinel's absolute purity ... so perhaps it should be Martes Nilsson 1820. If Nilsson should not pass, either, then the name is lost because the next reference, Wagler, 1830, uses Martes for a group of viverrids...."

Hershkovitz (1948a) says that Palmer in 1941 in private conversation denied the validity of Frisch's names, which Hershkovitz did also. The same author (Hershkovitz 1948b) reasserted his opinion, saying that Frisch was non-Linnaean, and persisted only because Palmer and Allen (Bull. Amer. Mus. Nat. Hist. 1902, 16: 13-22) had employed them. In 1949 the same author denied the validity of Oken's (1816) use of Tayra for the martens, saying the author was non-Linnaean. Ellerman and Morrison-Scott (1951) suggest that Brisson's names could not be considered Linnaean and that Oken's names fall into much the same category. Concerning Frisch's terminology they report that the International Commission in Paris in July, 1948, declared his work to be unavailable (Bull. Zool. Nomenclature 1950, 4:549). I have been unable to examine this journal. To summarize the above, it appears that by strict application of International Regulation, Mustela should be used as the generic term for the martens but that common usage and consideration of types gives the term Martes priority (Brongersma 1941, Thomas 1911). Although Frisch was the first to use the term, his names have been declared illegitimate (Ellerman and Morrison-Scott 1951) and the authority for the name must lie with any of Brisson (1762), Pinel (1792) or Nilsson (1820). Brisson has generally been considered unavailable, and so it appears likely that Pinel will retain permanent authority for the term. For these reasons I accept Martes Pinel as designating the genus.

In 1918, Pocock, on the basis of the structure of the baculum of the Indian and Malaysian species M. flavigula and M. guatkinsi, separated them as the distinct genus Charronia.

Ognev in 1928 showed that this name was preoccupied by Charonia Gistel 1848, p. 559, for a genus of Molluscs, and replaced it with the name Lamprogale. Ognev in 1931 and Pocock in 1936(b) accepted the change but Howell 1929, Allen 1938 and 1940, Simpson 1945 and Tate 1947 retained Charronia, Allen and Simpson insisting that the change was not merited. Most recent authors, however, refuse to accept Pocock's distinction as generic, and Ognev (1931), Carter Hill and Tate (1944), Bobrinskoy et. al. (1944) and Ellerman and Morrison-Scott (1951) consider Charronia or Lamprogale merely a subgenus of the genus Martes, which interpretation is accepted in this paper.

TAXONOMIC POSITION

The martens and fishers (Martes) have invariably been placed within the family Mustelidae, although how this family lies relative to the Arctoids and Aeluroids has never been precisely determined. For convenience it has generally been considered to lie nearer the former, however.

Within the Mustelidae a great many subfamilies have been devised, especially by Pocock, although most authors e.g. Simpson and Ellerman, Morrison-Scott name only four or five. Martes is generally placed in the subfamily Mustelinae, although some, for example Pocock and Allen (1938 and 1940), name both the Martinae and Mustelinae, the first for the martens, the last for the weasels etc. For greater detail see Simpson (1945).

For ordinal characters of the family Mustelidae, and the sub-family Mustelinae see Miller 1912a, Pocock 1921a and b, Allen 1938 and 1940, Stiles and Baker 1935.

About a dozen recent genera of Mustelinae are considered to exist today (Simpson 1945) but other authors have named more. About another twenty to twenty-five genera have been named as fossil forms but again there is great disagreement among authors. Keys to the recent genera are given by Gray 1865, Miller 1912a, Pocock 1921b, Allen 1938-40, Dammerman 1940, Ognev 1931 and others. Keys to the fossil forms (now outdated) as well as the recent ones are given by Matthew 1924 and Winge 1941. The characters of the genus Martes have been given by many authors, including the following, Flower and Lydekker 1891, Miller 1912a, Pocock 1921a and 1921b, Ognev 1931, Stiles and Baker 1935, Hall 1936, Dammerman 1940, and Winge 1941.

There follows a summary of the characters of the genus, compiled from the above: are Mustelid carnivores with body long, slender and flexible, though less so than in Mustela; head somewhat triangular, muzzle pointed; limbs short, feet rounded, toes short, five toes on each foot; tail moderately long, more or less bushy; skull long, narrow and ranging in basilar length from 60 to 115 mm.; facial angle slight; tympanic bullae moderately inflated, with thin walls, not in close contact with paroccipital processes; palate extending behind last upper molars; the brain although large, is not excessively so; the anterior edge of the orbit, although slightly pushed forward, is not greatly displaced; the jugular process is distinct; dental formula $\frac{3.1.4.1}{3.1.4.2}$ inner moiety of M^1 large, at least as large as outer with two internal cusps (protocone and an accessory cusp) and a cingulum; P^4 with a single deuterocone, this forming a

distinct internal lobe; length of whole tooth greater than its width; lower M_1 with evident though small metaconid and entoconid (thus with a total of 5 cusps); trigonid always longer than talonid, the latter semibasened.

B. THE SUBGENERA OF MARTES

HISTORY OF CLASSIFICATION

Although Cuvier (1817) and certain other authors notably Lydekker (1885) used subgenera to separate the martens from the weasels, interest here must be restricted to subgeneric division within the martens themselves.

The first to interest himself in the problem was Gray, who in 1865 and 1869 named four subgenera, which with a modern interpretation of the species constituting them, follows:

Genus Martes:

Subgenus Martes: Martes martes, M. melampus, M. zibellina and M. americana.

Subgenus Pekania: Martes pennanti.

Subgenus Foina: Martes foina.

Subgenus Charronia: Martes flavigula and M. guatkinsi.

Pocock in 1918, as has been described earlier, reasserted the validity of Gray's subgenera Martes and Charronia, naming Charronia a full genus and basing distinction on baculum structure. Pekania, as a subgenus, was not considered but in North America at least has continued to persist as a taxonomic unit. Foina was not upheld by Pocock, nor has it persisted. Ognev, in 1928 (as discussed earlier) changed Charronia to Lamprogale. Certain

authors, namely Ognev (1928), Ognev (1931) and Pocock 1936b accept Lamprogale, but most (Howell 1929, Allen 1938 and 1940, Simpson 1945, Tate 1947 and Ellerman, Morrison-Scott 1951) retain Charronia. Howell, Simpson and Tate give Charronia full generic status, while Carter Hill and Tate (1944) and Ellerman, Morrison-Scott consider it a subgenus. Ognev 1931, Allen 1938-40 and Bobrinskoy 1944 give Lamprogale subgeneric status only.

In 1931 Hall named Martes gazini from the tertiary of North America and erected the new subgenus Tomictis for its use. Similarly in 1946 Shikama named the subgenus Ten for Martes ten from the Pleistocene of Japan.

We find then, that the following are the subgenera that have been named to constitute the genus Martes.

Subgenus Martes Pinel 1792, vol. 1, p. 55 fide Gray 1865 and 1869.

Subgenus Pekania Gray 1865, p. 107.

Subgenus Charronia Gray 1865, p. 108, Pocock 1918, p. 307, synonymous with Lamprogale Ognev 1928, p. 26 and 30, considered by some a genus.

Subgenus Foina Gray 1865, p. 108.

Subgenus Tomictis Hall 1931, p. 156.

Subgenus Ten Shikama 1946, p.

Only three of these subgenera have been held valid by students of recent mammals (e.g. Ognev 1931, Bobrinskoy 1944, Miller 1924, Anderson 1946, Ellerman Morrison-Scott 1951). These with their constituent species are as follows:

Subgenus Martes: Martes martes, M. foina, M. zibellina, M. melampus and M. americana.

Subgenus Charronia = Lamprogale: Martes flavigula

Subgenus Pekania: Martes pennanti.

Because this classification is currently accepted it is the one used in the present paper.

Although only two subgenera of fossil martens have been named, it appears likely that a critical examination of fossil members of the genus would result in the naming of several to many more. Nor is it known with a few exceptions what fossil species are represented in the subgenera of recent martens.

TAXONOMIC CHARACTERS

It is generally stated that nine species of marten exist in the world today, these being "Martes americana", "caurina", martes, foina, zibellina, pennanti, flavigula, guatkinsi, and melampus. For reasons given elsewhere, however, this paper assumes the number to be only seven, by considering "M. americana" and "caurina" a single species (M. americana), and M. flavigula and M. guatkinsi another. As stated earlier, these are grouped into the following subgenera:

Subgenera Martes: Martes americana, martes, foina, zibellina, and melampus

Subgenus: Pekania: Martes pennanti

Subgenus Charronia (Flavigula): Martes flavigula

The characteristics of the subgenera Martes and Charronia have been carefully considered by Pocock (1918), Ognev (1931), Pocock (1936b) and Bobrinskoy (1944). The distinctive nature of the subgenus Pekania has never been considered seriously and in fact is not so clear cut as is that between the first

two named groups. A summary of the characteristics of the subgenera of martens follows.

1. Subgenus Charronia = Lamprogale. Colour varied black and yellow above; upper lip not divided by a distinct vertical groove; baculum distinctive, the distal end curved somewhat abruptly upwards and backwards in the form of a hook, the tip slightly expanded to produce four processes, each with a rounded condyle-like head.

Distribution: through the mountainous regions of northern India, northwards through China to Amur, and southward through Malaysia to Sumatra, Java and Borneo, also in the hills of southern India.

2. Subgenus Martes: Colouration generally monotone, brownish, but often with a lighter or yellowish spot on breast; upper lip divided by a distinct vertical groove; baculum not as above, gradually inclined upwards and forwards at its distal end, where it divides into two processes which remain separate, or which may unite.

Distribution: all of holarctic Europe, Asia and North America.

3. Subgenus Pekania: Colouration usually monotone, brownish, with chest spot absent or reduced, usually whitish; upper lip divided by a distinct vertical groove; baculum as in the subgenus Martes. It is so like the preceding subgenus that it is best distinguished by its relatively larger size, the length of its head and body being more than 570 mm. instead of less and its condylobasal length being more than 95 mm. instead of less.

Distribution: holarctic North America.

C. THE SPECIES OF MARTES

HISTORY OF CLASSIFICATION

In Eurasia

Adequate histories of the development of the present concepts of the classification of the genus Martes are not available, although attempts of varying degree have been made by de Blainville (1841), von Martens (1870) as summarized by Coues (1877) and Alston (1879). Much of what follows is collated from these.

It appears that the ancient Greeks were the first to recognize and name what we now place in the genera Martes, Mustela and Putorius. Three names were used for these, in their Anglicized form, Ictis, Gale and Mustela, but these terms were used rather indiscriminately. Aristotle compared Gale to Ictis, saying that the latter had a thicker pelage and a paler belly. Elsewhere he said that Gale of the forest waged war against rats. De Blainville believed that by Gale Aristotle meant weasel and by Ictis marten, and that the distinction of the two had been made by then. Gesner and later authors refer to the marten even more distinctly. It is believed, however, that these writers still confused the polecat (Putorius) with the weasel (Mustela) because Aristophanes used the word Gale to refer to an unclean woman, and Herodotus referred to a Gale of Africa, which was likely a Viverrid.

The Roman writers did not use the older Greek terminology, developing rather their own, e.g. Martes and Mustela, in their present form. Thus the origin of these words is nearly unknown, or at least obscure. In spite of this these are the

terms used by modern zoologists. In Leviticus 11, 29 Moses listed a number of animals that were considered impure. Among these was the Choleb which many translators have interpreted as Gale or Mustela. De Blainville believes this was the stone marten (Martes foina) of today.

It is uncertain who first made the distinction between the two species of European marten (Martes foina and the pine marten Martes martes). De Blainville attributes the first distinction to Pliny, who while transcribing Aristotle's statements referred to above, substituted the word Viverra for Gale and Mustela for Ictis. Ever since, he said, Mustela has appertained primarily to the stone marten. Viverra, it is assumed, was meant by Pliny to be the pine marten. Martial replaced the term Viverra with Martes, though providing no description to either. Most later authors, especially Agricola and Gesner, maintained the distinction, most applying Martes to the pine marten, Mustela to the stone marten, and Putorius and Ictis to the weasels and polecats.

Von Martens and Alston (1879) however, considered neither Aristotle nor Pliny to have recognized the distinction seen by de Blainville. It may have first been done by Albertus Magnus (who mentioned both Martarus or Martes fagorum and Martes abietum). Just as likely though, they believed, the distinction was not really made until as late as the time of Buffon and Linnaeus. The cranial and dental characters by which the pine and stone martens could be distinguished were first recognized and pointed out by Hensel in 1853 and further elaborated by

Blasius in 1857 (Saugethier Deutschlands, pp. 211-214), Gray 1865, Coues 1877, Alston 1879, Miller 1912a, Reynolds 1912, Ognev 1931, Bobrinskoy et al. 1944, Rode and Didier 1944, among others.

The origin of the name Mustela is believed by von Martens to originate in the word Mus. Sundevall believed further that it came from the Greek word for hunt, since Palladius referred to the mouse hunting ability of the animal and since it is still called Moustelle in Nice and Lorraine. Aubert and Wimmer, said von Martens, concluded, however, that all the older references are really to the stone marten in the strict sense, since it occurs throughout Greece (see also Rolleston 1868) and is still called Ictis there. The origin of the word Martes is still obscure.

Kerr (1792) considered the Satherius of Aristotle to have been the first reference to the sable, and Shitkov (1940) agrees. Pallas (1811) and Heptner (1934) attributed the name to Albertus Magnus, however, and de Blainville (1841) to Agricola. The first statement of the distinctive marks of the species was made by Aldrovandi and Ambrosini (according to de Blainville) and further elaborated by Brandt (1855), Gray (1865 and 1869) and others named above.

The specific names of the three species of martens discussed previously were considered by von Martens as follows: Zibellina has been known since the latter half of the middle ages under many variations such as sabelus, zibellina, zebel, sebeli, sable, sobol, soboli and samur. Graff says the Germanic term zebel is as old as the 9th century.

Martes now occurs in nearly all Germanic and Romantic languages as marta, martre, mart, martora, martin, marten, marter, mard, maar, meardtr and martarus. The word was first used by Martial as Martes, probably being taken from some non-Romantic language.

Foina is present in nearly all Romantic languages. Forms include fuina, fuinta, fouine, faina, faguino, fahino, fayne, fagina, farveina, fierna, feb, feh-wamme and fagorum. The Celtic, Slavonic, Finnish, Russian, and Magyarish words for the animal appear to be of totally different origin than the Latin term foina.

Martes martes has at times undergone various specific designations, these including sylvestris, sylvatica, vulgaris and abietum. M. foina has been named variously domestica and fagorum. It was not recognized by Linnaeus, who did not see it near his native Upsalla.

Ray introduced the concept of the genus and it was he who grouped the several species of marten then known into a single genus. He gave to this the generic name Martes. Later species of Asiatic marten were described by Boddaert in 1785 (Martes flavigula, the yellow bellied marten) and by Wagner in 1841 (M. melampus, the Japanese marten).

Buffon later described many discoveries from America "Pekan", "Martre", "Vison", etc., the first two of which are discussed subsequently.

In North America

Marten:

The classification of species of European marten was fairly well understood by the time Buffon and d'Aubenton (1758 and 1765) described the New World marten and it was with these that they were first compared.

Buffon employed French names rather than Latin binomials and hence his terminology has never been preserved in use.

Pennant in 1771 and again in 1781 first used Linnaean terminology to describe the New World forms, saying that two species of marten occurred there; these being Mustela martes and Mustela zibellina. Pennant said he had been informed by Dr. Pallas that no sables (M. zibellina) occur northeast of the "Anadyr" River in the country of the "Ichutki" Indians.

In 1772 Forster named the American marten Mustela martes after that name of Linnaeus. Pallas (1776-1780) named it Mustela zibellina. In 1792 Kerr renamed it Mustela zibellina americana being the first to apply the epithet americana to the New World form. He also named two other forms, Mustela martes and Mustela zibellina alba as being present. Thomas in 1879 and Allen in 1895 both believe Kerr should be given authority for the present usage of the current name Martes americana, but most subsequent authorities have attributed it to Turton. Allen says that Turton copied most of his names from Kerr and that the latter's work is "mere trash" compared to that of Kerr. For purposes of the present paper, I consider Kerr rather than Turton the authority for the epithet americana as applied to martens.

Turton in 1802 named the marten as Mustela americana. Coues in 1877 considered Turton's 1806 edition the authority of the specific name americana and although Rhoads (1902) pointed out that Turton first used the combination in his 1802 edition and although Sherborn does the same, most authorities refer the authorship to the 1806 volume. I have examined both editions of Turton's work, and find Rhoad's designation and not Coues' to be correct. Nevertheless for reason given previously, authority is given to Kerr for the name and not to Turton in either of his volumes. Gray 1865 and 1869 and Trouessart erroneously give authority for the name to a non-existent 1803 edition of Turton.

Ord in 1815 named three American species, namely Mustela martes, M. zibellina and M. americanus. Rafinesque (1819a and b) described a new species, Mustela vulpina from "the upper Missouri" which Coues (1877) concluded is really a white-tailed semi-albinistic individual of the typical form. Kuhl in 1820 named a form as Mustela leucopus which Coues (1877) considered a white-footed albinistic form. In 1823 Cuvier named a form Mustela huro, which Coues again explains as merely a light coloured individual of the typical eastern marten. Harlan (1825) considered two forms, Mustela zibellina and Mustela martes, to occur and confused these martens with the mink, Mustela vison, which he considered identical. Godman (1828) named two forms, Mustela martes and Mustela zibellina. American pine marten, he states, differ from their European equivalent in possessing a yellow rather than white breast. The sable is

much paler than most marten, he says, a specimen collected by Lewis and Clark being "bleached".

Griffith Smith and Pidgeon (1827) apply the name Mustela leucotis, this likely being a corruption of Kuhl's term leucopus. Waterhouse (1828) named only one form, Mustela zibellina, though ten years later Waterhouse (1838) considered zibellina to be absent from the continent and to be replaced by Mustela martes and M. foina. Richardson in 1829 believed only Mustela martes to be present, as did Gapper in 1830. The latter, however, pointed out that distinctions existed between the Old and New World forms. Godman (1831) named Mustela zibellina as the only form present, while Emmons in 1840, De Kay in 1842 and Linsley in the same year named Mustela martes. Gray (1843) named the marten Martes leucopus, using Frisch's generic name for the first time. Smith in the same year described three forms, Martes zibellina, Martes huro, and Martes leucotis, and Schinz (1845) named Mustela vulpine, Mustela leucopus and Mustela huro. Gesner in 1847 grouped all as Mustela martis [sic]. Audubon and Bachman (1845-48 and 1851-54) concluded that all martens they had examined were referable to Mustela martes and denied the presence of the sable on the continent.

Brandt in 1855, however, compared skins of Asiatic and American marten and concluded that the two were almost identical. The American form he named Mustela zibellina var. americana. Billings (1857) said that three species of martens occurred in the New World but did not name them.

Baird (1857 and 1859), after considering Brandt's views, expressed disagreement with him, concluding that two forms existed in America, one with a whitish head, lying near to the sable, and one with a darkish head near to the pine marten but both probably specifically distinct from the corresponding Old World forms. The name he used for both was Mustela americana. Ross in 1861 (a and b) concluded that two species occurred, these being Mustela americanus and M. zebillina [sic]. He believed the Mackenzie River form was only a colour variety of the Asiatic sable.

All workers up to this period worked primarily on colour and structure of pelage in their attempts to determine the species of marten present in the New World. For this reason it is not surprising that they referred American forms to either the pine marten (Martes martes), to the sable (M. zibellina) or named albinistic variants as distinct species (M. huro, M. leucopus). Before a better understanding of the status of the New World forms could be determined, it was necessary to examine cranial and dental characteristics. One of the first to do this was Gray, who in 1865 and again in 1869 concluded that the last upper molar in New World forms was small and quadrate, whereas in Old World forms it was large, massive and nearly twice as long on the inner as on the outer side. So long as one remembers that Gray had no specimens from the Cordillera and west coast of North America and that to these his distinction does not hold, Gray's separation is valid. He further divided "Martes americana" into three races, which as subspecies have been held as valid to the present.

These are: variety huro from Fort Franklin (the equivalent of "Martes americana actiosa"); variety abietinoides (now "Martes americana abietinoides"); and variety leucopus (now "M. americana americana"). Gray's work may be considered to mark the end of the exploratory period and the beginning of the scientific one, insofar as American marten are concerned.

Allen, in 1869, examined many Old and New World skins and skulls and concluded that all belonged to a single circumpolar species, with possibly one or two well marked continental races. Thus he named all marten, including the American martens, Mustela martes. Ames in 1874, however, named two species as being present, Mustela americana and Mustela martinus. He gave no description of either.

In 1876 (a) Allen reviewed his older paper and retracted the views it contained. He agrees to the distinctions made by Gray between the Old and New World forms and adds that while the character was inadequate for the separation of M. foina and M. americana the two could be distinguished by differences in the second lower molar which in all the Old World forms possesses an inner cusp lacking in the American form. Rhoads (1902) points out, however, that this distinction is invalid, or at least not constant, and my own studies have led me to the same conclusions. Allen also pointed out, quite correctly, that American marten increase in size from south to north in the fashion stipulated by Bergmann. All these he named Mustela americana.

Coues in 1877 monographed the Mustelid genera including the genus of martens. He agreed with Gray's separation of Old

and New World forms and through detailed comparison named other distinguishing characteristics. He concluded that M. americana lay nearest to the sable, of all Old World forms, a relationship not much doubted since. He disagreed with Gray's division of the species into three varieties, saying that they represented individual variation only. All forms he considered to be one species Mustela americana. In his 1884 catalogue, True listed Coues one species, M. americana, without comment, as did Tyrrell in 1889.

With Merriam, in 1890, began the third phase in the history of marten classification. His impress upon mammalian taxonomy in North America was extreme and the publication of his description of the species Mustela caurina resulted in what may be termed the phase of taxonomic splitting. From 1890 until recently the martens have been divided into thirteen or fourteen forms, all but one still considered valid. Much taxonomic splitting of the period is to be deplored, but it is a fact that Merriam's description of caurina from the Cordillera of North America marks the most basic division of marten that can be made. Merriam believed M. americana to lie nearest to M. zibellina of all Eurasian forms.

Flower and Lydekker (1891) regress to the conclusion that Mustela americana lay very near to M. martes and M. zibellina, and was difficult to distinguish from them. Herrick (1892) likewise emphasizes this lack of distinctiveness, as does Lydekker 1896.

Poland (1892) erroneously names the marten Mustela martes, saying it is indistinguishable from the Old World form and very nearly inseparable from M. foina. In spite of this, he provides a correct view of geographic variation in marten, showing extreme insight into the problem. Alaskan martens, he said, are large and pale; Californian animals are small and uniformly coloured; the Labrador marten is large and richly furred; those from southern Canada and the northeastern United States are small and more lightly furred. These are apt descriptions of the current forms "actuosa", "sierrae", "brumalis", and "americana". He concluded that "each district of North America has its own peculiar type".

In 1897 Bangs described as a distinct species Mustela atrata, the Newfoundland marten. The following year, the same author described another from Labrador, Mustela brumalis. In 1900 Osgood named Mustela americana actuosa from Alaska, Yukon and Mackenzie. In 1901 he described Mustela nesophila from the Queen Charlotte Islands.

Elliot (1901a) named five forms, Mustela americana, Mustela caurina, M. c. atrata, M. c. brumalis and M. c. actuosa. Miller and Rehn (1901) list them as M. americana, M. a. actuosa, M. atrata, M. brumalis and M. caurina. In 1902 Preble described Mustela americana abieticola from Manitoba, and Rhoads in 1902 Mustela caurina origenes from Colorado. Rhoads' work was revisionary in nature and he named the following forms: M. americana (with the subspecies abietinoides, actuosa and brumalis), M. atrata and M. caurina with its new subspecies origenes. Elliot

in 1903(a) described Mustela americana kenaiensis from the Kenai, Alaska, and in 1905(a) M. boria from Mackenzie. Elliot (1905b) listed six species of martens: Mustela americana (with subspecies abieticola, abietinoides, actuosa and brumalis), M. kenaiensis, M. atrata, M. boria and M. nesophila. In 1908 Preble synonymized M. boria with M. a. actuosa. Grinnell and Storer, in 1916, described Martes caurina sierrae from the Sierra Nevadas and Grinnell and Dixon in 1926, Martes caurina humboldtensis from the Coast Mountains of California and M. c. vancouverensis from Vancouver Island. These latter mark the last forms of recent North American marten to be described.

The systematic catalogues of the period 1912 to the present show a progressive attempt on the part of systematists to group the known forms of marten into realistic specific groups. Miller in 1912(b) listed six species: Martes americana (with subspecies americana, kenaiensis, abieticola, abietinoides and actuosa), M. atrata, M. boria, M. brumalis, M. caurina (with subspecies caurina and origenes) and M. nesophila. Anthony in 1917 named four species, using Miller's classification but omitting M. boria, origenes and nesophila.

Miller, in his Catalogue of Mammals, 1924, again listed six species, they being now Martes americana (with subspecies americana, kenaiensis, abieticola, abietinoides and actuosa), M. atrata, M. boria, M. brumalis, M. caurina (with subspecies caurina, sierrae and origenes) and Martes nesophila. Anthony, in his Field-book (1928) used Miller's classification, with the exception of M. boria which he omitted. It would appear that

Grinnell and Dixon (1926) were the first to suspect that only two major types (species) of martens occurred in North America. They wrote that "the material as yet available for study indicates the existence of two distinct species of marten in northwestern America -- Mustela caurina, with short bullae and other minor characters, on the Pacific coast from Admiralty Island south to east-central California; and Mustela americana, with long bullae, etc., in the interior of the continent and west at the north clear to the Alaska Peninsula. Each of these species contains several well marked geographic races". Allen (1942) employed the most modern classification of all, the one with which most systematists now concur. He also named only two species, Martes americana and Martes caurina, the first with the subspecies americana, kenaiensis, abieticola, abietinoides, actuosa, atrata, boria and brumalis; the second with the subspecies caurina, sierrae, origenes, nesophila, vancouverensis and humboldtensis. Anderson, in his Catalogue of Canadian forms (1946) followed Allen except that he omitted M. a. boria and the American forms M. c. sierrae, origenes and humboldtensis and raised M. atrata to specific status. Miller and Kellogg (1955) list all of Allen's subspecies except "boria", and name three species, "M. americana", "M. caurina", and "M. atrata".

The realization that only two major forms of marten exist on the continent was likely recognized by some systematists long before Allen put the idea into print. Just how these two forms (M. caurina and M. americana) were related to each other

(i.e. whether distinct species or subspecies) has only recently been made clear.

In 1936 Hall wrote that "critical study of the described species and subspecies of true martens in North America (subgenus Martes) almost certainly would show that the named forms belong to no more than two, and possibly only to one, full species". In 1942 Allen published his heretofore discussed volume in which he grouped all as subspecies of the two species M. americana and M. caurina. In 1946 Hall again wrote "I do not know whether caurina is a species distinct from americana and the species name should be regarded as tentative pending a revision of the genus". Rand in 1948(b) listed these as the only two species of marten occurring in Canada. Dalquest, the same year, studied the problem and concluded that "east of the Rocky Mountains the ranges of the two species approach closely but each retains distinctive characters.... On the basis of the evidence at hand, the two should be considered full species until positive proof of intergradation is established." Durrant in 1952 said that "my studies of martens cause me to doubt that M. caurina is distinct from Martes americana", but added no detail.

It remained for Wright (1950 and 1953) to provide the proof of conspecificity demanded by Dalquest. He showed that the two underwent complete intergradation in western Montana and central Idaho. On the basis of this, Wright listed all thirteen forms of marten as subspecies of the single species Martes americana. In view of the vital nature of Wright's work, it is reviewed in greater detail elsewhere in this paper.

Fisher:

Because fisher occur only in the New World and were discovered after the European forms were relatively well known, the problems of their nomenclature and classification are not the same as were those of New World martens.

Buffon, in 1765, published the first description of the Fisher and later the name was used by Brisson. In 1771 Pennant named and described not only Buffon's Fisher but another form he named Pekan. Concerning the first of these, he expressed belief that it might be identical to the sable of Asia, although in 1781 he retracted this view. Concerning the second, he said that he could not separate it from the Vison of Buffon.

Commenting on this situation Coues (1877) fide Baird (1857 and 1859) writes that Buffon, Brisson and Pennant all "described the animal from the same specimen - one in the cabinet of M. Aubry of Paris.... Pennant's account of his Fisher is unmistakable, but he describes in addition, the Pekan of Buffon, not recognizing in it the same species. These two accounts furnished for many years the bases of all the scientific binomial names imposed by various authors."

Erxleben, in 1777 gave for the first time a Linnaean binomial to the fisher, naming it Mustela pennantii, although very shortly later Schreber (1778) renamed it M. canadensis. Thus not only were two animals named from the same specimen, but two names were applied at nearly the same time to the same species. This situation provided much of the nomenclatural problem associated with the history of fisher taxonomy. In 1785, Boddaert

used the name M. melanorhyncha for the fisher and Kerr in 1792 named two forms, M. canadensis and M. zibellina nigra (both for the fisher). Shaw (1800) changed the generic name to Viverra, naming two forms, V. piscator and V. canadensis. Turton (1802) named Mustela nigra and M. canadensis and used the same nomenclature again in 1806. In 1815 Ord used the names M. nigra and M. hudsonius and used the term M. canadensis for the otter (Lutra canadensis) (Rhoads 1894). Desmarest (1820-1822) introduced the name M. rufa. In 1825 Harlan named only one form, calling this M. canadensis, while the following year Godman (1828) named a single form M. pennanti [sic]. Lesson (1827) named three species, all referable to the fisher. These being M. pennanti, M. canadensis, and M. piscatoria. Griffith Smith and Pidgeon, in 1827, followed Godman's nomenclature. Fischer (1829) used the term M. godmani (corrupted by Gray 1865 to M. goodmanii). Richardson (1829) named two forms, these being M. canadensis and a pale variant M. canadensis var. alba.

Swainson 1835, for the first time employed the generic name Martes for the fisher, naming it Martes canadensis. Emmons in 1840 remarked that earlier division of the fisher into two species was due to colour variation and grouped them together as one form, Mustela canadensis. Smith in 1843 named three species, Martes canadensis, M. nigra and M. pennantii. Gray in 1843 reduced all to the single species Martes canadensis. Schinz 1845 and Audubon and Bachman (1845-1848 and 1851-1854) named one form Mustela canadensis.

Baird in 1857 and 1859 was the first to attempt to systematize the chaotic nomenclatural state of the fisher. He

makes clear that, as pointed out previously, Buffon, Brisson and Pennant all named their fishers from the same specimen. Buffon named his Pekan, as did Brisson, but Pennant named both Pekan and Fisher, not knowing that both were the result of examination of the same specimen.

Baird then went on to the problem of priority of date between the two names, canadensis and pennanti applied to the species of Buffon and Pennant. "While Erxleben's work is dated 1777 and volume 3 of Schreber's work is dated 1778, Baird felt it possible that parts of Schreber's work may have been issued prior to 1777 and states as evidence that Erxleben quotes the plates of Schreber in various places. Nonetheless, in lieu of better evidence, Baird accepted Erxleben as having prior claim.

On page 455 of Erxleben, is described a Mustela canadensis, the synonymy of which includes both the Vison and Pekan of Buffon, but which in actual fact describes only the mink (Mustela vison). On page 470, however, Erxleben described under M. pennantii the Fisher of Pennant and concluded that the proper name for the species is Mustela pennantii Erxleben. He suggests elsewhere that two species, the fisher and the black cat, might exist, however.

In 1860 Godman described both Mustela pennantii and M. canadensis but expressed belief in Pennant's idea that the latter was named for a mink skin. Gray in 1865 used the binomial Martes pennantii, employing modern terminology for the first time.

Coues (1877) continued the clarification of nomenclature

begun by Baird. He concluded that Erxleben 1777 (Mustela pennanti), Shaw 1800 (Viverra piscator), Turton 1802 and 1806 (Mustela nigra), Lesson 1827 (Mustela piscatoria) and Boddaert 1785 (Mustela melanorhyncha) all named their forms after the Fisher of Pennant. Schreber 1778 (Mustela canadensis) named his after the Pekan of Buffon. Erxleben named a M. canadensis but applied it to Mustela vison. Shaw named a Viverra piscator whose origin Coues could not determine. Turton named a Mustela nigra for both Buffon's Pekan and the otter (Lutra) which he considered identical. Like Baird, he concluded that the fisher's name should rightly be Mustela pennantii Erxleben. Elsewhere, however, Coues drops the double i ending of pennantii, reducing it to pennanti. The current use of the shortened epithet may be said to date from Coues.

True in 1884, used Coues' term, M. pennanti, as did Tyrrell 1889.

Rhoads (1894) considered the nomenclatural problem and concluded as did Baird and Coues, that the proper name was Mustela pennantii. In 1898, however, in his revision of the species, he employed the name M. canadensis Schreber. Contrary to earlier opinions he concluded that since Erxleben made reference to Schreber's plates, and also on Sherborn's opinion, that Schreber was published (or the illustrations at least) prior to the issuance of Erxleben's work in 1777 and that he thus gained priority. Rhoads, in this paper, described a new subspecies from the Pacific coast, M. c. pacifica. This has been the first named subspecies to persist in the literature. Allen, in 1898, replied to Rhoads decision, saying that since

Schreber's plate name M. canadensis is preceded by the plate name M. lutra canadensis, it preoccupies the epithet canadensis as applied to the fisher. Hence Allen concluded, the proper name for fisher was Erxleben's M. pennanti.

In 1899 Elliot used the contracted epithet penanti, this probably being a lapsus, Miller 1900, Miller and Rehn 1901 and Elliot 1901, returning to the orthodox pennanti. Bangs in 1910 used the term pennanti. In 1912(b) Miller using Thomas' (1911) precedence, made it Martes pennanti, which form it has held to the present, with few exceptions (see Jordan 1929, Warren 1942 for exceptions).

In 1935 Goldman named the third and last subspecies to be accepted by modern workers. This was M. p. columbiana from the Rocky Mountains, which intergraded in the Prairie Provinces, he believed with typical M. pennanti. All three "subspecies" are listed in Miller and Remington's (1955) catalogue.

Some criticism has been directed towards the division of fisher into subspecies. Grinnell in 1933 and in 1937 (Grinnell, Dixon and Linsdale 1937) wrote that after critical examination of the specimens in the United States National Museum, he was unable to separate M. pennanti pacifica from M. p. pennanti and concluded they were all to be named simply M. pennanti. Hall, in 1936, working with fewer specimens, came to the same conclusion. None of them considered M. p. columbiana, of course, which was not described until 1935 (Grinnell's later manuscripts being completed before this date).

In 1950 (Hemming 1950) redrafted Article 14 of the

International Rules such that trivial names based on a male person's surname should "consist of the exact surname ... to which should be added ... the termination in the genitive case ... -i". Thus the epithet pennanti is given validity over the older form pennanti by the Regulations.

The currently accepted classification of the fishers is as follows:

"Martes pennanti pennanti" Erxleben 1777.

"M. p. pacifica" Rhoads 1898.

"M. p. columbiana" Goldman 1935.

SYSOPSIS OF THE SPECIES AND SUBSPECIES OF MARTEN

Comparisons of the distinctive qualities of the various species of marten have been made in the past by the following authors: Allen 1876(a), Allen 1938-40, Alston 1879, Blanford 1888-91, Bobrinskoy et al. 1944, Bonhote 1901, Brongersma 1941, Coues 1877, de Blainville 1841, de Vos 1952, Didier 1947, Ellerman, Morrison-Scott 1951, Flower 1885, Gerrard 1862, Gray 1865 and 1869, Hall 1926, Kneeland 1859, Merriam 1890, Miller 1912(a), Ognev 1925, Ognev 1931, Owen, 1853, Pocock 1918, Pocock 1921(a and b), Pocock 1936(b), Reynolds 1912, Rode and Didier 1944, Schmidt 1943, Tate 1947, and Bannikov 1953. At no time, however, have more than three or four species been compared simultaneously. The synopsis provided below, prepared through reference to the above named authors and by examination of specimens, attempts to help remedy this lack.

For those interested in the general anatomy of the martens the reader is referred to the writings of de Blainville

(1841), Reynolds (1912), Hall (1926 a and b), and Cooper (1954). Dental terminology is given in an illustration by Gregory (1951) fig. 20.08.

I have no way of knowing how carefully the specific distinction of species of marten in a biological sense has been determined. It is likely that the species of the subgenera Pekania and Charronia are truly species. Within the remaining subgenus Martes, the situation is less likely. The sympatricity of the ranges of M. martes and M. foina suggests their distinct specificity. Streuli (1932) says that not a single hybrid or intermediate was found among several hundred specimens of the two forms examined although Schmidt (1943) says Severtzov reported hybrids in the Tienschan Mountains. Rode and Didier (1944) report that 42 skulls of the two species were distinctive in every case. Severtzov (1876) considered M. intermedia intermediate between M. foina and M. martes but he apparently worked only with skins. Ellerman, Morrison-Scott (1951) conclude, however, that the two species are not always easily distinguishable, which suggests the possibility that intermediates may sometimes occur.

Martes zibellina has a range that barely overlaps that of M. martes; it is uncertain that it is in contact with that of M. foina, although Schmidt (1943) cites Severtzov as saying that in the Tienschan Mountains M. foina has been crossed with the sable. The cranial characteristics of all three are marked in the specimens I have examined, but Ponomarev in 1946, recorded that he obtained hybrids from M. zibellina and M. martes crosses.

Whether this situation occurs under natural conditions I do not know.

Martes melampus has always been considered a distinct species. Ellerman, Morrison-Scott (1951) say that while its coloration is near M. zibellina the skull is nearer M. foina and M. martes and conclude that it is an "isolated and valid species". Its true status is unknown to me, since older students have never considered its specificity in a critical fashion.

It has never been demonstrated that North American martens are specifically distinct from Old World forms. M. americana americana is morphologically distinct from M. zibellina, its nearest Old World neighbour, but this cannot be said to be marked in the relationship of M. americana caurina to M. zibellina. These two can almost always be separated, but their distinctions are small, far smaller in fact than exist between the two true subspecies M. americana americana and M. a. caurina. It is quite possible that the Asiatic and American forms will eventually be shown to be potentially capable of interbreeding, as Rausch (1953) and Bobrinskoy (1944) believe to be the case in many Siberian-Alaskan forms. If this is found to be so, M. americana will be reduced nomenclaturally to a subspecies of M. zibellina or of M. martes. The relationship between Asiatic and American forms is considered elsewhere in greater detail.

In order to facilitate the identification of unknown skulls, a key is provided below, which is based almost completely on dental characteristics. It makes no attempt to denote relationship and is completely artificial. It is based largely upon a series of indices devised by Brongersma (1941) which were

enlarged upon during the course of the present study. These indices are given in detail in Appendix A. The key considers M. flavigula and M. guatkinsi to be conspecific, and further, takes M. americana to subspecies.

1. Width of inner lobe of P^4 x 100/width of trenchant part of P^4 more than 65 2
- 1b. Less than 65 7
- 2a. Greatest width of canines at base x 100/bulla length more than 100.5 3
- 2b. Less than 100.5 5
- 3a. Mesial length of M^1 x 100/breadth of M^1 more than 55 4
- 3b. Less than 55 M. flavigula (including M. guatkinsi)
- 4a. Width of inner lobe of P^4 x 100/length of P^4 more than 28 M. melampus
- 4b. Less than 28 M. americana caurina
- 5a. Lateral length of M^1 x 100/mesial length of M^1 more than 79 M. americana americana
- 5b. Less than 79 6
- 6a. Greatest width of canines at base x 100/bulla length more than 95.5 M. martes
- 6b. Less than 95.5 M. zibellina
- 7a. Breadth of M^1 x 100/length of P^4 more than 89.. M. foina
- 7b. Less than 89 M. pennanti

Where the key proves inadequate for the identification of specimens, I suggest reference be made to the statistics on which it is based, given in Appendix A; even when identification

appears fairly certain, I would suggest that the reader make comparison to these. Other keys to a restricted number of species are given by Miller 1912(a), Ognev 1931, and Bobrinskoy et al., 1944. Diagrams of the skulls of the various species of marten are given on Figures 1 and 2.

Maps showing the distribution of Eurasian forms are given on Figures 3, 4, 5 and 6; these have been prepared from many sources, but chiefly from the maps of Kozhantschikov (1930), Ognev (1931), Stirton (1939), Schmidt (1943) and Bobrinskoy et al. (1944) and from the accounts of Sowerby (1922, 1930), Allen (1938-1940), Chasen (1940) Brongersma (1941), Harper (1945), and Ellerman, Morrison-Scott (1951).

Synonymies for the species and subspecies considered in this paper are, because of their lengthy nature, summarized alphabetically in Appendix B. The measurements of condylobasal length provided are meant to give some idea of geographic variation. They have been compiled from the specimens examined and the literature. Because the samples are small, only the means, observed extremes, and sample size are given, measurements being in centimeters. The classification that follows is that of Ellerman, Morrison-Scott (1951 and 1953) and Chasen (1940). Other recent classifications of importance are given by Miller 1912(a), Ognev 1925, Ognev 1931, Pocock 1936(b), Schmidt 1943, Bobrinskoy et al., 1944, and Harper 1945.

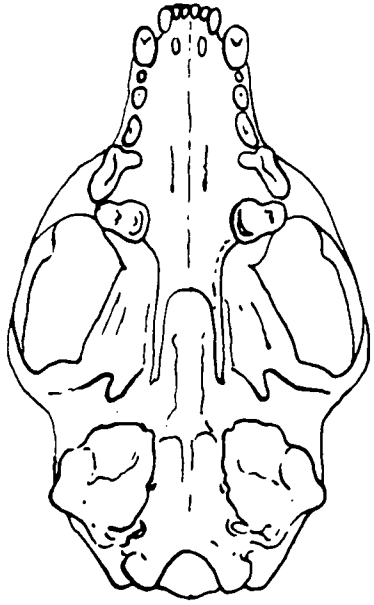
Martes martes (Linnaeus 1758) = M. sylvestris, sylvatica, vulgaris and abietum of authors (see Appendix B for detail).

Type locality: Upsala, Sweden.

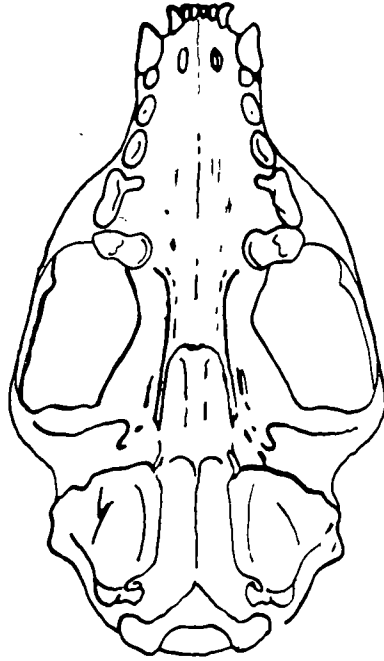
Range: British Islands including Ireland, Norway, Sweden,

Figures 1 and 2.
(To face page 42)

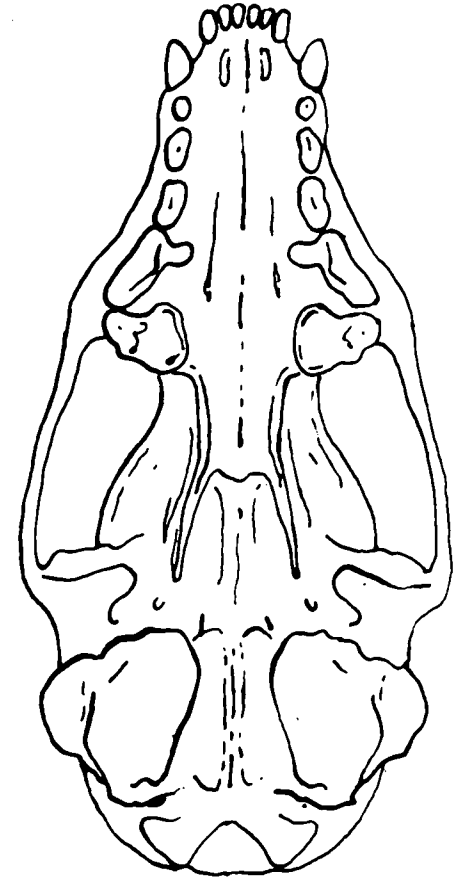
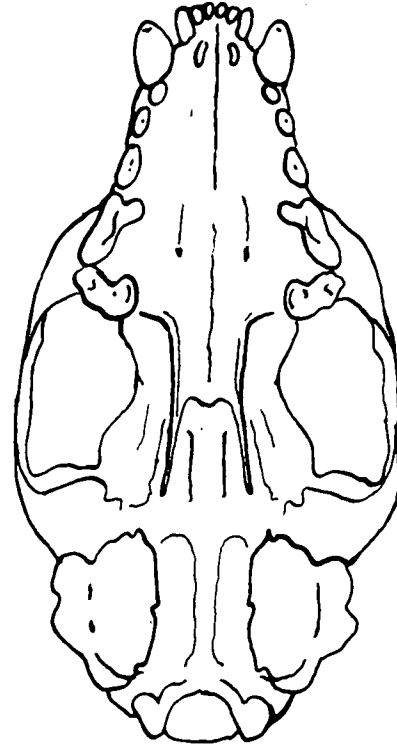
Figures 1 and 2. The skulls of the species of the world's marten, in ventral aspect. From sources referred to in the text, and from original material.



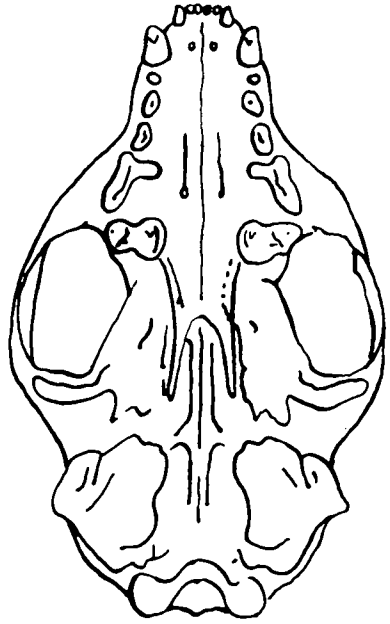
CAURINA



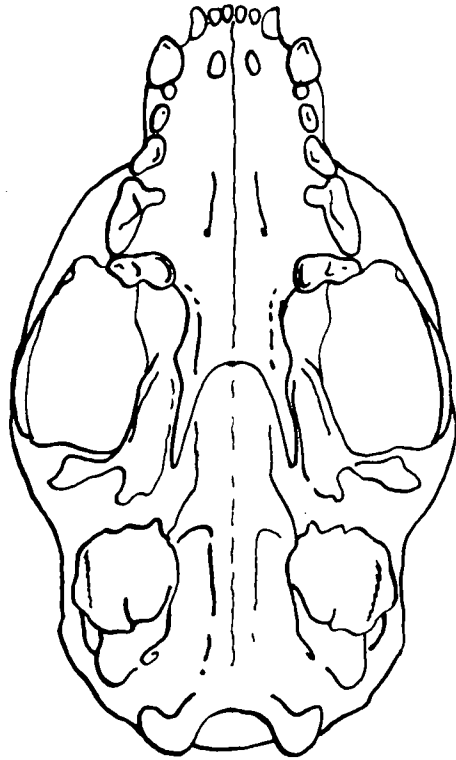
AMERICANA MELAMPUS



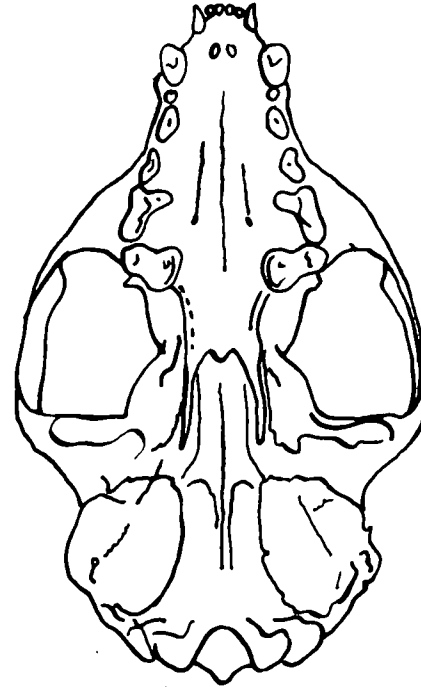
PENNANTI



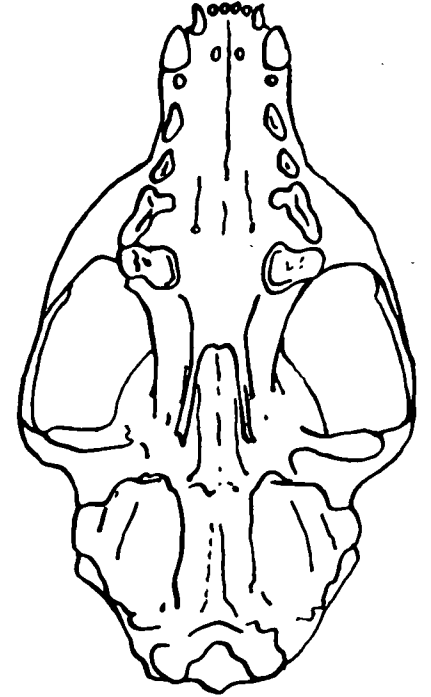
FOINA



FLAVIGULA



MARTES

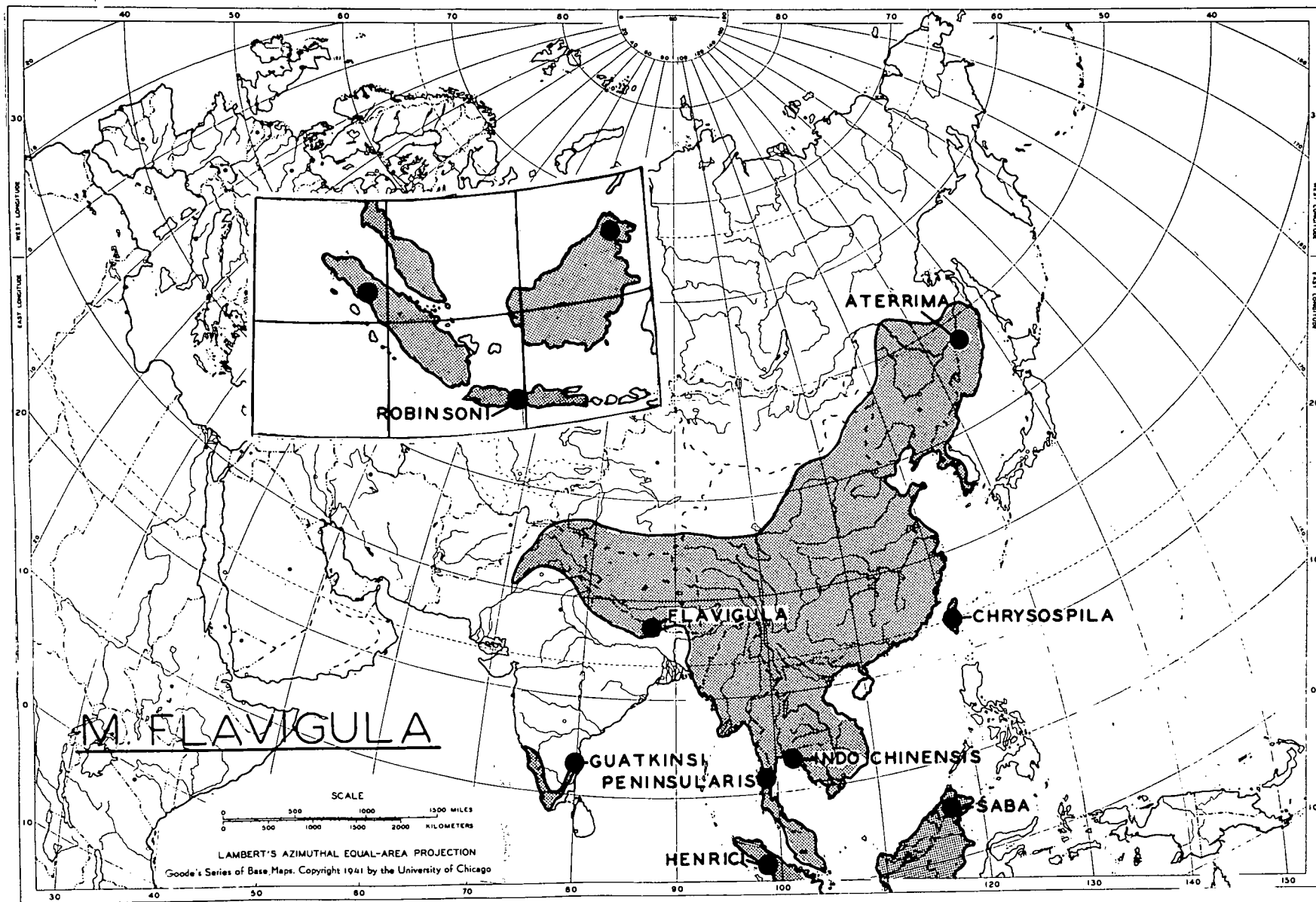


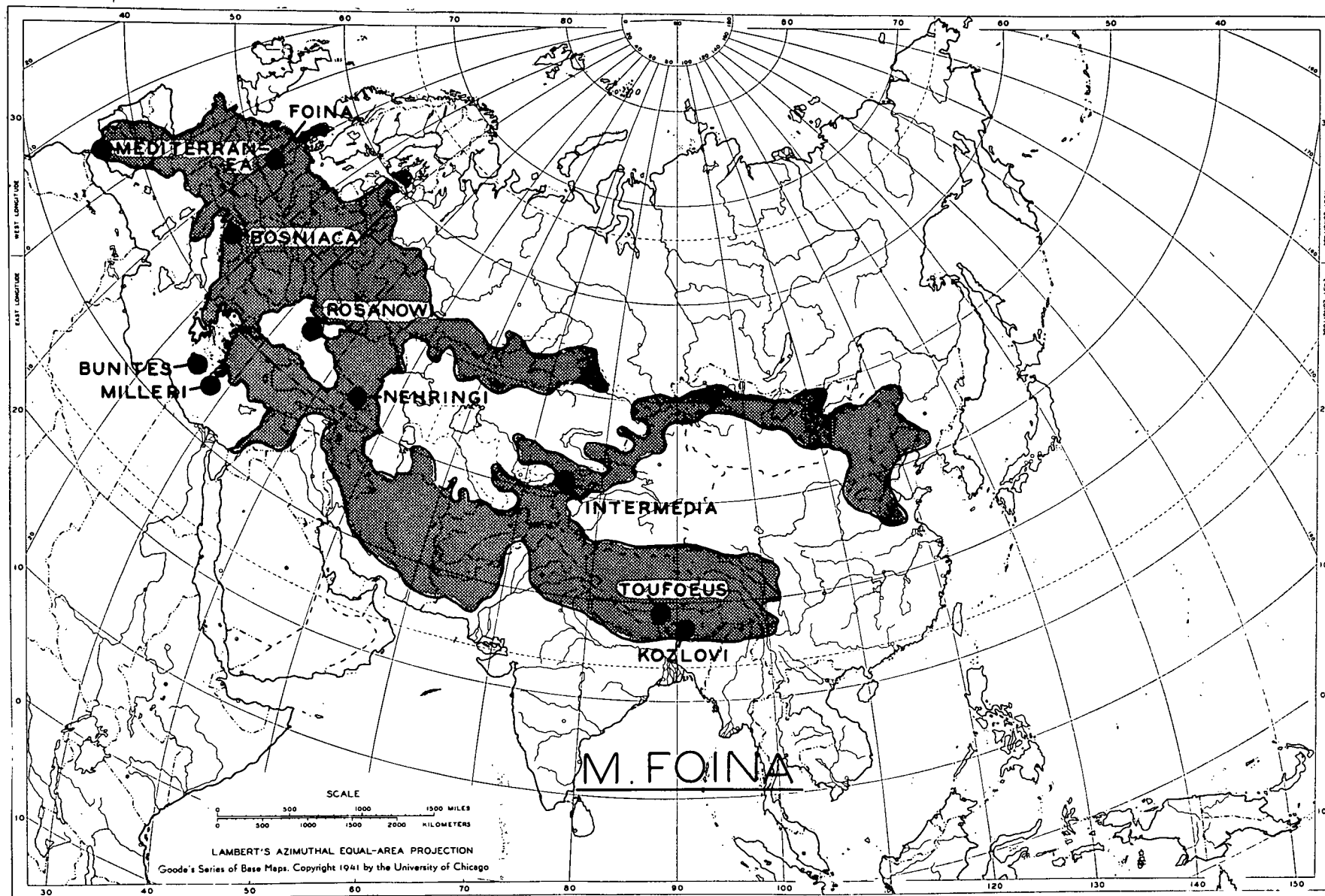
ZIBELLINA

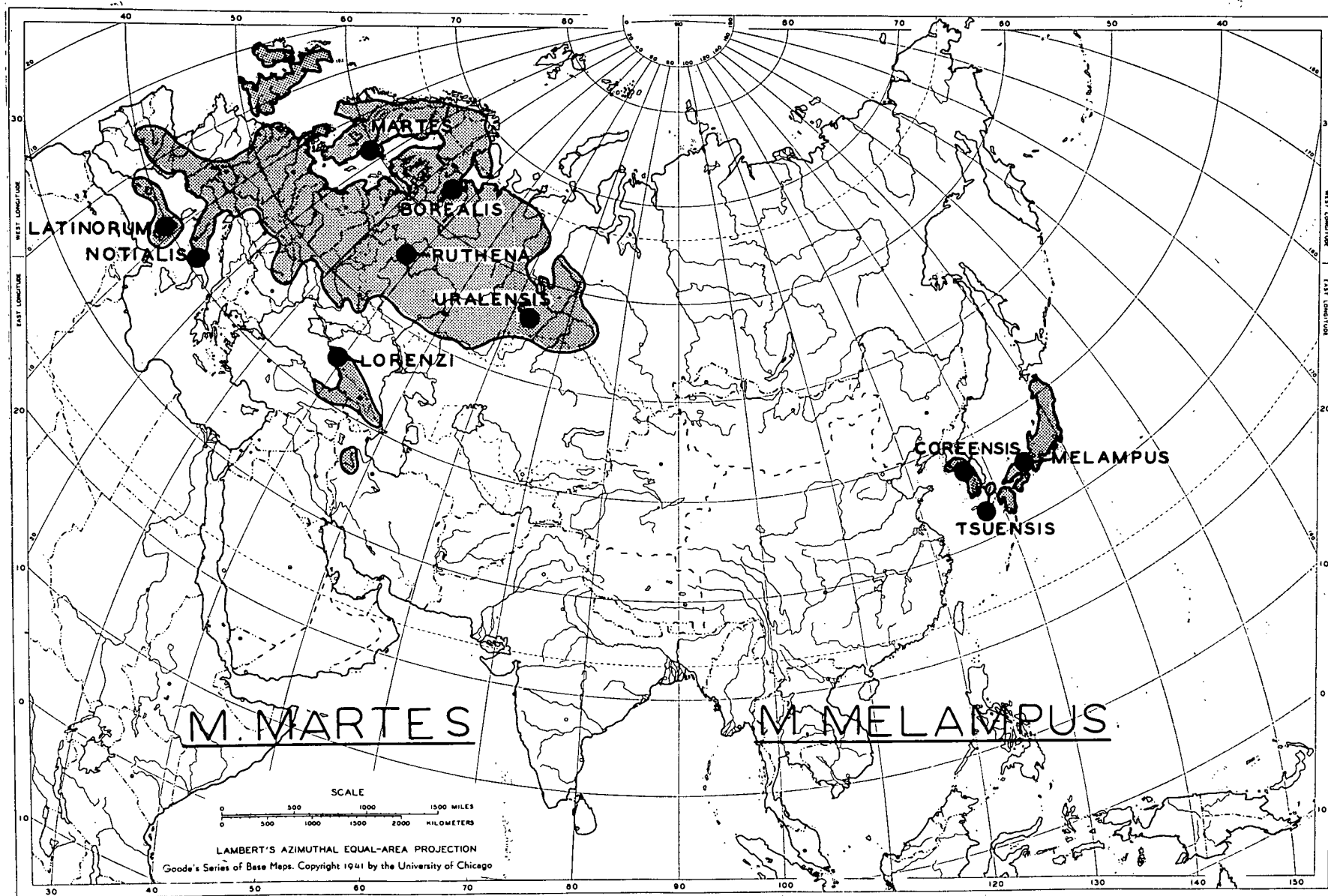
Figures 3, 4, 5 and 6.

(To face page 42)

Figures 3, 4, 5 and 6. The distribution of Eurasian marten. Collated from Kozhantschikov (1930), Ognev (1931), Schmidt (1943), Bobrinskoy et al (1944) and many other sources. Type localities are given for the classifications of Ellerman, Morrison-Scott (1951 and 1953) and Chasen (1940).









Denmark, France, Belgium, Holland, Switzerland, Italy, northern Spain, Balearic Islands, Sardinia, Bohemia, Poland, to Russia and the very southwestern parts of Siberia, to the Ob and Ertischa Rivers, the White Sea and the Caucasus, also Asia Minor and Persia (Bobrinskoy 1944 and Ellerman, Morrison-Scott 1951). Sowerby (1922-30) lists them from Heilungkiang and Kirin in Manchuria, and Sowerby (1916) from southwest Kansu and northwest Szechuan. Brongersma (1941) records a specimen very near to M. martes from Nepal, possibly another from Tibet.

Skull diagrams and photographs: Coues 1877, pl. 3; Alston 1879, fig. 2; Reynolds 1912, pl. 2; Miller 1912(a) figs. 76, 77, 78, 79 and 80; Ognev 1931, vol. 2, pp. 593, 600, 601 and 602; Schmidt 1943, figs. 8 and 9; Rode and Didier 1944, figs. 357, 358, 359, and 360. Other sources are given by Ognev 1931, vol. 2.

Specimens examined: twelve from Europe

This forest dweller is a typical occupant of the old hardwood or coniferous second growth forests. It lives in woods of up to 2000 meters in the Caucasus. It feeds on nuts, insects and berries. The den is built in a cavity 5 to 30 meters high in trees. Infrequently it uses the dens of wild pigs. The period of heat begins in February and reaches its peak in July. Gestation lasts for eight months (270 to 285 days). The litter of two to six, is born in April or May (Bobrinskoy 1944, Schmidt 1943). Geographic variation, according to Bobrinskoy (1944) chiefly expressed in size and colour. Jurgenson (1951) says much geographic variation in skull and teeth is associated with

the type of food eaten.

Characteristics: More active than M. foina; smaller and lighter (males weighing 1200-1650 grams, females 800-1350 grams); body long and slim with short limbs; length of head and body less than 57 cm.; fur fine, soft, brown below and above, rarely slatey; outer fur rich brown, under fur red grey with red yellow tips; top of head same colour as spine; often with a light coloured throat patch of yellow, which extends behind rear of forelegs; upper lip with distinct vertical groove; tail bushy, rather short, being considerably longer (without tip hairs) than one half the length of head and trunk (Ellerman, Morrison-Scott 1951 say only 49% length of head and trunk); tail vertebrae said to be variously 20-22, 17, 18-19, 18, 10+, 18-33, 17-19, 18-19 (Bobrinskoy et al. 1944, Ognev 1931, Gray 1869, de Blainville 1841, Flower 1885, Reynolds 1912, Schmidt 1943, Gerrard 1862); hair endings of tail long, being more than quarter length of tail; tip of tail rounded; soles of feet covered with thick hair; skull massive, zibellina shaped, i. e. long, narrow, and rather produced, thin and deep when seen from behind; skull and braincase less massive, especially in the posterior part; condylobasal length 70 to 90 mm.; zygomatic width about 48 mm., the zygomatic width being rather more than half condylobasal length; zygomatic arches highest at rear, whence they slope suddenly down and forward, being longer and narrower; sagittal crest heavy, only rarely completely absent; rostrum with parallel sides, narrow and elongate; anterior nares oval in shape; nasal bones with moderate central constriction; frontal profile only slightly sloping, concavity of profile not very pronounced; supraorbital

constriction moderate, pointed, rather deep and always present; post orbital process nearly midway between point of greatest constriction of cranium and the anterior root of zygoma, usually weak, occasionally absent; postorbital region (in front of point of greatest constriction) short and convex; palate relatively narrow and long (about 4.3 cm. in length), often with a distance azygos notch on rear surface; anteorbital foramen relatively large; bullae moderate in length and rather widely spaced, so that twice the distance between carotid canals is greater than the greatest length of the bullae; the distance between the outer edges of the jugular foramina is shorter than the greatest length of the bullae; distance between the carotid canals equals about half the distance between the foramen lacerum posterio and the eustachian foramen; bulla containing three or more chambers, with partitions strongly developed; mastoid process extends somewhat beyond the edge of the meatus; general dentition rather strong; upper premolars not crowded and straight; PM^3 strongly convex on inner surface, strongly concave on outer; relatively large PM^4 with thick inner cusp, its width being equal to its length and nearly equal to width of trenchant part, trenchant portion as long as M^1 is wide; M^1 is large, massive, inner moiety large - twice as large as outer moiety and one third longer, waist separating the two strongly constricted; M_1 with a slightly developed inner tubercle at base of main cusp (i.e. hypoconid); M_2 with inner cusp only slightly developed; baculum of the Martes type gradually bending upward throughout its distal third, 35 to 45 mm. long ending either in two vertical

prongs, or these being closed to form a transverse perforation (according to Pocock 1918 always forked, which conclusion I find to be incorrect).

Martes martes martes (Linnaeus 1758)

Type locality: Upsala, Sweden.

Range: Europe north of the Mediterranean east as far as the White Sea, Kiev and Vetebsk in Asia. Large and dark in colour (Bobrinskoy et al. 1944).

Condylbasal length: males 8.66 (8.41-9.00) n = 6; females 7.90 (7.78 - 8.16) n = 3.

Martes martes borealis Kutznetzov 1941 (according to Bobrinskoy et al. 1944).

Type locality: not known.

Range: northern parts of European Russia, excluding the Kola Peninsula.

Very like M. m. ruthena, but with winter pelage lighter (Bobrinskoy et al. 1944).

Martes martes latinorum (Barrett-Hamilton 1904)

Type locality: Nurri Mountains, Sardinia.

Range: Italy, Sardinia, Balearic Islands (Ellerman, Morrison-Scott 1951). As in M. m. martes but with pelage lighter in colour, throat patch yellower (Miller 1912a).

Condylbasal length: males 8.66 (8.50 - 8.80) n = 3; females 7.89 (7.70 - 8.30) n = 6.

Martes martes lorenzi Ognev 1926.

Type locality: Storojevaia, Kuban District, Caucasia.

Range: the forested area of the whole Caucasus. Large, as in M. m. martes, but with winter fur coarse and thick, dark brown with a characteristic red-olive cast (Ognev 1926, Bobrinskoy et al. 1944).

Condylbasal length: males 8.53 (8.41 - 8.66) n = 4; females 7.89 (7.70 - 8.30) n = 6.

Martes martes notialis (Cavazza 1912)

Type locality: South of Abruzzi, southern Italy.

Range: Italy. Smaller, paler than M. m. martes, with less dense pelage (Cavazza 1912).

Martes martes ruthena Ognev 1926.

Type locality: Dmitrovsk Subdistrict, Moscow Government, Russia.

Range: central part of European Russia. Smaller than M. m. martes and lighter in colour with a reddish sandy cast (Ognev 1926, Bobrinskoy et al. 1944).

Condylbasal length: males 8.20 (7.89 - 8.66) n = 22; females 7.57 (7.11 - 8.01) n = 11.

Martes martes uralensis Kutznetzov 1944 (according to Bobrinskoy et al. 1944).

Type locality: unknown.

Range: the whole of the Ural Range. Colour very much as in M. m. ruthena and borealis but larger in size than either (Bobrinskoy et al. 1944).

Martes foina (Erxleben 1777) = domestica, alba, fagorum.

Type locality: Germany.

Range: Europe, except southern Spain and Italy and the British

Isles; present in northern Spain and Italy, Bosnia, France, Belgium, Holland, Germany, Denmark, Switzerland, Crete, Poland, Finland, Ukraine, Crimea, Caucasus, Transcaucasus, Russian and Eastern Turkestan, northwards to the Altai, Asia Minor, Persia, Afghanistan, Syria, Palestine, Baluchistan, Kashmir, Himalayas and the Tibetan Plateau, Punjab, Chinese Turkestan, Mongolia, Manchuria, and probably parts of northern China, northern Chili, Shansi and into West China, probably not much further south than Shansi and Szechwan. (Sowerby 1922-30, Sowerby 1916, Ognev 1931, Allen 1938-40, Brongersma 1941, Bobrinskoy et al. 1944, Tate 1947, Ellerman, Morrison-Scott 1951, and Bannikov 1953).

Specimens examined: 81 from Europe and Asia.

Skull diagrams and photographs: de Blainville 1841, pl. G4 and G13; Bronn 1874-90; Klassen und Ordnungen vol. 1, pt. 5, pl. 15; Coues 1877, pl. 4; Alston 1879, fig. 1; Miller 1912a, fig. 80; Festa 1914, pl. 1; Ognev 1931, vol. 2, pp. 623, 625, 626, 627, and 628; Migulin 1938, p. 167; Schmidt 1943, figs. 8 and 9; Bobrinskoy et al. 1944, fig. 77; Rode and Didier 1944, pp. 127 and 128; Baumann 1949, figs. 365, 366, 367 and 368; Bannikov 1953, p. 40. Other sources are named by Ognev 1931, vol. 2.

This marten is unlike M. martes in that while it is found in woods, it also occurs in barren rock slides. Its den is made in crevices in the rock and unlike M. martes it does not avoid human habitation, often living in abandoned dwellings. It feeds on rodents, birds, birds' eggs, frogs, various insects,

berries, and grapes. It lives in the hills to an altitude of 3000 meters. Time and length of the period of reproduction is as in M. martes (Bobrinskoy et al. 1944). Asdell (1946) says that in England it mates in July and August and that the gestation period is 8.5 to 9.6 months. In India, according to Blandford (1888 - 1891) mating occurs in February and gestation lasts nine weeks. This interpretation may be a result of lack of knowledge concerning delay in implantation of the blastocyst, but Asdell suggests that if it is correct that delayed implantation occurs only in the northern part of the animal's range and not in the southern, it may be a function of seasonal daylength.

According to Bobrinskoy individual variation in M. foina is very great, while geographic variation is only slight.

Characteristics: A sluggish animal, being relatively large and heavy (male weighing 1700 - 2100 gms., females 1100 - 1500 gms.); body broad and compact with long limbs; length of head and body less than 57 cm.; fur coarse, less soft, brown above and below, often slaty; outer fur dull grey brown, under fur greyish white; top of the head same colour as spine; usually with a lighter coloured throat patch, usually white or creamy, not extending between legs but rather forking, each branch running down the front legs; upper lip with distinct vertical groove; tail bushy, rather short, though somewhat longer than in M. martes, without hair tips, considerably longer than one half head and body length (Ellerman, Morrison-Scott say actually 49% of head and trunk length); tail vertebrae various-stated to be 17 - 19, 18 and 20 - 22 (Schmidt 1943, de Blainville 1841, Bobrinskoy 1944 and

Ognev 1931); hair endings of tail long, being more than half length of tail; tip of tail pointed; soles of feet lacking hair; skull light, flavigula shaped (i.e. swollen, flattened, with short nose); skull broad, more massive, especially in posterior part; condylobasal length 70 - 80 mm. usually less than 83 mm., zygomatic width 48 mm., being much more than half condylobasal length; zygomatic arches regularly curved, broadest and highest near their middle, broader and shorter; sagittal crest absent or very weak; rostrum wide and short, with converging sides; anterior nares heart shaped; nasal bones strongly constricted; frontal profile more sloping, concavity much more pronounced; supraorbital constriction slight, flat, blunt and often absent; postorbital process much nearer point of greatest constriction than anterior root of zygoma; always present, strong, coming to a distinct point; postorbital region (in front of point of greatest constriction) long and straight; palate relatively broad and short (35 mm. long), truncated at posterior margin; antorbital foramen relatively small; braincase broader, less extended; bullae short and widely spaced so that the distance between carotid canals is greater than the greatest length of the bullae; the distance between the outer edges of the jugular foramina is the same or more than the greatest length of bulla; distance between carotid canals equals two-thirds the distance between foramen lacerum posterior and eustachian foramen; bulla with 3 or more chambers, the partitions less well developed than in M. martes; mastoid process extends somewhat beyond edge of meatus; general dentition

weaker, upper premolars crowded, often placed diagonally; PM^2 evenly biconvex, somewhat small; PM^4 with inner cusp small (total width less than length, and barely half width of trenchant part); inner cusp usually placed diagonally to axis of trenchant part; length of PM^4 greater than width of M^1 ; M^1 small, inner lobe small, hardly larger than outer lobe; constriction of waist weak; M_1 with a well developed hypoconid; M_2 likewise with an inner cusp present and well developed; baculum of the Martes type, bending gradually upward throughout its distal third, 56 to 59 mm. long, occasionally with two vertical prongs at tip, these most often united to produce a transverse perforation.

Martes foina foina (Erxleben). Type locality: German; Range: Europe, except southern Spain, probably eastwards into Russia (Ellerman, Morrison-Scott 1951). The type form, with longer hairs of back tipped with sepia, the general hue of upper parts drab (Miller 1912a).

Condylobasal length: males 8.19 (8.90 - 8.46) $n = 5$; females 7.77 (7.40 - 8.00) $n = 5$.

Martes foina bosniaca Brass 1911 (in Aus der Reich der Pelze)

Type locality: Bosnia, Yugoslavia.

Range and characteristics uncertain.

Martes foina bunites (Bate 1906).

Type locality: Kontopalo, Kania, Crete.

Range: Crete. Near to M. f. intermedia but with shorter fur

of a duller, more uniform colour, without any gloss, tail less bushy and shorter (Bate 1906).

Condylbasal length: males 7.72 (7.64 - 7.84) $n = 2$; females 7.00 $n = 1$.

Martes foina intermedia (Severtzov 1873)

Type locality: Basin of the Chu, Tallas and Naryn, eastern Turkestan.

Range: Russian and Chinese Turkestan, Tianshan, Afghanistan, Baluchistan, western Persia and Kashmir (Ellerman, Morrison-Scott 1951). Bannikov (1953) says it occurs in Mongolia. The most distinctive of all subspecies of M. foina; compared to M. f. foina are small in size, light in colour and with comparatively little fur (Bobrinskoy et al. 1944).

Condylbasal length: males 8.04 (7.60 - 8.46) $n = 15$; females 7.48 (7.37 - 7.80) $n = 9$.

Martes foina kozlovi Ognev 1931

Type locality: Kam (valley of River Mekong, eastern Tibet.

Range: the Tibetan Plateau and Himalayas. Characteristics uncertain.

Condylbasal length: males 8.10 $n = 1$; females 7.52 $n = 1$.

Martes foina mediterranea (Barrett-Hamilton 1898)

Type locality: Sierra de Jerez, Cadiz, Spain.

Range: southern Spain. Compared to M. f. foina with the longer hairs of back tipped with light yellowish brown, the general hue of the upper parts lighter, yellower, and less drab (Miller 1912a).

Martes foina milleri Festa 1914.

Type locality: Aghios Isidiros, Island of Rhodes, eastern Mediterranean.

Range: Island of Rhodes. Characteristics uncertain.

Martes foina nehringi (Satunin 1906), in Mitt. Kauk. Mus. Tiflis 2 : 120,292.

Type locality: Tiflis, Transcaucasia.

Range and characteristics uncertain.

Condylbasal length: males 8.30 (8.10 - 8.51) n = 4; females 7.58 (7.21 - 7.90) n = 4.

Martes foina rosanowi Martino 1917.

Type locality: north-western slope of the Chatyrdag Mountains, Crimea.

Range: Crimean Peninsula. Characteristics uncertain.

Condylbasal length: male 7.87 n = 1; females 7.57 (7.42 - 7.68) n = 3.

Martes foina syriaca (Nehring 1902)

Type locality: Wadi Syr (which runs into Wadi Kefren, a tributary of the lower Jordan), Syria.

Range and characteristics uncertain.

Martes foina toufoeus (Hodgson 1842). In the Journal of the Asiatic Society of Bengal, II, p. 281).

Type locality: Lhasa, Tibet.

Range: Tibet, Himalayas and Afghanistan (Jerdon 1874). Colour of head and body above is light yellowish gray; the extremities are blackish, the chin, throat and breast pure white (Horsfield

1851). Possibly quite similar to M. f. intermedia and M. f. Kozlovi. Ellerman, Morrison-Scott remark: "Despite Pocock's contention that this is allied to M. melampus, it looks much more like M. foina. Its range is adjacent to that of foina, very far from melampus. From notes left by him, Chaworth-Musters evidently intended to treat it as foina. See also Pocock (1941, p. 322 footnote). We cannot trace that the form 'kansuensis' noted by him on this page was ever described."

Martes zibellina (Linnaeus 1758)

Type locality: "Asia septentrionali"; according to Ognev (1925) this must be redesignated, after Gmelin, as "Surroundings of Tobolsk, Tomsk Government, Siberia."

Range: Siberia, from the middle of Pechora to the lower Leni, and from the Altai to the Ussuri region, also Kamchatka, Sakhaline, northern Japan (Hokkaido and the Kuriles), Korea, Manchuria, northern Mongolia and Tannu-tuba. Now highly fragmented (Bannikov 1953, Bobrinskoy et al. 1944) and with range much reduced (Harper 1945). According to Jerdon (1874), Blyth took a specimen in Tibet he was inclined to identify as M. zibellina (Bobrinskoy et al. 1944, Sowerby 1922-30, Ellerman, Morrison-Scott 1953, Kozhantschikov 1930, Ognev 1931). Zhitkov (1937) titles a paper "On the former distribution of the sable in Europe"; whether it occurred here formerly I do not know, not having examined the paper. Harper (1945) says that in the past it has extended as far west as the Kola Peninsula or even Lapland.

Specimens examined: 77 from Asia.

Skull diagrams and photographs: de Blainville 1841, pl. G7 and G13; Ognev 1925, pl. 26; Ognev 1931, vol. 2, pp. 563, 587, 591, 593 and 594; Bobrinskoy et al. 1944, fig. 77; Bannikov 1953, p. 40. Other sources are named by Ognev 1931, vol. 2.

This animal is a forest dweller, usually living in hilly country interspersed with moss covered rock slopes. All of its range is characterized by the presence of spruce and pine (i.e. typical taiga forest) and where these are absent, so is the sable. It is nocturnal, and spends more time on the ground than do Martes foina and M. martes. Its food is chiefly small nuts, berries and all small animals to the size of a rabbit or grouse. The den is made in the crevices of roots and rocks. In February they undergo a "False drive" which lasts for three or four weeks. In July is the real "drive" which is followed by mating. The gestation period is nine to nine and a half months (270 - 285 days). The young number two to four, rarely five or six and are born in April, or early May. They are born blind. On the 31st to 34th day, their eyes open. They suckle for about two months and in the sixth or eighth week first leave the nest. By August they are fully grown. Maturity is reached in the second year, according to one author, the third year according to another and the fifth according to a third. "False drive" occurs in the fall, reaching its extremity in October (Bobrinskoy et al. 1944, Kozhantschikov 1930, Schmidt 1943, Ponomarev 1938).

Variation in the sable is rather great. Ponomarev (1938) says that within a given region albinism, semi-albinism, white spotting, and a general mottling occur. On the Island

of Fekliston white headedness occurs, which he attributed to the activity of a single recessive gene. Normal sable colour, he believed is a typical quantitative character controlled by several genes. The colour and shape of the throat patch he attributed to a single gene.

Geographic variation is likewise marked. According to the same author the center of darkest colouration is found on the northeast coast of Lake Baikal.

Kozhantshikov (1930) reported that the characters assigned to the continental subspecies of sable are variable and insignificant but that insular forms and those from Kamtschadka were quite distinctive but probably derived from the continental form. He concluded that there were essentially only two types (subspecies ?) of sable - the continental and those remaining.

Ognev (1925) came to somewhat different conclusions. In colour, at least, he concluded, decided geographic variation occurs. According to him, the animals of the mountains are small, with very dark pelage, the underfur being characteristically slaty. The sables of the forest and low country are larger, with paler fur, less slaty underfur, and generally less dense, less soft pelage. The sable of the very northern tundra-taiga is the largest sable of all but its fur is coarse and light, the underfur yellowish.

Bobrinskoy et al. (1944) state that the chief characteristics marked by geographic variability are size, colour of fur, and quality of fur. The largest sables, he says, are found in two localities, one being the western parts of its range (Altai

and the Ob lowlands), the other in Kamtschadka. Medium and small sized sables occur in central Siberia and in the Amuro-Ussuriski districts. Colour and silkiness of fur change correspondingly and are evidently conditioned by the continentality of the climate. The darkest and silkiest live in the Transbaikal and southern Yakutia regions, whereas to the east and west of these places, the fur gradually becomes lighter and coarser; however, in the mountainous regions the colour again turns somewhat darker. It is interesting to note that in neither the sable nor the European martens does Bergmann's Rule appear to strictly apply (above named authors and Schmidt 1943).

Characteristics: An active form; weight uncertain, but probably more than in M. martes and M. foina; length of head and body less than 57 cm.; fur usually fine, soft, brown both above and below, often grading to blackish, underfur brown to yellowish, to slate and steel grey; top of head lighter in colour than spine; throat patch often absent, or at least very small, rarely reaching to fore legs; dusky salmon in colour; upper lip with distinct vertical groove; tail short, with hair endings less than one half length of head and trunk and barely reaching to end of outstretched legs; tail about five to seven inches long; tail vertebrae variously numbered as 15 to 16, 13, 18, 16, 12-15 (Bobrinskoy et al. 1944, Ognev 1931, Gray 1869, de Blainville 1841, Flower 1885, Schmidt 1943, Owen 1853); hair endings of tail less than quarter tail length; skull light, never massive, elongate as in M. americana americana, not short as in M. foina, narrow and deeper with nose somewhat produced;

condylobasal length 70 - 90 mm., rarely 96 mm.; zygomatic width about 48 mm., about one half condylobasal length; zygomatic arches highest at rear, whence they slope suddenly downward and forward, tend to be narrow, long; sagittal crest heavy, only rarely absent; rostrum sides convergent, but very narrow and long; nasal bones with only slight constriction; frontal profile not steeply sloping, concavity of profile not pronounced; supraorbital constriction moderate, pointed, rather deep, always present; postorbital process midway between point of greatest constriction and anterior root of zygoma, is usually weak, often lacking; postorbital region short and convex; palate relatively narrow and long, often with a distinct azygos notch on its posterior edge; anteorbital foramen small; braincase high, narrow and extended; bullae long and placed close together so that twice the distance between carotid canals equals the greatest length of the bulla; the distance between the outer edges of the jugular foramen is less than the greatest length of the bulla; distance between carotid canals is less than one half the distance between the foramen lacerum posteriore and the eustachian foramen; mastoid process fail to extend beyond edge of meatus; general dentition weak; upper premolars not crowded; PM^3 rather large, strongly convex on inner, strongly concave on outer side; PM^4 with inner cusp placed at right angles to trenchant part, large and thick, but with width less than total length, although nearly equal to width of trenchant part: PM^4 longer than width of upper molar; M^1 wide, inner moiety large (as in M. martes) twice as large as outer part and one third longer, waist strongly

constricted; M_1 with well developed inner tubercle (hypoconid) at base of main cusp; unlike M. martes and M. foina the last several caudal vertebrae all possess transverse process (according to Schmidt 1943) baculum 38 mm. long, of the Martes type, bending gradually upwards throughout its distal third, ending often in a biforked tip, according to Ognev (1931) but equally often the ends of bifurcations uniting to produce a transverse perforation.

Martes zibellina zibellina (Linnaeus 1758)

Type locality: "Surroundings of Tobolsk, Tomsk Government, Siberia" (Ognev 1925).

Range: Pechora basin, northern Urals, and Ob Plain (Ognev 1925) and 1931, Bobrinskoy et al. 1944, Ellerman, Morrison-Scott 1951). With long nose, short braincase. Colour dull and pale even in dark individuals, varying from cinnamon drab to dark brown, the underfur retaining its lightness of tint. In the Urals tends to be smaller, with darker denser fur, with a large bright throat patch (Ognev 1925).

Condylbasal length; males 8.59 (8.39 - 8.92) $n = 6$; females 7.83 (7.73 - 7.93) $n = 4$.

Martes zibellina arsenjevi Kuznetzov 1941 (according to Bobrinskoy et al. 1944).

Type locality: Ussuri Basin, eastern Siberia.

Range and characteristics uncertain.

Martes zibellina averini Bashanov 1943.

Type locality: Katon-Karagai region, southern Altai.

Range and characteristics uncertain (Ellerman, Morrison-Scott 1953), but occurs in Mongolia, according to Bannikov (1953).

Martes zibellina brachyura (Temminck 1844)

Type locality: Yeso, Japan.

Range: Hokkaido Island, Japan, and the Kurile Islands.

Inferior to the continental forms in fineness and length of fur; back and tail dark brown, sides and limbs lighter; hair of feet long, concealing the claws; tail short, only, 3.5 inches in length (Temminck).

Martes zibellina hamgyenensis Kishida 1927 (In Dobuts Zasshi Tokyo 39 : 509).

Type locality: Korea.

Range: so far as known, the range of the species is Korea, possibly north to near the type locality of M. z. arsenjevi.

Characteristics uncertain.

Martes zibellina kamtschadalis (Birula 1918) in Comptes Rendus Mus. Zool. Acad. Sci. Petrograd, vol. 821)

Type locality: Kamtchadka.

Range: the Kamtchadkan Peninsula. A strongly characterized sable, being much larger and with more robust dentition than any other subspecies. Colour ranges from warm sepia to mars brown, throat patch variable (Ognev 1925).

Condylbasal length: males 8.95 (8.50 - 9.50) n = 22; females 8.08 (7.86 - 8.41) n = 15.

Martes zibellina princeps (Birula 1922) In the Ann. Mus. Zool. Acad. Sci., St. Petersburg 22:)

Type locality: Baragusin Mountains, Transbaikalia.

Range: the mountain forests of Transbaikalia, i.e. in the Baragusin Hills and the branches of the Stanavoy Mountains, and through parts of Mongolia. Formerly between the Olekma and Witim Rivers. A medium sized sable, near that found in the Sajon Mountains, but with much longer bullae and braincase. Fur long, dense and soft, of a dark black-brown, with underfur bluish grey and with brown at base of tip. Throat patch reduced, often invisible (Ognev 1925, Bannikov 1953).

Condylbasal length: males 8.10 (7.82 - 8.35) $n = 9$; females 7.48 (7.43 - 7.53) $n = 5$.

Martes zibellina sahalinensis Ognev 1925

Type locality: Wedernikovo, Sakhalin Island.

Range: Sakhalin Island. Skull distinctive, fine and weak, with strong contraction in the interorbital region and with short bullae. Dentition weak. Colour, as in M. z. kamtschadalis, but commonly more cinnamon (Ognev 1925).

Condylbasal length: males 7.97 (7.63 - 8.20) $n = 13$; females 7.41 (7.26 - 7.59) $n = 6$.

Martes zibellina sajanensis Ognev 1925.

Type locality: Orsyba River, northern Sayan Mountains, middle Siberia.

Range: the mountain forests of northwestern Mongolia including the Usa and Kasyr Rivers. Skull short, both in nasal and cranial regions. Colour dark brown, the underfur pale yellowish. Throat patch varies from dusky brown to brilliant salmon (Ognev 1925, Allen 1938-40, Bannikov 1953).

Condylbasal length: males 8.24 (8.16 - 8.40) n = 6; females 7.36 (7.32 - 7.40) n = 2.

Martes zibellina schantarica Kuznetsov 1941 (according to Bobrinskoy et al. 1944).

Type locality: Shantar Islands, lower Amur, eastern Siberia.

Range: the Shantar Islands. According to Bobrinskoy is very like M. z. sahalinensis.

Martes zibellina tungusensis Kuznetsov 1941 (according to Bobrinskoy et al. 1944).

Type locality: Basins of the Nizhaya and Podkamennaya Tungush, middle Siberia.

Range: presumably as the type locality. Characteristics uncertain.

Martes zibellina yeniseensis Ognev 1925.

Type locality: Forest on plain along Yenesei River, Krasnoyarsk district, eastern Siberia.

Range: Taiga between the Angerra and Sayan foothills (Bobrinskoy et al. 1944, Ellerman, Morrison-Scott 1951, Ognev 1925). Near to M. z. zibellina but with shorter nasal region, longer cranial region, wider zygomatic arches and postorbital processes. The colour of the fur is a more dusky warm brown.

Condylbasal length: males 8.27 (8.00 - 8.70) n = 13; females 7.43 (7.20 - 7.70) n = 7. Ognev (1925) suggested that another distinct, but un-named, subspecies was to be found in the Tunguska River region, near Turuhansk. Bobrinskoy 1944 suggests distinctive forms may occur in the Altai and in southeastern Yakutia.

Martes melampus (Wagner 1841)

Type locality: Southern Hondo, Japan (Thomas 1905a)

Range: Hondo, Shikoku, Kiushii and Tsushima Islands, Japan and western Korea.

Specimens examined: eight from Asia.

Skull diagrams and photographs: Temminck 1844, figs. 3 and 4.

This appears to be a poorly understood animal; at least I have been able to locate almost nothing on its structure, life history, ecology or true relationships to the other forms. Some data may possibly be obtained from Okada 1938, or Kuroda 1940 which papers I have not seen. Ellerman, Morrison-Scott have this to say: "In the London material, this has the tail an average about 44 - 47 per cent of the head and body length (resembling zibellina therefore in rather short tail); a white throat patch seems fairly constant, and, at least in winter, the head tends to be paler than the back, all characters reminiscent of zibellina except the throat patch. But the bullae seem to be definitely of the martes--foina type, and do not seem to resemble those of zibellina. The forelimbs are clearly contrasted blackish, more so than in our zibellina skins, therefore the conclusion has been reached that melampus is an isolated and valid species, partly combining the characters of the other two groups. So far as colour is concerned, it in no way resembles the subgenus Charronia...." Described by Gray 1865 and 1869 as: fur soft, brown or yellow brown, underside scarcely paler, shoulder and outside of thigh blacker; feet blackish; head, chin and upper part of throat dark red brown; blackish streak from orbit to nose. Throat and sides of neck yellow or white,

crown paler.

Characteristics. Length of head and body less than 57 cm.; fur a rich golden brown to a deep brown; top of head lighter in colour than the spine; throat patch usually present, white in colour; upper lip presumably with a distinct vertical groove; tail short, with hair endings about 44 to 47 per cent length of head and body; skull very massive, foina shaped, or perhaps intermediate between foina and martes, not quite so broad, low and short as in M. foina.

Condylobasal length 84 to 85 mm.; zygomatic width greater than half condylobasal length, averaging about 48 mm.; zygomatic arches highest at rear, whence they slope suddenly downward and forward; relatively broad and short; sagittal crest strong, rarely absent; rostrum sides convergent, the rostrum being wide and short; nasal bones with no constriction; nasal profile rather sloping, with pronounced concavity; supraorbital constriction slight; postorbital process near middle or slightly nearer point of greatest constriction than anterior root of zygoma, is strong, coming to a distinct point. Postorbital region long and straight; palate relatively broad (.09 mm.) and short (86 mm.) with distinct azygos notch on rear surface; anteorbital foramen small; braincase broad, not relatively extended; bullae short, as in M. foina, and rather less inflated; widely spaced, so that the distance between the outer edges of the jugular foramen is greater than the greatest length of the bullae; so that the distance between the carotid canals equals about five-sevenths of the distance between foramen lacerum posteriore and the eustachian tube foramen; mastoid

process extends somewhat beyond edge of meatus; general dentition stronger; upper pre-molars sometimes rather crowded; PM^3 convex on inner side, concave on outer; PM^4 with inner cusp heavy, its width equalling its length and equalling three-fourths of the width of the trenchant part placed diagonally to axis of main cusp; length of PM^4 greater than width of M^1 ; M^1 large, massive, inner moiety large, intermediate between that of M. martes and M. foina, one and a half to two times as large as outer moiety, and twice as long; M_1 with inner cusp well developed; M_2 the same; baculum presumably of the Martes type, though as far as I know, never positively determined as such.

Martes melampus melampus (Wagner 1841)

Type locality: Japan (Wagner 1841), Southern Hondo, Japan (Thomas 1905a, b, and c).

Range: Hondo, Shikoku and Kiushiu Islands, Japan. With a rich golden brown pelage, the back usually much browner and with a bright orange throat patch (Thomas 1905a, b, and c). Condylobasal length: males 8.52 (8.50 - 8.55) $n = 2$; females 7.50 $n = 1$.

Martes melampus coreensis Kuroda and Mori 1923.

Type locality: Tenan, southern Chusei district, Korea.

Range: Korea. Near to M. m. melampus but general colour of upper parts yellow washed with fox-red instead of rich orange yellow and the ashy white of head extending farther to the nape instead of confined to the forehead. Separated from

M. m. tsuensis by much paler colouration throughout.

Martes melampus tsuensis (Thomas 1897)

Type locality: Kamoze, Tsushima Islands, Japan.

Range: Tsushima Islands, Japan. Similar to the typical form in all characters but colour of fur. General colour above in winter dirty yellowish brown instead of rich golden brown; muzzle and lips black instead of brown; throat patch white instead of yellow. In summer pelage much darker than the typical form, all brown parts being black as are the whole of the limbs; throat patch yellow (Thomas 1897).

Condylbasal length: females 7.80 n = 1.

Martes americana (Kerr 1792) including "M. caurina" (Merriam 1890)

Type locality: eastern North America.

Range: Holarctic North America.

Because this species will be treated in detail elsewhere, only those aspects needed for comparison to Eurasian species and the fisher will be utilized here. Because the two subspecies to be considered differ morphologically, comparison will be made for both of these.

Characteristics: Active forms, body long and slim with short limbs. Length of head and body less than 57 cm.; weighs about 700 - 1200 gms. in males, 600 - 800 gms. in females; outer fur dark brown, under fur longer in americana than in caurina, light yellow in both; top of head lighter in colour than is spine; throat patch in americana usually present, varying from white to

orange, but usually yellow, in caurina, always present, usually large (extending to base of forelegs), yellow or orange; upper lip with distinct vertical groove; tail in americana short with hair endings about one half a head and body length; in caurina, tail somewhat shorter equalling less than one half the head and body length; tail vertebrae average 17 (Cooper, 1953) in americana, 14 in caurina. According to Hall (1926a) it possesses an abdominal skin gland. Skull in americana light, narrow, elongate; nose rather produced; braincase not massive, especially in posterior part; in caurina more massive, broader, flatter, nose less produced; braincase more massive, especially in posterior part;

condylobasal length 67 mm. to 88 mm.; zygomatic width about 48 mm. in both, in americana being about one half condylobasal length, in caurina slightly more; arches in americana highest at rear, whence they slope suddenly downward and forward, being narrow and long; in caurina regularly curved, broadest and highest near their middle, broader and shorter; sagittal crest in americana only rarely absent, in caurina often weak or absent; rostrum, in americana narrow and long, rostral sides parallel; in caurina short and wide, sides convergent; in americana anterior nares oval, nasal bones with moderate constriction; frontal profile rather sloping, concavity pronounced; in caurina anterior nares more heartshaped, nasal bones with no constriction, frontal profile less sloping, concavity less pronounced; supra-orbital constriction in americana moderate, always present, in caurina, slight, sometimes absent; postorbital process in americana midway between point of greatest constriction and anterior

root of zygoma, usually weak; postorbital region short and convex; in caurina much nearer point of greatest constriction than anterior root of zygoma and stronger, postorbital region long and straight; palate relatively long and narrow, often with azygos notch on posterior surface in americana, in caurina shorter and broader, usually truncate behind; anteorbital foramen relatively large, in both; braincase markedly elongate, more so than in any other marten, in americana; less extended, broader and lower in caurina; bullae in americana long, narrow, highly inflated and situated near to each other, so that twice the distance between the carotid canals is the same or slightly less than the greatest length of bulla; distance between the outer edges of the jugular foramen is less than the greatest length of bullae; distance between the carotid canals is one half the distance between the foramen lacerum posterioire and the eustachian foramen; in caurina the bullae are less inflated, shorter, broader and more widely separated so that of the three measurements above, the first two are greater than the greatest length of bulla, and the distance between the carotid canals equals two-thirds the distance between the other two foramina; in americana the mastoid process does not extend beyond the meatus, in caurina it does; general dentition in americana weaker, upper premolars only occasionally crowded, in caurina stronger, premolars often crowded; in both PM^3 strongly convex on inner, concave on outer side; PM^4 in americana with inner cusp small, width being much less than length and only half the width of the trenchant part, placed nearly at right angles to

main axis of tooth, is as long as M^1 is wide; in caurina PM^4 has the inner cusp large and thick, its width nearly equal its length and more than one half the width of trenchant part and placed diagonally to main axis of tooth, not as long as M^1 is wide; M^1 in americana small, quadrate, always smaller than in Old World forms, inner moiety small, very little larger or longer than outer moiety and one third smaller than in caurina, in the latter form M^1 is large, massive, inner moiety one and a half to two times as large as outer moiety and twice as long; M_1 with an inner cusp present in both, more often absent in americana than in caurina; M_2 with inner cusp weak or absent in americana, present and well developed in caurina; baculum in both of the Martes type, bending gradually upwards throughout its distal third, ending in two prongs, or more, usually uniting to produce a transverse perforation.

Two subspecies are accepted in this paper.

Martes americana americana (Kerr, 1792)

Type locality: eastern North America.

Range: North America west to the Coast Range, excepting the Rocky Mountains south of central Idaho and Montana; also Newfoundland, Cape Breton Island and Prince Edward Island.

Martes americana caurina (Merriam 1890)

Type locality: Gray's Harbor, Chehalis County, Washington.

Range: the Coast Mountains, Coast Ranges, Cascade Mountains, Sierra Nevada and the Rocky Mountains, south of central Idaho and Montana, also Vancouver Island, the Alexander Archipelago and the Queen Charlotte Islands.

Martes pennanti (Erxleben 1777)

Type locality: Eastern Canada

Range: Holarctic North America

As in the case of M. americana, only those aspects important in comparison to other species are made here.

Characteristics: Active; elongate with short limbs; length of head and body usually greater than 57 cm. (ranging from 50 to 62 cm.); weight from 1500 to 4500 grams; fur coarse, less soft than in the martens; colour dark brown to blackish; outer fur brown-black with often a white subterminal area on each hair; usually without a throat patch, when present small and white; generally darker below than above; tail, without hair tips about one half the length of head and body, at least one third the length; tail relatively long, with variously 20 to 21 vertebrae (Kneeland 1859, Gerrard 1862); according to Hall (1926a) lacking an abdominal skin gland; skull not massive, although large; skull elongate, narrow, deep; nose rather produced; braincase not massive especially behind; condylobasal length usually more than 95 mm., varying from 92 to 122 mm.; zygomatic width from 55 to 60 mm., being more than one half condylobasal length; arches highest at rear, whence they slope suddenly downward and forward, are broader and shorter; sagittal crest strong, only rarely absent; rostrum long, narrow; rostral sides parallel; anterior nares oval; nasal bones slightly constricted; frontal profile rather sloping, concavity pronounced; supraorbital constriction moderate, always present; postorbital process about midway between point of greatest constriction and anterior root of zygoma, usually weak; postorbital region (in

front of point of greatest constriction) short and convex; palate relatively long (65 mm.) and narrow (10 mm.) usually with distinct azygos process on rear; antorbital foramen small; braincase light, extended; bullae long, but rather widely spaced so that twice the distance between the carotid canals is greater than the greatest length of bulla; the distance between the outer edges of the jugular foramen is the same or slightly more than the greatest length of bulla; the distance between the carotid canals equals two thirds the distance between the foramen lacerum posteriore and the eustachian foramen; the mastoid process extends beyond the edge of the meatus; general dentition weak; upper premolars not crowded; PM^3 convex on inner side, concave on outer; PM^4 with inner cusp small, width less than its length and only half that of trenchant part, placed diagonally to main axis of tooth, is longer than M^1 is wide; M^1 is light, quadrate but with inner moiety small as in M. americana americana, only slightly larger than outer lobe; waist moderately constricted; M_1 has well developed inner cusp at base of main cusp; M_2 likewise with strong inner cusp; baculum of the Martes type, gradually bending upward throughout its distal third, and with either two prongs at the tip, or these united to form a transverse perforation.

Of supposedly three subspecies, here not accepted.

Martes flavigula (Boddaert 1785) = Charronia flavigula Pocock 1918 = Lamprogale flavigula Ognev 1928 = Martes guatkinsi Horsfield 1851.

Type locality: Unknown, but considered by Pocock to have been

fixed by tradition as Nepal.

Range: The Amur and Ussuri regions of eastern Siberia, south through most of China, Tibet, Burma, Assam, thence westwards to Kashmir and North-West Frontier, and south into Indo-China, Siam, Malay States, Formosa, Sumatra, Java, Borneo and Banka; also the Nilgiri Hills, Coorg and Travancore, southern India (Sowerby 1916, Ellerman, Morrison-Scott 1951, Brongersma 1941). Brongersma adds that other unverified records exist in the literature for Palawan, Great Naturna, Balabac, and Calamianes, Cuyo, Subu, Sibutu, the Paternosters and Sebuko Islands. Jerdon (1874) says it occurs on Ceylon, but later authors do not authenticate this.

Specimens examined: 32 from Asia.

Skull diagrams and photographs: Blanford 1888-91, p. 157; Ognev 1931, vol. 2, pp. 635, 636 and 637; Pocock 1936b, fig. 2; Brongersma 1941, pl. 4 and fig. 1; Colbert and Hooijer 1953, pp. 51 and 52. Other sources are given by Ognev 1931, vol. 2.

According to Allen (1938-40) it is an animal of wooded mountainous country, fairly well distributed over most of southern and central China south of the Gobi. The same author records their feeding on honey bees, which are apparently a favourite food. They are also reported to feed on nectar and to run down and kill fawns of the barking deer. See also Appelman 1940, and Hutton 1949, not examined during this study. Characteristics: Length of head and body usually more than 57 cm. (Varying from 50 to 80 cm.); general colour black-brown above and yellow below; underchin white, chest, neck and under

belly yellow, occasionally tending to white; throat patch almost always extending so as to include the belly; upper lip never with vertical groove; tail long, but not bushy, its length (without hair tips) being two thirds the head and body length; tail vertebrae 24 (Blanford 1888-91, Owen 1853); soles of feet covered with hair (excepting in insular forms); skull massive, swollen, broad and flat, with short nose; condylobasal length 90 to 110 mm., occasionally as small as 70 mm.; zygomatic width about 60 mm., always greater than one half condylobasal length; arches regularly curved, broadest and highest at their middle, broader and short; sagittal crest absent or very weak; rostrum wide and short with convergent sides; nasal bones strongly constricted; frontal profile not steep, concavity not pronounced; supraorbital constriction moderate, pointed, always present; postorbital process about midway between point of greatest constriction and anterior root of zygoma, often absent, always weak; postorbital region short and convex; palate wide and short, truncated at hinder margin; anteorbital foramen small; braincase massive, especially at hinder end; bullae short and widely spaced so that twice the distance between the carotid canals or the distance between the outer edges of the jugular foramina are both greater than the greatest length of bulla; distance between the carotid canals is two thirds the distance between the foramen lacerum posteriore and the eustachian foramen; bulla with only two chambers, never three or more as in M. martes or M. foina; mastoid processes do not extend beyond the edge of the meatus; general dentition weaker; upper premolars not crowded; PM³ strongly convex on inner, concave on outer side;

PM⁴ with inner cusp small, width less than length and much less than width of trenchant part, placed at right angles to axis of main part, longer than width of M¹; M¹ small to moderate in size, inner moiety small, of about same length and size as outer moiety, waist only slightly constricted; the details of the lower molars are unknown to me; baculum distinctive, being easily separated from all other species of the genus, as pointed out by Pocock, curving up abruptly in its distal sixth, its tip being nearly vertical, length 65 - 80 mm., the tip is divided into four subsymmetrically arranged processes, each with a rounded condyle-like head (for details see Pocock 1918, 1936b and 1941, and Ognev 1931).

The two most recent classifications of the species (including M. guatkinsi) have been made by Pocock (1936b), Ellerman, Morrison-Scott (1951) and Chasen (1940). All of these authors, as well as considering M. flavigula and M. guatkinsi distinct, divide M. flavigula into eight subspecies (using quite distinct terminology for two of them). The classification of the latter two authors is given below, subjugating M. guatkinsi to subspecific status.

Martes flavigula flavigula (Boddaert 1785)

Type locality: fixed by Pocock as Nepal.

Range: Kashmir to Tibet and upper Burma and southern China, north to Shensi, Kentsu (Ellerman, Morrison-Scott 1951) Pocock 1936b). Characterized by the narrowness of the inner lobe of M¹, which is the same width throughout and in no way widened or flattened on its innermost margin (Bonhote 1901). Muzzle

and top of head black or dark brown; shoulders and back tawny brown to nearly white. Abdomen brown to whitish; throat rich yellow to nearly white; hair on rear foot extending back to and beyond the plantar pad. In India the soles are without hair. (Jerdon 1874, Bonhote 1901, Pocock 1936b).

Condylbasal length, males 10.06 (9.05 - 10.60) n = 19;
females 8.97 (8.20 - 9.70) n = 20.

Martes flavigula aterrima (Pallas 1811) = M. f. borealis Radde (1862) of Pocock.

Type locality: between the Uth and Amur Rivers, eastern Siberia, northern China and Korea (Ellerman, Morrison-Scott 1951, Pocock 1936b). Rather larger than typical flavigula and the colour of the back is much more yellow, the colour of the throat much more whitish (Bonhote 1901, Pocock 1936b). According to Howell (1929) individual colour variation is exceedingly high in the area occupied by this subspecies.

Condylbasal length: males 10.72 (10.20 - 11.00) n = 6;
females 9.63 (9.25 - 10.03) n = 2.

Martes flavigula chrysospila Swinhoe 1866 = M. f. xanthospila Swinhoe (1870) of Pocock.

Type locality: Mountain forests of Formosa.

Range: Formosa. Described by Bonhote (1901) as intermediate between the southern forms (peninsularis and henrici) and the typical form to the north. Small in size, with only moderately long fur; differs from typical flavigula by the head being deeper brown; back of the foreleg with a whitish patch (Bonhote

1901, Pocock 1936b).

Condylobasal length: males 9.20 $n = 1$; females 8.20 (7.60 - 8.80) $n = 2$.

Martes flavigula henrici (Schinz 1845)

Type locality: Sumatra.

Range: Sumatra, Banka and part of Borneo (Chasen 1940).

According to Pocock (1936b) occurs only on Sumatra. In shortness of fur and naked soles, resembles peninsularis; separated from it by its smaller skull and darker colouration, especially on the abdomen (Bonhote 1901, Pocock 1936b). Brongersma (1940) says a specimen of Mustela lutreolina from Sumatra in the Leiden Museum was originally mis-identified as M. f. henrici. Whether this casts doubt on the validity of the subspecies, or of the presence of the species on the island I do not know.

Condylobasal length: males 9.23 (8.75 - 9.70) $n = 4$; females 8.10 $n = 1$.

Martes flavigula indochinensis Kloss 1916.

Type locality: Klong Menao, southeastern Siam (Ellerman, Morrison-Scott 1951), Kohtak, southeastern Siam (Pocock 1936b).

Range: Siam, northern Tenasserim and Annam (Pocock 1936b).

Distinguished from typical flavigula and aterrima by a naked area of skin between the lobes of the plantar pad on the hind-foot, by the shorter winter coat, with a more yellowish tint, and by the paler patch beneath the eye (Pocock 1936b).

Condylobasal length: males 10.00 (10.00 - 10.00) $n = 2$; females 9.03 (8.80 - 9.20) $n = 3$.

Martes flavigula peninsularis (Bonhote 1901).

Type locality: Bankachon or Bankasun, Victoria Point, Tennes-serim.

Range: southern Tenasserim through the Malay Peninsula (Pocock 1936b, Ellerman, Morrison-Scott 1951). Similar to indochinensis in having the skin above the hind plantar pads naked, but differs in having the head brown, not black, shoulders and back less yellow and the abdomen dark brown. The coat is short and thin, varying little seasonally (Bonhote 1901, Pocock 1936b). Condylbasal length: males 9.75 ((.70 - 9.80) n = 2; females 8.67 (8.40 - 9.00) n = 4.

Martes flavigula robinsoni (Pocock 1936a).

Type locality; Tjbodas, Java.

Range: Java (Pocock 1936a). Distinguished from the Malayan and other insular forms in having the crown, nape and shoulders buffy grey and the line separating the white from the brown on the cheek poorly delineated (Pocock 1936 a and b).

Condylbasal length: females 9.10 n = 1.

Martes flavigula saba Chasen and Kloss (1932).

Type locality: near Sandakan, British North Borneo (Pocock 1936b)

Range: Parts of Borneo. Distinguished from henrici by its slightly smaller skull and its slightly smaller carnassial teeth (Pocock 1936b).

Condylbasal length: males 8.82 (8.60 - 8.95) n = 4; females 8.00 (7.80 - 8.20) n = 4.

Martes flavigula guatkinsi Horsfield 1851 = M. guatkinsi of authors.

Type locality: Madras, India.

Range: Nilgiri Hills, Coorg and Travancore, southern India.

The baculum, according to Pocock (1936b) differs somewhat from that of the other subspecies of M. flavigula in that the four distal processes are quite short, the left of the anterior pair being represented merely by a small tubercle. Skull distinctive in being depressed, as in an otter's, much flatter and less convex on its dorsal surface than in the other subspecies of flavigula, the frontal region being less swollen, with the occiput less sloped and the zygomata less arched. PM¹ may be absent. Colour dark, as in M. f. saba uniformly dark above; unlike saba metatarsal area above the plantar pad not naked (Bonhote 1901, Pocock 1936b).

Condylbasal length: males 8.90 n = 1; females 8.60 (8.20 - 9.00) n = 2.

Six to eight subspecies of Martes flavigula have been described from China, Mongolia and eastern Siberia. Pocock in his 1936(b) revision, reduced the number of these to two, but Howell 1929, Allen 1938-1940 and Brongersma 1941 say even these two fall within the range of individual variation and name all of them simply as M. flavigula flavigula admitting the possibility of the existence of the northern race, M. f. aterrima.

According to Allen, Thomas has concluded that M. f. indochinensis is an invalid form and Brongersma (1941) concluded that three insular forms (henrici, saba and robinsoni) all fell

within the range of individual variation and represented only a single subspecies M. f. henrici (called M. f. lasiotis by Brongersma). These forms are supposedly characterized by slightly smaller size, thinner pelage and naked feet.

Martes flavigula guatkinsi has been to the present considered a distinct species, in part at least because it is isolated geographically from M. flavigula. Jerdon (1874) says, however, that while Horsfield applied the name to the south Indian race, originally it was given to a Himalayan specimen. Tate 1947 says that M. guatkinsi is only "sometimes treated as a separate species". Pocock (1936b and 1941) considered the species distinct and pointed out what he considered important distinctions. Little is gained, however, by splitting M. flavigula into two species and I have here considered it a single form.

To summarize the above, it appears that while Pocock (1936b, 1941), Ellerman, Morrison-Scott (1951) and Chasen (1940) consider nine forms of the species to exist, the recent tendency has been towards simplification and these forms may be reduced to five as follows:

Martes flavigula flavigula

Martes flavigula chrysospila

Martes flavigula henrici

Martes flavigula peninsularis

Martes flavigula guatkinsi

RELATIONSHIPS OF THE MARTENS

The eventual answer to the puzzling problem of the relationship of the world's marten will be answered, likely through the study of genetics and paleontology. Some material concerning the latter is given elsewhere. Concerning the genetics of marten, I know only that Erlich (1949) reports that M. foina like most other carnivores, has a $2n$ chromosome number of 38 with heterogamic (x - y type) males. I presume that all species of the genus possess the same sort of chromosome structure.

This discussion is concerned primarily with a comparison of the morphology of the various species. It should be read in conjunction with the discussions elsewhere concerned with fossil marten, zoogeography, etc.

I have elsewhere discussed the "specific" status of the various species of marten in the world. I have pointed out that Severtsov (1876) considered the Tienschan Mountains of Eurasia to be the "homeland" of all marten and that here M. foina had been crossed with M. martes and M. zibellina, but that most other workers have found few or no hybrids elsewhere.

Schmidt (1943) concluded that the separation between M. martes and M. zibellina was considerably greater than that between M. martes and M. foina. His distinction would thus be:

- A. M. zibellina
- B. M. martes and M. foina.

Bonhote (1901) related M. flavigula upon the basis of its skull conformation to M. foina. Pocock's work on the baculum

of these species led to the relegation of M. flavigula to a distinct subgenus. When considering the New World forms in relation to the Old, we may immediately distinguish the fisher and thus arrive at:

- A. M. zibellina
- B. M. martes and M. foina
- C. M. flavigula (including M. guatkinsi)
- D. M. pennanti

We have not yet considered the relationship of M. a. americana and M. a. caurina to these, and it is this problem that we are primarily concerned with here. The "ecology" of the various species here suggests a clue. Marshall 1942, correctly I believe, points out that M. americana, M. martes and M. zibellina have, according to available information, so similar a pattern of behaviour and response as to be essentially the same. M. foina, M. flavigula and M. pennanti are, on the other hand, quite significantly different in their biology from each other and from the preceding, and hence might be grouped thus:

- A. M. americana, M. martes and M. zibellina
- B. M. foina
- C. M. flavigula
- D. M. pennanti

This scheme differs somewhat from that above with regard to M. americana, M. foina, M. martes and M. zibellina. It is of interest to compare them to that given by Gray (1865 and 1869), the last worker to so classify all of the world's species of marten. His scheme follows:

- A. M. martes, M. zibellina, M. americana and
M. melampus
- B. M. foina
- C. M. flavigula
- D. M. pennanti

Aside from the introduction of the species M. melampus, not yet considered, it will be seen that Gray's scheme lies nearest to the ecological one of Marshall and the one here accepted. The classification currently accepted by taxonomists is essentially this, so that M. foina is grouped with M. martes, M. zibellina, M. americana and M. melampus as the subgenus Martes; M. pennanti as the subgenus Pekania, and M. flavigula (including M. guatkinsi) the subgenus or genus Charronia or Flavigula. It is thus within the subgenus Martes that we must search primarily for relationship. I think we may accept that M. flavigula (upon the basis of its peculiar baculum) and M. pennanti (upon the basis of its size and biology) are distinctive from all others, although the degree of difference between the subgenera Charronia and Martes is probably greater and more fundamental than that between Pekania and Martes. There has been disagreement here in the past. Poland (1892) believed M. pennanti to be closely related to M. flavigula, so much so that he called the latter the "Afghan Fisher" and remarked on the disjunction in the distribution of the two. Schmidt (1943) considered M. flavigula the Asiatic counterpart of M. pennanti, but these workers did not know of, or in Schmidt's case did not take seriously, the fundamental distinction of the baculum in M. flavigula and their suggested relationship cannot be accepted.

Returning to the subgenus Martes, I can offer little concerning M. melampus. Ellerman, Morrison-Scott (1951) say that its colouration is near M. zibellina, but that its skull is nearer M. foina and M. martes, and they conclude that it is an "isolated and valid species". Other detail is given subsequently.

It has already been shown that early workers in North America often considered North American marten to be merely representatives of M. zibellina or M. martes but never of M. foina or M. melampus. Between 1771 and 1869, of those workers who named New World marten referable to Old World species, eleven referred them to M. zibellina and fourteen to M. martes (five of these referring them to both species). The honours then, have lain about equally between M. martes and M. zibellina and not to other species. We may devise from this again a scheme of relationship:

- A. 1. Martes martes, M. zibellina and M. americana
- 2. M. foina
- 3. M. melampus (possibly with M. foina)
- B. 1. M. pennanti
- C. 1. M. flavigula

The earlier workers on the problem, Gray (1865), Brandt (1855), Baird (1857), Allen (1869), and Coues (1877) came to the conclusions referred to above. Gray distinguished M. americana americana from the Old World forms on the shape and size of the upper molar. Brandt and Allen employed only characteristics of pelage. Baird employed both cranial and pelage characteristics as did Coues. All related M. americana to M. martes or M. zibellina and Coues, the last of the group, reviewed the findings

of the earlier workers and found closest relationship to M. zibellina of the two.

Coues and the earlier workers were unfortunate in that they did not recognize that a distinctive marten occurred on the west coast of North America (M. a. caurina) and it must be assumed, built their case around representatives of M. a. americana. In 1890 Merriam described caurina and said that in cranial and dental characters it departed from M. a. americana in the direction of M. zibellina.

Rhoads (1902) reviewed the problem in some detail. M. a. americana he considered totally distinct from all other forms on the basis of the smallness of the inner lobe of M^1 , as first outlined by Gray and the smallness of the lower molar and the small size of the inner cusp of M_2 . In general shape of skull M. a. caurina was nearest to M. foina but in the large size of the inner lobe of the upper molar and the large size of the lower first molar this form was very similar to M. martes and M. zibellina, not at all to M. americana americana to the east. In shape of skull, then, Rhoads related M. zibellina to M. americana and M. martes; M. foina to M. a. caurina. On the basis of dentition, however, M. a. americana was distinct, and M. a. caurina, M. martes and M. zibellina closely related and M. foina itself distinctive. He concluded of M. a. caurina that "its homologies connect it far more closely with the Eurasian than the American [M. a. americana] type of marten.... [It] is an isolated member of the martes - zibellina group".

Lydekker (1901 - 1904) stated that he believed the marten of North America were so nearly related to M. martes and M. zibellina that they should possibly be considered only varieties of these. He added no detail.

Ognev (1931) reviewing the marten of Russia said that M. zibellina lay intermediate in cranial and dental characteristics between M. martes and "M. americana". Subsequent description of "M. americana" makes it clear that Ognev was referring to M. a. americana and that he was giving no consideration to M. a. caurina.

Allen in 1938-40 said only that "Probably ... the sable (martes zibellina) ... finds its counterpart in the American Pine Martens (M. americana and races), but the Beech Marten (M. foina) is not represented in the New World".

My own interpretation of the relationship of martens, based upon examination of skulls of the species involved, leads me to conclude that the above writers are nowhere really wrong, and that M. a. caurina is most nearly related to M. martes and M. zibellina. M. a. americana is distinctive with some features allying it to M. zibellina and that M. melampus is to some degree related to martes and zibellina.

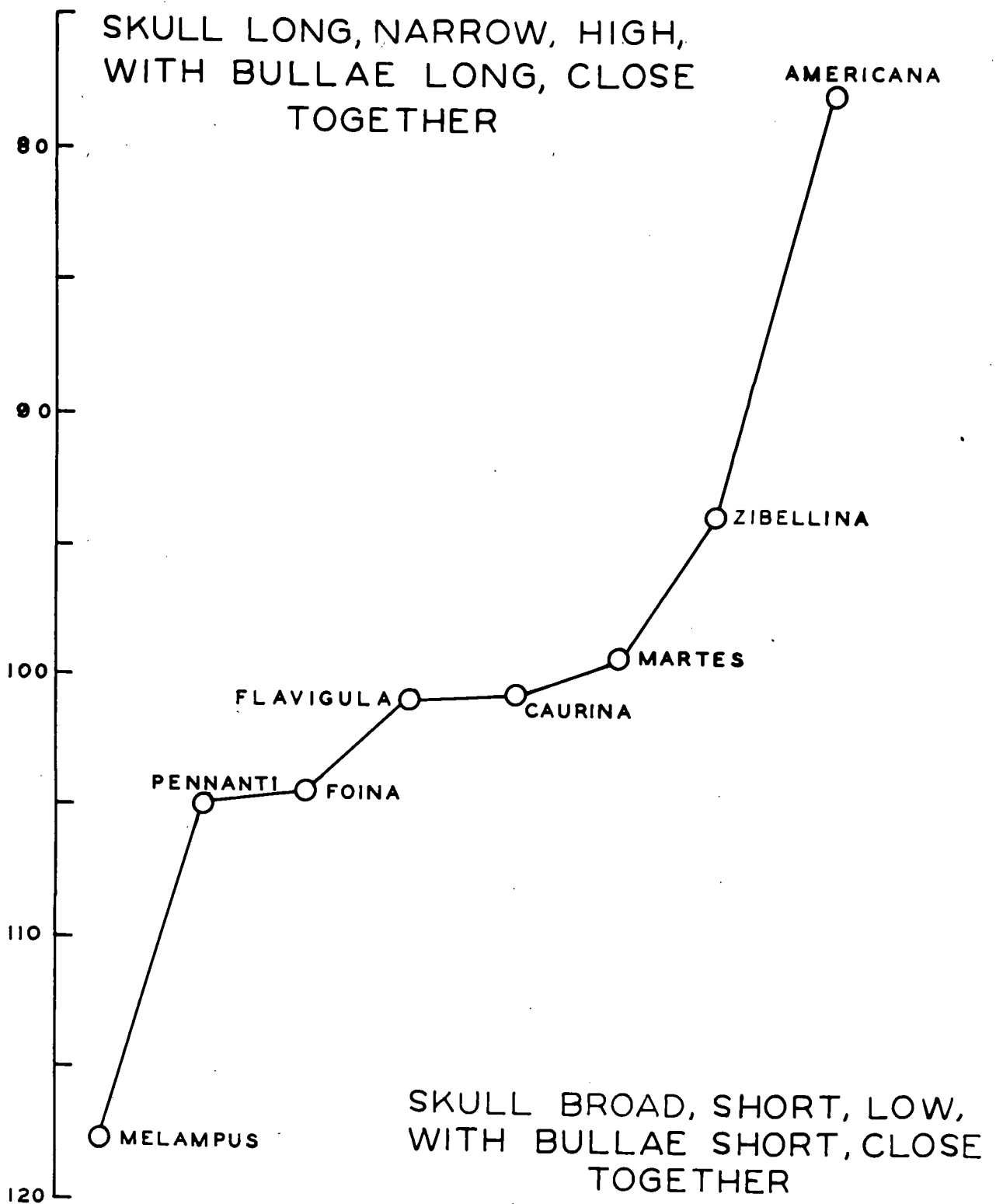
When I first began my study of skulls of all the species of marten, I was impressed by the fact that two basic types of skull existed. At the one extreme was the short, broad, and rounded skull, with short widely spaced bullae, and at the other, the long closely spaced bullae. The species of marten, placed in order, going from the former type to the

latter, would fall in this sequence: M. melampus, M. pennanti, M. foina, M. flavigula, M. a. caurina, M. martes, M. zibellina and M. a. americana (see Figure 7). The greatest division between the two groups occurs between M. melampus and M. pennanti and M. martes and M. zibellina. I felt that I could at that point divide martens into two basic divisions. I was puzzled, however, by the fact that both M. flavigula and M. pennanti fell so clearly within the first group and yet be so distinctive otherwise as to merit subgeneric status. Perhaps M. pennanti should not be so distinguished, but M. flavigula in view of its distinctive baculum, biology, distribution and antiquity, as shows in the palaeontological record could not be so ignored. It seemed that the two schemes of classification were mutually exclusive. In attempting to resolve the problem, help was given by Alston (1879) who remarked on the following findings of Blasius, with which Alston himself agreed: that the differences of proportion in the skulls of M. martes and M. foina are less conspicuous when a skull of an aged M. foina is compared to that of a young M. martes, than when individuals of the same age were contrasted. The implication that was made was that at a younger stage M. martes is more similar to M. foina than it is later on in its life.

I myself have been fortunate enough to examine five skulls of very young marten (perhaps two or three months old) two referable on geographic grounds to M. a. americana and three to M. a. caurina. I have been led to conclude from these that at this very young stage, the skulls of the two races are nearly indistinguishable, and what is more, both are marked to a greatly

Figure 7
(To face page 86.)

Figure 7. Ratio of canine width to bulla length in the skulls of the world's marten. This ratio approximates an index combining the characteristics of skull length, height and breadth.



exaggerated degree by a skull conformation of the foina - caurina type with short widely spaced bullae, broad low braincase and short rather broad rostrum, rather than the elongate skull of the zibellina americana type.

I conclude that the short, broad and low skull is characteristic of all martens in their youth; that in some (e.g. M. pennanti, foina, flavigula, caurina and martes) it is lost only to a slight degree with maturity. In the remaining species (M. zibellina and M. americana americana) while in youth they have the same skull type, with maturity it becomes elongate, high, narrow, and with long bullae. Thus, again referring to Figure 7, it is hypothesized that the pennanti - melampus group are neotenic; that is, the development of the skull is either primitive or retarded, while the americana - zibellina end of the scale is a result of hypermorphosis or acceleration in development, or possibly it is a primitive condition (i.e. neoteny and hypermorphosis are mutually exclusive conditions; which of the two exists is not known).

While I have no means at present of testing this hypothesis for the time being I accept it. If it is to be accepted, certain conclusions follow. The most important of these is this, that while all species possess skull types that fall within two extreme kinds, forming a gradient, two of these do not belong, because of other distinctions (M. pennanti and M. flavigula). It follows that the neotenic or hypermorphotic condition has arisen several times in quite distinctive groups;

thus we may make a classification of species, something like this:

Skull broad
and short

Skull long
and narrow

Subgenus Martes: melampus, foina, caurina, martes, zibellina,
americana

Subgenus Pekania: pennanti

Subgenus Flavigula: flavigula

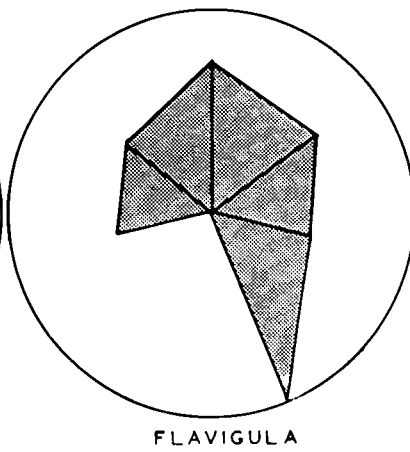
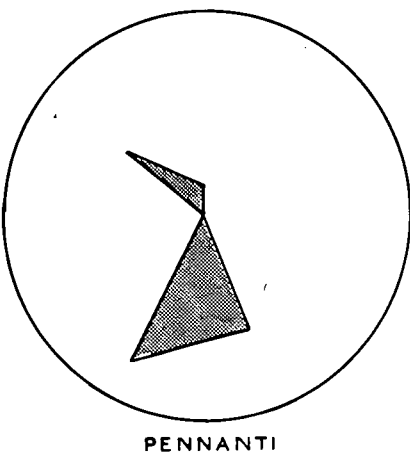
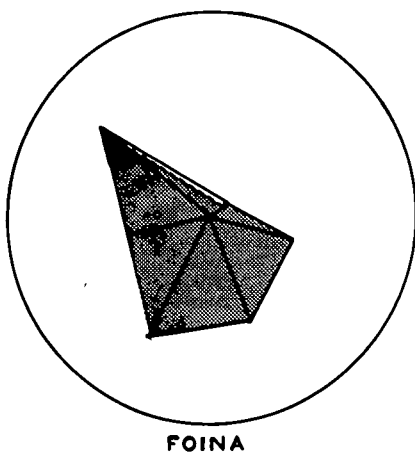
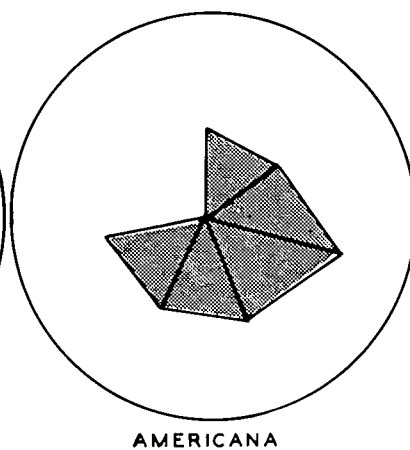
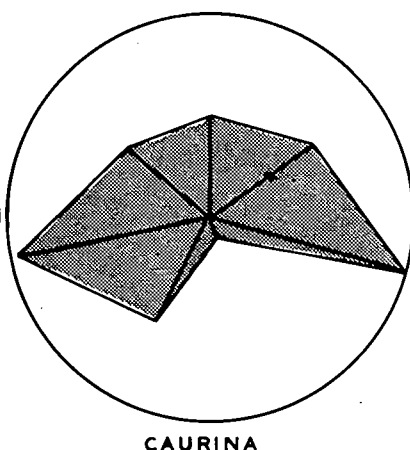
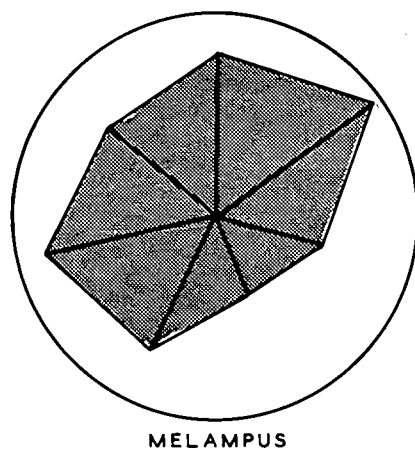
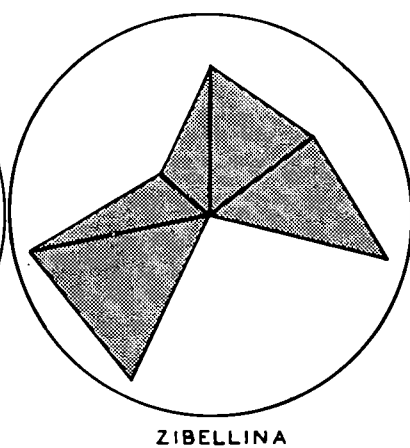
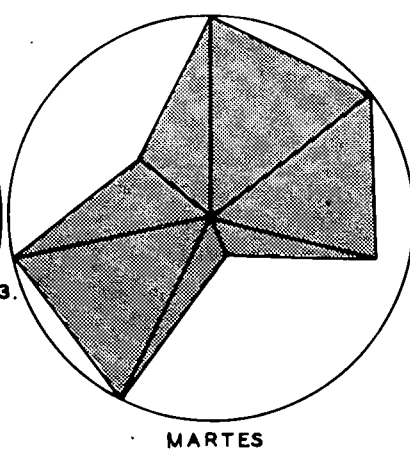
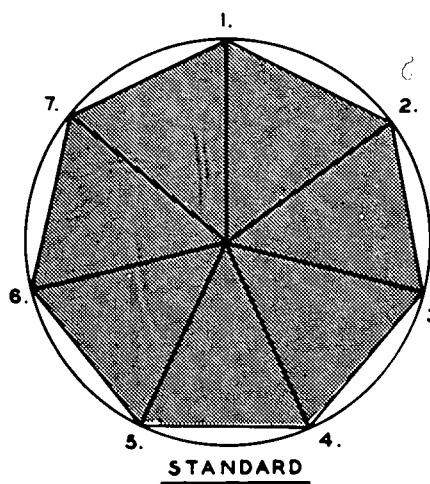
We come now to the problem: is the sequence shown in skull shape within the subgenus Martes a real one? To attempt this one must consider dentition. Figure 8 depicts pie diagrams of ratios, given in percentage, made from measurements taken from teeth of the various species. These are essentially the ratios devised by Brongersma (1941) and referred to previously. These diagrams show basic similarity in the combinations of the six dental ratios depicted for the following species: M. melampus, M. a. caurina, M. martes and M. zibellina. Of these M. a. caurina is apparently the most distinctive. M. a. americana and M. foina are totally distinctive, and strangely, are to a surprising degree similar in dental conformation though distinctive in skull shape. I assume that these relationships are real and in view of the lack of other evidence, that within the subgenus Martes, M. melampus, M. a. caurina, M. martes and M. zibellina are closely related species. M. foina and M. a. americana are distinctive in dental characteristics and within

Figure 8
(To face page 88)

Figure 8. Pie diagrams depicting certain characteristics of the skulls of the world's marten. The indices used are, with the exception of one, those devised by Brongersma (1941). The values graphed are not absolute, but rather percentages, the smallest mean equalling 0 in the pie cut, the largest 100.

The pie cuts are as follows:

1. $\text{Width of inner lobe of } P^4 \times 100 / \text{width of trenchant part of } P^4$
2. $\text{Width of inner lobe of } P^4 \times 100 / \text{length of } P^4$
3. $\text{Breadth of } M^1 \times 100 / \text{length of } P^4$
4. $\text{Lateral length of } M^1 \times 100 / \text{mesial length of } M^1$
5. $\text{Mesial length of } M^1 \times 100 / \text{breadth of } M^1$
6. $\text{Breadth of } P^4 / \text{length of } P^4$
7. $\text{Canine width at base} \times 100 / \text{bulla length}$



themselves are similar in this respect, but are so different cranially and in their biology as to be likely distinctive within themselves. On zoogeographic grounds, and pelage structure and colour, M. a. americana shows a degree of relationship with M. zibellina and M. martes, but for the time being it is here considered otherwise. Thus a scheme of relationship within the subgenus might be drawn up thus:

	Skull broad, short	Skull long, narrow
P ⁴ small, with		
small inner		
lobe; M ¹ with	<u>foina</u>	<u>americana</u>
small inner		
moiety		
P ⁴ large, with		
large inner		
lobe; M ¹ with	<u>melampus</u>	<u>caurina</u> <u>martes</u> <u>zibellina</u>
large inner		
moiety		

A hierarchical classification designed to show these relationships may be prepared as follows. It must be remembered that this does not attempt to represent phylogeny, though to a degree it might. For the time being it attempts rather to depict morphological similarity of crania.

Subgenus Martes: 1. M. melampus, americana caurina, martes
and zibellina

2. M. foina

3. M. americana

Subgenus Pekania: 1. M. pennanti

Subgenus Charronia:

1. M. flavigula

The baculum of M. pennanti is so similar to that of the species of the subgenus Martes, that its relationship to that subgenus must be considered much closer than is the relationship between the subgenera Martes and Charronia.

There is one problem more to be considered. The evidence appears such that M. a. americana and M. a. caurina are as morphologically distinct between themselves as either is compared to any of the Old World species. In fact, M. a. caurina appears much more closely related to M. melampus, M. martes or M. zibellina than M. a. americana does to M. a. caurina. And yet, as Wright has shown, M. a. americana and M. a. caurina interbreed, and must be considered to represent the same biological species. If this is so, one wonders how it is that the Eurasian species, so much more similar morphologically, have maintained their specific distinction in the eyes of systematists. It has occurred to me that M. martes and M. zibellina may possibly interbreed where their ranges meet in north central Russia and that M. zibellina and M. melampus interbreed where their ranges meet in Korea. It is significant that the ranges of these species are nowhere sympatric. One wonders, too, if

M. a. caurina and hence M. a. americana might not prove to be conspecific in the same sense with M. zibellina. If this were shown to be so, it would reduce the number of species of marten in the world from eight as here interpreted to a maximum of four as follows:

M. martes (including M. zibellina, M. melampus and
M. americana)

M. foina

M. flavigula (including M. guatkinsi)

M. pennanti.

D. THE MARTENS OF THE NEW WORLD

LIFE HISTORY

Brief accounts of the life histories of the European forms have been given in the pages preceding. Schmidt (1943) assures us that the natural history, reproductory and food habits of Martes foina, martes and zibellina are in every respect almost identical to those of M. americana and M. pennanti. Thus it would appear that what is briefly stated below may be attributed also to the Eurasian forms named above.

Martes americana: Birth occurs usually in April, less often in May and June (la Berée, Brassard and Bernard 1939, Schmidt 1943, Lensink 1953, Pearson and Enders 1944 a and b). According to Pearson and Enders (1944a) this period can be shortened by three or four months by means of artificial lighting, and since the long gestation period has been shown by the above authors to be caused by delayed implantation of the blastocyst, they concluded

that implantation is controlled by day length in spring. Oddly enough, although the long gestation period has only recently been determined, Kerr in 1792 wrote that the period was said to be nine months. The litter size is one to six, averaging 2.6 to 3.0 (Brassard and Bernard 1939, Markley and Bassett 1942, Marshall 1951, Schmidt 1943, Lensink 1953). The animals are born toothless, and the permanent adult dentition is attained by the 16th to 18th week (Brassard and Bernard 1939, Schmidt 1943). Both above authors give detailed descriptions of the sequence by which adult dentition is attained. The young leave the nest at the earliest by the 44th day, but usually by the eighth week, this being most often sometime in mid-July (Brassard and Bernard 1939, Schmidt 1943). The full adult weight is approximated by the end of the third month (Rand 1948a, Grinnell, Dixon and Linsdale 1937, Bailey 1936, Brassard and Bernard 1939) though the animal continues to fill out until its third year (la Beree 1941). The animals first mate in their second year, giving birth to their first litter in their third year (la Beree 1941, Markley and Bassett 1942, Marshall 1951, Schmidt 1943). According to Lensink they occasionally mate for the first time at fifteen months, usually at twenty-seven months of age. They are usually considered polygamous (Marshall 1951, Schmidt 1943). One litter is produced every year thereafter until death, the oldest known animal being seventeen years old when it died (la Beree 1941, Seton 1925-1928, Lensink 1953). Growth curves for the early stages of marten life are given by Markley and Bassett 1942, Remington 1952, and Schmidt 1943.

As remarked on earlier, the animals occur in greatest numbers in coniferous forests, especially those dominated by spruce (Picea). Densities of the animal per unit area vary from locality to locality. The area covered by individuals appears to vary with sex, season and age. Marshall (1951) believed the winter range of marten to be about ten to fifteen miles. Males appear to hunt over a wider area than females (Yeager 1950). Lensink (1953), reviewing the literature of de Vos (1952) and Yeager (1950), who had both reviewed the earlier literature, and including with these his own figures from interior Alaska and figures based on skulls used in the present study, found that 159 males were trapped for every 100 females. Various authors have, however, suggested that this difference may only be a result of the wider cruising radius of the male and not a real deviation from a 1 : 1 ratio. Quick (1953) in northern British Columbia found the ratio in 1947 to be 1 : 1, in 1948 1.2 : 1. Lampio (1951) likewise found a nearly 1 : 1 ratio to exist in M. martes in Finland. Lensink (1953) concluded that nearly 50% of the marten population was made up of immature (non-breeding) animals.

Lensink (1953) reviews the literature on foods eaten by Marten (Cowan and Mackay 1950, Marshall 1946, Newby 1952, Remington 1950 and others) adding his own observations to these. Microtines comprised by far the largest proportion of food taken, except in Washington where squirrels appear the most eaten. Other foods include animals to the size of rabbits, insects and berries. See also Newby and Hawley (1954) not examined during this study.

Martes pennanti: Birth occurs from March 15 to the end of April (Douglas 1943, la Beree 1941, Hodgson 1937, Seton 1925-1928, Enders and Pearson 1943a and b, Schmidt 1943, Hall 1942), as in marten probably varying with latitude. Mating occurs from three days to eighteen days after birth, probably about a week as a rule. Dates of birth given in the literature vary from March 15 to April 27 (Douglas 1943, la Beree 1941, Hodgson 1937, Enders and Pearson 1943a and b, Schmidt 1943, Hall 1942). The gestation period is stated to vary from 210 to 370 days, averaging about 350 days (Douglas 1943, la Beree 1941, Hodgson 1937, Pearson and Enders 1944a and b, Hall 1942, Schmidt 1943, de Vos 1952). According to Enders and Pearson 1943a and b, the period of delayed blastocystic implantation is nine or more months. The litter size is said to be one to five, averaging two or three (Douglas 1943, Hodgson 1937, Schmidt 1943, de Vos 1952, Seton 1925-1928. The features coincident to the attaining of adult dentition have yet to be worked out, but in view of the similarity of the other features of the life history to that of the martens it is probably quite similar. The young leave the nest at nine to ten weeks (Schmidt 1943) and are full sized by seven months (Hodgson 1937). Mating first occurs during the second year, the first litter being born in the third (Douglas 1943, Hodgson 1937, Hall 1942). The animals are said to be polygamous (Douglas 1943).

Fisher tend to occur in lower altitudes than marten (Edwards 1950, de Vos 1952). De Vos considers in rather great detail the habitat requirements of the animal. The animals

appear to vary in density geographically, staying generally within an area of two to six square miles (de Vos 1952, Quick 1953). Unlike marten, there appear to be more females than males per unit area, trapping figures giving 49 males to 51 females (de Vos 1952) and one male to two females (Quick 1953). Animals captured by fisher as food are largely grouse, red squirrels, hares, shrews, porcupines and others (de Vos 1952, Quick 1953).

VARIATION

Non-geographic variations

There are several kinds of non-geographic variation, namely that which occurs by sex, by age, by season and that which is characteristic of individuals of the same sex and age, here termed individual variation, whether genetic or otherwise. Since any attempt to describe geographic variation must be preceded by some understanding of the non-geographic sort, so that the two may be distinguished a brief account follows. Burt (1953) records the taking of about 400 marten from Fort Nelson British Columbia, which should be of use to anyone studying non-geographic variation.

Sexual variation: We may consider here only the more obvious of the secondary sexual characteristics. The most important of these is size. The males in all species of martens and fishers are considerably larger than the females. For martens in terms of weight, it may be stated as a general rule that the female weighs approximately two-thirds that of the male. The pelage

of the male is thicker, with longer hairs and a greater elasticity to the fur (see Brassard and Bernard 1939, de Vos 1952, Markley and Bassett 1942, Lensink 1953, Lampio 1951). The under fur anterior to the urethral aperture on the midline of the belly lies forward, rather than backward in the male (Lampio 1951, Lensink 1953).

The skulls of the males are plainly heavier and more robust than those of the females. The canines and the dentition in general is heavier and the sagittal crest more likely to be highly developed in those forms where it occurs. For Martes americana americana and M. a. caurina the measurements of large samples of six skull characteristics arbitrarily chosen were compared by sex and it was found that all of these averaged 1.10 times larger in the male than in the female, and the X^2 probability that these averages came from the same supply was far beyond the 99% level. The characters employed were condylobasal length, rostral width, upper tooth row, bulla length, rostral width / bulla length and upper molar width plus length. The use of the above index would allow one to predict the skull size and characteristics of both sexes of any unknown form of North American marten, if only one sex is known. No comparable comparisons were made for Eurasian martens or M. pennanti. Hall (1934) says the figure is about 1.6 compared to 1.1 in marten.

Most of the specimens of both marten and fisher used in this study were already designated to sex. Where the sex of an animal was not known, it was identified by comparison to bar graphs of condylobasal length and other measurements drawn up

from larger samples of known sex, from the same general area.

Age Variation: As marten advance from maturity (second year) into old age, the following changes have been noted to occur: the condylobasal length increases (Lensink 1953, Wright 1953), the zygomatic breadth increases (Grinnell, Dixon and Linsdale 1937, Wright 1953), the braincase is said to decrease in size (Grinnell, et al., 1937), the postorbital constriction narrows (Grinnell et al., 1937, Wright 1953), the rostrum narrows and lengthens (Grinnell et al., 1937), the naso-maxillary sutures fuse (other sutures ankylose very early) (Grinnell et al., 1937, Rhoads 1902, Lensink 1953, Marshall 1951), the postorbital process becomes more prominent (Grinnell et al., Lensink, Marshall), the baculum increases in weight (Marshall).

During the early stages of life, age may be obtained by use of growth curves (Markley and Bassett 1942, Remington 1952, Schmidt 1943) or to the eighteenth week by the sequence of tooth eruption (Brassard and Bernard 1939, Schmidt 1943). Working with "M. c. caurina" of central Idaho, Marshall (1951) concluded that the presence of a sagittal crest in a female or one longer than 2 mm. in a male implied sexual maturity (two years or older). Likewise Marshall concluded that a baculum heavier than 100 mg. implied sexual maturity.

Lensink (1953), working on the marten of interior Alaska, concluded that he was able to tell the age of males to four years, of females to five years by means of weight of baculum and height and length of sagittal crest. His table of measurements is reproduced below.

Males

Age	Baculum weight (mgs.)	Height of sagittal crest (mm.)	Length of sagittal Crest (mm.)
0 - 1	Less than 130	0	0
1 - 2	130 - 205	Less than 16	1 - 20
2 - 3	206 - 260	16 - 19	25 - 40
Over 4	More than 260	More than 18	41 - 50
Over 5	More than 260	More than 18	More than 45

Females

Age	Length of sagittal crest (mm.)	Height of sagittal crest (mm.)	Min. separation of temporal muscle scars (mm.)
0 - 1	0	0	More than 5
1 - 2	0	0	Less than 5
2 - 3	1 - 20	0	0
3 - 4	25 - 37	0	0
Over 5	More than 38	0	0

Lensink's work comes closest to providing a means to age marten skulls, and in systematic work, to break samples into age subsamples. However, one result of the present study has been to show that marten from different localities possess bacula of significantly different weights at maturity and acquire sagittal crests of different sizes at different ages.

At the beginning of this study, twenty-four characteristics were selected from a population of marten of restricted geographic extent (Banff region, Alberta). These were broken into two age groups by use of the following single characteristic:

fusion or lack of fusion of the naso-maxillary suture. Where fusion was complete, the animals (fide Rhoads 1902) were considered adult; where unfused, immature. Wright (1953) has done the same and in common with him I found that the following characters varied significantly between the two age groups: greatest and condylobasal length of skull; zygomatic breadth, postorbital constriction, postorbital width, vomerine width, width of incisor row at base, rostral width and length and lower jaw length. Mastoid breadth, interorbital breadth, height of cranium, size of auditory bullae, and size of teeth did not vary (Wright found no variation also in rostral width, concerning which see above, basilar length, palatal length).

Of the twelve measurements used in the present study, those found to change with age were measured only in adults, the remainder on both adult and immatures, as follows:

1. Condylobasal length. Adults only.
2. Rostral width. Adults only.
3. Upper tooth row. Adults and immatures.
4. Canine width at base. Adults only.
5. Bulla length. Adults and immatures.
6. Upper molar width. Adults and immatures.
7. Upper molar inner moiety length. Adults and immatures.
8. Palatal length. Adults and immatures.
9. Mastoid width. Adults and immatures.
10. Height of skull at bullae. Adults only.
11. Length of last upper premolar. Adults and immatures.
12. Palatal width. Adults only.

Details of the above measurements and those given below for fisher are given in Appendix C. In general, where large samples were available, only the adult portion (by the naso-maxillary test) were measured.

In fisher, the following characteristics are known to change as old age is attained: lightening in pelage colour (Rhoads 1903); an increase in condylobasal length (de Vos 1952); increase in the weight of the skull, the male about 25%, the female about 9% (Grinnell et al.); an outward bowing of the zygomatic arches (Coues 1877, Thomas 1886, Grinnell et al., de Vos); the postorbital constriction narrows (Coues, Thomas, Grinnell et al.); the lambdoidal crest increases in size (Coues); the sutures of the nasal region and basi-cranium ankylose (Coues, Grinnell et al., de Vos); the canines become longer (Thomas); the interorbital width increases (de Vos); the sagittal crest increases in height and length (Coues, Thomas, Grinnell et al.); the mandible increases with depth (Hall 1942); and the baculum increases in weight (de Vos). According to de Vos a male with no sagittal crest is juvenile, with one less than 62 mm. long is adult, and with one longer is old adult. Of females, only old adults bear a crest.

As in the case of marten, a large number of characteristics were measured for a sample limited geographically (Stuart Lake, British Columbia), these being broken into "subadult" and "adult" on the basis of degree of fusion of the naso-maxillaries. No significant variation was found in the upper tooth row,

mastoid width, palatal length, preorbital and postorbital widths, and size of teeth. These measurements were henceforth taken on all "adult" and "immature" animals. The remaining characters were found to vary with age, and were measured only on "adults". These included condylobasal length, canine width at base, rostral width, bulla length, and palate length.

As in marten, where large samples were available, only "adults" were measured.

Rhoads in 1898 expressed the belief that the white patches on the breasts of fishers were lost with age. In 1903 he suggested further, that the oldest specimens are the lightest coloured, some becoming nearly white.

Seasonal variation: This kind of variation is concerned chiefly with variation in the condition of fur. Surprisingly little is known concerning the moulting of marten and fisher.

Grinnell, Dixon and Linsdale (1937) reported one complete annual moult in the marten of the Sierra Nevada. This proceeded slowly through the autumn months. It begins in the tail, about the end of August. They also report a loss of hair with no renewal in the spring months, for summer skins are less dense in pelage than are the winter ones. Summer and winter skins, they reported, are closely alike in colouration, the former being only slightly the paler of the two.

Markley and Bassett 1942 reported that during the summer moult the colour changed from "dark brown to light tan". The moult began on the tail tip, then moved to the legs, the mid-dorsal region and the face, in that order.

According to Schmidt (1943) European marten undergo two annual moults. The hair begins to fall at the end of April or beginning of May and lasts until the beginning of June. Moulting begins on the face and works back to the tail. The summer coat is darker than that of the winter. Pregnant females end their summer moult much earlier than non-breeding ones.

The fall moult begins in August, and ends by November. Here the order of hair loss is reversed; as in Grinnell's animals, the first part affected being the tail, the last the neck and head.

Grinnell et al. concluded that California fisher show only one annual moult, this occurring slowly, in the fall. With the advance of summer a slight fading of tones appears.

It seems likely then, that fisher and marten undergo a fall moult, and a spring loss of hair, at least. My own detailed examination of skins has been largely restricted to specimens taken from the Canadian Rockies. These show a summer pelage far darker and thinner than the winter one. The fall moult appears to occur considerably later than it does in the Californian specimens examined, time of moulting likely being, as Bissonnett (1944) shows in weasels, a function of day length.

In general, where I have attempted comparison of skins, I have divided them into three groups, summer, winter (by date of capture) and moulting (by appearance). Comparison has then been made within each of the classes "summer" and "winter".

Individual variation: Individual variation has been recorded for a long time in martens and is known to be extreme, especially

with regard to colour of pelage. All writers, however, have failed to distinguish between variation that might be due to sex, age or season, which makes the situation a difficult one to interpret.

In 1875 Cartwright wrote that the marten "varies the most in colour, in the same region, of any animal; some are light yellow, some are dark brown, and others are black". Macfarlane (1905) wrote that he had "seen several albino examples and also a considerable number of bright yellow and dark orange coloured martens ..., particularly while stationed in the districts of Mackenzie River and Athabasca". Hardy in 1910 recorded the taking of a very dark specimen from Maine. It was "the darkest furred one I ever saw south of the St. Lawrence" he reported, adding that he had examined over 20,000 pelts from the region, but none so dark as this. Cory (1912) remarks that in eastern marten the brown colour is lighter or darker in different individuals, the throat patch varying from orange to yellowish white.

Markley and Bassett 1942 reporting on marten of Idaho and Wyoming, say that "evident at once is a great individual variation in extent of the throat patch. Its shape, always irregular, in several specimens was restricted to a number of detached spots on the lower throat and breast, while on others it became a solid patch extending from the upper throat to the abdominal region. On a prime winter pelt the tail and legs became nearly black on some individuals."

A detailed account is given by de Vos (1952). The colour of the fur, he concludes, is "extremely variable". He presents a series of skins, selected from a collection of 450 pelts trapped from November 1st to March 31st of two consecutive years. These varied from "a very pale yellow-orange marten of a partly cromistic, partly albinistic type, "with an entirely white head" and with white underparts, feet and tail the same colour of the upper parts and with no throat patch to a "very dark marten with a large number of white guard hairs ..., the underparts ... of a similar colour ... with a large orange throat patch." He also records a dark, possibly melanistic specimen, but no albinos, though Ponomarev (1938) found them in Russian sables. Ponomarev reported also a tendency toward geographic colour variability and de Vos likewise found the marten of Algonquin Park, Ontario, to be, on the average, slightly paler. De Vos concluded that "the variability in a local series indicates that one should be on his guard when making comparisons between series from different localities, and that one preferably should compare large series." Wright in 1953, working with 300 specimens designated M. a. abietinoides from Montana and Idaho, likewise found great variability; dorsally they varied from Isabella color or Mouse Grey to Mummy Brown, and ventrally from Isabella or Mouse Grey to nearly black. The throat patch varied from almost complete absence to five or six inches square and from Pale Orange-Yellow to Capucine Yellow or Deep Chrome (colours from Ridgway, 1912).

Size variation, within a limited area, appears to be rather less than one might expect on superficial examination of skins and skulls. A sample of 100 skins taken from Ontario, when divided into male and female, but not into age groups, give the following average coefficients of variability: total length 4.2%; tail length, 6.1%; hind foot 6.0%; and weight 13.2%. Another sample of 21 "adult" males from near Banff, Alberta, when measured for twenty-four skull characteristics, gave an average coefficient of variability of 3.3%, with a maximum much higher in only one characteristic (7.5% for postorbital width).

I believe that fishers show rather less variability than do martens. De Vos (1952) examined 200 skins from Ontario taken between late November and late March. He remarked "Colour variations between individuals are fairly striking. No such variations could be detected between local populations. The overall colour of the dorsum varies from pale grey to practically black This is true for both sexes, although the gray colour predominates in males. A reddish brown tinge can be noticed occasionally.... On the ventral side there is not much variation between individuals, although light backed specimens are slightly paler than dark ones. No large throat patches ... were observed, although a few individuals had one or a few white spots on the throat. The largest white patch is usually found on the belly, anterior to the anus. In some animals white spots are present in the axillas of the front legs which may occasionally be fused on the mid ventral line and extend anteriorly for a short distance."

Audubon and Bachman (1851-1854) say they had examined a specimen that was "nearly white with a brown head". Elliot (1901a) says they vary from glossy black to gray or grayish white on the upper parts. Grinnell, Dixon and Linsdale (1937) working with Californian animals, however, concluded that colour variations were slight, being expressed chiefly in amount of white on the underparts.

Size variation is about the same as in marten. Merriam 1882-1884 and 1886, however, records the taking of one in New York, that was estimated to weigh 40 pounds and the skin of which was that of "a good sized otter". He records another from the Adirondacks with a skull 12.5 cm. long. Merriam concluded that giantism in fishers occurred only among males.

A sample of sixteen male fisher, from Ontario, not divided into age groups gives the following coefficients of variability for external measurements: total length 6.8%; tail length 8.0% and hind foot 3.7%. A sample of thirty-three male adult skulls from the intermontane plateau region of middle British Columbia gives an average coefficient of variability for fourteen characters of the skull of 4.1, none being higher than 8.6% (width of postorbital constriction).

I have myself carefully examined only a relatively small number of skins (about 75 marten, about 40 fisher), although a larger number were briefly examined and measurements recorded. The reason for the smallness of the number examined carefully was that the colour of pelage seemed to be an unreliable solution to the problem. The degree of individual colour variation was

so extremely high, especially in marten, that I have concluded that very little can be determined by it, and that the rather careful descriptions of pelage colour made by earlier describers in many cases provide disappointingly little help. As will be outlined later, this does not mean that pelage colour is not of some use to the systematist, however. Martens can be broken into several distinctive geographic colour types as follows. Those from Labrador are dark, those from Ontario and southeastern British Columbia are intermediate, those from Alaska, northern British Columbia and the northern Prairie Provinces are paler, especially about the head. Marten from the northern Coast Ranges, Cascades, Coast Mountains and the American Rockies are dark, while those from California tend to be lighter.

The situation with fisher is less distinct. While they appear to vary less in pelage individually, they also vary much less geographically. It is unlikely that usable samples from the west can be distinguished from those further east.

In view of these findings it was very early decided that this study would need to be based almost wholly on cranial characteristics. While external measurements show variability almost as low as do cranial ones, these are usually limited to three or four taken at time of skinning, and hence are of restricted use. The cranial measurements used, and the conclusions derived from them follow.

Methods of study of geographic variation

In attempting to solve the problems presented by the martens, I was faced with that of obtaining statistical estimates

of the parameters to be studied quickly.

The subsamples to be compared to each other were obtained by accretion; that is, by taking reasonably large samples from near a given type locality as standard for a subspecies and adding to it similar forms, working away from the type locality, until I reached samples whose statistics lay nearer to those of another type locality. This is admittedly an unsatisfactory technique, but presumably is the one used by other systematists and at the time was accepted by me as the one to be used.

The next problem to unravel was this: how randomly distributed were the subsamples thus obtained. Dice (1952) points out that most collections in our natural history museums were not collected by random sampling methods and hence are not really suited to the application of statistical methods. Dice is certainly correct in this assumption. Mine being a study carried on indoors, however, no means of correcting this situation was available to me, and I have been obliged to construe my samples to be of random distribution although I know they are not.

The next problem was one of homogeneity. It was possible that each subsample (when age, sex, etc. were taken into consideration) could consist of more than one natural population. Ideally each subsample should have been tested for skewness or kurtosis; perhaps analysis of variance would have worked well here. Harding (1949) has reported a method that might work equally well. Time restricted me to the simple expedient of

calculating the coefficient of variability in place of the other techniques. This statistic does not measure homogeneity in the true sense, nonetheless I have been obliged to consider a CV of less than about six to indicate a normally distributed sample. Where it has been higher than six, I have attempted more refined means of determining its cause.

The comparison of samples may be done in complex, satisfying fashion, or more simply and perhaps less revealingly. I would think that the several methods of multivariate analysis available (see for example Fisher 1938, Mather 1947, Stone 1947, Storer 1950) would be the most efficient, or perhaps the simple method of trivariate analysis suggested by Burma 1948. Time has again limited this study to a simple comparison of two variates, these being made singly through all of the samples. The simple "t" test is much used here and has been simplified by Simpson and Roe (1939) and Mayr, Linsley and Usinger (1953) by using the standard error of the difference of the means. Even simpler than these are the comparative graphs first used by Dice and Leraas (1936). Different authors have suggested different levels of probabilities should be used, Dice and Leraas suggesting the use of the $\bar{x} \pm 2$ or $3 SE_{\bar{x}}$; Simpson and Roe (1939) $\bar{x} \pm 3 SE_{\bar{x}}$; Amadon (1949) $\bar{x} \pm 3.24 SD$; Hubbs and Perlmutter (1942) $\bar{x} \pm 1 SD$; Mayr, Linsley and Usinger (1953) $x \pm 1.5 SD$; Hubbs and Hubbs (1953) $\bar{x} \pm 2 SE_{\bar{x}}$. Actually as satisfactory as any of these, should be the use of " $1_1 1_2$ ". I have, however, restricted myself to the use of $\bar{x} \pm 2 SE_{\bar{x}}$ in comparing subsamples and using "t" where n in either or both was less than ten.

Clark (1952) suggested the use of a "coefficient of divergence" for comparing the degree of dissimilarity or similarity of a number of variates of a number of subsamples simultaneously. I have not employed his technique but feel that it might offer a more precise means of evaluating degree of similarity or otherwise than any of the techniques I have employed.

All of the methods so far discussed are analytical. I discovered too late a method of almost synthetic viewpoint that had I known of it would have been the major technique employed in this study. I report it in some detail here, wishing that I might have used it and hoping that some other systematists may see its essential worth. This technique, devised by Womble in 1951, is essentially a method of summing and weighing morphological values and mapping them two-dimensionally on a map. The method is this: the values of each trait are recalculated to a scale of 0 to 1, these representing the minimum and maximum averages for each trait. Each trait is then, if so desired, weighted according to whatever degree of genetic worth it is valued at, the values for each rescaled and weighted trait are then mapped, a contour interval selected and isopleths or "isophenes" drawn. A random selection of slopes between isopleths is taken, each for convenience multiplied by 10,000 and these again mapped and isopleths again drawn. At randomly selected points, the slopes for all the traits are summed (if weighted are then divided by the sum of the weighting factors) the sums are plotted on a map and isopleths again drawn. This is the final map. Its topography shows the rate of trait change

geographically. Ridge lines mark areas of rapid change, basins areas of uniformity.

Because Womble's excellent technique could not be used, I have attempted to simplify it by mapping the distribution of a single characteristic. The most important of these are condylobasal length and canine width at base / bulla length, which are presented on Enclosure A (inside back cover) and Figure 11, for martens. Too few specimens of fisher were available to allow its use in these animals. I consider these diagrams close to the most important contributions this paper has to offer, and believe that they come closer to depicting a true picture of variation than any other method I have seen. The exception of course would be Womble's method, which if further refined so as to remove errors of sampling could be a most worthwhile tool in the hands of the systematist.

MARTENS

Distribution

The distribution of marten in North America appears to be governed very closely by the distribution of the northern evergreen forest (Seton 1925-1928, Grinnell, Dixon and Linsdale 1937, Bailey 1936, Dalquest 1948, Merriam 1886, Merriam 1882-84, de Vos 1952). Lensink (1953) concludes, for example, that the marten distribution in Alaska is coincident with the distribution of white and black spruce, "which is apparently the critical element in their habitat". Edwards (1950) believed that those coniferous forests of highest market value supported the greatest

number of marten. Anthony (1917) believed, however, that "it does not appear to be particularly attached to coniferous woods, living in them simply because such forests prevail to a great extent in the geographical areas it inhabits". Ponomarev's (1944) experiments give credence to this view, in that he concluded that the Eurasian martens (M. martes, M. foina and M. zibellina) had their distribution controlled chiefly by the presence or absence of low temperatures (20° C and less). Nonetheless, most authors name the humid upper transition, the Canadian and the Hudsonian life zones as those occupied by the marten (Rhoads 1903, Cary 1917, Grinnell and Storer 1924, Skinner 1927, Williams 1930, Bailey 1936, Grinnell, Dixon and Linsdale 1937, Hall 1946, Rust 1946, Dalquest 1948, Yeager, Denney and Hammit 1949, de Vos and Guenther 1952, Durrant 1952, Sumner and Dixon 1953).

Marten have been also recorded outside the evergreen type forest. While de Vos (1952) and most writers consider them scarce or absent in hardwoods, others report them common there. Emmons (1840) stated they were common in the beech woods of Massachusetts. Adams (1873) said they occur in the hardwoods of New Brunswick. Rhoads (1903) concluded that the hardwood timber of New Jersey and Pennsylvania was preferred to coniferous forests. Allen (1904) reported that they occurred in beech forests throughout New England. De Vos (1952) says that they may have occurred in the northern hardwoods of Ontario before western settlement occurred. That this relationship exists not only in North America is shown by Jurgenson (1939)

who states that Martes martes prefers a mixed deciduous-coniferous forest to any other, in Russia.

In mountainous regions martens have been known to frequent talus slides (Turner 1886, Grinnell and Storer 1924, Clarke 1940, Hayward 1952 and Marshall 1951). They are also known to occur far from timbered areas on tundra and mountain meadows (Turner 1886, Cary 1911, and Clarke 1944).

However, it is essentially true that the distribution of marten fits very closely the distribution of the northern coniferous forests as comparison of the distribution of martens and forest types obviously indicates.

A distribution map of martens has been prepared and is included in this paper (Enclosure B, inside end cover). This is based on the specimens examined and an extensive, but by no means complete survey of the literature. The limits of the animal's range are based chiefly on the vegetation maps of Zon and Sparhawk 1923, Munns 1938, Preble 1908, Anderson 1934a and b, Davis 1939, Pitelka 1941, Robertson 1945, Raup 1945 and 1946, Villeneuve 1946, Camsell 1947, Munro and Cowan 1947, Anon. 1948, Villeneuve 1948, Dayton 1949 (after Shantz and Zon 1924), Gutsell 1949, Hustich 1949a and b, Braun 1950, Hare 1950, Department of Mines and Technical Surveys of Canada Map, 1950, Edwards 1950, Macleod 1950, Bandy 1952, Webb 1952, Candy 1951, Hustich 1951, Macdonald 1951, Nicholson 1951, Whitaker and Ackerman 1951, Hare 1952, Halliday 1937 and 1952, Putnam 1952, Muesbeck and Krombein 1952. To these were added the material obtained from the marten distribution maps given by Seton 1909, Cary 1911, Cory 1912,

Grinnell and Dixon 1926, Seton 1925-1928, Anderson 1934a, Brouillette 1934, Bailey 1936, Grinnell, Dixon and Linsdale 1937, Melven 1938, Dufresne 1942, Hamilton 1943, Hall 1946, Twining and Hensley 1947, Dalquest 1948, Burt 1948, de Vos 1952, Durrant 1952, Webb 1952, and unpublished maps for Colorado and Montana kindly prepared by Mr. Richard Denney and Dr. Philip Wright respectively. The remaining sources from which these maps and the account following has been prepared are given in Appendix D and the account following.

It is well known that the numbers of martens throughout the continent have steadily decreased in the past several hundred years (Henderson and Craig 1932, Seton 1925-1928, Allen 1942, Yeager 1950, Minville 1946, Innis 1927, Anon. 1927-1950, Squires 1946, Butler 1950).

Alaska: All of forested Alaska, as far west as Norton Sound and Kotzebelle Sound (Nelson and True 1887) and nearly to the mouth of the Yukon River (Dice 1921) and as far north as the head of the Nunatog River (lat. 68°) (Nelson and True 1887) and Anaktuvak Pass in the Brooks Range (Rausch 1950 and 1951); the Kenai Peninsula and the Panhandle; the following at least of the Alexander Archipelago; Admiralty Island (Swarth 1911, Dufresne 1946, and specimens examined), Etolin Island (specimens examined), Kodiak Island (Nelson and True 1887), Kuiu Island (Swarth 1911, Dufresne 1946, and specimens examined), Kupreanof Island (Dufresne 1942 and 1946 and specimens examined) and Revillegigedo Island (Dufresne 1946 and letter of Calvin Lensink). In 1934 marten were transplanted to Prince of Wales and

Chichagof Islands (Dufresne 1946). Marten were being trapped during the winter of 1948-49 (Yeager 1950). Localities not mapped include: Savioyok Valley, Brooks Range (Rausch 1951), Bering Sea, Coast of Alaska (Elliot 1905a) and Salcha (U.S. Fish and Wildlife Service File).

British Columbia: Occur through all of the following biotic areas of Munro and Cowan 1947: Cariboo Parklands, Columbia Forest, Subalpine Forest, Boreal Forest, Peace River Parklands, Coast Forest, Queen Charlotte Island, Vancouver Island (many sources and specimens examined). Are present on both Graham and Moresby Islands of the Queen Charlotte group (specimens examined). Macleod (1950) says they have been trapped on Pitt, McCauley, Hawksbury Islands and suggests that they occur on still others. Mr. Charles Guiget says they have been reported from Hunter Island. Marten were being trapped in the winter of 1948 - 49 (Yeager 1950).

California: The forested parts of the Klamath Mountains and Coast Mountains as far south as Sonoma County (Grinnell 1933, Twining and Hensley 1947, Grinnell, Dixon and Linsdale 1937) and the Sierra Nevadas as far south as Tulare County (Grinnell, Dixon and Linsdale 1937). One specimen from the U. S. National Museum (no. 32033) from San Joseph Island in lower California is named a marten, but it is almost certainly referable to Bassariscus astutus. Marten were being trapped in the winter of 1948-49 (Yeager 1950). Localities not mapped include Rush Creek and Bear Creek Kellogg 1916).

Colorado: Everywhere in the higher mountains (above 9,500 feet) (Williams 1947, Remington 1950, Yeager, Denney and Hammit 1949) from the northern to the southern boundaries of the state and as far east as western Arapahoe County (Yeager 1950) and western Huerfano County (Denney, letter). Remington (1950) reports a specimen from Camp Hale which I have possibly mistakenly located in Yuma County. F. C. Kleinschultz (letter) believes the marten to be found in the following counties beyond those mapped: Alamosa, Archuleta, Chaffee, Conejos, Custer, Delta, Dolores, Fremont, Gilpin, Hinsdale, Huerfano, Lake, La Plata, Mesa, Moffat, Ouray, Pitkin, Rio Grande, Saguache, San Miguel, and Teller. Martens were being trapped in the winter of 1948-49 (Yeager 1950). Localities not mapped are East Spanish Peak and Bennett's Well (Cary 1911).

Connecticut: Linsley (1842) lists marten as occurring in the state but Goodwin (1935) found no authentic record of its former presence. He believes that it may once have occurred in the mountains of the northwestern and possibly northeastern part of the state, however. Two specimens from the American Museum of Natural History (41340 and 41335) collected in Greenwich are variously labelled "M. foina" and "M. americana" and to the second is appended the statement "this may be an introduced species". My examination of these leads me to conclude that while the first specimen may be representative of M. americana, the second is not, and is referable instead to M. foina of Eurasia.

District of Columbia: Captain John Smith (1607-08) recorded "martens" from the district (according to Mansueti 1950).

McAtee (1918) said that "according to Wm. [sic] Palmer there is a fairly certain record as late as about 1880". Bailey (1926) concludes that marten once occurred, as does Mansueti (1950).

Idaho: The forested mountains of Idaho, as far south as Ada, Elmore, Blaine and Fremont Counties (Baird 1857 and 1859, Suckley and Gibbs 1860 and specimens examined). Davis' (1939) vegetation map suggests that it may occur in Caribou, Bonneville and Bear Lake Counties. It was still being taken in the winter of 1948-49 (Yeager 1950). A locality not mapped is the Kanisku region (Rust 1946).

Illinois: Kennicott (1859 and 1855) records the former presence of marten in Cook County. Sanborn (1925) says they were once present about the Chicago region. Hahn (1909) and Cory (1912) say a skeleton of a marten was held by the Chicago Academy of Sciences and that it was said to have been collected in the northern part of the state many years before. Shorger (1942) concludes that they once occurred in the strip of pine timber along the shore of Lake Michigan. Mohr (1943) says that recent reports (U.S. Forest Service 1937) have listed marten as occurring in the state. Mohr says these reports are incorrect and that the animal has been extinct for a century or so.

Indiana: Hahn (1909) considered the animal a "hypothetical intruder" in the state. Lyon (1936) believed that if it

occurred in Illinois (see above) it "probably" occurred in Indiana. Shorger (1942) concluded that it formerly penetrated into the strip of pine timber that ran along the shore of Lake Michigan.

Iowa: Scott (1937) cites papers by Goding and Osborn as listing marten for the state, but considers these doubtful. He concludes that that animal "may have entered northeastern Iowa as a straggler many years ago"

Kansas: Cockrum (letter, citing Cockrum 1952) considers the former presence of marten as hypothetical. He writes that Mead (1899) wrote "martens were rare", and that on this basis Hibbard (1933) listed it as a former member of the state's fauna. He concludes that "I think the marten has not occurred in Kansas within historic time."

Maine: Occurs throughout the mountainous northern part of the state. Seton (1925-1928) says they are "rarely seen now in the southern part of the state." They are reported to have once occurred as far south as Muddy River (Topsham) about 1915, and from New Gloucester over 100 years ago and are known from the shell heaps on Goose Island (Norton 1930). Coues (1877), Allen (1876b) and Anderson and Sclater (1881 and 1891) report them from as far south as central Oxford County. The last specimen in the state was taken in 1936 (Yeager 1950).

Manitoba: All of Manitoba originally, except perhaps the extreme southwest portion and the barrens of Hudson Bay. Now very rare

south of latitude 53N. (Melven 1938). The most southerly records are Aweme (Criddle 1929) and Pembina Mountains (Seton 1925-1928). R. W. Sutton (letter) reports the taking of a marten in the poplar bluffs about the Delta Research Station in the winter of 1951-52. Marten were regularly being trapped during the winter of 1948-49 (Yeager 1950). The chief collecting points are Nelson House, Lac du Brochet, and Shamatawa (L. Butler letter).

Maryland: Scharf 1882 stated that "marten occurred in western Maryland". Mansueti (1950) says it "has been completely extirpated in Maryland for at least 70 years.... Its distribution probably was not widespread...." J. W. Aldrich (letter) reports that there appear to be no definite records for the state.

Massachusetts: Formerly present in the Berkshire Mountains of Berkshire County (Emmons 1840, Allen 1869, Coues 1877, Allen 1904). Hamilton (1943) suggests it may still occur in the area.

Michigan: Formerly all of the timbered areas of the state as far south as Allegan County, and on Isle Royale. None has been taken in twenty-five years and is now rare or absent in the state (Burt 1948). Pruitt (1951) records their presence on Sugar Island.

Minnesota: Northern Wisconsin, as far south as Polk County (specimen examined) and Crow Wing County (Swanson, Surber and Roberts 1945). Originally common, rare by 1900, and probably now extinct, although possibly still existing in Superior and

Chippewa National Forests (Shorger 1942, Swanson, Surber and Roberts 1945, Gunderson and Beer 1953, Stenlund 1955). The last specimen was taken in 1953 in St. Louis County (Stenlund 1955). De Vos says they are still present in the northern part of the state.

Montana: The northern regions of the Montana and Bitterroot sections of the northern Rocky Mountains, as far east as Western Cascade County (Wright 1953) and as far south as Ravalli County (specimens examined) also present in Madison County (U. S. Fish and Wildlife Service File), Sweetgrass, Stillwater, Carbon and eastern Park Counties (specimens examined). Marten are still common in the state (Yeager 1950, Wright letter)

Nebraska: Swenk (1908) cites an undated publication of Aughey who reported that they have been taken in the northwestern part of the state, but that they were rare. Swenk considered them extinct at time of writing.

Nevada: Reported to occur in the southwest portion where the Sierra Nevadas enter the state, from Mount Rose south to Monument Peak. One specimen is known from Marlette Lake (Hall 1946).

New Brunswick: Formerly common throughout all of Nova Scotia (Chamberlain 1884 and 1892). At present greatly reduced and restricted to the more remote areas (Allen 1942, Morris 1948). No specimens have been taken since 1945-46 (Yeager 1950). Specimens not mapped include Lake Edward (Chamberlain 1884 and 1892), between Lake Edward and Salmon Lake (Elliot 1901a and b), and Salmon Lake (Chamberlain 1884 and 1892).

Newfoundland (excluding Labrador): Originally common in all the wooded areas (Reeks 1870 and 1871), but now very scarce (Bangs 1913, Allen 1942). A. Cameron (letter) says the animal is "quite rare" and confined to the more inaccessible regions. D. H. Pimlott (letter) reports that marten have, for the past two years, been reported from the lower Grand Lake and Gambo Lake areas only.

New Hampshire: Found originally in the White Mountains and northward (Allen 1904). Very nearly extirpated now, if not completely so (Preble 1942-43). Norman Preble (letter) has sent me the following information: one specimen is known from the state, from Coos County in the New England Museum of Natural History (Boston Museum of Science). Common 100 years ago in the Crawford Notch region of the White Mountains, but now rare, the last specimen being taken in 1936. Alfred E. Preble observed an animal on Mount Washington in 1930 that was likely either a marten, a fisher, or a tame Bassariscus. Another marten was reported at the same place in the spring of 1944. All records from the state are in Coos County, except one from Laconia in Belknap County taken between 1931 and 1934 (Helenette Silver, letter, after Jackson 1922). According to Monahan (1953) have been recently reintroduced into the northern part of the state.

New Jersey: "Once abundant in the mountain regions. Now wholly absent from the state. Probably exterminated fifty years ago" (Rhoads 1903). I know of no other record.

New Mexico: Present, but by no means common, in the high mountains of the northern part of the state, especially the San Juan and Sagre de Cristo Ranges (Bailey 1931). Records known are from Chama (specimen examined), Taos (Wheeler 1875), Truchas Peaks (Bailey 1931), Las Vegas Mountains (Durrant 1952). The last locality named is the most southerly record for the animal in North America. An unmapped locality for which marten is recorded is Twining (Bailey 1931). Allen (1942) believed they still existed in the state, at time of writing; whether or not they are still present I do not know.

New York: Formerly common in the Adirondacks and possibly the Catskills until 1890 (De Kay 1842, Merriam 1882-84 and 1886, Mearns 1898, Miller 1899 and 1900) but trapped almost to extinction since that time (Seton 1925-1928). The most southerly records are those from the Catskills (Audubon and Bachman 1851-1854, Mearns 1898). An unmapped locality is Averyville (Harper 1929). The last specimen taken was in 1938 (Yeager 1950).

North Dakota: Common a century ago in the wooded northeastern part of the state, but have been long extinct (Bailey 1926a, Allen 1942). Known records are from Pembina County (Bailey 1926a), Walsh County (Bailey 1926a, Swanson, Surber and Roberts 1945) and Grand Forks County (Bailey 1926a). An unmapped record is the Hair Hills (Bailey 1926a).

Northwest Territories: All of the Territories south of the barrens (Ross 1861a and b and 1862, MacFarlane 1905, Mair and Macfarlane 1908, Preble 1902 and 1908). Banfield (1951)

records one taken seventy-five miles west of treeline near Contwoyto Lake, and Dergbol and Freuchten (1935) record the taking of one just south of Chesterfield Inlet far from the forest edge. Clarke (1944) likewise has observed that marten have been taken far from timberline near Tuktoyoktuk. The greatest numbers of martens were taken during the period 1840 to 1860, according to Seton (1925-1928), but since then the numbers available have steadily decreased (many authors). The annual catch in the years 1851-60 exceeded 30,000 pelts, but by 1930 the average had dropped to about 5,000 pelts. The chief collecting places are now Forts Simpson, Good Hope, Norman, Aklavik, Rae, Smith, Resolution and Providence in that order of importance (Robinson and Robinson 1946). An unmapped record is Fort Anderson (Preble 1908).

Nova Scotia: Originally probably all of Nova Scotia (Smith 1940) and according to Coues (1877) and Bailey (1896) once very common. Now very rare, and found only in restricted areas (Smith 1940). No specimens have been legally collected for some time, but Rand (1933) had heard of one smuggled out shortly before. Are, or were, present on Cape Breton Island (Rowan 1876, Rand 1944b).

Ohio: Kirtland (1838) reported that "the pine weasel is admitted to the state's fauna on the authority of Dr. Ward, who informs me that it was taken in the vicinity of Chillecothe". Brayton (1882) quoting a letter of one Emory Potter, listed it as "extinct in Ohio". Bole and Moulthrop (1942) have examined

two specimens believed collected from Ashtabula County. They conclude that it has been extinct for about one hundred years. The Chillecothe record, if correct, marks the most southerly marten records known for the area east of the Great Plains.

Ontario: Apparently once common through all of the province except for the barrens just south of Hudson Bay. It now occurs no further south than the southern limits of Algonquin Park (Cross and Dymond 1929, Downing 1948, de Vos 1952) and is made up of many small disjunct populations, the largest centering around the area fifty to seventy-five miles west of Timmins (de Vos 1952). An unmapped locality is Quinte Forest District (de Vos 1952). Apparently at one time it occurred all through southern Ontario, at least as far south as Essex County and Rondeau, as the following evidence indicates. Small and Lett, 1884, (Trans. Ottawa Field Nat. Club 6.2 : 280-283, and 150-151) and Rand (1945a) say it occurred near Ottawa about 1840 and Seton (1925-1928) says it was found between Lake Simcoe and Ottawa in the 1870's. It occurred at Whitechurch, ten miles north of Toronto (Seton 1925-1928) and near Toronto in 1830 and "much later" (Faull 1913).

They were considered to have once occurred near Hamilton by Warren (1950) in the upper Thames watershed (Richardson 1952) and Saunders (1932) was told in 1899 that they had been seen at Rondeau. De Vos (1952) says that Volume 3 of the Census of Canada, 1870-71, records fur returns from the following ridings: Essex, Kent, Brant, Simcoe, Victoria and Peterborough. Marten skeletons have been found in the late pre-European middens of

Prescott, Brantford and London (Wittsburg 1919, 1939 and 1948). Marten refuges have recently been formed on the east coast of James Bay and on Akimiski Island (de Vos 1952). I do not know whether marten have ever occurred naturally on the island.

Oregon: Throughout the Coast Mountains and Cascade Mountains from the northern to the southern boundaries of the state, as far east as western Crook County (Bailey 1936) and DesChutes River (eastern Wasco County) (specimen examined). Also present in the Blue Mountains of the north eastern part of the state, as far west as Grant County (Bailey 1936, Anon. 1951 and 1952) and as far south as Prairie City (Grant County) (specimen examined). Marten were being trapped in 1952 (Anon. 1952). A locality unmapped is Olive Lake (Bailey 1936).

Pennsylvania: Once abundant in the northern mountains of the state, but were exterminated by 1900 (Rhoads 1903, Richmond and Roslund 1949). Its southern limits in the state appear to have been Crawford, Forest, Elk, Cameron, Clinton, Tioga, Sullivan, Columbia, Wyoming and Wayne Counties (Rhoads 1903, Shoemaker 1919). Rhoads (1903) also says they once occurred in Lancaster County; if this is so it is, as Rhoads (1896) points out, the most southerly known record for marten in the Appalachian Mountains, aside from an Ohio record (see above).

Quebec, including Labrador: Commonly throughout all of the two, Quebec and Labrador, north to the tree line (Bell 1884, Low 1895, 1896 and 1897, Bangs 1898, Anderson 1931-32, Strong 1930, and Tanner 1944). Inland it was abundant everywhere

(Stearns 1883) but north of Misstassini it occurs chiefly in the forested river valleys only (Low 1895 and 1896, Strong 1930). The numbers trapped per year have dropped from 12,000 in 1870 (Minville 1946) to 1200 in 1949-50 (Anon 1927-50). Originally it occurred as far north as Chimo, as far west as George and as far east as the barrens edging the Labrador Coast (specimens examined). There are no records for its former occurrence in the eastern townships though Hall (1861) recorded it from near Montreal, Cameron and Orkin (1950) from Laurentides Park just north of Montreal and it is known to be present although scarce on the Gaspé (Cameron 1953 and specimens examined). Verrill (1862) and Rowan (1876) reported that marten occurred on Anticosti Island. Hunter (1907) said he had examined specimens of these, but Newsom (1937) said he could find no one on the island to confirm the story, though he did not doubt their reports that at one time they had occurred there. D. H. Pimlott (letter) writes that Mr. C. McCormick, the chief Game Warden on the island reports that the last specimen taken was trapped in 1926, and that tracks have not been seen since 1931.

Saskatchewan: The northern wooded portion of the province, probably as far south as the southern limit of Aspen Parkland, and at least as far south as the southern limit of the coniferous forest. Records for the province are scarce, the most southerly being Ile a la Crosse in the west and the Pas Mountains (Butler, letter) and Redearth in the east (specimens examined), although I have examined a specimen from Duck Mountain in

Manitoba, just across the border from Saskatchewan, about 150 miles south of the preceding locality. Twenty-five hundred skins were taken in 1919-20, but this has been reduced to 375 in the winter 1949-50 (Anon. 1927-50). The chief collecting points are Fond du Lac, Isle a la Crosse, and Pelican Narrows (L. Butler, letter).

South Dakota: "A specimen ... was taken in the Black Hills near Custer in January, 1930, which is the only authentic record for the state. However, there is every reason to assume that before the white trapper entered the region the pine marten roamed in the wooded area up the eastern side of the state and in the Black Hills as a straggler". (Over and Churchill 1945). A record of a marten taken from Pringle in the Black Hills is held in the files of the U. S. Fish and Wildlife Service.

Utah: Occurs through the Wasatch and Uinta Ranges of the middle Rocky Mountains as far west as Salt Lake and Utah Counties and as far south as Lost Lake, Wasatch County, if not farther. They occur also in the Colorado Plateau region of the southeastern part of the state, in San Juan and Grand Counties (Durrant 1952 and specimens examined). Small numbers of marten were collected in 1949-50 (Yeager 1950).

Vermont: Originally common throughout the mountainous portions of the state (Kirk 1916, Osgood 1938). Reported scarce by 1840 (Seton 1925-1928) and nearly extinct at present (Osgood 1938, Foote 1944). Osgood (1938) says the last specimen taken was in

1926. Records are known from Rutland, Bennington, and Windham counties only (Kirk 1916, Osgood 1938).

Virginia: Bailey (1946) states that "the account showing the quantity of skins and furs exported annually ... from Virginia from ... 1698 to ... 1715" lists marten as being taken, and that Thomas Jefferson in his "Notes on the State of Virginia" (1801) likewise included it. Audubon and Bachman (1851-54) report that "we have sought for it in vain on the mountains of Virginia, where notwithstanding, we think a straggler will occasionally make its appearance." Anthony (1928), Bailey (1946), and Brown (1952) all list it as a likely former inhabitant. Handley and Patton (1947) review the situation and reach the following conclusion: "although its range has been given by dozens of authors, even to the present day as 'extending south in the mountains to Virginia', we have been unable to find record of any specific evidence of its occurrence south of Pennsylvania. It is not inconceivable, however, that it might have occurred in the ... spruce forests that formerly covered eastern West Virginia and extended into the Virginia Mountains...."

Washington: Occurs in the Olympic Peninsula and south in the Coast Mountains at least to Chehalis (specimens examined), the Cascade Mountains from the international boundary to the Columbia River, west to Camp Skagit, Mount Vernon, and Hamilton (specimens examined) and east to eastern Chelan County and Chelan (Dalquest 1948 and specimens examined). Present in the Columbia, Bitterroot

and Selkirk Ranges of the northeastern part of the state (Dalquest 1948, Anon. 1931 and specimens examined) and the Blue Mountains of the southeastern corner (Dalquest 1948). The range is now more restricted according to Dalquest. The last specimens were collected in 1946-47, the season since being closed (Dalquest 1948).

Wisconsin: Formerly in the wooded portions of the northern part of the state, at least as far south as St. Croix, La Crosse, Jackson, Juneau and Brown Counties (Shorger 1942). Nearly extinct by 1900 (Jackson 1908, Cory 1912, Barger 1951). Shorger (1942) says the last specimen taken was in 1925 and believed by Barger (1951) to be completely gone from the state, but reported by de Vos (1951) as still present. Stated by Shorger (1942) as present in 1934 on Outer Island of the Apostle Island group in Lake Superior.

Wyoming: Reasonably common in the forested areas of the Wasatch and Yellowstone sections of the Middle Rocky Mountains of the western part of the state (Cary 1917, Seton 1925-1928, Bailey 1930, Calhalane 1943, Anon. 1950, Thomas 1952b). Occurs from Yellowstone Park south to La Barge Creek, Lincoln County (specimens examined) and as far east as western Park County (U.S. Fish and Wildlife Service card file) and Dinwoody Canyon, western Fremont County (specimen examined). No specimens were trapped in the year 1948-49 (Yeager 1950).

Yukon Territory: Present through all of the forested part of the territory, at least as far north as the Macmillan River (Mason 1924, Rand 1945d). The present status of marten is good, and promises to remain so (Rand 1944c) although the present total take is not equal to that of the catches of some single trappers thirty-five to forty years ago (Rand 1945b). Specimens were still being taken in 1949-50 (Anon. 1927-50). A locality record not mapped is the lower Yukon region (Twitchell 1921).

Synoptic examination

Having determined that North American marten fall into two distinctive morphological types (americana and caurina), whether they be of "species" or subspecies grade, and knowing that all New World marten are referable to these two basic groups, it becomes important to consider the many other named groups that remain and to examine their validity.

In 1942 Allen correctly recognized that marten fell into the two groups named above and considered them to be distinct "species", i.e. "Martes americana" and "Martes caurina". Wright, as pointed out elsewhere, in 1953 showed that these two supposed "species" actually intergrade and hence must be considered subspecies of M. americana. The taxonomic difficulties resulting from this conclusion are discussed elsewhere, but for the time being (insofar as this stage of the paper is concerned), we here utilize Allen's classification, believing that it is unsatisfactory, but recognizing that it is the more convenient of the two.

Reference is made throughout this discussion to Enclosure A (inside back cover) showing the geographic

distribution of condylobasal length in male marten. This was made by obtaining the mean condylobasal length in males for each local subsample, mapping them, and joining points of equality by lines (isopleths). While more than one cranial character might have been used to advantage, lack of time made such an approach impossible, and is perhaps not as vital as at first it might appear to be, since most geographic variation within any "species" (caurina, americana) is reflected in size (i.e. condylobasal length). All other characters (including external measurements) closely follow the pattern shown by condylobasal length.

Detailed synonymies are provided in Appendix B. Only the name combinations used are given below; for author, date and citation the reader must refer to the appendix.

"Martes americana" (Kerr 1792)

Detailed characteristics given elsewhere, but easily distinguished by long, narrow, high skull, small upper molar and long highly inflated bullae. Width of inner lobe of P^4 x 100 / length of P^4 always less than 25.8; breadth of M^1 x 100 / length of P^4 always less than 97.15; lateral length of M^1 x 100 / mesial length of M^1 always more than 77; breadth of P^4 (across inner lobe) x 100 / length of P^4 always less than 64; canine width at base / bullae length always less than 94.

"Martes americana americana" (Kerr 1792)

Synonymy: Martes (or Mustela) martes, zibellina, americanus, americana, vulpina, leucopus, huro, leucotis, sinuensis, zibellina americana, zibellina var. americana, americana var.

leucopus, martinus, or vison.

Most writers attribute the epithet americana to Turton 1802 or 1806. However, Kerr in 1792, was the first to employ the term and authority for the name must now be attributed to him. Type specimen: None that I know of.

Type locality: Variouslly designated as "the North of ... America" and "North America, especially in Canada" (Kerr 1792); "North America" (Turton 1802 and 1806); "Country ... watered by the Missouri ..." (Rafinesque 1819a and b); "In Canada" (Kuhl 1820); "the habitat of the Huron Indians, fide Milbert, viz., region east and south of Georgian Bay, west peninsula of Ontario" (Cuvier 1823); "Eastern North America" (Miller 1900); "Upper Missouri?" (Elliot 1901a after Rafinesque 1819a and b); "The region occupied by the small pale martens of southern Canada and the northern United States" (Rhoads 1902); "Probably came from Ontario or Quebec...." (Rhoads 1902).

Although Cuvier's type locality is probably the most clearly defined, it is now likely without martens, and most authors since the turn of the last century have used Miller's (1900) designation "Eastern North America". Because this could be interpreted to include the "races" "atrata", "brumalis" and "abieticola", it is likely best to restrict it to Ontario or the United States east of the Mississippi.

Dr. E. R. Hall has kindly written to point out that Rafinesque's (1819a and b) Mustela vulpina, since it was taken from the "Upper Missouri River = Idaho or southwest Montana" should be considered a synonym of "M. caurina" which occurs there and

indeed, should actually replace the name "caurina" for the "species". Dr. Hall mistakenly stated that Rafinesque's specimen was taken from the "Upper Missouri". Rafinesque said only that it was taken from the "country ... watered by the Missouri ...", the change to Hall's locality being made by Elliot (1901a). While it is possible that M. vulpina was taken from Idaho or Montana, it could also have been taken in the Dakotas or Iowa, and since both Elliot and Rhoads (1902) considered it synonymous with "M. americana" ten years after "M. caurina" had been described, I am obliged to make the same interpretation. It is notable, however, that Gray 1865 and 1869 considered M. vulpina to be synonymous with "M. a. abietinoides".

Rafinesque's specimen was a semi-albino, so that the description of pelage cannot be safely used in identifying the specimen. He does say that the total length of the specimen was twenty-seven inches, the tail length nine inches. M. vulpina was thus a large marten, much nearer to "M. caurina" than to "M. americana americana", although perhaps near to "M. a. abieticola" so that the problem can not be said to have been closed. As Dr. Hall says in his letter, if it can be shown to have been a specimen of "M. caurina", the name caurina will need to be changed to vulpina.

Pelage: The coat is usually said to be yellowish brown, legs, feet and tail tipped with black and with a whitish yellowish throat patch (Emmons 1840, Miller 1900, Elliot 1901a, Rhoads 1902 and 1903, Cory 1912). De Vos (1952) described it as with "head usually lighter in colour than the body and normally

light gray brown, the inner sides of the ears are dull white. The dorsal parts are normally dark brown, but may range from light pale yellow to nearly black. The limbs and tail are normally slightly darker than the rest of the body. The ventral parts and flanks are of a lighter colour than the dorsal parts. The throat and breast patches, which may be of different sizes and shapes, and the median ventral stripe are generally yellowish-orange, but may vary from pure white to brownish-yellow or may be entirely absent." Elsewhere he says that "the colour of the fur ... is extremely variable", ranging from very pale yellow-orange, with an entirely white head and no throat patch to very dark, with a large number of white guard hairs, with a large orange throat patch.

Rhoads (1902) stated that this "subspecies" was distinctive from others by the paleness and yellowness of the outer fur, the clear ash of the basal under fur, and the strongly contrasting colours of the foreparts compared to the hinder parts.

Almost all authors have remarked on the small size of this "race" compared to all others.

The pelage descriptions given above are in accord with my own findings. It is generally, as Rhoads pointed out, the palest, yellowest and most thinly furred of all the "races" of "M. americana", although as de Vos points out, variation can be extreme. It is likewise small, being, aside from "M. a. abietinoides" in the Canadian Rockies, the smallest marten of the "species".

Geographic variation: Marten from Algonquin Park, and from extreme northwestern Ontario are, according to de Vos (1952), paler than the average Ontario skin. Those from eastern Ontario are said by Bachrach (1946) to have very short guard hairs and underfur. Marten from the north shore of Lake Superior are, according to Richardson (1829) and Rhoads (1902) very near to black in colour, and according to Allen (1876a) are slightly larger than those from New York and Maine.

Adams (1873) described this "subspecies" as it occurs in Nova Scotia in some detail. He said that two types occur, a light coloured one (orange and saffron) from the hardwood forests, and a dark coloured one from the pine forests. Any large series of skins, he said, showed these two types, and intergradation between the two occurred. Rowan (1876) said that marten from the north shore of the St. Lawrence were darker than those from Nova Scotia (grading towards "M. a. brumalis"?) while those south of the St. Lawrence, in Quebec, were paler, yellower and more thinly furred. Those from the Gaspé, however, were much darker and richer than those from New Brunswick. Rhoads (1902) reported that specimens from about Lake Superior and New Brunswick tended to largeness and darkness.

Poland (1892) said that the poorest and palest skins came from the northeastern part of the United States. Rhoads (1902) came to the same conclusion. The martens from the Adirondacks of New York and from Pennsylvania are especially pale according to Rhoads (1903) and Grant (1906).

The marten on Anticosti Island were described by Hunter

in 1907 as being peculiar and distinct in having in almost all cases the forepaws and the end of the tail tipped with white. They were otherwise as dark and well furred as those from Labrador ("M. a. brumalis"). Newsom (1937) was unable to verify this report.

I am unable to add much to this discussion of pelage variation, except that I have also found that specimens from the United States are on the average considerably paler in colour than those from Ontario and that regional populations appear to vary somewhat in overall hue, though this is only to be determined from large samples.

Geographic variation in condylobasal length in males, as mapped on Enclosure A, is of interest. The average condylobasal length of the total sample of this race was 7.87 cm. (n = 118), but specimens from the northern part of Ontario averaged 8.10 cm. or more, while those from the area about Algonquin Park averaged 8.20 cm. and those from the Adirondacks of New York and the central Quebec-Ontario boundary less than 7.60 cm. These differences are significant at or very near the 95% level, and indicate that not only does pelage vary geographically within the "race" but that skull length and presumably total length does also. I am unable to account for the peculiar "islands" or largeness and smallness within the range of this "subspecies". De Vos (1951 and 1952) has mapped the distribution of marten in Ontario and this map shows the Algonquin Park and Ontario-Quebec boundary populations to be disjunct and quite isolated from other nearby populations. Hamilton (1943) maps the marten of the

Adirondack Mountains as being equally isolated. It is possible, I suppose, that the differences marking the marten of these "islands" is a result of the so-called Sewell-Wright effect on small isolated populations. If this is so, it means that they have likely occurred since these populations have become disjunct, a period of time probably not exceeding a century and in some cases probably considerably less.

Cranium: Since this is the standard against which other "subspecies" of the "species" are to be compared, little needs to be said except that it is marked by all the characteristics of the "species" and that the skull is exceedingly small, being equalled in this respect only by "M. a. abietinoides", comparison with which is made under that "subspecies".

Two "subspecies" have ranges contiguous to the range of this "subspecies", namely "M. a. brumalis" to the northeast in Quebec and Labrador and "M. a. abieticola" to the west, in Manitoba. The samples of crania of "M. a. americana" are distinct from these to the 95% level as shown by all of the fourteen characters studied except the following: upper molar width, upper molar inner moiety length, narrowest width of palate, canine width at base / bullae length, and upper molar width plus inner moiety length, females only. These likely fail to show distinction because of the small sample size ($n = 3$) of female "M. a. abieticola".

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	7.86	.23	2.94	118	7.08	.24	.34	81
Rostral width	1.46	.07	5.18	120	1.28	.07	5.37	82
Upper tooth row	2.87	.10	3.61	69	2.55	.13	5.08	45
Canine width at base	1.40	.06	4.62	120	1.24	.06	5.00	82
Bulla length	1.64	.06	3.71	119	1.54	.06	3.70	82
Upper molar width	.73	.08	10.53	120	.65	.03	5.38	82
Upper molar inner moiety length	.45	.03	7.31	119	.38	.02	6.51	82
Palate length	3.92	.15	3.94	66	3.47	.15	4.21	44
Mastoid width	3.44	.13	3.92	66	3.10	.11	3.70	44
Height of skull at bullae	2.94	.11	3.81	66	2.53	.14	5.44	44
Length of last upper PM	.77	.03	4.54	118	.68	.03	4.37	80
Narrowest palate width	.76	.06	7.27	110	.70	.04	6.30	68
Canine width base / bullae length	.85	.03	3.76	118	.80	.03	4.35	82
Upper molar width plus inner moiety length	1.19	.06	5.36	118	1.04	.06	5.75	82
Total length	60.00	1.96		80	53.80	2.74		33
Tail length	17.50	1.02		80	15.60	1.15		33
Hindfoot	8.90	.31		80	7.70	.66		33

Distribution: Hamilton (1943) considered all marten east of the Mississippi River in the United States to belong to this "subspecies". Cory (1912) mapped its range and showed it occurring everywhere within the "species" range south of a line

connecting southern James Bay, Lake Mistassini and Godbout, and east of a line in western Ontario connecting (approximately) Bemidjii (Minnesota), Sioux Lookout and central James Bay (Ontario). Further detail concerning these marginal limits are given subsequently.

This "subspecies" has been reported to occur in the following provinces and states, not all, however, being based on examination of specimens: Ontario (Downing 1948, Cross and Dymond 1929, Anderson 1946); Southern Quebec, Gaspé and Eastern Townships (Anderson 1934b, Cameron 1953); New Brunswick (Morris 1948); Nova Scotia (Smith 1940); North and South Dakota (Bailey 1926a, Over and Churchill 1945); Minnesota (Swanson, Surber and Roberts 1945); Iowa (Scott 1937); Wisconsin (Barger 1951); Illinois (Cory 1912); Michigan (Burt 1948); Ohio (Bole and Moulthrop 1942); Pennsylvania (Williams 1930, Grimm and Whitebread 1952); New Hampshire (Carpenter and Siegler 1945); Vermont (Osgood 1938); Connecticut (Goodwin 1935); Maryland (Mansueti 1950); Virginia (Handley and Patton 1947).

This "subspecies" is presumed to be the form present on Prince Edward Island and Cape Breton Island. The marten of Anticosti Island are described by Hunter (1907) as possessing a rich dark pelage that suggests that it lies nearer to "M. a. atrata" or "M. a. brumalis". The vegetation of Anticosti is reported by Halliday (1937) and Hustich (1949b) to be most closely related to that of the Mingan area directly to the north, so that I make the assumption that the nearest relative of the Anticosti marten may be "M. a. brumalis", the Labrador marten.

My examination of specimens and of the literature leads me to believe that the marten of the following provinces and states can be properly referred to this "race": central, eastern and southern Ontario, southern Quebec, Eastern Townships and Gaspé, New Brunswick, Nova Scotia, Prince Edward and Cape Breton Islands, and doubtfully Anticosti Island, eastern and central Minnesota, Wisconsin, Iowa, Illinois, Michigan (including Isle Royale), Indiana, Ohio, Pennsylvania, New York, Vermont, New Hampshire, Maine, Massachusetts, Connecticut, and other adjacent states where they may have once occurred. Specimens from western Minnesota, western Ontario and North and South Dakota may be referable to this "race", or may be more nearly allied to "M. a. abieticola" as discussed below. The marten from the Black Hills of South Dakota, a specimen of which was recorded taken by Over and Churchill (1945) and which is listed in the files of the U. S. Fish and Wildlife Service is considered by the above named authors to be representative of "M. a. americana" but may really represent "abieticola" or as likely "M. caurina" which occurs only 175 miles to the southwest of the Black Hills.

To the northeast and into northern Quebec and Labrador, "M. a. americana" grades into "M. a. brumalis", as the isopleth map clearly shows. Just where the range of "americana" ends and where "brumalis" begins is a matter of opinion. The localities following have provided specimens that have been, or are, referable to "M. a. brumalis": George River (Rousseau 1949), Chimo (Anderson 1946), Matamak (Eidmann 1935), L'anse au Loup (Bangs 1910), Fort George, Nichuchin, Chimo and Northwest River

(Low 1896). On the other hand the following localities have been referred in the literature to "M. a. americana": Lake Edward (Bangs 1898), Lake Mistassini (Anderson 1946), James Bay region (Anderson 1934), Straits of Belle Isle (Rhoads 1902; Anderson 1946), James Bay region (Anderson 1934), Straits of Belle Isle (Rhoads 1902, Anderson 1934b, 1938 and 1940). Low (1894 and 1896) was the first to suggest that the two "races" underwent gradual intergradation into each other. Bangs (1898) did not believe that such intergradation occurred, but Anderson (1934b, 1938 and 1940) expressed belief that while the line of intergradation could not be accurately drawn, it did exist. Cory (1912) mapped the southern limit of "brumalis" as extending from southern James Bay, through northern Lake Mistassini, to about Clarke City, and showed an area about fifty miles wide to the south of this in which it intergraded with "americana". Anderson names the area of intergradation to be in the region north of Lake Mistassini.

I have examined most of the specimens seen by Bangs and Anderson, and many of those examined by Low, and conclude with Anderson that a cline exists between the small pale "race" to the south ("americana") and the larger, darker "race" to the north ("brumalis"). Examination of the isopleth map for condylobasal length indicates this gradation well. The area of most rapid rate of change, as exemplified by this map occurs from southern James Bay to the north shore of the Saguenay River (where the average condylobasal length increases by 2 mm. in a belt not much more than 50 or 75 miles wide). This area might be said to mark

a good point of division between the two "subspecies". However, Anderson considers the skull and pelage of the Mistassini specimens to lie closer to "M. a. americana" than to "M. a. brumalis". Further, since the mean condylobasal length of the sample of "M. a. americana" males is 7.86 cm. ($n = 118$, $SD = .23$), while that of "M. a. brumalis" is 8.56 cm. ($n = 55$, $SD = .18$), we might set the point of division midway between the two means, i.e. set the point of division at that area characterized by martens with an average condylobasal length of 8.21 cm. Referring again to the isopleth map, this isopleth is found to run from the region about the base of Hudson Bay, through the northern end of Lake Mistassini, to about Betsiamites on the St. Lawrence River. This line perhaps fits Anderson's interpretation better than does the previously suggested one.

Actually of course, as discussed elsewhere, the problem cannot be solved. What is significant is that "Martes a. americana" of Ontario, as one moves north into Quebec becomes gradually darker and larger until its maximum of largeness and darkness is attained along the Labrador coast. Any boundary line that one may set up to mark the geographic limits of the two "races" will have to be wholly arbitrary, and not particularly significant.

The western boundary of "M. a. americana", where it intergrades with "M. a. abieticola" is likewise difficult to state. It has been described variously as "the western shores of Hudson Bay" (Anthony 1928), "Ontario, west of Hudson Bay" (Cross and Dymond 1929), eastern limit of the western Hudson Bay drainage system (Anderson 1937), or "extreme western Ontario or

eastern Manitoba" (Anderson 1946). Cory (1912) maps the eastern limit of "abieticola" as passing from about Moorhead, Minnesota, through Lake of the Woods, Sioux Lookout to the middle reaches of the Winisk River, Ontario. He shows it intergrading with "americana" in a belt 75 to 100 miles wide to the east of this.

Of the specimens I have examined, the most westerly in Ontario (Goldpines and Sioux Lookout) are referable to "M. a. americana", while those most easterly in Manitoba (York Factory, Oxford House, Red River) are referable to "M. a. abieticola", though averaging slightly smaller than typical. Reference to the isopleth map shows that "abieticola" begins to grade into "americana" on about a north south line bisecting Manitoba, reaching the dimensions of "M. a. americana" somewhere west of Goldpines and Sioux Lookout. One specimen from Grand Forks, Minnesota, appears to lie intermediate between the two "races" as are skin measurements given by Gunderson and Beer (1953) for Minnesota marten. I would suggest that the Ontario-Manitoba boundary line marks as well as any other line the approximate area of greatest change between the two "races". The midpoint between the means of condylobasal length of the males of the two "races", 8.13 cm., is, however, as I have mapped it, somewhat to the east of this line.

Specimens examined: 413 specimens, from Ontario, Quebec, New Brunswick, Minnesota, Michigan, New York, and Connecticut.

Skull diagrams and photographs: De Kay 1842, vol. 1, pl. 11 and 19; Boddaert 1785, pl. 36; Baird 1857 and 1859, pl. 36 and 37;

Coues 1877, pl. 5; Osgood 1900, pl. 7; Elliot 1901a, fig. 66; Cory 1912, p. 382; Pratt 1923, fig. 126.

"Martes americana brumalis" (Bangs 1898)

Synonymy: Martes (or Mustela) brumalis, atrata brumalis, caurina, brumalis, americana brumalis.

Type specimen: Museum of Comparative Zoology, Cambridge, Massachusetts, Bang's Collection no. 7417 (Allen 1931, Anderson 1946).

Type locality: "Okkak, Labrador" (Bangs 1898); "Okak, Labrador" (Miller 1900); "Okak, Labrador, Canada, now Newfoundland" (Anderson 1938).

Pelage: Long recognized as distinctively large and dark coloured, when compared to "M. a. americana" to the south (Gilpin 1860, Rowan 1876, Poland 1892, Low 1895 and 1896, Bangs 1898, Rhoads 1902, Hunter 1907, Hardy 1910, Cory 1912, Anderson 1934b, 1938, 1940 and 1946, Tanner 1944, and 1947, Rousseau 1949).

The original describer, Bangs, saw no skins of this "race", the first description of the colour being made by Rhoads (1902), who described it as "separable from any other eastern interior form on account of its darker shades and its longer guard hairs, and distinct from the equally large Alaskan marten (M. a. actiosa) by its much darker colour".

Rhoads' interpretation of this "subspecies" is quite correct and I conclude with him that in colour and size it is

quite distinctive from any other "subspecies" of "M. a. americana". It is always very much darker than any other "race", being a rich glossy chocolate brown, often nearly black, with guard hairs long and glossy. In darkness of pelage it is approached only by the Newfoundland marten ("M. a. atrata").

Cranium: The original description of this "race" was made by Bangs from skulls, which he described as follows: "skull large, powerful, and heavy; rostrum very short and broad; frontals highly arched; auditory bullae very large and deep; dentition extremely heavy throughout, the last uppermolar in particular being very large; the tooth row a good deal crowded ... their large size, short wide rostrums, and enormous teeth at once distinguish them."

Rhoads, in 1902, validated Bangs' description, adding to it its distinctive pelage characteristics and pointing out the similarity of the skull of this "race" to that of "M. a. actiosa". Rhoads, unlike Bangs, recognized too that "brumalis" should properly be considered a "subspecies" of "americana" and not a distinct "species".

My examination of skulls of this "race" show it to be very much larger than those of "M. a. americana" to the south, being equal in size to those of "kenaiensis", "abieticola" and "actiosa", the ranges of which it does not meet.

Comparison of cranial statistics with "M. a. americana" have already been made. Comparison with "M. a. atrata" is made under that "subspecies" topic. Compared to "abieticola", "actiosa" and "kenaiensis", they show a condylobasal length

significantly greater than any, and hence are the largest marten in North America. Statistical significance is also shown for upper tooth row (from male "actuosa" only), canine width at base ("kenaiensis" only) upper molar width (males of "kenaiensis" and "actuosa" only), upper molar inner moiety length (from "actuosa" and "kenaiensis"), palate length (from "kenaiensis", "actuosa" and "abieticola" in males, but only "abieticola" in females), mastoid width (from "kenaiensis" and "actuosa", males only), length of last upper premolar (from "actuosa", males only), canine width at base / bullae length (from "kenaiensis") and upper molar inner moiety length plus width ("actuosa" and "kenaiensis", males only). Thus of fourteen cranial characters considered, this "race" is significantly different from "kenaiensis" by ten in males and three in females; from "actuosa" by eight in males and one in females; and from "abieticola" by two in males and one in females. The implied greater similarity to "abieticola" is due likely to the smallness of the sample of that "race" studied (n = 18) and to the large standard deviations thus obtained.

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	8.56	.18	2.06	55	7.66	.15	2.01	48
Rostral width	1.63	.06	3.80	58	1.44	.06	3.88	49
Upper tooth row	3.13	.07	2.67	35	2.79	.05	1.76	23
Canine width at base	1.57	.06	4.01	58	1.38	.06	4.05	49
Bullae length	1.75	.05	3.09	58	1.62	.05	3.20	49
Upper molar width	.80	.03	3.97	58	.70	.03	4.55	49

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Upper molar inner moiety length	.49	.03	5.66	58	.42	.02	5.25	49
Palate length	4.35	.11	2.57	36	3.81	.08	2.05	23
Mastoid width	3.79	.08	2.13	36	3.45	.08	2.29	23
Height of skull at bullae	3.22	.08	2.42	36	2.89	.08	2.80	23
Length of last upper PM	.84	.03	4.14	58	.75	.02	2.93	49
Narrowest palate width	.84	.03	4.14	35	.76	.03	4.19	23
Canine width base / bullae length	.90	.04	4.45	58	.85	.04	4.57	49
Upper molar width plus inner moiety length	1.30	.05	4.22	58	1.12	.05	4.54	49
Total length	68.00	-	-	1	58.5	-	-	1
Tail length	19.50	-	-	1	17.90	-	-	1
Hind foot	11.50	-	-	1	9.1	-	-	1

Geographic variation: Anderson (1934b) says that this "race" is "more or less variable in any district" but adds no detail. Writers who have lived in the district (Rowan 1876, Low 1895 and 1896, Tanner 1944 and 1947) say that the largest and darkest martens are to be found in the very northern part of the "sub-species" range. Low says "the largest and darkest skins are taken along the edge of its northern limits", and Tanner remarks that "the darker and thicker the black spruce woods are, the darker and richer are the skins of the marten living there...."

We have already pointed out that as our isopleth map indicates, a steady decrease in size (and presumably of darkness) occurs from the Labrador coast southwest into the region about James Bay and the Saguenay River. The very largest specimens appear to be taken from the area about Cartwright and the region about the mouth of the Eagle River on the southern Labrador coast. Specimens from Chimo, Grand Falls and Northwest River are nearly as large, and larger than those from the adjacent coast, suggesting an "island" of largeness in the region of the Torngat Mountains, Labrador.

Distribution: All authors appear to agree that the northern limit of this "race" is the northern limit of marten and is coincident with the tree-limit in Labrador and Quebec, and the southern limit of the semi-barrens (Low 1895 and 1896, Anderson 1934b, 1938 and 1940, Tanner 1944 and 1947). Low adds that north of this line it is found "only in the wooded stretches of the river valleys" While a large proportion of the specimens I have examined are labelled as coming from the Labrador coast it is quite likely that many were trapped inland and later brought to the coast.

The southern limits of this "race" have been discussed under the topic "M. a. americana" and the reader should refer to this. In brief, it may be said to grade through the length of most of the Quebec-Labrador peninsula into "M. a. americana" somewhere in the region about southern James Bay and Lake St. John.

It has already been pointed out that this may be the

"race" that once occupied Anticosti Island.

Specimens examined: 128 specimens from northern Quebec and Newfoundland Labrador.

Skull diagrams: Bangs 1898, p. 503; Osgood 1900, pl. 7.

"Martes americana atrata" (Bangs 1897)

Synonymy: Martes (or Mustela) atrata, caurina atrata, americana atrata.

Type specimen: Museum of Comparative Zoology, Cambridge, Massachusetts, Bangs' Collection no. 5752 (Allen 1931, Anderson 1946).

Type locality: "Bay St. George, Newfoundland" (Bangs 1897).

Pelage: The characteristics of the Newfoundland marten are not well known, presumably because of its scarcity. Almost all writers (Gilpin 1860, Bangs 1897, Miller 1900, Elliot 1901, Cory 1912, Bangs 1913 and Anderson 1946) describe it as dark chocolate in colour, with lustrous pelage and orange throat patch. Most distinguish it from the much paler coloured "M. a. americana" and ally it with the similarly coloured "M. a. brumalis" of Labrador and Quebec. Reeks, in 1870, in comparing it to the Labrador "race" described it as "much lighter throughout, but especially in the head and ears". Bangs, in his original description described it as about the same size, or perhaps slightly larger than "M. a. americana" (i.e. a small marten), with

colouration more like that of a mink than that of a marten.

"Deep chocolate becoming black on back, head, arms, legs, rump and tail; a few white hairs scattered along the back; chest and under side of neck irregularly blotched with orange; a median line of orange on belly; ears black, narrowly bordered all around with dull white; a patch of yellowish-white hairs in front of the opening of ear...." Bangs later (1913) redescribed it as a "rather small species..." as did Miller in 1900, who said it could always be told from "brumalis" by its smaller size and from "americana" by its much darker (never pale yellowish) pelage. Cory (1912) added that it may always be told from "M. a. americana" by its more orange throat patch.

I have examined no skins of this "race" and hence cannot add to the descriptions above, except to point out, as is done below in greater detail, that Bangs and later authors were mistaken in believing that this "race" is as small as he believed. In size it lies much nearer to "M. a. brumalis".

The Newfoundland marten shows, in all the skulls I have studied, all of the characters of the "species" "M. americana" and must be considered to belong to it. Bangs when he described the race considered it to be a distinctive species ("Mustela atrata"). Elliot in 1901a incorrectly considered it a subspecies of "M. caurina". Rhoads (1902) although he saw no skulls of the "race" correctly recognized from Bangs' description that it was closely allied to "M. a. americana", although he made no nomenclatural change. Allen, in 1942, first named it a subspecies of "M. americana" and de Vos, in 1952, although unaware of Allen's

change, expressed a correct interpretation of the relationship of atrata as a subspecies of "americana". Miller and Kellogg (1955) however, gave it specific status.

Bangs, in his description of the "race", did not recognize that the specimens on which he based his account were females; it was by comparing these to males of "M. a. americana" and "M. a. brumalis" that he concluded "atrata" to be very little larger than "M. a. americana". Of the eleven skulls of this "subspecies" that I have examined, three were male, and it is evident from these that in size "M. a. atrata" lies very near to "M. a. brumalis" rather than to "M. a. americana" as Bangs believed. The mean condylobasal length of males of this "race" (8.39 cm., n = 3), while not so large as that of the samples of "M. a. brumalis" from the Labrador coast, equals those (as the isopleth map shows) from extreme western Newfoundland-Labrador, which is very much larger than those of typical "americana" from Ontario. Since in size "atrata" lies close to the average specimen of "M. a. brumalis" and since descriptions of its pelage show it to be dark as in "brumalis" (not pale as in "americana") we must conclude that it is closely related indeed, to the Labrador "race" and not to "M. a. americana". I conclude, in fact, that there have been no distinctions shown to exist between "atrata" and "brumalis" and that both are best considered one "subspecies", "M. a. atrata" (Bangs).

In addition to the similarity of "atrata" to "brumalis" and its dissimilarity to "americana" stated above, I add the following based on statistical comparison of the three samples studied. Of the fourteen cranial characters studied, when

"atrata" is compared to "americana" all but the following differ significantly to the 95% level; upper molar width, palate length and upper molar width plus inner moiety length. On the other hand, when compared to "brumalis", "atrata" shows significance in the following only: upper molar width (females only), palate length (males only), mastoid width (females only) length of last upper premolar, canine width at base, bullae length (males only) and upper molar width plus inner moiety length. Two other characters approach but do not attain significance (rostral width, males only, canine width at base, females only). By summing significances we find that "M. a. atrata" shows over twice as many significant distinctions when compared to "M. a. americana" than when compared to "brumalis".

The following are cranial statistics for the Newfoundland "race":

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	8.39	.16	1.85	3	7.37	.08	1.04	5
Rostral width	1.67	.02	1.20	3	1.42	.03	2.25	8
Upper tooth row	3.13	.09	2.71	3	2.74	.06	2.01	8
Canine width at base	1.58	.03	1.90	3	1.35	.02	1.63	8
Bullae length	1.73	.03	1.73	3	1.59	.03	2.07	8
Upper molar width	.76	.04	4.59	3	.66	.03	3.78	8
Upper molar inner moiety length	.46	.01	3.02	3	.40	.03	6.23	8
Palate length	4.28	.10	2.34	3	3.68	.06	1.69	8
Mastoid width	3.79	.09	2.37	3	3.36	.06	1.63	8

	<u>Male</u>				<u>Female</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Height of skull at bullae	3.21	.05	1.40	3	2.95	.11	3.60	8
Length of last upper PM	.82	.00	.00	3	.71	.02	2.39	8
Narrowest palate width	.87	.03	3.45	3	.77	.03	3.91	8
Canine width base / bullae length	.91	.00	.00	3	.85	.02	2.59	8
Upper molar width plus inner moiety length	1.23	.05	4.08	3	1.06	.05	4.52	8
Total length	-	-	-	-	552*	-	-	3
Tail length	-	-	-	-	185*	-	-	3
Hind foot	-	-	-	-	88*	-	-	3

*From Bangs 1897 and
Miller 1900

Geographic variation: Nothing is known regarding this.

Distribution: Restricted to forested Newfoundland, where it is considered the only form of marten to occur. It is possible (if "atrata" and "brumalis" were to be considered distinct) that this "race" (and not "brumalis") is the one occurring on Anticosti Island.

Specimens examined: 11 specimens from Newfoundland

Skull diagrams and photographs: None that I know of.

"Martes americana abieticola" (Preble 1902)

Synonymy: Martes (or Mustela) americana abieticola

Type specimen: U. S. National Museum no. 19256/34962 (Poole and Schantz 1942, also seen by myself).

Type locality: "Cumberland House, Saskatchewan" (Preble 1902).

R. Macfarlane, who collected the type for Preble, wrote (1905) that it was obtained from an Indian chief, "I think the Chief told me that he had trapped it in the Pas Mountain, some sixty or seventy miles to the southward of Cumberland House".

Pelage: This "race", like that preceding, is a puzzling one, in that it has never been properly defined and limited. Preble, when first he described the "form" properly recognized it as a "subspecies" of "M. americana", but did little to distinguish it from other "subspecies" of the "species", especially "M. a. actuosa". Subsequent authors have added almost nothing to his description.

Preble described the skin as follows: "type in winter pelage: general color of body rich dark yellowish brown, darkest on middle of back; legs and tail darker, the latter almost black at tip; an irregular blotch and a small spot on chest, ochraceous; face and cheeks greyish brown; ears edged with whitish". Anderson in 1946 described it simply as "a large dark brown race". Preble recognized it to be much larger than "M. a. americana" to the east, although he considered it rather smaller than the Alaskan marten "M. a. actuosa".

My examination of Preble's skins from Manitoba leads me

to agree that it is a much larger and darker "race" than is "M. a. americana" from Ontario. The colour tends to be richer, browner, and longer furred than the smaller "race" and browner and less grey than the pale headed Alaskan "race", though of about the same size. There is, however, sufficient variation in the colour of the fur of the Alaskan "race" (see under that topic) especially in Mackenzie, to lead one to believe that "abieticola" falls within its range of colour.

Cranium: This is described by Preble as "much larger than in M. americana americana ..., more angular, the sagittal crest being more highly developed; zygomata more bowed outward posteriorly; dentition much heavier except last upper molar, which is usually about the same size." Elsewhere he remarks that "this form approaches in some of its characters Mustela a. actuosa from Alaska, but though smaller has heavier dentition than that species, and consequently more crowded molars."

The distinctions that Preble makes between "M. a. americana" and "abieticola" are, I find, perfectly real and valid, although it is evident that the two "races" intergrade, and are closely related. However, Preble fails to show that "abieticola" is really distinctive from "M. a. actuosa" to the northwest. His distinctions between these two "races" are essentially these: that "abieticola" is darker in colour, slightly smaller in size and with slightly heavier and more crowded dentition. I have already pointed out that the difference in colour may easily fall within the range of "actuosa". Further, this "race", contrary to Preble, is not smaller than the Alaskan "race", but rather about

equals it. Insofar as crowding of and heaviness of dentition is concerned, while these are difficult to measure quantitatively, I conclude that there is no essential difference here between the two "races". In other words I conclude that aside from conformity to precedence, there is yet no basis for the maintenance of this "race", and here name them one, "M. a. actuosa" (Osgood). Comparison of this "race" to "americana" has already been made. Compared to "actuosa" of the fourteen characters studied, only one (upper tooth row) in females only, shows significance at the 95% level.

Cranial statistics of "M. a. abieticola" taken from Manitoba follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	8.40	.19	2.30	12	7.56	.07	.86	3
Rostral width	1.61	.06	3.53	15	1.43	.05	3.70	3
Upper tooth row	3.08	.06	1.04	14	2.72	.00	.00	3
Canine width at base	1.57	.06	4.08	15	1.37	.07	5.10	3
Bullae length	1.74	.07	4.13	15	1.63	.06	3.38	3
Upper molar width	.80	.03	4.02	15	.70	.06	8.61	3
Upper molar inner moiety length	.48	.03	6.20	15	.41	.04	9.09	3
Palate length	4.22	.13	3.10	14	3.73	.04	1.07	3
Mastoid width	3.73	.09	2.36	14	3.38	.07	2.16	3
Height of skull at bullae	3.19	.07	2.13	14	2.83	.08	2.94	3
Length of last upper PM	.84	.04	4.31	15	.74	.03	3.78	3
Narrowest palate width	.81	.04	4.57	14	.75	.04	4.69	3
Canine width base / bullae length	.90	.04	4.89	15	.85	.05	5.92	3

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Upper molar width plus inner molety length	1.29	.07	5.13	15	1.10	.09	8.52	3
Total length	62.30	4.02	-	5	55.50	-	-	2
Tail length	19.50	1.97	-	5	17.70	-	-	2
Hind foot	9.50	.90	-	2	9.40	-	-	1

Geographic variation: Discussed under "M. a. actuosa", whose range has never been properly distinguished from that of this "subspecies". It may be stated here, however, that the largest marten of this "race" appear to be found in southeastern Mackenzie.

Distribution: Preble, when he described this "race", identified specimens from Norway House, Oxford House, York Factory, lower Churchill River, Cross Lake and Fort Churchill and of course from the type locality in eastern Saskatchewan as belonging to it. We may assume, therefore, that he considered most of forested Manitoba to be occupied by it. Other authors have tended subsequently to extend this range, often it appears, without reference to specimens. Its eastern limit has been discussed under the topic "M. a. americana". I have placed it at about the Manitoba-Ontario boundary, although it grades to this "race" from about central Manitoba to about Goldpines and Sioux Lookout, Ontario.

The western limit of the "race", where it intergrades with "M. a. actuosa", and possibly "M. a. abietinoides", is reported as lying somewhere west of the Athabasca River, Fort

Macmurray and Lac la Biche in eastern Alberta (Seton 1911); "Saskatchewan north to the tree limit" (Anthony 1928); west of the "Athabasca River to Lesser Slave Lake, and perhaps Sturgeon Lake", east central Alberta (Soper 1948); the western limits of the Hudson Bay drainage system including at least parts of Manitoba, Saskatchewan and Alberta (Anderson 1946); "northeast Alberta" (Rand 1948a). The U. S. Fish and Wildlife Service card file records the identification of specimens from parts of Manitoba, Saskatchewan, Alberta and Keewatin to this "race"

Because I find it extremely difficult or impossible to separate individuals of this "race" from those of "M. a. actiosa" it is hard to determine what constitutes the western boundary of the "race". If, however, we examine the isopleth map for condylobasal length, we note that there is an arm of smaller martens extending from north west British Columbia to Great Slave Lake. This isopleth (the 8.20, 8.30 or 8.40 cm. isopleth, but especially the first of these) reaches the western shores of Great Slave Lake, and together with the lake effectively marks a boundary between the large martens of Saskatchewan and western Manitoba ("M. a. abieticola") and those of Alaska and northern Mackenzie ("M. a. actiosa"). The arbitrary use of the above boundary has certain advantages, so long as we remember that the boundary is wholly artificial. First, around Great Slave Lake and northern western Alberta at least, it marks an area of relatively rapid change of size. Second, it is in accord with the conclusions of Seton (1911). A disadvantage to this limit is however, that the marten to the north and west, supposedly

"M. a. actuosa" show as much or more geographic variability, none of which is considered worthy of taxonomic mention. Another approach would be to take the midpoint between the means of condylobasal length of male "abietinoides" and "abieticola". The isopleth of the midpoint (8.15 cm.) approximates the distribution of the 8.20 cm. isopleth referred to above, and is consistent with its use.

For those who, like myself, see this "subspecies" as being essentially synonymous with "M. a. actuosa" this problem has no importance. For those systematists, who insist upon the maintenance of the "race", however, I offer the suggestion that the northern and western limit of the "race" be defined somewhat as follows: north to the tree limit in Keewatin and eastern Mackenzie, west to Fort Reliance and the shore of Great Slave Lake; the southern shore of the lake west to about the mouth of the Hay River, and thence south along the 8.30 cm. isopleth, about as I have marked it, which includes approximately the eastern half of Alberta, south to Edmonton and the open prairie, it being understood throughout that this is a general approximation of a broad and complex region of gradation into the smaller marten of the cordillera to the west, and of south eastern Yukon.

Specimens examined: 52 specimens from Manitoba, plus another 50 from Saskatchewan and Alberta, whose identity is somewhat less certain, as pointed out above.

Skull diagrams and photographs; none that I know of.

"Martes americana actuosa" (Osgood 1900)

Synonymy: Martes (or Mustela) americana actuosa, atrata actuosa, actuosa, caurina actuosa, americana var. huro, boria, americana boria. I include within the scope of this "subspecies" the two named forms "Mustela americana actuosa" Osgood 1900 and "Mustela boria" Elliot 1905b, which were synonymized by Preble in 1908.

Type specimen: "M. a. actuosa", U.S. National Museum no. 6043 (Poole and Schantz 1942); "M. a. boria", Chicago Natural History Museum no. 13484 (Sanborn 1947). Osgood's type is here considered the proper one.

Type locality: "Fort Yukon, Alaska" (Osgood 1900); "Lower Mackenzie River district, toward Arctic Ocean; exact locality unknown" (Elliot 1905b). As pointed out above, only Osgood's locality is accepted here.

In 1865 and again in 1869, J. E. Gray described Martes americana var. 2., huro, from Fort Franklin on the southwest shores of Great Bear Lake. This he described as "yellow-brown; head and ears whitish; throat pale yellow; legs, feet and tail blackish". The locality from which this specimen was taken lies well within the range of "M. a. actuosa" as determined by Preble (1908) and by myself. The paleness of the head, as described by Gray leads further to this conclusion. It is peculiar that none of Osgood, Rhoads or Preble noticed that Osgood's description of "actuosa" was really nothing more than a redescription

of Gray's huro, which pre-dates it by thirty-five years.

However, Gray was not the first to use the epithet huro in describing martens. It was used earlier by Cuvier (1823), Richardson (1839), Schinz (1845) and Smith (1843). All but Schinz gave no type locality or "habitat" for their marten, and I have not examined Schinz's paper. It appears to me that if strict priority were to be adhered to, Osgood's epithet "actuosa" should be replaced by Gray's huro. Little other than inconvenience would result from making the change, however, and I endorse the continued use of Osgood's better known terminology.

Elliot, 1905b, described as a new species of marten "Martes boria" from the lower Mackenzie River region. Elliot's description is given elsewhere. What is important here is that in 1908 Preble examined Elliot's type and topotypes and concluded that "boria" represented merely "the dark phase of color which this animal M. a. actuosa exhibits throughout its range". Compared to large series of "actuosa" from Fort McPherson, Fort Yukon and Fort Simpson, "boria" fell well within the range of darker individuals of the former "race", and Preble therefore synonymized the two "forms". I have compared a series of skulls, and a smaller series of skins of the two named "forms" and agree completely with Preble's conclusion. Thirty skulls from the region about the mouth of the Mackenzie showed no significant differences from typical "actuosa" from Alaska.

Pelage: The fact that the marten of Alaska and the Canadian northwest is distinctively large, thickly furred, and pale headed has been recorded by nearly every author concerned with them

(Ross 1861, Gray 1865 and 1869, Allen 1876a, Nelson and True 1887, Poland 1892, Russell 1898, Osgood 1900, Elliot 1901a, Rhoads 1902, Elliot 1905a, Preble 1908, Osgood 1909, Mason 1924, Bachrach 1946, Boyd 1951, Rausch 1951 and 1953).

Osgood described the "race" as with "posterior half of upper parts pale ochraceous buff, shoulders and anterior part of upper parts gradually becoming grayish; entire upper parts, except head, overlaid with coarse brown hairs; head including cheeks and throat, pale grayish-white lightly mixed with brown, especially on nose and chin; inside and edges of ears whitish outside and bases of ears brown; underparts similar to upper parts, but darker and more brownish on chest; an irregular patch of creamy buff mixed with white on chest; legs and feet dark brown, front of legs with mixture of gray hairs; tail brown, somewhat darker at tip, and with a slight mixture of gray hairs". Elsewhere he says that "in a good series of actuosa from Fort Yukon and Fort McPherson the characters are very constant. A large number of skins from these localities present very little variation and nearly all are quite light colored like the one described above". This description is repeated in abbreviated form by Elliot (1901a).

Ross, in 1861a and b, described this (then unnamed) "race" as with "legs and tail blackish, general color a deep and rich orange brown clouded with black along the back. Head generally light colored, with the tips of the ears and a stripe along the cheeks yellowish white. A broad orange patch is visible in the throat in some, in others this is nearly pure white, and in many entirely wanting...."

Poland (1892) and Preble (1908) say that some marten from Alaska have the head almost white, and that white tailed and near albinos have been reported. Rhoads (1902) assured us that Osgood's original description of the "race" was based on a paler than average individual.

That this "race" is among the largest to occur in North America has been known for a long time.

I have quoted the descriptions of pelage in "M. a. actuosa" given above, because these authors have examined a far greater number of skins than I have. From those that I have seen, however, I conclude that they are quite correct in their descriptions. The most characteristic quality of the skins of most individuals of this "race" is the paleness of the head and shoulder region, this being at least pale grey, and occasionally almost a dirty white. Only exceptionally are individuals of any other "race" of marten in American, except "abieticola", so coloured.

Cranium: The skull was described by Osgood as "similar to that of M. brumalis ... but somewhat larger; relatively longer and narrower; interorbital space slightly narrower; audital bullae very much larger and longer; dentition relatively much weaker; last upper molar decidedly smaller.... This form is the largest of the subspecies of Mustela americana. M. brumalis is also large, but does not equal actuosa and notwithstanding its smaller size has heavier dentition. The enormous audital bullae of actuosa are not equalled by those of any other member group. The

skulls of americana ... are so very much smaller ... that they do not need to be closely compared".

Rhoads (1902) concluded that Osgood had characterized the "race" correctly, but believed the distinctions between "actuosa" and "brumalis" were less than Osgood had stated, to which conclusions I agree.

In 1876 (a) Allen pointed out that a gradual increase in marten skull size occurred as one moved northwest from New York and Maine, across Canada into Alaska. The average "skull length" of males from New York and Maine he found to be 7.46 cm. (n = 3); from Fort Good Hope and Pell River 8.28 cm. (n = 9); and from the Yukon River 8.32 cm. (n = 8). Allen did not, however, attempt to name any of the northwestern "forms" on the basis of this distinction.

Osgood's description of the cranium of this "race" is, I find, quite adequate. It is large, as he points out, but not so large (as he believed) as the largest skulls of "M. a. brumalis"; in many localities (see below) it is quite considerably smaller. Osgood's emphasis on the distinctive nature of the auditory bulla in this "race" is no longer supportable, it being actually no larger than that found in "brumalis".

Statistical comparison of the skulls with those of "M. a. brumalis" has been made under that "subspecies" topic. Compared to "M. a. americana" it differs significantly in all fourteen characters studied (being very much larger). Comparison to "M. a. abietinoides" and "M. a. kenaiensis" is made under those "subspecies" descriptions.

The following are the statistics obtained from samples of this "race" which includes also small numbers from Alberta and Mackenzie that might more properly have been referred to "M. a. abieticola".

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	8.38	.27	3.17	187	7.62	.21	2.73	91
Rostral width	1.63	.09	5.40	198	1.45	.07	4.89	94
Upper tooth row	3.07	.08	2.68	104	2.78	.09	3.39	54
Canine width at base	1.60	.09	5.44	197	1.41	.07	4.64	92
Bullae length	1.75	.06	3.50	191	1.64	.06	3.48	92
Upper molar width	.78	.04	5.00	197	.69	.04	5.21	94
Upper molar inner moiety length	.47	.03	6.75	198	.41	.03	6.86	94
Palate length	4.22	.15	3.46	105	3.79	.15	3.98	52
Mastoid width	3.73	.11	2.89	100	3.42	.14	4.16	51
Height of skull at bullae	3.19	.12	3.79	100	2.92	.10	3.50	51
Length of last upper PM	.82	.04	5.12	198	.74	.04	4.87	94
Narrowest palate width	.81	.05	5.54	114	.75	.04	5.48	60
Canine width base / bullae length	.91	.04	4.86	190	.86	.04	4.19	91
Upper molar width plus inner moiety length	1.25	.06	5.10	197	1.10	.06	5.17	94
Total length	63.31	2.04	-	137	57.33	2.32	-	75
Tail length	19.20	1.04	-	92	17.13	1.10	-	75
Hind foot	10.18	.42	-	107	8.93	.67	-	37

Geographic variation: The marten of central and eastern Alaska, as has been pointed out previously, tend to thick fur and paleness, especially about the head. Preble (1908) pointed out that while individual variation might be relatively slight in this region, as believed by Osgood, it likely varied in degree of variation, geographically. Nelson and True (1887) report that specimens taken near the coast in northern Alaska have a light coloured, short, harsh pelage, compared to those taken inland, while those taken in southwest Alaska are long haired and dark. Ross (1862) said that those from the Yukon are furred and coloured very like the Asiatic sable and Boyd (1951) says that in the whole Yukon Territory they are pale but with a very fine, silky fur. Mason (1924) reported that marten from the Porcupine River in Alaska are occasionally very black and always of a fine thick fur.

The Brooks Range of Alaska supports marten that while cranially no different from those to the south differ considerably in pelage (Rausch 1951 and 1953). "The ochraceous colouring is limited to the posterior third of the dorsal part of the body. The head is very pale grey, with a slightly darker median streak which gradually darkens and extends the full length of the body. No throat patch is present, and the entire throat is greyish buff. The forefeet and legs are nearly black and the hindfeet and legs are very dark with a light area on the front of the leg just above the foot. The tail is mostly dark. ... The dorso-posterior third of the body is bright orange, similar to Ridgway's Ochraceous Orange".

Like the marten of Alaska, those of the Mackenzie River region are heavily furred, though supposedly "thinner about the gills and sides ..." (Boyd 1951, Bachrach 1946). According to Bachrach, Ross (1862) and Preble (1908), marten at the very northern limits of this part of their range, average considerably darker, or at least are subject to a degree of melanism. It was from this region, lower Mackenzie River, that Elliot, in 1905b described his darkly coloured "M. boria". It was, he said, with "sides of head grayish white; nose and top of head light brown and gray mixed; entire body above and below burnt umber; blackish on dorsal region; entire throat region black; tail black ..., ears like body externally, white internally."

The marten of the middle and lower reaches of the Mackenzie are considered paler (nearer the Alaskan type?) than are those further north by Mason (1924) and Preble (1908), although Mason says that specimens from Fort Norman are often dark. In the region south of Great Slave Lake, about the Alberta boundary, they tend again to become darker, so that in the Peace, Athabasca, Slave and Liard regions of Alberta and British Columbia they are distinctively darker and browner (Russell 1898, Preble 1908). The more easterly of these, south of Great Slave Lake, might more properly, it has been pointed out, be considered representative of "M. a. abieticola" rather than of this "race" (see Seton 1911), although I synonymize the two.

I have little to add to this account of variation as it is reported to exist in this "race". I agree with the above

named authors that considerable geographic variation in pelage occurs, and that the marten of east central Alaska are pale, those from the northern Mackenzie darker, those from about Great Bear Lake including both dark and pale skins and that those from Alberta tend to darkness again. I have seen one of Rausch's Brooks Range skins and agree that it is as distinctive as he says. The marten south and east of Great Slave Lake, while darker, are often referred to "M. a. abieticola", but specimens from other places within the range of actuosa are just as dark, and are given no subspecific status. The darker specimens from western central and southern Alberta might more properly be considered representative of "M. a. abietinoides".

Variation in size, as exemplified by condylobasal length of the skull is rather extreme in this "race". Allen (1876a), as has been pointed out, believed that slight increase in size of skull occurred between Great Slave Lake and Alaska. Preble (1908) added to this, that marten grew slightly smaller between Fort McPherson and the Athabasca River below Grand Rapids, Alberta. The smallest specimens were to be found, he concluded, about Fort Rae. Preble also noted two very small specimens ("basilar lengths" 68 and 69 mm.) taken near Leith Point, Great Bear Lake, and remarked that "these in conjunction with their very small size, have very small teeth and may represent a dwarfed race occupying the extreme edge of the timbered belt". I have not examined Preble's small specimens, but find that other specimens from nearby localities fail to show the small size described by him for the marten of the region. In

contradistinction, an immature male from Fort Resolution (U. S. Biol. Surv. Coll. 263348) had the amazing condylobasal length of 9.69 cm. This, if truly a marten, was a gigantic one; I suspect, however, that it is really a misidentified fisher skull, and regret not having made more positive identification at the time of examination.

Allen's and Preble's accounts of size variation are very general, and a more detailed understanding of it may be obtained from the map of condylobasal length isopleths. It will be seen from this, that allowing for the likelihood of sampling error in the samples used, variation is considerable within the supposed range of the "race", grading from about 8.00 cm. in northern British Columbia to 8.80 cm. or more at the base of the Seward Peninsula in Alaska. Further, the geographic distribution of this variation is complex and best understood from examination of the map, a brief account of which follows. An area of smallness (8.40 cm. isopleth and lesser ones) extends from Norton Sound, through the Central Uplands and Plains of Alaska, and the southern Brooks Range, through most of Yukon Territory and western and southern Mackenzie into British Columbia, and all of Alberta except the extreme north eastern part. These might properly be referred to "M. a. kenaiensis". In Alaska, north and west of the area above described, the marten become considerably larger (to 8.75 cm. at the base of the Seward Peninsula). South of the Uplands and Plains, in the Alaska Ranges and Alaska Basin sections, the marten again become larger (to 8.65 cm.), growing smaller south of this region in the Chugach and St. Elias

Ranges and into the Yukon. East of the Mackenzie, Ogilvie and Selwyn mountains, in the Mackenzie District, larger marten are found, these increasing in size until on the eastern shores of Great Bear and Great Slave Lakes they attain a condylobasal length of 8.65 cm. This region of largeness extends south of Great Slave Lake, where it enlarges to include most of eastern Mackenzie, Saskatchewan and western Manitoba, which portion most authors have considered to constitute the range of "M. a. abieticola."

I believe that "M. a. actuosa" is the geographically variable of the named "races" of "M. americana" as the above accounts indicate. This extreme variability, in my opinion, casts doubt on the validity of the "race" preceding, and that following. The other possibility, the naming of more "races" to encompass the range of variation shown by "actuosa" offers little satisfaction, I believe.

Distribution: Although first described from Alaska, the range of this "race" was by the time of Anderson's catalogue (1946) extended so as to include the "timbered districts of Alaska (exclusive of Kenai Peninsula and adjacent range of M. a. kenaiensis), Yukon, Mackenzie district of Northwest Territories, northeastern British Columbia and northwestern Alberta, ... presumably intergrading with abietinoides in northern or central British Columbia ."

Specimens from Alaska (excepting the Kenai Peninsula, the panhandle and Alaskan Islands) have been referred to this

"subspecies" by all authors. In the Mackenzie district, the following localities have either had specimens referred to this "subspecies" or mention made of the taking of large, pale headed martens: Fort McPherson (Osgood 1900, Preble 1908); Mackenzie River region (Ross 1861a and 1861b, Preble 1908); Slave River, Great Bear Lake, and Forts Rae, Simpson and Franklin. In the Yukon Territories, the whole region (Rand 1945d); Canol Road (Rand 1945b); Macmillan region (Osgood 1909). In Alberta, Wood Buffalo Park (Soper 1942); Grand Prairie and Peace River area east, to but not including Athabasca and Lesser Slave Lake (Soper 1948); Athabasca River region, Peace River, Slave River and Henry House (Preble 1908); northwest Alberta (Rand 1948a). In British Columbia, Fort Halkett (Baker 1951); Driftwood River, Bear Lake and Bulkely House (Stanwell Fletcher 1943); Peace River district (Cowan 1939); Laurier Pass (Sheldon 1932); Fort Nelson (Quick 1953, Boyd 1951); Prince George (Boyd 1951); Liard River (Preble 1908). Swarth (1936) and Rand (1944c) would not hazard "subspecific" determination for specimens taken from Atlin and the Alaska Highway.

It is extremely difficult, because of the great range of variability found within this "race" to determine any usable limits to its distribution. We have already pointed out that Great Slave Lake marks a reasonably satisfactory southeastern limit, and that this coincides well with the opinions of earlier workers. We are left then with the problem of finding an adequate southern limit. Examination of the isopleth map for condylobasal length shows how impossible a task this is. If

we choose that isopleth marking the midpoint between the lumped samples of male "actuosa" and "abietinoides" (8.10 cm.), we find that it passes from the mouth of the Iskut River, British Columbia, northeast to the Yukon Mackenzie boundary, thence south again to about latitude 57° in northeast British Columbia, then east to Hay Lake in Alberta, then southeast along the eastern edges of the Rocky Mountains in Alberta to about Calgary. Further, a "finger" of largeness is seen to extend from Dease Lake, British Columbia, southeast to the Takla Lake region and beyond. The use of this arbitrarily selected isopleth fits surprisingly well, the ideas of distribution of the "race" at its southern limits as described by the above named authors. It suffers, however, from two points: first, we have determined that this "race" is so extremely variable that any mean condylo-basal length determined from a large sample may be quite inaccurate as a parameter, unless each variant population were to be sampled in numbers proportionate to its importance in the whole population. For this reason I suspect that my sample of "actuosa" emphasizes the smaller sized populations within the "race", at the expense of the larger. Second, while the 8.10 cm. isopleth falls approximately where earlier writers would place the southern limit of the "race", in detail it fails to include some marginal limits. Our map is not completely accurate and also subject to sampling error, and in addition the northern part of British Columbia is poorly represented by samples. Nonetheless to the present, it must be used until better maps are prepared. Another difficulty is that

specimens to the south of the 8.10 cm. isopleth are represented by skins that possess heads fully as pale as are many of those from Alaska, and very much paler than the dark heads of the "race" to the south. Localities supporting these pale headed individuals extend as far south as Bulkely House, Bear Lake, Omineca and Finley Rivers, British Columbia and all points north of Peace River Station, Alberta. Thus we might arbitrarily conclude that the facts are best fitted, and earlier opinion least offended, by considering a proper division between the two "races" as being made along the Omineca and Peace Rivers in British Columbia and the Peace River in Alberta. Actually the whole area is one of intergradation, there being a cline of decreasing size from Alaska south into northern British Columbia. It is interesting to note that the rate of decrease in size does not occur in the same fashion as pale headedness, which occurs south to the region north of the Peace River and then apparently suddenly changes to dark headedness.

Since the days of the very early workers in the north west (Pennant 1771 and 1781, Pallas 1767-80, Kerr 1792, Brandt 1855, Baird 1857 and 1859 and Ross 1861a and b) speculation has been made concerning the possible presence of the Asiatic sable (M. zibellina) in Alaska. Dr. Henry Setzer of the U. S. National Museum kindly brought the problem to my attention when he showed me one of Rausch's Brooks Range specimens referred to above, and pointed out the similarity of the skin to that of the sable. Of all the Alaskan skulls I have examined, however, none has been even doubtfully referable to the Old World species.

Mr. C. Lensink, of the University of Alaska, kindly gave me the following information: "I am told that there are rumors that during the period of the Russian rule that sable might have been introduced - hearsay only! We do know that during the period of the last charter of the Russian American Company, excellent conservation practices were followed.... Dr. C. E. Hulley, who has just finished a history of Alaska, tells me that he is certain that he has seen references to transplants of native furbearers to areas where they had been depleted during that period (1844 to 1867)". I am unable to add more to the solution of the problem.

Specimens examined: 551 specimens, from Alaska, Yukon, Mackenzie, British Columbia and Alberta, some of which might be referred to as "M. a. abieticola".

Skull diagrams and photographs: Osgood 1900, pl. 71.

"Martes americana kenaiensis" (Elliot 1903a)

Synonymy: Martes (or Mustela) kenaiensis, americana kenaiensis

Type specimen: Chicago Museum of Natural History no. 9847 (Sanborn 1947).

Type locality: "Kenai Peninsula, Alaska" (Elliot 1903a).

Pelage: "M. a. kenaiensis" is one of the forgotten "races" of "M. americana" that has never been reconsidered since Elliot's description in 1903, yet whose status has never been questioned.

Elliot described the animal as with "size smaller than in M. a. actuosa, with longer tail, shorter feet, and general color darker.... Upper parts tawny buff mixed with black, darkest on dorsal region, which part in one specimen is almost wholly black; top of head dark gray; forehead, top of nose and sides of head brownish white; sides of nose dark brown; chin and throat uniform dark ochre without spots, under parts darker than back, uniform dark chocolate brown, ungual region paler, inclining to a pale buff, no spots on abdomen; upper part of forelegs on top chocolate brown, feet and under part black with a grayish white patch at base of toes beneath; hind legs and feet blackish above and below; with a chocolate patch at base of toes on top; tail black inclining to chocolate at base; ears brownish black externally, white internally and on edges; nails white". He continued that the specimens he examined "at once attracted attention by their dark color and absence of gular and abdominal markings on the majority.... Of the six specimens four are entirely lacking beneath in ochraceous or yellowish markings of any kind; one of the two remaining has a diamond shaped yellowish white spot on the throat, and one smaller spot on the breast, rest of underparts being a uniform chocolate brown; the other specimen has a dark buff line on one side of the throat going to the breast and passing half way across the latter, the rest of the underparts being a uniform dark chocolate brown.... Much darker and richer and more buffy than actuosa.... Color ... nearest to brumalis but hardly as dark, viz.: less chocolate.... Smaller than ... actuosa, ... with relatively longer tail...."

I have examined no skins of this "race", but must conclude that if Elliot's sample of six skins is representative of marten from the Kenai, they are indeed darker than typical "M. a. actuosa" and distinctive in lack of throat patch, but are no more distinctive than was "M. boria", now a synonym of "M. a. actuosa".

Cranium: Osgood, in 1901, (two years before the "race" was described) reported that two marten skulls from the Kenai Peninsula were of about the same size and proportion as skulls of "M. a. americana" from New York. Allen, in 1902b, said that a single skull from the same locality was "much too large for M. americana americana, and though smaller than the male type of actuosa may well be a female of that species". The same author, in 1903, examining two other skulls from the same locality, said that they "greatly exceed in size the very largest skulls of a large series of M. americana americana from New Brunswick, but fall considerably short of the measurements given by Mr. Osgood for the type skull of M. a. actuosa."

Elliot, in his description of the race, described the skull as with "audital bullae large ridged [sic], rectangular, longitudinally produced. Molars heavy; sagittal crest prominent...."

I have examined a fairly large series of skulls from the Kenai Peninsula, and find that qualitatively and quantitatively, they fall within the range shown by skulls of "M. a. actuosa" from Alaska, with the exceptions shown below. Rostral

width is larger and bullae length is somewhat less (approaching significance in males only, but not reaching it) so that the ratio canine width at base / bulla length is significantly larger (above the 95% level of probability) in both sexes of "kenaiensis" than in "actuosa".

All the skulls are, of course, referable to the species "M. americana" in spite of the fact that Elliot 1905b gave it specific status ("Mustela kenaiensis"). Examination of the isopleth map for condylobasal length indicates that the condylobasal length of males (about 8.35 cm.) while approximating that for the summed total for "actuosa" is actually considerably smaller than that animal in parts of its range, especially in Alaska, and equals those martens found in southeastern Alaska and much of Yukon Territory.

We may conclude that "kenaiensis" differs from "actuosa" in its darker pelage, absence of throat patch, greater rostral width and smaller bullae length. I do not think these distinctions merit subspecific status. The pelage distinctions may easily fall within the range of variation shown in "actuosa", but the cranial distinctions likely are real. Because the Kenai Peninsula is in effect nearly an island, it is doubtless true that a restriction in gene transmission across to the mainland is in effect; this being so, the Sewell-Wright effect on small populations might be sufficiently active to assure us of a distinctive "variety" of marten. I have, however, found "M. a. actuosa" so variable within itself that I believe little is gained by considering "kenaiensis" anything but a local

variant of the northern "race", and suggest it be synonymized with it.

Statistics obtained from a sample of this "race" follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	8.35	.11	1.32	14	7.66	.13	1.70	15
Rostral width	1.67	.05	3.24	15	1.47	.04	2.44	15
Upper tooth row	3.05	.10	3.25	13	2.78	.09	1.58	15
Canine width at base	1.63	.05	3.32	15	1.43	.05	3.15	15
Bullae length	1.70	.06	3.35	15	1.61	.05	3.17	15
Upper molar width	.78	.03	3.35	15	.70	.03	3.98	15
Upper molar inner moiety length	.46	.03	6.09	15	.39	.03	8.14	15
Palate length	4.23	.15	3.43	13	3.82	.10	2.70	15
Mastoid width	3.71	.09	2.48	12	3.39	.06	1.83	15
Height of skull at base	3.20	.12	3.63	13	2.96	.11	3.82	15
Length of last upper PM	.82	.03	3.92	15	.74	.02	2.99	15
Narrowest width of palate	.82	.04	4.78	13	.76	.05	6.18	15
Canine width base / bullae length	.96	.05	4.92	15	.89	.03	3.37	15
Upper molar width plus inner moiety length	1.24	.05	3.89	15	1.10	.05	4.29	15
Total length	79.00	-	-	1	-	-	-	-
Tail length	29.30	-	-	1	-	-	-	-
Hind foot	9.00	-	-	1	-	-	-	-

Geographic variation: Nothing is known regarding this.

Because the range of the animal is so restricted, it is likely rather small.

Distribution: Considered by all authors to be restricted to the Kenai Peninsula. If the "subspecies" were to be retained it should also perhaps include the small marten of southern Alaska and Yukon.

Specimens examined: 49 specimens from the Kenai Peninsula, Alaska.

Skull diagrams and photographs: Elliot 1903a, pl. 32.

"Martes americana abietinoides" Gray 1865.

Synonymy: Martes (or Mustela) americana var. abietinoides, americana abietinoides.

Type specimen: None designated that I know of. According to Rhoads it is to be found in the Drummond and Lord Collection in the British Museum.

Type locality: "Rocky Mountains" (Gray 1865 and 1869); "Edge of the humid western slope of the Rocky Mountains, somewhere between Kicking Horse Pass and the Columbia River" (Rhoads 1902).

Rhoads changed Gray's type locality because he recognized that it included part of the range of "M. caurina". By referring to Richardson (1829) he concluded that Gray's

specimens could on geographic grounds, not include "M. caurina", and contrariwise, must have been "M. americana".

Pelage: Described by Gray (1865 and 1869) as "black brown; ears pale; head grizzled with white hairs, more or less grey; throat yellow or yellow spotted; throat spot large or broken up into small spots; the head sometimes with only a few grey hairs, and the throat with only a few distinct small spots". Redescribed by Rhoads (1902) as follows: "the color ... answers exactly Gray's description of 'black-brown'. In this respect it is instantly distinguished from all other of the specimens as well as the uniformity of its coloration. In terms of Ridgway's Nomenclature of Colors, this specimen is seal-brown throughout, both above and below, with exception of the sides of the head, the interior of ears and a small irregular throat patch. The shade of seal-brown is blackest on tail, feet, legs, and middle back. On sides, underparts, neck and head it is more of a vandyke-brown, but nowhere buffy, ochraceous or orange, as in all other martens I have examined. A cheek patch between ear and eye and the insides and margins of ears are grayish-drab, but the rest of head above and below is not noticeably paler than neck as in all others of the americana group.... Scattered white hairs are noticeable among the dark above and below, being more numerous about head, neck and breast. The narrow irregular throat patch reaches from angle of lower jaw to near base of neck, being about two inches long and three quarters of an inch broad in the widest part. The color is ochraceous buff. The fullness, density and length of pelage is noticeable, and the slight

contrast in color of the basal portion of the fur with that of the apical half is unique, so far as I have examined specimens." Rhoads goes on to say that in all other martens, the hairs are tricolour, not bicolour as in "abietinoides".

Wright (1953) examined 300 skins of this "race" of marten from the Whitefish Range of Montana. He concluded that the light coloured patch between the eyes and ears described by Rhoads from his single specimen was uncommon, and not observed in any of his specimens. The colour varied from Isabella Color (Ridgway) or Mouse Gray, both dorsally and ventrally, to Mummy Brown dorsally and Black ventrally. Over one half of his sample, however, were Cinnamon Brown to Dresden Brown dorsally, and Antique Brown, Brussel Brown, Sudan Brown or Mummy Brown ventrally. In all but the darkest skins, the heads are nearly all grizzled and generally lighter coloured than the back, but the lightness does not extend behind the ears. In some of the darker skins, however, the top of the head was almost as dark as the rest of the body. The throat patch varies from five or six inches square to almost complete absence; the colour from Pale Orange-Yellow to Capucine Yellow or Deep Chrome. The hairs, when blown apart are bicolour, as Rhoads pointed out. The under fur is dense and dark. Wright concluded that since the large Montana sample, and twelve skins from Jasper and Banff Parks show very dark skins to be outnumbered by lighter coloured individuals, Gray and Rhoads who described the darker forms did not see enough animals to know that their descriptions applied only to a minority of animals.

I have examined far fewer skins from marten of this "race" than has Wright, and hesitate to disagree. I find that marten of a darker hue than Wright found in Montana, predominate the small samples I have seen from central British Columbia. Wright's descriptions and Rhoads' detail fit otherwise most of what I have observed. I find further that the bicolour characteristic of the fur of "abietinoides" is usually distinctive, the fur of almost all individuals of other "races" of the "species" "M. americana" being tricolour. This in conjunction with the dark pelage, and small size, mark it as easily distinguished from all other "races" of the "species".

Cranium: Rhoads wrote that two skulls of this "race" show, in comparison with female skulls of same age from the Mackenzie River regions, that "abietinoides" is not only specifically identical with "M. a. actiosa" but that it is only slightly smaller in size, being intermediate in the latter feature between "M. americana americana" of Lake Superior and Arctic examples of actiosa.... The teeth, audital bullae and the proportions and configuration of skull in abietinoides are precisely as in the americana, as contrasted with the caurina type of cranium."

Rhoads is correct in allying "M. a. abietinoides" with "americana" rather than "caurina". He is wrong, however, in believing that in size it lies between "M. a. actiosa" and "M. a. americana". "M. a. abietinoides" is actually almost identical in size to the small eastern "race" ("M. a. americana") and is, indeed, difficult to separate from it cranially, as

Hollister (1912) has pointed out. It is, however, significantly larger compared to "americana" in rostral width, canine width at base, bullae length (males only), upper molar inner moiety length (males only), mastoid width, height of skull at bullae, and the ratio canine width at base / bullae length.

When compared to the sample of "M. a. actuosa", significant differences exist for all of the fourteen characters studied. Compared to the sample of "M. a. abieticola", it shows significant differences in all characters but the following: canine width at base / bullae length, upper molar width (females only), height of skull at bullae (females only), narrowest palate width (females only), upper molar width plus inner moiety length (females only), and bullae length (females only). The last two characters listed above also approach but do not quite attain significance in males also.

Much of the apparent overlap in characteristics in the female samples must be attributed to the small sample of female "abieticola" and the consequent large estimate of error.

Cranial statistics obtained from the sample of this race that were studied follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	7.87	.23	2.95	204	7.12	.20	5.53	152
Rostral width	1.52	.07	4.81	211	1.35	.06	4.38	161
Upper tooth row	2.89	.09	2.94	150	2.59	.11	4.21	88
Canine width at base	1.45	.06	3.80	185	1.28	.06	4.30	124

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Bullae length	1.69	.14	8.07	185	1.56	.05	3.46	123
Upper molar width	.75	.04	5.36	185	.66	.04	5.45	124
Upper molar inner moiety length	.47	.02	4.73	205	.39	.03	8.16	160
Palate length	3.95	.14	3.47	157	3.49	.13	3.69	116
Mastoid width	3.53	.11	3.09	158	3.23	.10	3.00	116
Height of skull at bullae	3.02	.30	9.97	156	2.81	.10	3.38	113
Length of last upper PM	.77	.07	8.55	181	.69	.03	4.04	122
Narrowest palate width	.76	.05	6.14	154	.71	.04	5.19	91
Canine width base / bullae length	.87	.05	5.38	185	.82	.05	5.46	122
Upper molar width plus inner moiety length	1.21	.07	5.70	184	1.05	.07	6.19	124
Total length	59.51	2.72	-	25	57.87	2.45	-	40
Tail length	17.35	1.36	-	25	15.02	1.20	-	40
Hind foot	9.50	.84	-	25	8.70	.74	-	40

Geographic variation: Geographic variation has not been well documented in this "race". Boyd (1951), a fur expert, says that the "best" colours are obtained in the Arrow Lakes and Golden districts of British Columbia. Hall (1934) says that three skins from the Bowron Lake region of British Columbia differ considerably in possessing "a relatively clear gray head and extreme dark tail and hind feet with a smoky suffusion over the remainder of the pelage". Hall considered them so distinctive

that he termed his identification to "abietinoides" as only tentative.

I have already pointed out that there is a possibility that there exists a larger proportion of dark coloured individuals in south central British Columbia than in northwestern Montana.

For data concerning variation in size, we must refer to the isopleth map for condylobasal length. This indicates that rather a surprising amount of variation occurs within the range of this "race". As pointed out elsewhere, there is a gradual decrease in size from north to south, as one passes from the Yukon Territory into Northern British Columbia, and another from east to west as one moves from eastern Alberta and Great Slave Lake to the Finlay River region in British Columbia. The smallest martens occur in the Blue River, Golden, Lardeau, Revelstoke region (the Selkirk and Columbia Ranges) and in the eastern portions of the Fraser and Stikine Plateau regions, centering about the Finlay, Parsnip and McGregor Rivers east to the Hudson Hope, Fort St. John areas. These two regions of smallness are separated by a region of slightly larger marten from just north of Jasper, through Albreda, Prince George, Fort St. James, Stuart Lake and Takla Lake northwest to the Dease Lake area. In the very southern part of the "race's" range, where it intergrades with "M. caurina" about Manning Park, Rossland and Grand Forks, British Columbia, and Couer d'Alene, Idaho, and south of Flathead Lake, Montana, the size of marten increases slightly. It is possibly slightly larger too, along the eastern slopes of

the Coast Mountains in British Columbia, where it intergrades with "M. caurina".

Distribution: Although distinctive in pelage and size, this "race" has had its limits only generally defined; this, of course, because it grades gradually into the surrounding larger forms. Rhoads, in 1902, described the range as restricted to the "humid interior region of British Columbia, peculiar to the Selkirk and Gold Ranges". Anderson (1946) gave the range as "humid parts of mountains in southern British Columbia, particularly the Selkirk and Gold Ranges; east in Rocky Mountains to Banff and Jasper National Parks; northern limits of range unknown, but presumably intergrading with actuosa in central British Columbia". Under the topic "M. a. actuosa" I have referred to those localities in British Columbia and Alberta that have provided specimens referable to "actuosa". References of "abietinoides" of a marginal nature include the Chilcotin (Racey 1936), Cariboo Parklands (Munro and Cowan 1947), Bowron Lake (Hall 1934), and Manning Park, British Columbia (Carl, Guiget and Hardy 1952), Banff and Jasper Parks, Alberta (Anderson 1946). Specimens available, however, extend the limits considerably beyond what is implied above. The western limit of the "race" in British Columbia, because it is also the western limit of the "species", is relatively easily determined, and appears at present to be at the eastern side of the Coast Mountains. Marginal specimens have been examined from the junction of the Stikine and Iskut Rivers, Tahtsa Lake, and the eastern side of Manning Park. Carl, Guiget

and Hardy (1952), without reference to specimens, recognized the limit of the "race" when they stated that both "M. caurina" and "M. a. abietinoides" likely occurred within the Park. My examination of specimens verified this conclusion and suggests further (as detailed elsewhere) that the two "forms" intergrade within the Park.

The difficulty of assigning an eastern limit has been discussed under "M. a. abieticola", where an approximate limit for the latter "form" was suggested as from western Great Slave Lake south through central Alberta. In actual fact, as the isopleth map indicates, east of the foothills in Alberta a gradual increase in size occurs, until the large size characteristic of "abieticola" is attained in eastern Alberta or western Saskatchewan. The difficulty of naming a northern limit has been pointed out under the topic of "M. a. actuosa", where an arbitrary limit was set at the Omineca and Peace Rivers in British Columbia, and the Peace River in Alberta. I can add little to these, since any limit is artificial and should properly be said to be non-existent, all changes being gradual and extending over relatively large geographic areas.

To the best of my knowledge, until Wright in 1953 made his important study of marten in Montana and Idaho, the presence of "M. a. abietinoides" in the United States had never been acknowledged. Rust, in 1946, identified specimens from Shoshone and Kootenai Counties, Idaho, as "M. caurina" and concluded that this was likely the only form present in the state. Davis, in 1939, had come to the same conclusion, naming all Idaho specimens

"caurina". Dalquest (1948) working on the marten of Washington, likewise concluded that all specimens from that state were referable to the "species" "M. caurina". Wright (1953) showed, however, that "M. a. abietinoides" occurred in both northern Idaho and northwest Montana, where they then intergraded with "M. caurina". He concluded that specimens from northern Idaho, and the Whitefish Range, Montana, lay nearest to "abietinoides", while those from the Swan, South Fork, and Sun Rivers, Montana, were intergrades which ran into "M. caurina" in the Sapphire, Clearwater, and Red Lodge regions. My own examination of specimens (many of them kindly lent me by Dr. Wright) leads me to conclude that the following counties are represented by marten lying nearest to "M. a. abietinoides": eastern Bonner and Shoshone Counties, Idaho and most of Lincoln, Sanders, Mineral, and very western Missoula, Lake and Flathead Counties, Montana.

Specimens examined: 587 specimens, from British Columbia, Alberta, Idaho and Montana.

Skull diagrams and photographs: Wright 1953, pl. 1.

"Martes caurina" (Merriam 1890)

Detailed characteristics given elsewhere, but characterized by shorter, broader flatter skull (compared to "M. americana"); large upper molar, and short, broad, less highly inflated bullae; width of inner lobe of P^4 / length of P^4 always more than 25.8; breadth of M^1 x 100 / length of P^4 always more than 97.5; lateral length of M^1 x 100 / mesial length of M^1 always less than

77; breadth of P^4 (across inner lobe) x 100 / length of P^4 always more than 64; canine width at base / bullae length always more than 94.

"Martes caurina caurina" (Merriam 1890)

Synonymy: Martes (or Mustela) caurina, americana caurina, atrata caurina, caurina caurina. Reference to the possibility that Mustela vulpine Rafinesque 1819a and b should precede Merriam's term "caurina" is considered under the discussion of "M. a. americana".

Type specimen: U. S. National Museum Collection no. 186,450 (Poole and Schantz 1942 and seen by myself).

Pelage: Merriam (1890) described it as follows: "In external appearance Mustela caurina differs little from M. americana, the chief difference being that the irregular markings of the throat and under surface generally are orange-red instead of whitish or yellowish...." Rhoads (1902) says that "it is of a richer brown than in any of the americana group, more inclining to cinnamon in upper body color. This shade is more uniform throughout the entire length of upper parts to head, which is not so distinctly lighter in color as in all other average East American martens. The head is an almost uniform shade of pale Mars-brown [Ridgway], not lightening on cheeks and ears as in eastern American types. A marked difference peculiar to caurina is found in orange-buff throat patches. This area begins at the angles of the jaw, reaches up along sides of neck

to and including inner bases of forelegs, and stretches by spotted interruptions almost to the vent, the main body of color terminating on lower breast.... A tendency to scattered long silvery hairs through the upper pelage is noticeable as contrasted with americana.... In external character the length of tail is greater than in any other form of American marten except origenes...."

Wright (1953) examined 80 skins of this "race" from the Sapphire and Bitterroot Ranges of Montana and Idaho. He described them as much more uniform in colour and inferior in quality to those of "M. a. abietinoides". The backs are mostly near Sudan Brown (Ridgway), occasionally Brussels Brown, Prouts Brown, Antique Brown, Amber Brown, and a few near Mars yellow. The venter was Sudan brown or Amber Brown. As in "M. a. abietinoides" (and contrary to Rhoads' conclusion), the head was grizzled and lighter. The throat patch was large, and in some extending continuously to the anus. The colour of the throat patch ranged from Capucine yellow to Cadmium orange, with most being orange. Compared to "abietinoides" it had, generally, shorter fur, and conspicuously less under fur. Markley and Bassett (1942), working with captive marten of this "race", remarked on the "great individual variation" they observed in the throat patch. "Its shape, always irregular, in several specimens was restricted to a number of detached spots on the lower throat and breast, while on others it became a solid patch extending from the upper throat to the abdominal region. On a prime winter pelt the tail and legs became nearly black on some individuals."

My own conclusion from examination of skins agrees with the above descriptions. Specific comparison with "M. americana" is made elsewhere.

Cranium: Merriam (1890) and Rhoads (1903) point out in detailed fashion the distinctions of the skulls of "M. caurina" and "M. americana" but provide nothing of value concerning "subspecific" characteristics. The distinctions between species are made elsewhere. Here we need only list cranial measurements, since comparison will be made to this standard.

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	7.89	.23	2.90	151	7.17	.18	2.57	53
Rostral width	1.62	.08	4.82	158	1.43	.08	5.26	54
Upper tooth row	2.96	.08	2.77	116	2.65	.07	2.61	22
Canine width at base	1.52	.07	4.48	153	1.34	.07	5.36	50
Bullælength	1.50	.07	4.46	151	1.41	.05	3.82	50
Upper molar width	.83	.05	5.44	154	.75	.04	5.24	50
Upper molar inner moiety length	.54	.04	7.65	160	.46	.03	7.11	54
Palate length	3.99	.13	3.31	116	3.51	.14	3.84	25
Mastoid width	3.67	.12	3.17	114	3.32	.11	3.29	26
Height of skull at bullæ	2.91	.10	3.47	114	2.66	.10	3.73	26
Length of last upper PM	.83	.03	3.96	153	.75	.04	4.81	49
Narrowest palate width	.84	.05	5.45	132	.78	.04	5.40	38
Canine width base / bullæ length	1.01	.10	9.39	148	.95	.05	5.15	50

	191							
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Upper molar width plus inner moiety length	1.37	.08	5.93	154	1.21	.07	5.62	50
Total length	63.78	1.97	-	80	58.74	1.83	-	63
Tail length	21.02	1.07	-	80	18.98	1.00	-	61
Hind foot	9.07	.44	-	23	8.18	.64	-	5

Geographic variation: Almost nothing concerning geographic variation within this "race", as it is currently understood, has been recorded in the literature. Dalquest (1948) says that in Washington, fur graders distinguish between a dark "coast marten" and a paler "Cascade marten". Boyd (1951) says that the "coast marten" of British Columbia and Washington are "quite woolly and reddish in colour". The "Cascade marten" in the two areas is "not as woolly as the coast type, and is quite a bit finer in quality".

Mr. K. Racey has pointed out to me that skins he has collected from the Alta Lake district, British Columbia, are unusually pale and yellow, especially when compared to specimens taken further north in the province.

The marten of northeast Washington and the Blue Mountains of that state, are according to Dalquest (1948) with paler heads and yellower throat patches than usual. Wright (1953) reported that marten from south central Montana appear to have slightly broader skulls than those in the north. Durrant (1952) considered Utah marten to lie intermediate between "M. c. caurina" and "M. c. origenes" but nearer the latter.

Considerable variation in size is shown, however, (see

isopleth map). In the Coast Range of British Columbia and Alaska northward, increase in size occurs. The smallest specimens from this area are found just north of the Fraser River at about latitude 50 (condylobasal length 7.60 cm. in males). South of this, at the Fraser, they increase to 8.00 cm. North of this, increase in size occurs to about 8.50 cm. and larger at Yakutat, Alaska. Areas of very rapid increase in size occur in the region about River's Inlet, British Columbia (7.50 - 7.70 cm.), and about the Skeena River, British Columbia (8.00 - 8.30 cm.). The marten of the Cascade Range of Washington are relatively large, averaging 7.90 - 8.00 cm. in male condylobasal length. Those in the Olympic and Coast Mountains and Willamette Valley of Washington are slightly smaller (7.75 - 7.95 cm.), the largest occurring in the Olympic Peninsula, the smallest about the Columbia River. The Coast Range and Cascades of Oregon support somewhat smaller marten, ranging from 7.90 cm. in male condylobasal length in the region about Portland, and the southern section of the state, to 7.60 cm. on the southwest coast and 7.40 cm. on the east central side of the Cascades.

The martens of the northern Rocky Mountains of Montana, Idaho, Washington and Oregon vary in size from 8.25 cm. to 7.65 cm. The largest are found in the southwestern part (northeast Oregon and southwest Idaho), the smallest in Montana, where intergradation with "M. a. abietinoides" occurs.

The central Rocky Mountains of southern Montana, very eastern Idaho, and Wyoming, support an apparently homogenous

population, those in the northwest half averaging a male condylo-basal length of 8.00 - 8.05 cm., those in the southeast part averaging .05 cm. smaller.

Distribution: Merriam, when he described this "race" in 1890, considered it to occur in "the dense spruce forests of the heavy rain-fall belt along the northwest coast from northern California to Puget Sound, and doubtless ranging much farther north...." Rhoads, in 1902, extended the range to include the "humid Coast and Cascade Mountain region of western United States, British Columbia and probably southern Alaska, from northern California northward, east to summit of Cascade Range." Rhoads knew that this "species" occurred in Colorado, naming it a new "race" "M. caurina origenes", which he said occurred in the "southern Rocky Mountain region; higher ranges of New Mexico (?) northward; probably replaced in the Canada Rockies by a race of americana". He elsewhere said that it was likely the "race" that occurred in the Purcell Range, Montana.

Because Rhoads' new "race", "M. c. origenes", is so similar to typical "caurina" subsequent workers have been confounded when attempting to designate martens from the region separating the two, chiefly in the northern and middle Rocky Mountains. Specimens from New Mexico have always been designated as "M. c. origenes" (Anthony 1928, Bailey 1931, Bailey 1936, Thomas 1952b, Durrant 1952 and the U. S. Fish and Wildlife Service card file). Marten from Colorado have likewise always been placed in "origenes" (Cary 1911, Bailey 1936, Warren 1942,

Yeager, Denney and Hammitt 1949, Rodeck 1952, Thomas 1952b, and the U. S. Fish and Wildlife Service card file), as have those from Utah (Barnes 1927, Bailey 1936, Hayward 1945 and Durrant 1952). Skinner, in 1927, named Wyoming marten as "M. c. caurina", but Cary 1917, Bailey 1930, Bailey 1936, Thomas 1952b and the U. S. Fish and Wildlife Service card file name them "M. c. origenes". Montana marten were considered "origenes" by Rhoads 1902 and the U. S. Fish and Wildlife Service card file, "M. c. caurina" by Bailey and Bailey 1918, and "M. c. caurina" and "M. a. abietinoides" by Wright 1953.

Specimens from Idaho were considered to be referable to "M. c. origenes" by Bailey 1936, Dalquest 1948 and the U. S. Fish and Wildlife Service card file. Davis 1939 and Rust 1946, considered, however, that they should be named "M. c. caurina", and Wright 1953 believed both "M. c. caurina" and "M. a. abietinoides" occurred within the state.

Dalquest (1948) believed "M. c. origenes" to be the "race" represented in northeast Washington and the Blue Mountains of that state, and Bailey (1936) believed it to be the "race" present in the Blue Mountains of Oregon.

To summarize the problem, it appears that when Rhoads first described "M. c. origenes" from Colorado, he suspected that it occurred throughout all of the American Rocky Mountains. The tendency since then has been to restrict its range more and more, so that the martens from the northern and middle Rocky Mountains have come to be considered to be "M. c. caurina". This is the view adopted here, although Miller and Kellogg (1955) following Bailey, Davis and Dalquest, consider all marten of

the Rocky Mountains in the United States referable to "M. c. origenes".

Bailey, in 1936, when determining that "M. c. origenes" occurred in the Blue Mountains of Oregon, apparently examined specimens, but did not tell how he reached his conclusion. He considered specimens from coastal Oregon to be referable to "M. c. caurina". Dalquest (1948), naming Blue Mountain and northeast Washington marten "M. c. origenes", does not indicate that he examined specimens from here, though he says that they possess paler heads and yellow instead of brown throat patches, compared to the coast and Cascade marten. These latter Dalquest considered typical "M. c. caurina".

Davis (1939), working with Idaho marten, named all "M. c. caurina" saying that "they may interbreed with M. c. origenes in southeastern Idaho and southern Wyoming". He distinguished all of his specimens from "M. a. abietinoides" by means of the short, broad rostrum, small bullae, large upper molar, bright orange throat patch, and longer tail, and from "M. c. origenes" by the whiteness of the inner surface and edge of the ear. Wright (1953), as has been pointed out, showed that "M. a. abietinoides" occurs in the northern part of the state, and concluded that "M. caurina" from the central and southern part of the state were closest in cranial and skin characteristics to the "subspecies" "caurina" and not "origenes". Rust (1946) named his specimens from Shoshone and Kootenai Counties, northern Idaho, as "M. c. caurina" (identification being made by H. H. T. Jackson). Wright (letter), and my own

examination of specimens, leads to the conclusion that this area really supports "M. a. abietinoides" tending slightly to "M. caurina" and not "M. caurina" properly.

Wright (1953), in his excellent study of marten in Montana, showed that "M. a. abietinoides" occurred in the northwestern part of the state, and that it intergraded with "M. caurina" in the southwestern part. "M. caurina", on comparison with the typical coast form, he referred to the "subspecies" "caurina". Those marten from the south central part of the state (just north of the Wyoming border), he said, though "represented by only a small series of skulls [twelve] is clearly of the caurina type. However, there is some suggestion that these animals may have broader skulls.... The possibility remains that this population may eventually be found by further investigation to belong to the subspecies origenes, or perhaps to some undescribed subspecies, but for the present they are referred to as caurina."

Durrant (1952) reviewing the marten of Utah, examined three skulls and one skin from the state, and said that they lay intermediate in cranial characters between specimens from New Mexico ("origenes") and those from Washington and British Columbia ("caurina"), but lying nearer to the former, and hence were referable to "M. c. origenes".

I have examined most of Bailey's, Davis', Rust's, Durrant's and Wright's specimens, together with a large series from Washington. I conclude that the most critical and dependable conclusions are those of Wright, with whose opinions I

agree for the most part, and with whose views I largely sympathize. Statistical comparison of these series of crania indicate the following. If large samples of skulls from the following populations are compared statistically, each may be separated from the other by one or more cranial characteristics at the 95% level of probability. The subsamples compared are "M. caurina" from the Coast Range north of the Fraser River, British Columbia; from the Coast Mountains and Cascade Ranges of Oregon and Washington; from the northern Rocky Mountains of eastern Oregon, Idaho and western Montana; the middle Rocky Mountains of southern Montana, eastern Idaho and western Wyoming; the Wasatch and Uinta Mountains of Utah; and the southern Rocky Mountains of Colorado and New Mexico. Since the last named population is classically referred to "M. c. origenes", it will not be considered further for the present. The statistics of the other subsamples follow on page 198.

Comparison of these statistics, as well as examination of the isopleth map for condylobasal length in males, shows that geographic variation occurs within this "race", but suggests that Wright is correct in allying the marten of southwest Montana with those of the coastal regions ("M. c. caurina") rather than with those to the south ("M. c. origenes"). Wright suggests that there are possibly more "subspecies" to be described, but as explained elsewhere, this does not seem to be the best solution.

As one moves from the northern Rocky Mountains through the middle Rocky Mountains into the Wasatch and Uinta Ranges, the marten become larger, so that in the Wasatch-Uinta population,

MALES

	Coast Range, B. C.			Coast Mts. and Cascades, Wash. and Oregon			Northern Rocky Mts.			Middle Rocky Mts.			Wasatch and Uinta Ranges		
	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n
Condylobasal Length	7.80	2.79	33	7.93	.19	67	7.87	.23	51	8.00	.18	18	8.08	.07	2
Rostral Width	1.64	.09	34	1.62	.06	72	1.61	.09	52	1.68	.06	19	1.72	.05	2
Upper Tooth Row	2.90	.10	22	2.97	.08	59	2.96	.07	35	3.01	.10	15	2.96	-	1
Canine Width at Base	1.52	.09	34	1.52	.06	72	1.51	.07	47	1.58	.07	19	1.64	.06	2
Bulla Length	1.49	.10	34	1.51	.06	70	1.50	.05	47	1.55	.05	19	1.55	.06	2
Upper Molar Width	.81	.04	34	.83	.04	73	.85	.05	47	.86	.05	19	.90	.06	2
Upper Molar Inner Molety Length	.51	.04	34	.53	.03	73	.56	.04	53	.57	.04	19	.62	.03	2
Palate Length	3.91	.16	22	4.01	.11	58	3.99	.13	36	4.10	.12	14	3.94	-	1
Mastoid Width	3.65	.13	22	3.64	.12	56	3.70	.10	36	3.76	.07	14	3.85	-	1
Height of Skull at Bullae	2.94	.12	22	2.87	.09	56	2.96	.08	36	2.99	.07	14	3.01	-	1
Length of Last Upper Premolar	.83	.03	34	.83	.04	73	.84	.04	46	.86	.03	19	.92	.03	2
Narrowest Palate Width	.83	.05	30	.85	.04	65	.84	.05	37	.83	.04	15	.79	-	1
Canine Width at Base / Bullae Length	1.03	.07	32	1.01	.05	69	1.00	.04	47	1.02	.04	19	1.05	.00	2
Upper Molar Width Plus Inner Molety Length	1.32	.07	34	1.36	.07	73	1.41	.09	47	1.43	.08	19	1.52	.08	2

FEMALES

	Coast Range, B. C.			Coast Mts. and Cascades, Wash. and Oregon			Northern Rocky Mts.			Middle Rocky Mts.			Wasatch and Uinta Ranges		
	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n
Condylobasal Length	7.22	.28	13	7.18	.15	16	7.13	.14	24	7.22	.20	17	7.40	.09	4
Rostral Width	1.47	.10	13	1.42	.06	16	1.40	.06	25	1.48	.07	18	1.47	.02	4
Upper Tooth Row	2.64	.10	7	2.68	.04	6	2.64	.05	9	2.71	.08	7	2.72	.04	4
Canine Width at Base	1.40	.10	13	1.34	.04	16	1.31	.05	21	1.39	.07	19	1.38	.05	4
Bulla Length	1.42	.06	13	1.41	.06	16	1.41	.05	21	1.42	.05	17	1.44	.03	4
Upper Molar Width	.74	.05	13	.74	.03	16	.75	.04	21	.77	.03	19	.77	.02	4
Upper Molar Inner Moiety Length	.47	.04	13	.44	.03	16	.48	.03	25	.49	.05	19	.51	.03	4
Palate Length	3.57	.18	6	3.60	.07	6	3.45	.11	13	3.63	.16	7	3.67	.03	4
Mastoid Width	3.30	.16	7	3.33	.07	6	3.32	.10	13	3.43	.10	7	3.45	.06	4
Height of Skull at Bullae	2.62	.18	7	2.69	.03	6	2.66	.05	13	2.74	.11	7	2.74	.06	4
Length of Last Upper Premolar	.77	.04	13	.74	.03	16	.74	.03	20	.77	.04	19	.79	.02	4
Narrowest Palate Width	.78	.03	13	.79	.06	13	.76	.04	12	.77	.04	7	.77	.02	4
Canine Width at Base / Bullae Length	.99	.06	13	.95	.04	16	.92	.03	21	.99	.05	17	.96	.04	4
Upper Molar Width plus Inner Moiety Length	1.21	.09	13	1.19	.05	16	1.23	.07	21	1.26	.07	19	1.28	.05	4

most characteristics are significantly larger than those in the northern Rocky Mountains, while those in the middle Rocky Mountains are intermediate between the two. Since "M. c. origenes" is as small in most characteristics as is the northern Rocky Mountain population, and is indeed very difficult to separate from it cranially, it seems inadvisable to consider the Utah population as nearest to "M. c. origenes". In actual fact, "M. c. origenes" is more similar to the marten of the northern Rocky Mountains and the coast than are those from Utah and the Middle Rocky Mountains. For the time being, then, I conclude that the range of "M. c. caurina" in the American Rockies should be considered to include the Wasatch - Uinta and the Middle and Northern Rocky Mountain populations, restricting "M. c. origenes" if it were to be maintained to the area of its type locality, the Southern Rocky Mountains and New Mexico. In making this interpretation, it must be remembered that marten from the Middle Rocky Mountains and the Wasatch - Uinta Ranges are considerably larger than those farther north, while those farther north lie nearest the Colorado population ("M. c. origenes"). I conclude, however, that there is no reason for maintaining "origenes", and synonymize it with "caurina".

The northern limit of the "subspecies" in the Coast Range of British Columbia or Alaska has not been determined. Grinnell and Dixon (1926) said it extended as far north as the coast opposite Admiralty Island, while Anderson (1946) gave its northern limit as the Alaska Panhandle. Because this "species" likely intergrades with "M. americana" at its northern limit here,

one would think that it should be easy to determine the edge of its range, but specimens from the region are so few that one can arrive at no positive conclusion. Two specimens from just south of Juneau (Taku) are definitely referable to "M. caurina". One specimen from the mouth of Cross Sound (Dundas Bay) was so smashed it could not be properly identified. One specimen from Yakutat (identified on its tag as "M. c. nesophila") lies intermediate between "M. americana" and "M. caurina". This last is the most northerly specimen of marten even doubtfully referable to "M. caurina" that I have examined, but Zon and Sparhawk (1923) and Anon. (1948) map the Coast Forest (Sitka spruce and Western Hemlock) as occurring as far northwest along the coast as the Kenai Peninsula and Kodiak Island.

The southern limits of this "race", along the Pacific coast have likewise not been carefully determined. Grinnell and Dixon (1926) say that "M. c. humboldtensis" likely occurs in the Coast Mountains of California north into Oregon. Bailey (1936), writing on the marten of Oregon, says that "specimens from southern Oregon are included in M. c. caurina but are grading towards Martes caurina sierrae...." Grinnell, Dixon and Linsdale (1937) write that "a good representation of martens from the Trinity Mountains, California region, is not quite typical of sierrae nor, as might have been expected, intermediate between it and humboldtensis; the tendency is rather toward caurina of the Puget Sound region. Probably geographic intergradation takes place to the north of California between each of these subspecies, separately and caurina".

I find all Oregon specimens sufficiently large to be referred to "M. c. caurina"; another from northwest Del Monte County, California, is equally large, while two from about only forty miles to the south east of the latter locality is fully .50 cm. smaller, and well within the range of typical "M. c. humboldtensis". These are extremely small samples to consider seriously, yet they suggest that the area of intergradation between the two "races" is narrow, and occurs in the very northwest of California. I find very little cranial distinction between "M. c. sierrae" and "M. c. caurina", but comparison of Bailey's and Grinnel, Dixon and Linsdale's distribution maps shows that "M. c. sierrae" is geographically isolated from "M. caurina caurina" in extreme north central California.

I conclude that a conservative interpretation of the distribution of this "race", excluding "origenes" which is here synonymized with it, may be summarized as follows. The Coast Range of British Columbia, east to the edge of the Intermontane Plateau, and including the Coast Forest Biotic Area of Munro and Cowan (1947), north in the forest coast of the Alaskan Panhandle, at least to Yakutat, and possibly farther; south through the Olympic and Coast Mountains and Cascades of Washington, the Coast and Cascade Mountains of Oregon and possibly intergrading with "M. c. humboldtensis" in northern Del Monte and northwest Siskiyou Counties, extreme northwest California; the Blue Mountains of Washington and Oregon, and Idaho south of Lewis, and Clearwater Counties; Montana south of the range of "M. a. abietinoides", and including southern Mineral, Lake, Missoula and

Ravalli Counties; the Middle Rocky Mountains of south central Montana, southeastern Idaho, and western Idaho; the Wasatch and Uinta Mountains of Utah and presumably of very southeast Idaho, and very northwest Colorado. No specimens of the marten of Grand and San Juan Counties, Utah, were examined, hence no designation of their status can be made. Durrant (1952) saw no specimens from this area, but considered all Utah marten to be "M. c. origenes".

Reference has already been made to the marten of the Black Hills, South Dakota. Over and Churchill (1945) assumed it would be referable to "M. a. americana" without having seen a specimen, but they could as likely be referable to "M. caurina".

Specimens examined: 615 specimens from California, Oregon, Washington, British Columbia, Alaska, Idaho, Montana, Wyoming and Utah.

Skull diagrams and photographs: Osgood 1901, pl. 5; Grinnell, and Dixon 1926, figs. 5 and 6; Hall 1926c, fig. 3; Marshall 1951, pl. 11; Wright 1953, pl. 1.

"Martes caurina origenes" (Rhoads 1902).

Synonymy: Martes (or Mustela) americana origenes; caurina origenes.

Type specimen: U. S. National Museum Collection, no. 112,170 (Poole and Schantz 1942, and examined by myself).

Type locality: "'Marvine Mountain' (Garfield County?), Colo." (Rhoads 1902); "Marvine Lodge, Garfield Co., Colo." (Seton 1925-1928); "Marvine Mountain, Rio Blanco County, Colorado" (Warren 1942).

I have been unable to locate a Marvine Lodge or Mountain in Garfield County, but I have found a Marvine Mountain in eastern Rio Blanco County, and I presume this to be the proper type locality. The two counties are adjacent, however, and do not cast doubt on the validity of Rhoads' designation.

Pelage: Described by Rhoads, chiefly on the basis of pelage and distribution as follows. "Strikingly different from all other American marten except caurina in the absence of the light colored cheek patches. Head relatively darker, as compared with upper body colors, than in caurina; ears lacking a white border or inner lining of white hairs. Gular and pectoral patch extensive, wide, connected by interrupted streaks along median abdominal line with well-defined narrow pre-ventral area of similar color. Color of gular patch a peculiar buffy-orange, as in caurina, lightening somewhat on belly, 'wood-brown', the longer, darker hairs of middle back and rump being 'broccoli-brown', and the brush of tail and soles of feet 'clove-brown'. The concolor appearance of origenes viewed from above is even more striking than in caurina, the whole of head excepting the ear margins being quite as dark as the neck and shoulders and those not noticeably darker than the back. The under parts show precisely the same color and pattern characters which distinguish caurina from americana.... Five skins and three skulls

of Colorado martens at hand ... all show with remarkable uniformity the constancy of the characters of the type as above given. ... It is a pale race of "caurina". Dalquest (1948) described the "race" as pale headed and with yellower throat patches.

Bailey, in 1936, described it thus: "size and proportions about the same as in caurina but colors generally lighter, more drab brown with more distinctly gray head, lighter yellow or occasionally white throat patch and light yellow traces along median line of belly...." Durrant (1952) described marten of Utah which he considered belonging to this "race" (but which I refer to "M. c. caurina"), as with "upper parts brown, darkest in mid-dorsal region; sides paler; tail like back proximally, but grading to black at top; top of head, face and chin grayish brown; throat, pectoral and inguinal regions orange; feet and legs dark brown; underparts pale brown except midventral line which is orange."

It appears that the characteristics assigned by Rhoads to this "race" are not as distinctive as he believed. Dalquest (1948) found that the marten of Idaho and northeastern Washington had the paler heads and yellower throat patches that Rhoads considered characteristic of "origenes"; these were, in fact, specimens that Dalquest considered to be "origenes". Wright (1953) wrote that "the type specimen of origenes in the National Museum does not appear to me to differ markedly from the type of caurina. Surely there are much greater differences in color between selected specimens from the Whitefish Range in Montana than there are between the types of caurina and origenes. Since both subspecies were described from small series it seems desirable

that the status of origenes should be reinvestigated."

I myself have seen the types of both "races" and examined a moderately sized series of "caurina" and a small one of "origenes" and agree with Wright that the range of variability of the former is quite sufficient to encompass that of the latter. In fact, I have found Rhoads' characteristics quite insufficient to separate skins of "origenes" from coastal examples of "caurina", and synonymize the two.

Cranium: Rhoads' description of the "race" did not depend on cranial characteristics. He quite rightly concluded that its characters related it to the "species" "M. caurina", but did nothing to indicate cranial distinction from "M. caurina caurina". Bailey (1936) says "origenes" has a "slender rostrum", but does not say it is any slenderer than the relatively broad one of "M. caurina caurina". Durrant (1952) lists the following characteristics as being distinctive in separating the two "races", but does not say which "race" possesses a given degree of any of them. The characteristics he lists are shape of zygomatic arch, extension of palate behind last molar, shape of foramen magnum, size of upper molar, size of inner lobe of last upper premolar, shape of the interpterygoid space and rostral width.

I have made rather detailed statistical comparison of samples of the crania of this "race" with various geographic subsamples of "M. caurina caurina" and find that the crania of "origenes" fall well within the range of variation of "caurina caurina" and that in fact, various subpopulations of "caurina caurina" show greater deviation away from the mean of the whole

"race" than does "origenes" from the same mean. Of the fourteen characters studied, only mastoid width in females is significantly different (at the 95% level of significance), being larger in "origenes". I am lead to conclude that there is little reason left for supposing that "M. c. origenes" should be maintained as a valid "subspecies".

Cranial statistics for the "race", obtained from a sample from the Southern Rocky Mountains and New Mexico follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	7.92	.17	2.12	28	7.20	.21	2.86	19
Rostral width	1.64	.07	4.39	28	1.43	.07	4.62	19
Upper tooth row	2.96	.06	2.17	18	2.61	.09	3.33	7
Canine width at base	1.53	.05	3.45	28	1.36	.05	3.75	19
Bulla length	1.49	.04	2.69	28	1.41	.04	2.99	19
Upper molar width	.82	.04	4.51	28	.74	.03	4.47	19
Upper molar inner moiety length	.53	.04	6.82	28	.46	.03	7.03	19
Palate length	4.01	.11	2.74	18	3.51	.11	3.10	7
Mastoid width	3.71	.13	3.54	18	3.38	.12	3.61	7
Height of skull at bullae	2.95	.08	2.61	18	2.70	.08	2.99	7
Length of last upper PM	.83	.03	3.12	28	.75	.04	5.48	19
Narrowest palate width	.85	.04	4.73	18	.77	.03	3.27	7
Canine width base/ bullae length	1.03	.03	2.72	28	.97	.03	2.90	19
Upper molar width + inner moiety length	1.35	.06	4.22	28	1.19	.06	5.20	19
Total length	67.46	-	-	3	58.85	-	-	4
Tail length	21.90	-	-	3	18.53	-	-	4
Hind foot	9.03	-	-	3	8.20	-	-	4

Geographic variation: The literature records nothing concerning this. My specimens indicate so far as they are able that it is a homogenous population, with little variation within the confines of its rather limited range.

Distribution: An account of the various interpretations of the distribution of this "race" was given under the discussion of "M. c. caurina". It is here considered, if it were to be maintained, to occur only in the region of the type locality; that is, the Southern Rocky Mountains of Colorado, New Mexico, and likely very southern Wyoming; possibly also in Grand and San Juan Counties, Utah. It is, however, to be synonymized with "M. c. caurina".

Specimens examined: 151 specimens from Colorado and New Mexico.

Skull diagrams and photographs: Warren 1942, pl. 6.

Synonymy: Martes caurina humboldtensis; Martes americana humboldtensis.

Type specimen: Museum of Vertebrate Zoology, University of California no. 19158 (Grinnell and Dixon 1926).

Type locality: "Ridge about five miles northeast of Cuddeback (= Carlotta), Humboldt County, California" (Grinnell and Dixon 1926).

Pelage: As early as 1892, Poland described marten from California as "smaller than most other martens and ... of uniform brown or light brown colour". Described by Grinnell and Dixon as follows.

"In general external features, including dark tone of coloration, resembles Martes caurina caurina; ... decidedly darker, of richer golden brown tone, than M. c. sierrae...."

Grinnell, Dixon and Linsdale (1937) redescribed it as "similar to the Sierra Nevada pine marten, ... but slightly smaller, coloration darker, especially on under surface, and tone of brown more golden.... They contrast with prime pelts of the Sierran race in the following respects: there is a distinctly darker, more sooty 'overwash' apparently pertaining to the overhairs; the underfur, especially along the sides, shows through as a richer, golden brown tone; the feet and legs are more extensively blackish brown; the tail is black at the end, but this blackness extends farther toward the base than in the Sierran animal. There is far less orange-yellow color on the throat and chest, and the usual area of this color is much broken up by coarse spots and marblings of body brown...."

I have examined several skins of this "race", and can attest to the similarity of the colour of the skins examined to "M. c. caurina", and to the darker, richer colour compared to those of "M. c. sierrae".

Cranium: According to Grinnell and Dixon, the skull is smaller than in either "M. c. caurina" or "M. c. sierrae", "with rostrum slender, distinctly constricted behind root of canines; frontal region and postorbital constriction narrow; teeth small; molariform series not so crowded as in sierrae, so as to skew the premolars; last upper molar with heel greatly expanded entero-posteriorly, as much so, relatively to transverse diameter of

this tooth, as in sierrae, and hence more than in caurina."

Grinnell, Dixon and Linsdale (1937) described it as "rather sharply different cranially from sierrae. The skull ... is smaller and narrower, with a notably slenderer rostrum and the teeth are somewhat smaller, especially the carnassials and molars."

The small sample of this "race" that I have examined (twenty specimens) averages far smaller in size than any other marten of the "species" "M. caurina", excepting for a small subsample from eastern Oregon, which approximately equals it in smallness of size. Statistical significance at the 95% level with all other "subspecies" of "M. caurina" is shown in the following characteristics (all of which are smaller); condylo-basal length (females only); rostral width (males only); upper tooth row; canine width at base; bullae length (females only); upper molar width (females only); palate length; mastoid width; length of last upper premolar (females); canine width at base / bullae length (males only); upper molar width plus inner moiety length.

Cranial statistics for this race follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	7.66	.26	3.40	11	6.85	.11	1.66	8
Rostral width	1.51	.03	2.13	11	1.32	.03	2.43	9
Upper tooth row	2.77	-	-	1	-	-	-	0
Canine width at base	1.45	.05	3.11	4	1.21	-	-	1
Bullae length	1.48	.03	2.17	4	1.28	-	-	1

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Upper molar width	.82	.08	9.43	4	.67	-	-	1
Upper molar inner moiety length	.51	.06	11.23	4	.41	-	-	1
Palate length	3.63	-	-	1	-	-	-	0
Mastoid width	3.50	.08	2.40	8	3.13	.03	1.02	7
Height of skull at bullae	2.86	.05	1.58	8	2.60	.08	2.96	8
Length of last upper PM	.82	.06	7.71	4	.69	-	-	1
Narrowest palate width	.83	.00	.00	2	.76	-	-	1
Canine width base/bullae length	.98	.01	1.43	4	.95	-	-	1
Upper molar width plus inner moiety length	1.33	.13	9.74	4	1.08	-	-	1
Total length	61.00	-	-	4	58.70	-	-	2
Tail length	19.62	-	-	4	18.50	-	-	2
Hind foot	9.25	-	-	4	10.00	-	-	2

Geographic variation: Specimens from the Trinity Mountain region of extreme northwestern California are considered by Grinnell and Storer (1916) to lie near to "M. c. sierrae". Grinnell, Dixon and Linsdale (1937) reinterpret these specimens as really lying near to "M. c. caurina" and my examination of these specimens leads me to the same conclusion. Other than these, no geographic variation of note has been detected by me, or so far as I know, recorded in the literature.

Distribution: The Coast Mountains of California intergrading

with "M. c. caurina" in the very northwest California. No intergrades with "M. c. sierrae" are known, presumably because that "race" is completely isolated from it. For further detail on distribution see that topic under the description of "M. caurina caurina".

Specimens examined: 20 specimens, from California.

Skull diagrams and photographs: Grinnell and Dixon 1926, fig. 7; Grinnell, Dixon and Linsdale, 1937, vol. 1, fig. 66.

"Martes caurina sierrae" Grinnell and Storer 1916.

Synonymy: Martes caurina sierrae; americana sierrae; caurina nobilis.

Type specimen: University of California Museum of Vertebrate Zoology Collection no. 22112 (Grinnell and Storer 1916).

Type locality: "Head of Lyell Cañon, 9800 foot altitude, Yosemite National Park, California" (Grinnell and Storer 1916); "Head of Lyell Canyon, at 9800-foot altitude, Yosemite National Park, Tuolumne County, California" (Grinnell, Dixon and Linsdale 1937).

Pelage: Described by Grinnell and Storer as "similar to Martes caurina caurina, but general coloration paler both above and below, this paleness involving both overhair and fur; sides of face decidedly paler; pale ochraceous-orange of chest very extensive, spreading forward to throat and backward along median

line to belly; 'feel' of pelage softer.... The Yosemite series of specimens, as regards both skins and skulls, is notably uniform in characters...."

Described by Grinnell, Dixon and Linsdale (1937) as with "underfur long and lax; overhair sparse and fine. General coloration ... light golden brown, deepening to blackish brown on feet and end of tail; a broad patch of orange or yellowish color on throat or chest.... General coloration of body snuff brown. There is a darkening toward mummy brown down middle of back, owing chiefly to black tippings of overhairs there. A darkening also takes place down the legs, reaching mummy brown on tops and sides of feet (but woolly soles of feet light drab). Claws translucent yellowish white; color of tail at base is like that of body, but it gradually darkens toward end until blackish brown at tip; head paler than body, becoming light drab on face; muzzle dusky drab; nose pad and whiskers black; back of ear fuscus, rim ecru-drab, inside pale drab gray; chin and jaws brownish drab; a broad area from throat down front of neck onto chest, and reaching irregularly to insides of fore-legs, cinnamon-buff (even approaching ochraceous-orange in places); the same light color extends in a narrow line, more or less interrupted in different specimens, from chest down middle of belly to region of vent; in some specimens there is an unsymmetrical spotting of snuff brown on the light-colored chest area. Pelage everywhere copious, consisting chiefly of underfur; overhairs usually scanty, and short in relation to length of underfur.... Trappers have told us of marten pelts taken in a single

district that have been graded variously as 'light' and 'dark'. In the series of twenty-six skins before us there is remarkable uniformity in general tone of coloration. Two examples ... were sent to us ... as representing the light and dark types of coloration to be obtained.... The difference between them, while readily appreciable, is not as conspicuous as that found in a series of pelts of, say, red fox. There is no indication of the existence of two color 'phases'; the extremes mentioned can be accounted for by ordinary individual variation, and are within rather narrow limits. The chief singular feature of variation in our series is the extent of the yellowish white or orange-tinted throat patch; in most specimens this is very wide and long, but in a few ... it is restricted to an irregular area on the lower throat, and to detached spots and scattering white hairs on the middle of the breast. The intensity of the color of the throat patch varies in different individuals from dirty, dull, buffy, white to (in an extreme example) zinc orange.... As compared with the northwestern pine marten (Martes caurina caurina) from the Puget Sound region, the Sierra Nevada pine marten (M. c. sierrae) averages decidedly paler in general tone of color, and has finer textured pelage."

Hall (1946) said it was distinguished from "M. c. humboldtensis" in "larger average size, [and] darker coloration generally," It is told from "M. c. caurina" by "a more reddish (less yellowish) pelage" (compared to specimens from Idaho)

I have seen many of the skins examined by Grinnell and his co-workers and can add little to what they say. Like

them, I find that it is distinctly paler than "M. c. caurina", with a finer coat; compared to "M. c. humboldtensis" it is paler, and considerably larger in size.

Cranium: According to Grinnell and Storer (1916), "cranium with rostrum short as in caurina, but extremely narrow; whole cranium narrower with brain-case relatively higher; sagittal crest very weak; auditory bullae even smaller than in caurina." Grinnell, Dixon and Linsdale (1937) described it as, when compared to "M. c. caurina", with "more widely spreading zygomatic arches, narrower rostrum, weaker sagittal crest, and more crowded molariform teeth." Compared to "M. c. humboldtensis" they say the skull is larger and broader, with a broader rostrum, and the teeth, especially the molars and carnassials somewhat larger. Hall (1946) says it may be told from "caurina" by its narrower rostrum, and from "humboldtensis" by its larger skull and broader rostrum.

Hall, in 1926 (c) described as a new subspecies, "Martes caurina nobilis", a supposedly extinct Pleistocene marten, based on upper and lower jaws found in Samwell and Potter Creek Caves, California. At that time he believed it showed nearest affinity to "M. c. caurina", but in 1936, Hall reinterpreted this view to conclude that the new "race" should be considered nearest to "M. c. sierrae" and indeed, be synonymized with it, although averaging larger in size. Hall's earlier paper gives details of dentition that need not be reproduced here.

My examination of skulls of this "race" leads me to

conclude that the above descriptions are essentially correct, but that rostral width is alone insufficient to separate it from all populations of "M. c. caurina", some of which show the same narrow rostrum. Compared to "M. c. caurina" from Oregon and Washington, however, distinctions at the 95% level of probability occur in the following characteristics: bulla length (in which it is smaller) and upper molar width, upper molar inner moiety length, length of last upper premolar, and upper molar width plus inner moiety length (in males only, except in premolar length, which is significantly different in both males and females, and which in all are significantly larger in "sierrae" than in "caurina"). However, where the sample of "M. c. caurina" is broken into subsamples, all characters for "M. c. sierrae" fell within the range shown by one or another of the subsamples of "caurina". Greatest affinity is shown to the subsamples of "M. c. caurina" from Oregon and Washington, and those from the northern Rocky Mountains, though statistical distinction can be made from these (see above).

Compared to "M. c. humboldtensis", "sierrae" is distinctly larger, significantly so in the following characteristics: condylobasal length; rostral width (males only); bulla length (females only); canine width at base (females only); bulla length (females only); upper molar width (females only); upper molar inner moiety length (females only); palate length (males only); mastoid width (males only); length of last upper premolar (females only); upper molar width plus inner moiety length (females only). The third, eighth, ninth and tenth

measurements could not be compared in females.

I am not convinced that this race should be synonymized with "M. c. caurina", but suggest that for the time being at least, such procedure is warranted.

Cranial measurements for this race follow.

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	7.96	.13	1.63	12	7.08	.11	1.55	4
Rostral width	1.59	.06	3.52	12	1.40	.10	6.95	5
Upper tooth row	2.98	.05	1.58	8	2.70	-	-	1
Canine width at base	1.50	.05	3.40	12	1.31	.03	2.44	5
Bullae length	1.47	.03	1.77	12	1.36	.03	1.84	4
Upper molar width	.86	.03	3.24	12	.77	.04	4.66	5
Upper molar inner moiety length	.56	.02	3.58	12	.48	.05	11.30	5
Palate length	4.01	.11	2.74	8	3.53	-	-	1
Mastoid width	3.64	.07	1.95	8	-	-	-	0
Height of skull at bullae	2.89	.09	2.98	8	-	-	-	0
Length of last upper PM	.87	.02	2.30	12	.77	.01	1.81	5
Narrowest palate width	.85	.04	4.34	8	.79	.01	1.27	2
Canine width base / bullae length	1.02	.05	4.61	12	.97	.05	4.86	4
Upper molar width plus inner moiety length	1.42	.04	2.88	12	1.25	.08	6.40	5
Total length	60.00	1.82	-	35	55.23	3.01	-	6
Tail length	19.55	2.01	-	29	18.10	1.80	-	6
Hind foot	8.60	.70	-	28	7.80	.84	-	6

Geographic variation: Grinnell, Dixon and Linsdale (1937) assure us that geographic variation within the "race" is slight and I find no reason to disagree with them.

Specimens from the Trinity Mountain region of extreme northwestern California (Kellogg 1916, p. 355), are considered by Grinnell and Dixon (1926), while not typical of "sierrae" (tending toward "humboldtensis") referable to the former "race". Grinnell, Dixon and Linsdale (1937) come to the same conclusion, saying, however, that they tend not towards "humboldtensis", but rather towards "M. c. caurina". I conclude from examination of these skulls, that rather than being "sierra-caurina" intergrades they are really intergrades between "humboldtensis" and "caurina", being very near to the latter, and hence not involved in a discussion of variation in "M. c. sierrae".

Distribution: The Sierra Nevada of California, above the 6000 foot level, from Mineral King and Jordan Hot Springs to the Trinity Scott and Salmon Mountains. They are apparently isolated completely from nearby populations of "M. c. humboldtensis" and "M. c. caurina". "M. c. sierrae" is also present in extreme western Nevada, where the Sierra Nevada enters the state near Lake Tahoe (Grinnell, Dixon and Linsdale 1937, Hall 1936).

Elsewhere I have pointed out that specimens considered intermediate between "M. sierrae" and either "M. c. caurina" and "M. c. humboldtensis" have, I believe, been mididentified. Hall (1926c) however, refers to a specimen (M. V. Z. 13773) "regarded as intermediate between M. c. caurina and M. c. sierrae", but

does not state where it was captured. I have not seen this specimen and can add nothing to Hall's statement.

Specimens examined: 38 specimens from California.

Skull diagrams and photographs: Grinnell and Dixon 1926, figs. 4 and 8; Hall 1926c, figs. 1, 2 and 5; Grinnell, Dixon and Hinsdale 1937, vol. 1, fig. 66; Hall 1946, figs. 111, 112, 113 and 114.

"Martes caurina vancouverensis" Grinnell and Dixon 1926.

Synonymy: Martes caurina vancouverensis; americana vancouverensis.

Type specimen: University of California Museum of Vertebrate Zoology Collection no. 12,474 (Grinnell and Dixon 1926).

Type locality: "Golden Eagle Mine, 20 miles south of Alberni, Vancouver Island, British Columbia" (Grinnell and Dixon 1926).

Pelage: The pelage and skull were first described by Swarth in 1912, fourteen years before Grinnell and Dixon named it as a distinct "subspecies". Swarth described it thus: "the four males are in summer pelage, and consequently short-haired and with scanty under fur. In general appearance they are uniform dull brown (about Prout brown), darkening somewhat on rump, feet and tail where the long, dark-coloured hairs more effectively hide the yellowish brown underfur. The tip of the tail, of conspicuously longer hairs, is black. The inner surface of the

ear is very slightly grayish. On the throat there is an irregular patch of pale orange-rufous, disconnected spots of the same interspersed with a few white hairs extending onto the breast. The two winter skins are much more richly colored. They too, are uniform brown, with no trace of gray on the head, but the pelage is darker and much more glossy than the summer specimens, long outer hairs dark brown, about mummy brown; tail black. There are numerous white hairs scattered over the entire skin. The throat patch is of about the same color as the summer skins." Swarth correctly recognized that Vancouver Island marten belonged to the "species" Martes caurina".

Grinnell and Dixon, in their naming of this "race", say, concerning pelage only that it is "externally like Martes caurina caurina ...", making distinction wholly upon skull characteristics.

I have examined a fair sized series of skins of this "race", and find them indistinguishable from skins on the adjacent coast referred to "M. c. caurina".

Cranium: Described by Grinnell and Dixon as follows: "Externally like Martes caurina caurina ... but skull markedly different; rostrum shorter; frontal region, and indeed, whole cranium broader; zygomatic spread greater; molariform teeth more crowded and more skewed out of alignment; last upper molar decidedly smaller, and its heel far less expanded anteroposteriorly.... Skull in general proportions more nearly like that of Mustela nesophila ... but smaller ... and with weaker

dentition; last upper molar much smaller, and heel even less expanded, thus nearly as in Mustela americana". Elsewhere these authors say that "vancouverensis" very nearly bridges the gap between "M. c. caurina" and "M. c. nesophila".

My examination of a series of skulls from the Island leads me to conclude, that far from being intermediate between "caurina" and "nesophila", "vancouverensis" is almost indistinguishable from "M. c. caurina" and hence totally distinct from "nesophila". Statistical significance from samples of "M. c. caurina" is found only in height of skull at bullae in females. However, the inner moiety length of upper molar is so small as to equal that of "M. c. humboldtensis" and be nearly significantly distinct from all others. Similarly the skull height at bullae is so great as to be larger than in most subpopulations of "M. caurina caurina" and were it not for the high skulled marten of the middle and southern Rocky Mountains, would be significantly distinct. Significance is approached also in canine width at base and rostral width in females.

In comparing "vancouverensis" with "M. c. caurina" from the adjacent mainland of British Columbia, greater distinctions appear. Significance is shown here in larger condylo-basal length; canine width at base; bullae length; upper molar width; palate length; height of skull at bullae; and narrowest palate width (males only, tests with females not being made). "M. c. vancouverensis" shows greatest similarity, however, to marten of the middle Rocky Mountains, not that of the coast, although it shows lighter dentition than does the interior form.

When comparison is made to "M. c. nesophila", "vancouverensis" shows the following significant distinctions at the 95% level, all being smaller; condylobasal length (males only); rostral width; upper tooth row (males only); canine width at base; upper molar inner moiety length (males only); mastoid width; length of last upper premolar; narrowest palate width; canine width at base / bullae length; and upper molar width plus inner moiety length (males only).

We may conclude that "vancouverensis", although fairly easily distinguished from marten on the adjacent mainland falls within the range of variation shown by "M. c. caurina" in other parts of its range, and is hence not a particularly distinctive "race", and may be synonymized with "M. c. caurina".

Statistics of a sample of marten from Vancouver Island follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	7.97	.14	1.76	24	7.32	.30	4.03	11
Rostral width	1.67	.06	3.59	24	1.49	.07	4.90	11
Upper tooth row	2.90	.06	1.93	24	2.67	.16	6.04	8
Canine width at base	1.57	.05	3.11	24	1.41	.07	5.19	11
Bullae length	1.55	.04	2.26	24	1.46	.07	4.72	11
Upper molar width	.84	.03	3.09	24	.73	.09	12.14	11
Upper molar inner moiety length	.48	.02	4.20	24	.42	.09	22.30	11
Palate length	4.05	.09	2.25	24	3.67	.22	6.07	7
Mastoid width	3.64	.07	2.01	24	3.36	.13	3.72	7
Height of skull at bullae	3.04	.07	2.24	24	2.81	.13	4.53	7

	<u>Male</u>				<u>Female</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Length of last upper PM	.83	.02	2.63	24	.76	.03	3.30	11
Narrowest palate width	.87	.02	2.52	24	.79	.03	3.28	11
Canine width base / bullae length	1.02	.03	3.23	24	.97	.04	3.62	11
Upper molar width plus inner moiety length	1.32	.04	3.10	24	1.15	.06	5.38	11
Total length	61.00	-	-	4	58.70	-	-	2
Tail length	19.63	-	-	4	18.50	-	-	2
Hind foot	9.25	-	-	4	10.00	-	-	2

Geographic variation: None has been determined as far as I know, nor can I detect any.

Distribution: Vancouver Island, especially in the mountains (Swarth 1912, Grinnell and Dixon 1926).

Specimens examined: 51 specimens from Vancouver Island, British Columbia.

Skull diagrams and photographs: Grinnell and Dixon 1926, figures 2 and 6; Hall 1926c, figure 4.

"Martes caurina nesophila" (Osgood 1901)

Synonymy: Martes (or Mustela) nesophila, caurina nesophila; americana nesophila.

Type locality: "Masset, Graham Island, Queen Charlotte Islands,

British Columbia" (Osgood 1901).

Pelage: Originally described by Osgood from skulls alone. A single skin from Admiralty Island, Alaska, was described by Swarth (1912) as "quite different from any of the Vancouver Island specimens. It is of about the same shade of brown, but the whole body, except along the median line of the back, is strongly suffused with orange-red (somewhat darker than Chinese-orange), giving a very rich effect - a character, however, that according to Merriam (1890, p. 27), is sometimes present in caurina. Feet, legs and tail are lustrous black. The head is abruptly grayish, drab on the chin and lower jaw, broccoli brown, mixed with white hairs, above; tip of muzzle darker; inner surface of ear white. A large spot of orange-rufous on the throat and breast.... Taking this ... specimen as representative of the species [subspecies] it may be readily distinguished from the more southern form (caurina) by its gray head, and from the more northern one (americana) by its intensely dark coloration otherwise".

Anderson (1946) described it as "larger than M. c. caurina, and ... always light coloured and short haired as compared with the mainland form". Mr. K. Racey has pointed out to me, and it was verified by me, that the skins of "nesophila" that we have seen can often be identified by its relatively short ears, these being low and round compared to other "races" of the "species".

Examination of a small series of skins from the Queen Charlotte Islands has led me to conclude that this is perhaps

the most distinctive "race" of "M. caurina". The skins are thin and would pass as low grade by the furrier. The hair is coarse, not at all thick, and the colour is pale, especially about the head, with a large red-orange breast spot. The ears, as Mr. Racey points out, are short relative to those of any other member of the "species".

Cranium: Described by Osgood as "similar to Mustela caurina, but larger; rostrum shorter and heavier; dentition heavier; premolars larger and more crowded. Last upper molar similar to that of Mustela americana, internal length being more nearly equal to external length than in caurina.... The molar teeth of nesophila are heavier than in any other form of the group. The audital bullae are actually about the same size as in caurina and thus relatively smaller. The maxillary region between the intraorbital foramen and the alveoli of the upper molars is wider and heavier than in caurina. The most obvious cranial character, however, and the one which distinguishes nesophila from all other members of the americana [read caurina] group is the thick heavy rostrum."

Swarth in 1911, recorded the taking of a single skull from Kiui Island, Alaska, which he correctly, I believe, identified as "M. c. nesophila" although it differed slightly from it "in slightly greater width, with especially wide spreading zygomata...." He concluded that the "race" was distinctive by the "small audital bullae and short, heavy rostrum, with crowded upper tooth row and large sized upper molar." The following year (1912), Swarth obtained two more skulls from

Admiralty Island, Alaska, and said of these, together with that from Kiui Island referred to above, that they "are much like those from Vancouver Island, but somewhat larger, with smaller and less inflated audital bullae, and with appreciably larger last upper molar...." These he all referred to "M. c. nesophila", although in his earlier paper (1911) he had said that "should additional specimens show the wide spreading zygomatic arches to be a constant feature, the marten of the Alexander Archipelago should be considered a distinct species".

Osgood and Swarth both considered "nesophila" to be a distinct "species", but Grinnell and Dixon (1926) concluded correctly that it was related to both "vancouverensis" and "caurina", and should be considered a "race" of "M. caurina" (i.e. M. c. nesophila).

Examination of a series of skulls from Queen Charlotte Islands and Swarth's specimens from the Alexander Archipelago, leads me to conclude that the above description of crania is correct. "M. c. nesophila" is related to "M. caurina" and must be considered a "subspecies" of it. Furthermore, it is by far the most distinctive "race" of the "species", with the possible exception of "M. c. humboldtensis". It has those characters which distinguish "M. caurina" from "M. americana" in exaggerated form; a very low broad skull, wide rostrum, short bullae, large upper premolar and molar, compared to all other "races" of the "species". Further it is the largest marten of the "species" with exceptions referred to elsewhere. Almost all characters average larger than in the adjacent coastal "forms", all but the

following being statistically distinct (at the 95% level); Upper tooth row (males only); bullae length; upper molar inner moiety length; palate length (males only); mastoid width (males only); and upper molar width plus inner moiety length. Comparison to "M. c. vancouverensis" has been made under the discussion of that "subspecies". Statistics obtained from a sample of marten from the Queen Charlotte Islands and the Alexander Archipelago follow:

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	8.19	.11	1.39	14	7.49	.16	2.08	14
Rostral width	1.82	.05	2.47	16	1.58	.06	3.74	17
Upper tooth row	3.01	.06	1.93	10	2.73	.03	1.10	10
Canine width at base	1.71	.05	2.93	16	1.48	.05	3.52	17
Bullae length	1.51	.04	2.58	16	1.44	.06	4.10	16
Upper molar width	.85	.09	10.52	16	.76	.09	11.30	17
Upper molar inner moiety length	.53	.04	6.65	16	.46	.03	5.71	17
Palate length	4.11	.13	3.07	10	3.70	.05	1.38	11
Mastoid width	3.79	.10	2.51	10	3.52	.04	1.25	10
Height of skull at bullae	3.10	.05	1.65	10	2.84	.07	2.50	10
Length of last upper PM	.89	.11	12.54	16	.80	.03	4.00	17
Narrowest palate width	.93	.04	3.97	13	.72	.02	2.36	12
Canine width base / bullae length	1.13	.03	2.47	16	1.03	.05	5.16	16
Upper molar width plus inner moiety length	1.38	.04	2.90	16	1.22	.05	4.20	17
Total length	64.90	-	-	4	60.20	-	-	2
Tail length	20.40	-	-	4	17.00	-	-	2
Hind foot	9.00	-	-	4	8.30	-	-	2

Comparison of twenty-two skulls from Queen Charlotte Islands with twelve skulls from the Alexander Archipelago, shows those from the Charlottes to average very slightly larger in most characteristics, in none reaching significance, but approaching it in the following: canine width at base; bullae length, and length of last upper premolar. The Archipelago skulls thus appear so similar to those from the Queen Charlottes as to merit Swarth's designation of them to this "subspecies".

Geographic variation: It has been pointed out above that specimens from the Alexander Archipelago average very slightly smaller than those on the Queen Charlotte Islands. I have detected no other variation of significance in the sample studied.

Distribution: Although first described from Graham Island, Queen Charlotte Islands, I have examined specimens distinctly referable to it from Moresby Island, Queen Charlotte Islands, and from Etolin, Kupreanof, Kiui, and Admiralty Islands of the Alexander Archipelago. Marten are also recorded from Revillagigedo Island in the Archipelago, according to Dufresne (1946) and Nelson and True (1887) say they occur on Kodiak Island.

Dufresne (1946) says that marten were, in 1934, transplanted to Prince of Wales and Chichagof Islands in the Archipelago. Dufresne does not say where the marten were obtained, and hence what "subspecies" or "species" were involved.

One specimen of marten from Yakutat, Alaska, in the collection of the University of California Museum of Vertebrate Zoology (no. 4781) is labelled as being "M. c. nesophila". It is very large, having a condylobasal length of 8.53 cm., but in other aspects lying intermediate between "M. c. caurina" and "M. c. nesophila". This specimen leads one to wonder if "M. c. nesophila" or martens near it do not also occur on the mainland coast of the northern Alaska Panhandle, intergrading perhaps with "M. c. caurina" between Yakutat and Portland Canal, where more typical "caurina" occurs.

Specimens examined: 61 specimens from Graham, Moresby, Etolin, Kupreanof, Kiul and Admiralty Islands, British Columbia and Alaska.

Skull diagrams and photographs: Osgood 1901, pl. 5.

Summary: I have, in the account preceding, suggested that there is no reason for the further maintenance of the following "subspecies": brumalis, abieticola, boria, kenaiensis, origenes, vancouverensis, and with less assurance, sierrae. If any of these are to be maintained, sufficient geographic variation exists that many more "subspecies" need to be named. The classification of marten then, at this point in this paper, stands as follows:

Martes americana

Martes americana americana

Martes americana atrata (including brumalis)

Martes americana actiosa = huro (including abieticola, boria, and kenaiensis)

Martes americana abietinoides

Martes caurina

Martes caurina caurina (including origenes,
vancouverensis, and sierræ)

Martes caurina humboldtensis

Martes caurina nesophila

The "species" of North American marten

Status: To the present, in this paper, I have dealt with "M. americana" and "M. caurina" as if they were distinct "species". We must now examine in greater detail the validity of this concept.

It has been pointed out elsewhere that in the past up to six "species" of marten have been considered to occur on the North American continent (see, for example, Miller 1912b and 1924). Grinnell and Dixon, in 1926, concluded, however, that in western North America only two "species" occurred ("M. americana" and "M. caurina"), all other named forms being only "subspecies" of these. I have pointed out that Hall, in 1936, recognized that only two and possibly only one "species" existed, and in 1946 the same author again suggested that only one "species" might exist. Rand (1948b) named two "species" as occurring in Canada, and Dalquest (1948) expressed the belief that two "species" existed, the characters of the two were distinctive and did not overlap. Durrant, in 1952, expressed doubt over the specific distinction of americana and caurina.

Allen, in 1942, was the first author to state that all named forms of marten in North America belonged to the two

"species" "americana" and "caurina", and to refer named "subspecies" correctly to these. His classification is the one followed in the synopsis of named forms of North American marten given elsewhere in this paper.

My examination of specimens, especially of skulls, leads me to conclude that all marten on the continent may be clearly and easily referred to these two "species". Given a single skull, and knowing what distinctions to look for, one can always refer it to one or another of these two types of marten. In fact, while one can thus refer a single skull, only by the use of large samples can one identify subsidiary groups (what I have heretofore referred to as "subspecies" or "races"). This primary division is so basic and so obvious that I find it difficult to understand why earlier workers failed to observe it. I cannot stress too greatly that the martens of North America may easily (from specimens) almost always be identified to "species"; only with difficulty, and with large samples to "subspecies". There is an exception to this rule: in certain areas referred to below, intergradation between "americana" and "caurina" occurs, which specimens cannot be referred to one or the other "species".

P. L. Wright, in 1950, and in greater detail in 1953 has made an excellent contribution to our knowledge of the taxonomy of martens. Essentially he showed that in Montana and Idaho, "Martes americana" and "M. caurina" intergrade with each other (or rather that samples of the two races show intergradation) and that the two "species" meet all the requirements

of biological subspecies, as presently conceived. It seems odd in view of the sympatric distribution of these two "species" that this relationship was not guessed at by more workers than Hall and Durrant. I consider Wright's work so significant that I summarize it below. I must add that Dr. Wright kindly lent me all of his cranial material, together with a manuscript of his paper while it was still in press. I have recalculated all of Wright's computations by a slightly different method, looking especially for overlap rather than intergradation, and have been led to conclude that Wright was correct in his conclusions and that the two "species" intergrade. In discussing this situation with others, I have had it pointed out to me that Wright's work still does not prove the conspecificity of these two supposed "species". It seems to me, however, that Wright has gone as far as possible in indicating that these two forms interbreed in nature and that while absolute proof that they interbreed in nature can probably never be obtained, the onus of disproof now lies with those who would maintain their specific status, not Wright who has shown intergradation in his samples.

Wright studied 245 skulls from Montana, Idaho, southwest British Columbia and southeast Alberta, together with several hundred skins from these regions. He found that intergradation occurred in the following four characters: rostral width, cranial height, bullae length, and length of inner moiety of upper molar. He found that none of these characters varied with age within any single subsample. All conclusions are based on the 95% level of significance. Wright also found

intergradation in pelage characteristics. He wrote that "in view of the fact that the skulls from the Whitefish Range [northern Montana and Idaho] and from northern Idaho are essentially similar to those from Suswap and Barkerville, British Columbia, with respect to the size of the auditory bulla and other cranial characters, and that skins from the Whitefish Range exhibit the very dense underfur previously described as characteristic abietinoides from the Selkirk Range, these populations are classed as M. a. abietinoides. The series from the Sapphire Range and the Clearwater Region [central Montana], since they agree in regard to cranial characters with the published description of caurina from Washington ... and since the skins from these areas are very similar to the type specimen of this form, are classed as caurina. The specimens from the Swan, South Fork, and Sun River Regions are intermediate between these types as regards both cranial and pelage characters. Since intergradation is occurring between populations previously regarded as distinct species, it appears that we are dealing with only a single species. Accordingly Martes caurina is reduced to subspecific rank. Since the area of intergradation is very extensive, it would be very difficult to draw a line for separation of the subspecies. Accordingly it appears best to regard the population of the Swan, South Fork, Sun River Region, Montana, as one of intergradation.... As a result of the relegation of M. caurina to subspecific rank, the scientific names of the members of the caurina group are changed as follows: Martes americana caurina (Merriam); Martes americana origenes

(Rhoads); Martes americana nesophila (Osgood); Martes americana sierrae Grinnell and Storer; Martes americana humboldtensis Grinnell and Dixon; Martes americana vancouverensis Grinnell and Dixon".

In his paper Wright measured thirteen characters but graphed only three of these. Because of their significance, I here graph certain others, using Wright's computations rather than my own because they do not differ in any important respect, on Figure 9.

Carl, Guiget and Hardy (1952), on the marten of Manning Park, British Columbia, wrote without reference to specimens, that "the races occupying this area are M. caurina caurina (Merriam) of the coast which probably occupies most of the area, overlapping with M. a. abietinoides Gray toward the Princeton side". After reading this, and knowing of Wright's work, I was particularly interested in examining specimens from this area. Mr. R. Y. Edwards, knowing this, collected specimens from the area. As predicted by the above authors, both forms occur in the Park, and as in Wright's specimens, intergradation is indicated. Only twenty-nine specimens were obtained, and these when graphed (Figure 10) show intergradation in canine width / bulla length, and upper molar width plus inner moiety length, the only characters examined. Since intergradation of this sort occurs in no other samples except in Wright's (i.e. the two kinds are always elsewhere completely distinctive), I offer this as indicating added proof of Wright's conclusions. Dufresne (1946) relates that in 1934 marten were transplanted to Prince of Wales

Figure 9.
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Figure 9. Evidence of intergradation between "Martes americana" and "Martes caurina" in Idaho and Montana (after Wright 1953). The statistics graphed are \bar{X} and $\bar{X} \pm 3 SE_{\bar{X}}$

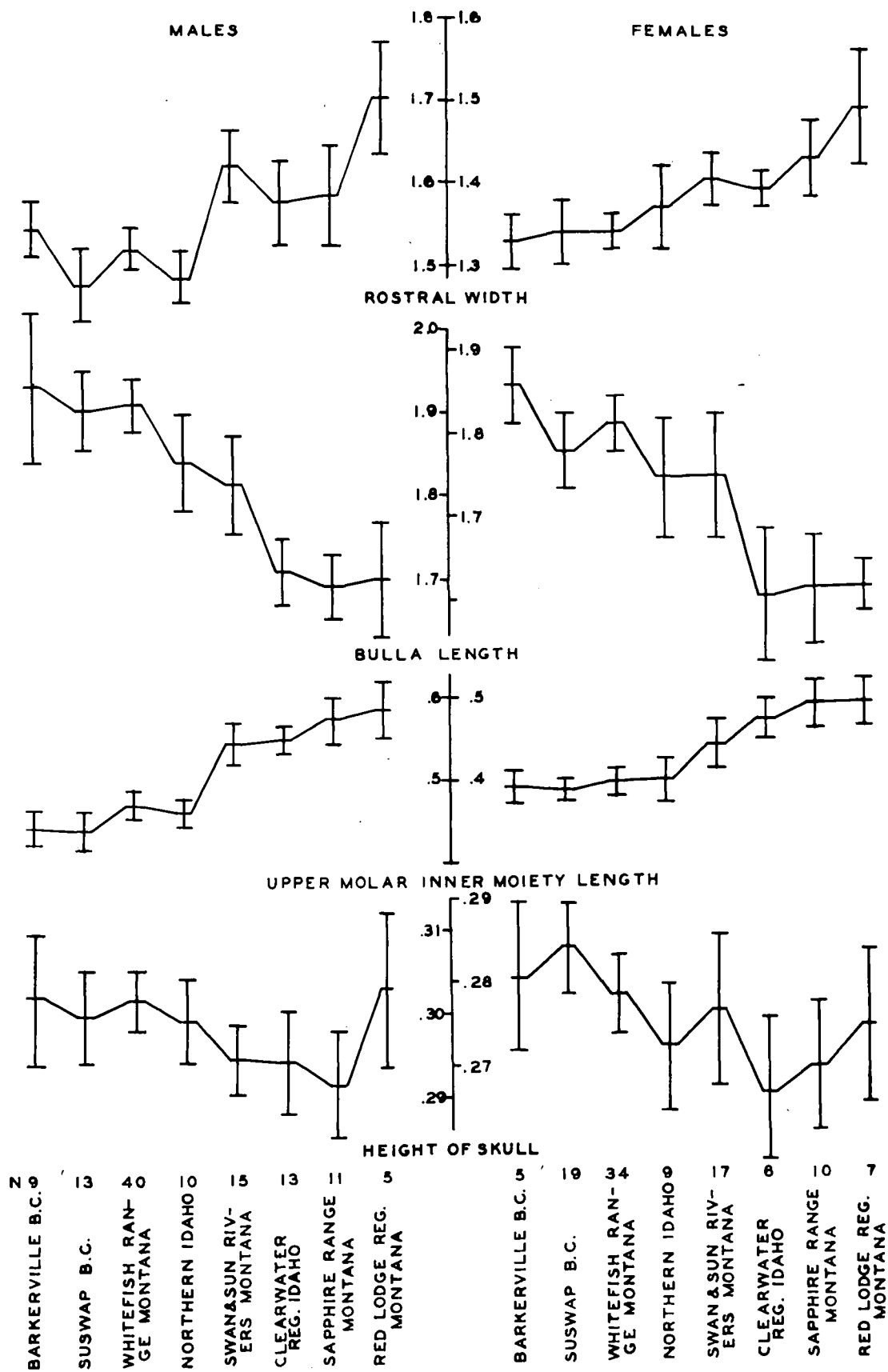
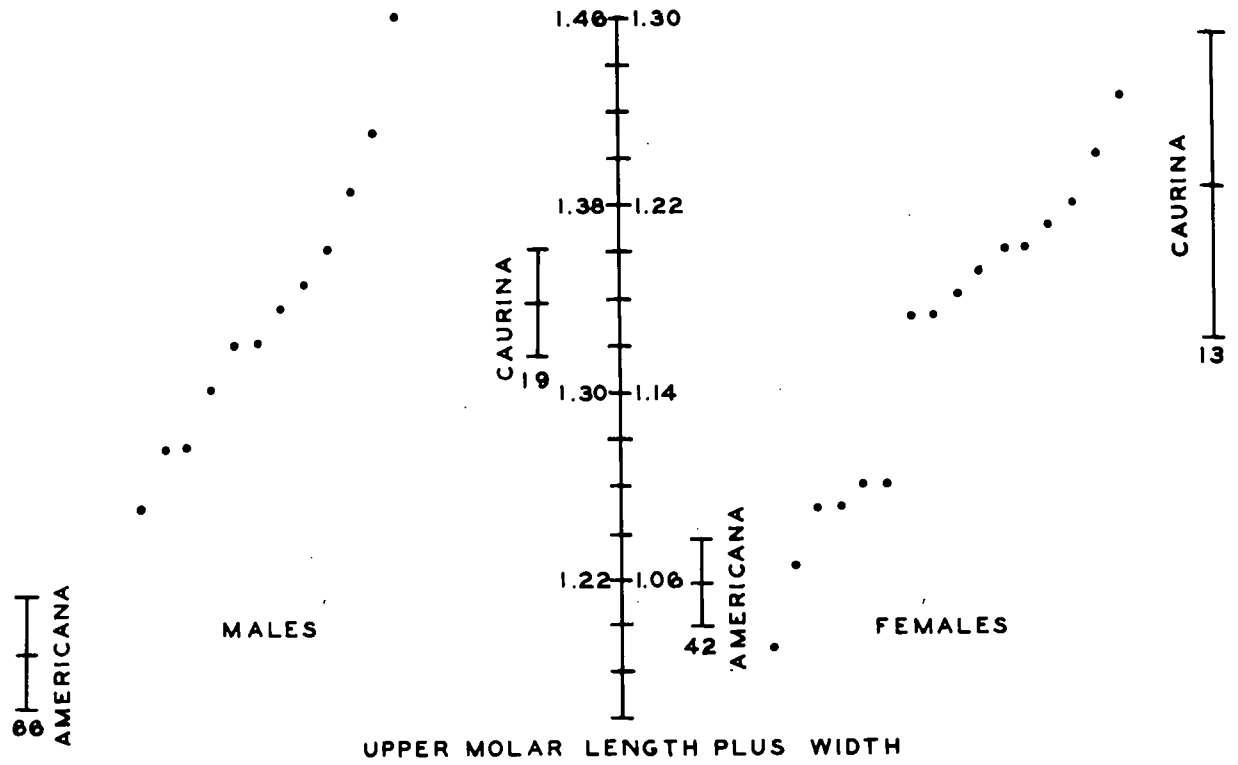
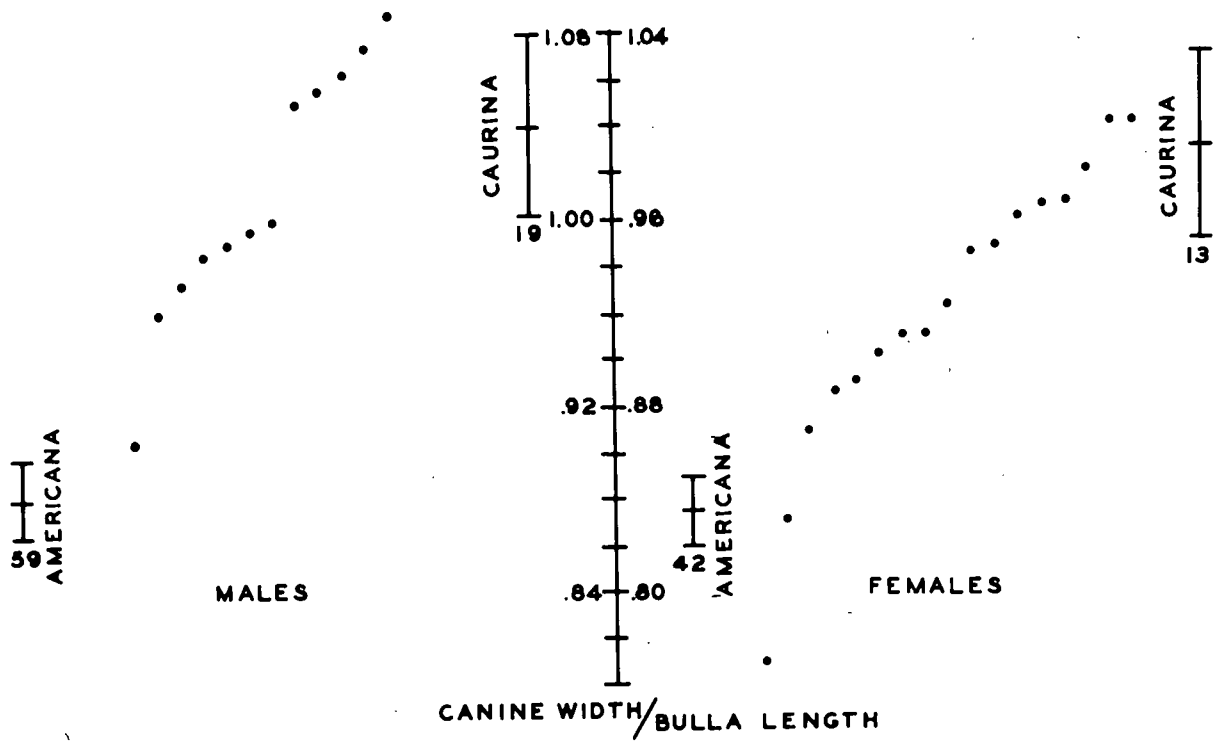


Figure 10
(To face page 235)

Figure 10. Evidence of intergradation between "Martes americana" and "Martes caurina" in Manning Park, British Columbia.

Each dot represents a single specimen.
Comparative samples from adjacent populations of americana and caurina are given, the \bar{x} and $\bar{x} \pm SE_x$ being shown.



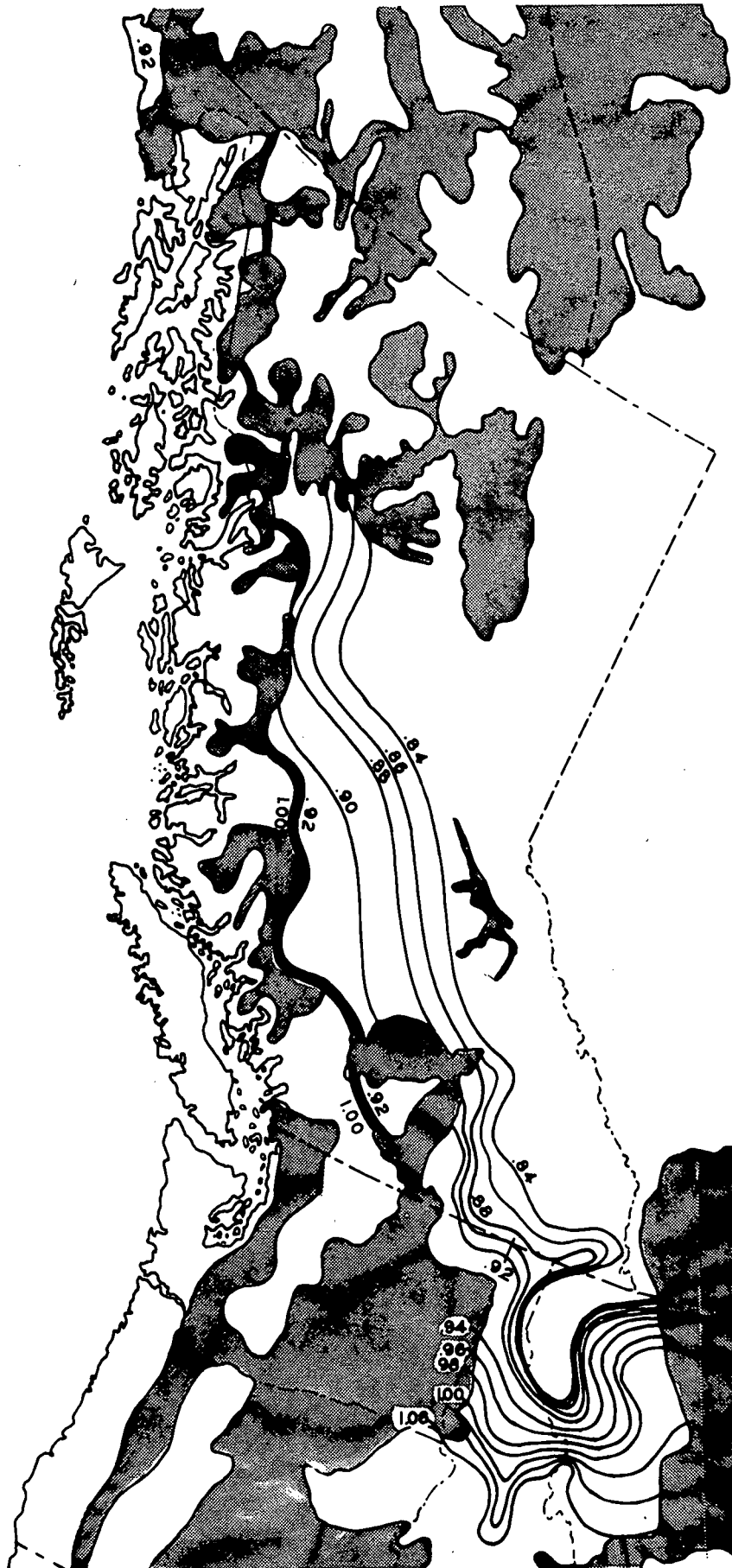
and Chichagof Islands of the Alexander Archipelago, Alaska. It is likely that if marten have ever occurred naturally they would be referable to "caurina". The possibility exists that the introductions were made from "americana" stock. If this is so, and native marten still occurred on the islands at the time of introduction, an opportunity for examination of the specific relationship of the two "species" would be available.

Since true intergradation appears to occur between these two primary kinds of marten, and since all other named forms are much less distinctive from each other (within their group americana or caurina), it follows naturally, I believe, that these lesser named forms almost certainly intergrade, or are capable of intergradation within themselves. I take this last conclusion for granted in the remainder of this paper.

Distribution: I do not know positively whether or not the supposed "species" "americana" and "caurina" intergrade everywhere within their range where they meet, but presume that they do. With this point in mind I have prepared a map showing the geographic distribution of the ratio canine width / bulla length, on Figure 11. This ratio is as easy a means of distinguishing the two "species" as any, although other characters or ratios or sums are nearly as valuable (Figure 9). The areas of greatest rate of change, as mapped by isopleths, have been determined from specimens in southern British Columbia, northeastern Washington, Idaho and Montana. In coastal British Columbia, and the Alaskan panhandle, they have been determined both by

Figure 11.
(To face page 236)

Figure 11. Distribution of the boundary separating "Martes americana" from "Martes caurina". The index mapped is the ratio canine width at base / bulla length.



reference to specimens and more so through reference to maps showing the distribution of the Coast Forest and mountains as mapped by Zon and Sparhawk (1923), Raup (1945), Munro and Cowan (1947), Macdonald (1951), Halliday (1952), Edwards (1950), Macleod (1950), Bandy (1952) and Webb (1952). This figure shows that, insofar as specimens allow determination to be made, the area of greatest change in Washington, Idaho, and Montana (ratio of canine width / bulla length changing from .88 to .92) occurs in a strip 40 to 80 miles wide through the following counties: northern Stevens and Pend Oreille Counties, northeast Washington; Boundary, Bonner, eastern Kootenai, Shoshone and northeast Clearwater Counties, northern Idaho; northeast Lincoln, southern Mineral, western Missoula, eastern Sanders, western Lake, central Flathead and western Glacier Counties, Montana. To the north of this area of intergradation, typical "M. americana (abietinoides)" is attained; south of it, however, gradation into "M. caurina" is more gradual, its effects being seen as far south as Idaho and Valley Counties, Idaho, and Lake, Missoula, Powell and Lewis and Clark Counties Montana. In actual fact, the exact intermediate isopleth between the two "species" is about .95, which lies about 40 to 60 miles south of the above named boundary. I choose the former (.88 to .92 isopleths) because here a much more rapid rate of change occurs.

The marten of northeast Washington, it will be noted, while not typical "caurina" (tending towards "americana") are best referred to that race.

In southern British Columbia, the area of rapid intergradation extends apparently through the Lumby area to the Okanagan dry belt area. West of this area, intergradation has been noted occurring in Manning Park; marten to the east, in the Merritt-Vernon area being "americana", to the west and south, "caurina".

I have detected no other direct signs of intergradation between the two "species", but conclude that it likely occurs in the river valleys cutting the Coast Mountains, on the eastern limits of the Coast Forest. The specimens at hand indicate this is so, or at least, all specimens west of this arbitrary limit are "caurina", all east of it "americana".

East of the Coast Mountain-Intermontane Plateau boundary marten show the "caurina" influence for a considerable distance, the .85 isopleth passing on a line drawn (approximately) from Revelstoke through Prince George. West of this line, to the boundary referred to above, the ratio value increases gradually, to the .90 isopleth, about 100 miles from the boundary in the Chilcotin River area. No specimens have been examined from this area to the coast. The "caurina" influence east of the Coast Range, is, I think, added proof of the idea that the two "species" intergrade on the eastern edge of the coast range.

The maps of Chantz and Zon (1923) and Raup (1945) indicate that the Coast Forest extends up the Alaskan panhandle in isolated patches, in the river valleys, as far as the Kenai Peninsula. While to the south, "caurina" appears restricted to this forest, I do not think it extends nearly this far north.

The most northern specimens definitely referable to this "species" are from near Juneau. One specimen is unusual in that it shows characteristics intermediate between "americana" and "caurina", but nearer the former (ratio of canine width / bulla length .92). This specimen is also extremely large and its proper designation is the more difficult. It is unfortunate that a larger sample from the area is not obtainable.

There is little reason for giving a detailed description of the ranges of these "species", these being given in the part above, in the "subspecies" descriptions and on the map referred to above (figure 11).

Characteristics: Having pointed out that all martens of North America are divisible primarily into two basic types, having shown that at least in part of their ranges these two basic types appear to intergrade, and having attempted to map the area of intergradation, it is important that the morphological characteristics of these two basic types, whether designated "species" or "subspecies", be discussed. In so doing, I use Allen's nomenclature for the time being, considering them distinct "species" for the sake of convenience.

The characteristics given in the original description of "Mustela caurina (= "Martes caurina caurina") by Merriam, and later by Rhoads, are still perfectly valid when applied at the "species" level to "Martes americana" and "Martes caurina". Much of the account that follows is built around their descriptions, but in all cases has been tested by myself, and added to, especially regarding quantitative data. A preliminary

description of the two "species" was given under the discussion of the species of the marten of the world. There comparison was made primarily to Old World forms. Here the comparison is explicitly restricted to the two New World kinds, and is of a different and more detailed nature.

It is suggested that the reader have specimens of the two "species" of marten before him as he reads this discussion; if none is available reference may be made to Figures 1 and 2.

"Martes caurina" may be distinguished from "M. americana" by the following characteristics: fur shorter, with comparatively less underfur; colour richer brown, inclining often more to cinnamon in upper parts; distribution of colour on upper parts more uniform with head not so much paler than spine, and ears and cheeks not so much paler than head; throat and breast patch usually larger, often extending to vent, orange red rather than whitish or yellowish; tail with hairs on tips relatively longer, without hair tips relatively shorter (less than one half head and body length rather than about equalling half of it), tail vertebrae averaging fourteen rather than seventeen; skull more massive, especially in posterior part, relatively broader and flatter, so that zygomatic breadth is slightly more than one half condylobasal length rather than about equalling it; less prone to the development of heavy sagittal crests; rostrum and interorbital area especially wider, the rostrum averaging less than 1.52 cm. in "americana" and more in "caurina", but with overlap between the ranges occurring; rostral sides convergent rather than parallel, and with a less

developed constriction behind canines; supraorbital constriction slight, sometimes absent, not moderate and always present; post-orbital processes nearer point of greatest constriction than to anterior root of zygoma, rather than being about midway between the two; frontal profile less sloping; zygomatic arches shorter, broader, highest near their middle, rather than their rear; palate shorter (averaging 3.8 rather than 3.9 cm., but overlapping), broader (averaging .83 rather than .79 cm., but overlapping), less extended behind plane of last molar, often truncate behind rather than marked by an azygos notch; bullae shorter, less inflated, and broader, squared anteriorly rather than rounded, so that the ratio of canine width at base / bulla length is almost always more than .96 cm. rather than less; the bullae are also more widely spaced so that twice the distance between the carotid canals is greater than the greatest length of bulla, rather than the same length or slightly less; the distance between the outer edges of the jugular foramina is greater than the greatest length of bulla, rather than being less; the distance between the carotid canals is about two thirds the distance between the foramen lacerum posterioire and the eustachean foramen, rather than being about one half the distance; the mastoid process extends beyond the meatus, rather than not; the lower jaw is heavier, relatively longer; the dentition generally is stronger, and more often crowded; PM^1 is smaller; PM^4 is larger, with inner lobe thicker, and often extending nearly to anterior edge of trenchant part, rather than not; inner lobe usually placed diagonally rather than perpendicularly to plane of

trenchant part; width of inner lobe x 100 / width of trenchant part nearer to 71 than 69; width of inner lobe x 100 / length of trenchant part nearer 27 than 25; breadth of PM^4 (across inner lobe) x 100 / length of trenchant part nearer 66 than 61; M^1 larger, with a relatively much broader inner lobe, hence the whole molar appearing triangular rather than rectangular in shape, and hence upper molar width plus inner moiety length nearer 1.29 cm. than 1.17 cm (though with overlap), and lateral length of tooth x 100 / mesial length nearer 72 than 82, and mesial length x 100 / breadth of same tooth nearer 65 than 62; inner lobe of M^1 with tendency toward a double median tuberculation rather than a single elongate tubercle; breadth of M^1 relatively greater than length of PM^4 , the ratio of the two being nearer 1.00 than .95; lower canine often less strongly curved; PM_1 smaller, PM_2 and PM_3 shorter, thicker; M_1 longer, thicker, higher, its length, however, usually less instead of more than the length of inner lobe of M^1 , and equalling instead of exceeding the greatest width of PM^4 ; inner cusp (protoconid) usually present in "caurina" more often rudimentary or absent in "americana".

The above comparison is rather detailed, yet once having examined specimens of the two "species", the reader will at once be able to distinguish the two. "M. americana" has essentially a long, narrow, high skull, with narrow rostrum, small upper molar and long well inflated bullae; "M. caurina" has conversely a shorter, broader, flatter skull with broader rostrum, larger upper molar and shorter, broader, less inflated bullae. The

best single index for separating the two, is the ratio canine width at base / bulla length, which is always more than .96 in "M. caurina", always less in "M. americana". If the sex of the specimen to be determined is known, an even more precise identification may be made; here males with a ratio larger than .965 are "caurina", with smaller "americana" and females with a ratio larger than .92 "caurina", and smaller "americana".

FISHERS

Distribution

The distribution of fisher, when compared to that of marten in North America, is similar, but by no means identical to it. Its northern limit is 10° south of that of marten, and while it extends as far down the Pacific mountains as that animal, it does not in the Rocky Mountains and conversely, in the east, it extends even further south.

Part of the explanation for the distinctive nature of the fisher's distribution may be found in its environmental needs. Meriam (1882-84 and 1886) reports that fishers are said to feed on beech nuts, though he concludes that it does not occur in his area of study. Rhoads (1903) said many were caught in the beech woods of Pennsylvania. Shorger (1942) said that although the fisher of the Lake States were "never as numerous as the marten, it was far more common than the latter in the hardwood timber". De Vos (1951) says that they are present in second growth forest where marten are absent. De Vos (1952) also says that while they prefer heavy timber, they are frequently seen

in open second growth stands and occasionally in recent burnt-over areas. In Ontario the animal is not too strict in its habitat requirements, in that it occurs in coniferous, mixed, and maple-yellow birch forests (de Vos 1952). Mason (1924) and Martin (1950) report it to range over burnt-over areas of Willow, birch and aspen. Barger (1951) said it lives through the hardwoods of Wisconsin. In the area about Great Slave Lake, the fisher often occurred in the grassy prairies at the mouth of the Slave River (Ross 1861a). Edwards (1950) also reports they occur in areas showing grassland influence.

Fisher are also supposed to stay at lower altitudes than marten. Rhoads (1903) says they prefer low, wet grounds and the banks of streams, in Pennsylvania, whereas the marten stays on the hills. In the mountain regions of the west the fisher is reported to live in the lowlands with the marten, but only the marten lives in the higher country (Rand 1944a, Edwards 1950, Webb 1952). The life zones in which the fisher lives are reported to be the humid Transition and Canadian zones (Rhoads 1903, Grinnell, Dixon and Linsdale 1936, Bailey 1936, Rust 1946, Dalquest 1948). Rhoads (1903) says that in Pennsylvania they also occur in the Hudsonian zone.

The distribution map of fishers (Enclosure C, inside end cover) is based on the specimens examined and a survey of the literature. The limits of the range are taken from the maps listed under the topic marten distribution, together with the fisher distribution maps of Seton (1925-1928), Seton (1909), Cory (1912), Hamilton (1943), Burt (1948), Anderson (1934a),

Brouillette (1934), Grinnell, Dixon and Linsdale 1937, Lyon (1936), Melven (1938), Dalquest (1948), Bailey (1936), de Vos (1952), Webb (1952), Bandy (1952), Macleod (1950), Edwards (1950). The remaining sources are listed in Appendix D.

The following authors have shown that fisher numbers have been greatly reduced in the last century: Seton (1925-1928), Allen (1942), Minville (1946), Innis (1927), Anon. (1927-1950), Henderson and Craig (1932). Locally, however, recent increases in numbers have been reported.

Fishers are known only from North America. Poland (1892) erroneously states, however, that "a few are still found in South America, and skins from these parts having only hair".

Alaska: Coues (1877) said that he examined specimens from Alaska, but did not give a specific locality of capture. Remarking on this, Osgood, in 1900, reported that "no specimens are at hand to corroborate this record, but there is little doubt that it occurs along the upper Yukon, as it is known from similar latitudes to the eastward". In actual fact, Turner (1886) has stated that it "occurs sparingly in the upper Yukon valley; rather more abundantly in the heavier timbered regions to the south". Other than the above statements I know of no record of the occurrence of fisher in Alaska. Macleod (1950) records it from the lower Iskut region of British Columbia, very near the border of Alaska and it may quite possibly occur in the very southern part of the adjacent panhandle.

Alberta: All of forested Alberta, at least as far south in the west as Prairie Creek near Rocky Mountain House (specimens examined) and in the east as far as the Athabaska River (Preble 1908). Rand (1944a) says it occupies two-fifths of the north and west of the province. L. Butler (letter) reports that Alberta has the last fisher of any of the three Prairie Provinces. Its catch has come chiefly from Fort Vermilion, Little Red River and Sturgeon Lake. Rand (1948a) says it is "now scarce in, or unreported from, many areas."

Arkansas: Brown (1908) reported a Pleistocene recovery of Martes pennanti from Conard Fissure in Newton County. Hall (1936) believes these may possibly be referable to M. diluviana (a small extinct fisher). No recent records of occurrence are known.

British Columbia: Still common through most of the forested part of the province. Occurs in the following Biotic Areas of Munro and Cowan (1947): Coast Forest, north to the Iskut River and south to the region about Namu and Rivers Inlet (Macleod 1950); apparently absent south of this area, excepting for the region about Manning Park (specimens examined, Carl, Guiget and Hardy 1952, Goldman 1935, Rhoads 1898, Edwards 1950); Subalpine Forest, at least as far north as Ware on the Finlay River (Bandy 1952) and as far south as Kamloops and Salmon Arm (specimens examined), Cariboo Parklands (Webb 1952 and specimens examined); the northern parts of the Columbia and Dry Forests,

apparently no farther south than about Invermere (Bandy 1952); Boreal Forest, east to the Alberta boundary (Edwards 1950, Rand 1944c, Quick 1953, Baker 1951, specimens examined and other sources), and west to the Lower Post area (Rand 1944c, Edwards 1950). Also present in the area about Dease Lake and Anvil Mountain (Edwards 1950). Are apparently absent northwest of a line connecting the Lower Iskut River, Dease Lake and Lower Post. Occurs in the Peace River Parklands, including the Peace River area (Cowan 1939, Edwards 1950) and the area about Fort Nelson (Quick 1953, Edwards 1950 and specimens examined). Does not seem to occur in the Parklands much east of Fort Nelson. Is absent from any of the islands along the coast. A specimen is listed in the U. S. Fish and Wildlife Service card file as having been taken from Graham Island, Queen Charlotte Islands, but Mr. J. A. Munro, the collector of the specimen, says this statement must be due to a clerical error. Two unmapped records for the province are New Caledonia (Macfarlane 1905) and Buckingham area (Rand 1944a).

California: The mountainous part of the state, from the Oregon boundary south to the Klamath and Coast Ranges to the region about Lakeport, Mendocino County and Lake County. It is also recorded from Main County. South in the Sierra Nevadas to Greenhorn Mountain, Kern County (Sumner and Dixon 1953, Grinnell Dixon and Linsdale 1937). According to most authors its numbers are now very much reduced. Records not mapped include Fort Crook (?), Cahlo, Big Creek, Mariposa County and Atwell's Mill (specimens examined).

Colorado: "Said to be more or less common in Park County ..."
(Allen 1874). Commenting on this, Cary (1911) says "I have made careful inquiry of old hunters and trappers throughout ... northern Colorado ... and have yet to meet one who ... has even heard of the animal within the state.... It seems probable that Allen's record is based upon erroneous information".

Warren (1942) says that "there have been rumours of ... [its] occurrence", but concludes that it has never occurred there.

Yeager, Denney and Hammit (1949) refer to it as "rare, if present at all in the original fauna, has been extirpated...." R. Denney (letter) says that two were imported from British Columbia five years ago, and are now living in captivity in the state. I know of no other records for the area.

Connecticut: Linsley (1842) listed the fisher as occurring in the state. Goodwin (1935) reported that it "has supposedly been extirpated for many years; it is not impossible, however, that a few individuals may still survive in the wilderness of the northwestern section of the state or in the highlands of the northeast". He states that 124 fishers were trapped in the state in 1924.

Idaho: The mountainous part of the state, including the Selkirk, Bitterroot and Salmon River Ranges, as far south originally as Sawtooth (specimen examined), Ketchum and Alturas Lake, all in Blaine County (Davis 1939). Now probably restricted to the northern and central part of the state (Davis 1939, Rust 1946) and very rare (Davis 1939).

Indiana: Apparently the fisher ranged originally through most or all of the state. Plummer 1844 says that it had not been seen since 1820, but that prior to that time "it was not uncommon". Lyon (1936) says the last specimen was taken in 1859. Lyon (1933) considered it a "wanderer from the north. ... [It] can scarcely be considered to have been a normal inhabitant of the state". Records are known from the following counties: Porter (Rand and Rand 1951), Hamilton (Lyon 1936), Wayne (Plummer 1844, Hahn 1900), Posey (Lyon 1936, Hahn 1909), and Ohio (Kirkpatrick and Conway 1948).

Illinois: Kennicott 1855 reported fisher from Cook County, saying they used to be common in the timber along Lake Michigan. The same author in 1859 said they occurred in the woods of the northern part of the state. Sanborn (1925) said they have occurred within historic times about the Chicago region. Forbes in 1912, reported they "have long been extinct in this state". The record from Posey County, Indiana, suggests that at one time they may also have occurred in the southern part of Illinois.

Iowa: Goding (1883) (after Scott 1937) considered the species "rare" in the state, and Scott (1937) cites Spurrell (1917) as reporting that fisher tracks were observed in Calhoun County in the 1850's, and that several skins were traded somewhere north of Sac County at about the same time. Scott considered these records open to question, but believed that the fisher may at one time have entered northeastern Iowa as a straggler before and during the days of early settlement.

Maine: In all but the southern part of the state occurring at least as far south as Brownfield (Coulter 1952), Lincoln (Rhoads 1898), and very southern Aroostook County (Hardy 1910). Coulter (1952) says "it is now common north and west of a general line from Brownfield to Rumford, Strong, Bingham, Guilford, and Katahdin Iron Works, thence north to Mt. Katahdin, Portage, and St. John Plantation. [Also found in] ...two districts in northwestern Franklin County close to the Canadian border". The same author adds that "one of the most remarkable changes in the distribution and abundance of any animal has been that of the fisher. It is now common ... [whereas] ten years ago it was reported as rare...."

Manitoba: Originally all of Manitoba south of a line connecting Stony Lake (Melven 1938), Churchill River (L. Butler, letter) and York Factory (Preble 1902) and north and east of Riding Mountain (Green 1932) and Assiniboine (Seton 1925-1928). "Are now found chiefly between the Ontario border and Lake Winnipegosis, with a few further north along the Churchill River. The province has the highest catch of any of the Prairie Provinces. The chief collecting points being Little Grand Rapids, Berens River and Norway House" (L. Butler, letter). Fisher were taken in 1952 in the following sections: Wabowden Lake, Sherridon Lake, Norway House, Oxford House, Island Lake, Pukatawagan, God's Lake, and Cross Lake (Malaher 1952). Mr. J. Bryant tells me that they have increased in numbers and extended their range in the past several years.

Maryland: Although no definite records exist for the state, Mansueti (1950) believes that it probably occurred in Garrett County and the portions of western Maryland more than two centuries ago. Hamilton (1943) records a specimen captured in 1921 in Holtwood, Pennsylvania, only about twelve miles from the Maryland border.

Massachusetts: Originally, at least, through the Berkshire Hills and Green Mountains of the western part of the state (Emmons 1840, Allen 1869, Allen 1904). According to Allen (1904) extinct at time of writing.

Michigan: Originally probably all of the northern peninsula, and in the southern part at least as far south as Wexford, Gratiot, Ingham, Washtenow and Wayne Counties (Burt 1948, and specimens examined). Pruitt (1951) says they have been known on Sugar Island. Shorger reports the last specimen trapped in 1930-31. Burt (1948) says it is now very rare or absent. Locality not mapped: Park Siding (Elliot 1907).

Minnesota: At one time fisher occurred throughout the northeastern half of the state, their southwestern limit being a line connecting eastern Pennington, southern Clearwater, southern Crowwing and southern Ransey Counties (Shorger 1942, Gunderson and Beer 1953, Swanson, Surber and Roberts 1945). Were formerly numerous, but are now rarer and restricted to the extreme northern and eastern portions of the state and are still taken there in small numbers. (Swanson, Surber and Roberts 1945, Gunderson and Beer 1953). An unmapped record is Big Bog (Shorger 1942).

Montana: Only three records within the state are known to me: these are Glacier National Park (Allen 1942), Swan River, South Fork and upper Swift Current River (Bailey and Bailey 1918). Only the first two of these have been mapped. Fletcher E. Newby (letter) informs me that these records are so unreliable as to be considered unauthentic. Because it occurs in central Idaho, and northern Wyoming, it seems hard to doubt that it may possibly have at one time occurred throughout much of the Montana section of the Northern Rockies, even though it is now absent from southeastern British Columbia.

Nebraska: Swenk (1908) believes that it likely occurred within the state, but finds no record of its presence.

Nevada: "Occurs in the Sierra Nevada of California and may occur in these mountains between Carson City and Reno". Satisfactory evidence of its presence within the state is lacking (Hall 1946). Grinnell, Dixon and Linsdale (1937) in their mapping of the fisher's distribution in California show it to extend its range into Nevada.

New Brunswick: Original range not known, but at present restricted to the central and northern parts of the province (Rand 1944a, Morris 1948). Bruce S. Wright (letter) says fisher tracks were observed in 1953 in the Burpee Game Reserve in Sunbury County, where a fisher brought from Ontario had been released in 1950. This record is the most southerly known in the province. Chamberlain 1884 and 1892 considered the fisher

rare at time of writing, but Wright (letter) says a few are still taken each year.

New Hampshire: Originally through all of the White Mountains and northward (Allen 1904). Records are known from the very northern part of Coos County to southern Cheshire County in the very southern part of the state (specimens examined). Carpenter and Siegler (1945) and Hamilton (1943) say it is still present, and N. Preble (letter) says two were taken in 1936. Helenette Silver (letter) says a specimen was trapped in 1951 at Warner, and adds that "I have heard well authenticated rumors of others being taken by trappers who were afraid to turn them over to us as they are fully protected.... It is probable that they are more common than we know". Mr. F. Fay, of the University of British Columbia, has kindly pointed out that he recollects that two young fisher were captured in 1949 or 1950 near Lake Ossipee in the east central part of the state, and that another was seen by Mr. Charles MacLaughlin, formerly of the University of New Hampshire, on the road at Pasaconaway near North Conway in 1948. Mr. Fay says he has seen fisher tracks at Pasaconaway himself at about the same time. An unmapped record for the state is "Greenough Trail" (Helenette Silver, letter).

New Jersey: Abbot in 1868 said that "about the mountains in the northern counties a few are still living". In 1889, Nelson reported a few to persist in the northern part of the state. Rhoads (1903) knew of no record other than Abbott's; he concluded

that "it undoubtedly occurred in former days in the northern sections...."

New York: Formerly throughout all but the southwestern part of the state, extending as far west as Buffalo (Miller 1899) and as far south as Buffalo, Munro County (specimen examined), northern Delaware County (specimen examined) and Rennselaer County (Audubon and Bachman 1851-54). Grant (1906) reports that it was largely confined to the Adirondacks by 1842, although Mearns in 1898, reported they were still occasionally taken in the Catskills, and Miller's Buffalo specimen was captured in 1899. By 1900 it was closely restricted to the Adirondacks (Grant 1906) where it still occurs. An anonymous article in the New York State Conservationist (reprint no. 12) says the fisher has recently been increased markedly in numbers. An unmapped record is Brownstract (specimen examined).

North Carolina: Known only from one specimen reported by Audubon and Bachman (1851-54) as taken from Buncombe County, in western North Carolina. Kellogg (1937) says it once occurred in the state. Aside from the Pleistocene fisher found in Arkansas, this is the most southerly record known east of the Great Plains.

North Dakota: Audubon and Bachman (1851-54) report having "seen many skins from the upper Missouri", presumably from this state. Bailey (1926a) says they formerly occurred in the northeastern part, but that they are now extinct. Records are known from eastern Cavalier, Pembina, Walsh, Grand Forks Counties and

Hair Hills. The last of these is unmapped (Bailey 1926a, Swanson, Surber and Roberts 1945, Over and Churchill 1945).

Northwest Territories: Known only from the Mackenzie District, never being recorded, to my knowledge, from Keewatin. Were originally well known as far north as Resolution on the shore of Great Slave Lake (Richardson 1829, Ross 1861a and b, Macfarlane 1905, Russell 1898, Preble 1908, Seton 1911), although never common at its northern limit (Ross 1862, Macfarlane 1905, Russell 1898). Russell says they are not found between Great Slave and Athabaska Lakes except along the Slave River, which is its eastern limit, although they were common on the numerous deltas of the Slave (Ross 1861a). Russell says that to the west they have been seen just north of Providence, and the Liard River has been considered a more westerly northern limit (Preble 1908, Seton 1911, Mason 1924). Seton (1911) said that the natives considered the point where the north Nahanni enters the Mackenzie the most northerly limit of the fisher in the District. Patterson (1954, pp. 76 and 180) saw fisher tracks on the south Nahanni northwest of Caribou Creek and in Deadman's Valley. Macfarlane (1905) says specimens have been taken at Whitefish Lake, which I locate about 125 miles east of Resolution, and Clarke (1944) says they have been taken at the headwaters of the Anderson River, which I map north of Great Bear Lake. Both of these are so far outside the range of fisher as I know it, that I must presume them to be errors of mapping. The numbers of fishers taken in the Territory has never been great, and now very low. Clarke (1944) says that "for a number of years no

fisher have been reported from the Mackenzie District except in the Fort Liard area. At this post a very few skins from the Mackenzie District are traded annually".

Nova Scotia: Gilpin (1868) listed it as present, but there has been no record of it since (Smith 1940, Allen 1942, Rand 1944b).

Ohio: Kirtland (1838) stated that two specimens had been taken in Ashtabula County in 1837. Brayton (1882) listed the fisher as a member of the state's fauna. Bole and Moulthrop (1942) say that a specimen taken in the state (possibly Kirtland's) was held in the Cleveland Museum of Natural History. Leedy (1950) considers the marten rare or absent in the state. No other records of the occurrence of fisher in the state are known to me.

Ontario: Formerly present, apparently through all of the province except the unforested lowlands bordering Hudson Bay. Now its range extends no further south than the French and Mattawa Rivers, and Algonquin Park (Rand 1944a, Downing 1948, de Vos 1952). De Vos (1952) map shows the population to be divided into three major groups, one centering around Central Patricia, one around Timmins and one around Algonquin Park. Originally the fisher occurred to the very southern end of the province as the following records show. Audubon and Bachman (1851-54) record one shot at Port Hope. Gapper (1830) mentions one taken between Toronto and Lake Simcoe. Saunders (1932) stated he had been told they had occurred at Rondeau at Burks Falls at the turn of the century. Richardson (1952) believes they once occurred in the upper Thames Watershed.

Wittemburg (1939, 1948) records them from the late pre-European middens of London and Brantford. Not mapped are McClure Township and Quinte Forest District (de Vos 1952).

Oregon: Through the Coast, Klamath and Cascade Ranges of the state, from the northern to the southern boundaries, as far east as eastern Hood River, eastern Douglas and central Jackson Counties (Bailey 1936). Also present in the Blue Mountains of the northeast, at least as far east as central Umatilla County, and as far south as southern Union County (Bailey 1936). According to Bailey, is united with the western population in the area north of the High Desert and the Harney Basin.

Pennsylvania: At one time through all of the northeastern half of the state (Rhoads 1903), occurring as far south as Forest, Elk, Clearfield, Centre, Cumberland, and Lancaster Counties (Rhoads 1898 and 1903, Shoemaker 1919, Hamilton 1943 and specimens examined). Roslund (1951) believes the fisher had become extinct in the state by 1903, but Hamilton (1943) records the taking of one in the southern part of the state in 1921. Localities not mapped include Second Mountain and Peter Mountain (Shoemaker 1919) and Mountain Bog above Strausstown (Poole 1932).

Prince Edward Island: "In Prince Edward Island ... there are now no fisher" (Rand 1944a). Whether Rand meant this to signify that fisher have been known from there or not I do not know.

Quebec: Known only from Quebec south of a line connecting the southern end of James Bay, Lake Mistassini, and Mingan (Bell 1884, Low 1895 and 1896, Anderson 1938 and specimens examined).

Stearns (1883) says it is found occasionally in the southern portion of Labrador, but I have no other record of this.

Eidmann (1935) says the natives report it to come occasionally into the Matamek region. Hunter (1907) says that " ... prior to about the year 1860 the fisher ... was ... unknown to the trappers on the north shore ... east of the Saguenay and it was only after that year that an odd one was trapped in that lower country...." On the south shore of the Saint Lawrence it is reported from Ile Ste. Helene (Achintre and Crevier 1876) and the Gaspé Peninsula (Goodwin 1924, Cameron 1853). Newsom (1937) says that no fisher are known from Anticosti and while two were released there a number of years ago, there was no trace of their presence at time of writing. Fisher have become very much scarcer throughout the province than they originally were (Neilson 1948, Cameron 1953, Minville 1946). Localities not mapped: Eureka Lake, Pontiac County (specimen examined).

Rhode Island: Included by Mearns (1900) in his list of extinct animals formerly present in the state. I know of no other records.

Saskatchewan: Forested Saskatchewan, as far south at least as Little Red River (L. Butler, letter), and Red Earth (specimens examined). While once present in Prince Albert Park, it was long considered absent; since 1945 a few animals have been observed in the area, however (Soper 1952). Are now collected chiefly near the Saskatchewan and Churchill Rivers, Lac la Roche, Montreal Lake and Cumberland House (L. Butler, letter).

South Carolina: Said by Seton (1925-1928) to occur as far south, in the mountains, as South Carolina. I know of no other record for the state and Seton's is probably incorrect.

South Dakota: "There is no authentic record that it was ever taken in South Dakota territory, but early trappers mention it as frequently seen in the Red River valley of North Dakota, and it is likely that before the advent of white man it inhabited the timber regions of the eastern side of the state.... No doubt it lived sparingly in the Black Hills in the early days" (Over and Churchill 1945).

Tennessee: Known only from specimens taken in western Cumberland County and Cocke County (Audubon and Bachman 1851-54), Merriam 1886 and Rhoads 1896). Has likely been extinct for at least 75 years.

Texas: Lydekker (1901-04) and Anthony (1917) both report it to occur in the northern part of the state. I believe both these records to be in error.

Utah: Durrant (1952) includes the fisher in the state's fauna on the basis of photographs of fisher tracks taken by William Marshall at Trial Lake in Summit County in 1938. Other tracks were seen in the same place the following year. Durrant considers the evidence for the fisher's presence in the state "unimpeachable".

Vermont: Known originally throughout the Green Mountains of the state from la Moille to Rutland Counties (Kirk 1916, Osgood

1938, Foote 1944 and specimen examined). By 1916 had been confined to "the wildest mountain districts" (Kirk 1916) and by 1938 was very nearly extinct (Osgood 1938). Its present status in the state is uncertain (Foote 1944). Locality record not mapped is Meridan (Kirk 1916).

Virginia: The "account showing the quantity of skins and furs exported annually ... from Virginia from ... 1698 to ... 1715" lists fisher as being taken, according to Bailey (1946).

Audubon and Bachman (1851-54) say they saw it on the mountains of the state, and Allen 1876b says it once occurred there.

Poland (1892) suggests that its German name "Virginian Fitch or Polecat" implies it was once found there. Handley and Patton (1947) report "we have been told by old residents of the Crab-bottom section that 'black foxes' had been killed in Highland County as late as 1890 ... and it seems reasonable to believe that these may have been Martes pennanti. Before the advance of civilization ... fishers were probably common in many parts of western Virginia...." Are now extinct (Handley and Patton 1947, Brown 1952).

Washington: Occurs in the Olympic and Coast Mountains from the northern tip south to Gray's Harbour (Dalquest 1948, Elliot 1907 and 1899 and specimens examined). Apparently absent from the Puget Lowland except at low altitudes in Mason and Pierce Counties (Scheffer 1938 and specimens examined). Present in the Cascade Mountains from the international boundary south to the Columbia River as far west as eastern Whatcom, Snonomish

and central King Counties, and as far east as central Okanagan, Chelan and Yakima Counties (Dalquest 1948, Scheffer 1938, Taylor and Shaw 1929, Rhoads 1898, Potts and Grater 1949, Baird 1857, 1859). Dalquest (1948) believes that it is possible a few exist, or have existed, in the Columbia, Selkirk and Bitterroot Ranges of the northeast, and in the Blue Mountains of the southeast part of the state. Localities not mapped are: Iron Creek (specimen examined), Billy Goat Mountain, Head of Cascade River, Granville, Suez (Scheffer 1938).

West Virginia: Originally through most of the mountainous parts, and apparently still present in very small numbers. Surber (1912) reported it formerly quite common, but rare at time of writing. Kellogg (1937) said they were formerly present, and A. B. Brooks (1924) records the taking of one in Upshur County. McKeever, Frum and Berard (1951) review the above records and add to them as follows. Fred Brooks reported in 1911 that it had been common fifty years earlier, but that it was rare or extinct at the time of relating. The same person reported three to have been caught in 1871, 72 and 73, in northern Boone County. A fisher was trapped in Gilner County in 1949, according to these authors and there appears to be no doubt as to its correct identity. Not mapped is a record from Clear Fork, Big Coal River (Kellogg 1937).

Wisconsin: Reported by Jackson (1908), Hollister (1910), Cory (1912) and Barger (1951) to have occurred at one time through almost all of the state, but to be lacking in any specific

records. Cory (1912) believed it possibly might still be present and Shorger (1942) says positively that it still existed in the state at time of writing. De Vos (1951) expressed belief that it might still be present, but Barger (1951) considered it to have become extinct by 1900. The only locality records available are those given by Shorger (1942) for la Cross, Sauk, Jefferson and Milwaukee Counties.

Wyoming: Known only from Yellowstone and Shoshone Counties in the northwest corner of the state (Skinner 1927, Cahalane 1947, Thomas 1952a and Anon. 1950). This is considered the southern limit in the Rockies (Seton 1929, Allen 1942, Handley and Patton 1947, Sumner and Dixon 1953) although it is now known from northern Utah. It is now considered extinct or nearly so (Skinner 1927, Anon. 1950, Thomas 1952a, James Grasse (letter)). According to Thomas (1952a) the first specimen taken in the state was captured early in the 1920's, although tracks had been observed previous to this time. None have been taken since about 1940 (Anon. 1950). Reports indicate they exist now only in the Absaroka Range of northern Park County (Thomas 1952a).

Yukon Territory: Rand (1944a) says it barely enters the southern Yukon. The same author (1945b) reports that "Mr. Drury of Whitehorse ... trades a few fisher, but they do not average one a year, and he did not know of a single pelt that had undoubtedly been taken in Yukon.... That fisher do occur in southeast Yukon, as usually assumed, is supported by trappers Leitman and Carmen of Tobally Lakes, and Larsen of Beaver River. The former have taken

three in several years trapping; the latter one fisher in several years trapping...." Rand (1945d) says 2 to 38 skins have been traded in Yukon, from 1920 to 1942, with no assurance that any were taken within the Yukon. Turner 1886 reported they occurred in the upper Yukon Valley, but I do not know if he meant that part in the territory or not.

Synoptic examination

An account of the fishers of North America is much simpler to prepare than that of the martens, since only three "forms" have been named, and these always accepted as "sub-species" of a single "species".

As in the case of marten, detailed synonymies are provided in Appendix B. Only the various name combinations are given below.

"Martes pennanti pennanti" (Erxleben 1777).

Synonymy: Martes (or Mustela) pennantii; canadensis; pennanti; melanorhyncha; zibellina nigra; nigra; rufa; piscatoria; godmani; goodmanii; canadensis var. alba; penanti [sic]; hudsonius; vison; lutreola; pennantii pennantii; pennanti pennanti; Viverra piscator; V. canadensis.

Type specimen: None designated that I know of.

Type locality: "North America" (Pennant 1771, Kerr 1792, Turton 1802); " 'New York and Pennsylvania' Pennant" and as a footnote, "typical canadensis [pennanti] must be restricted to the

Alleghenian form" (Rhoads 1898); "Canada" (Miller 1899); "Eastern Canada" (Miller and Rehn 1900); "Boreal America" (Elliot 1901a); "Eastern Canada, that is, Quebec" (Seton 1929); "Eastern Canada (= Province of Quebec)" (Miller and Kellogg 1955).

Most authors now consider Miller and Rehn's designation of "Eastern Canada" as the type locality of this "race", and it is quite adequate.

It has already been pointed out that "M. pennanti pennanti" (Erxleben) is given precedence over "M. canadensis canadensis" (Schreber) as the name for this animal.

Pelage: Described by Emmons (1840), working with Massachusetts specimens, as "Color mostly black; nose, rump, tail and extremities black; face yellowish-gray; ... ears ... with margins whitish ... the color of the head and shoulders lighter, being of a yellowish, or brownish, or ash-gray; hair and fur also of these parts shorter than on the rest of body, darker beneath than above; hair black or dark-brown at the extremity, then ash, and then darker at the roots; fur uniformly brown, and of one color over the body.... There are white spots at the base of the anterior, and a large one between the posterior legs, and a small one on the throat. In another individual there were no white spots. The general color of this was ash above, and nearly black beneath...." In 1792 Kerr had seen both white spotted and non-spotted specimens from eastern North America, but had considered them distinct "species" (Mustela canadensis and M. zibellina nigra).

Rhoads in 1898 gave the first detailed description of the "race" (but including in it "M. p. columbiana"). The colour of an adult male from Pennsylvania he described as with "head and one-half the length of body, gray and black mixed, gray predominating; throat darkest, with snout from tip to line of eyes dark brown. The hinder half of body gradually darkens into a deep chocolate color until it reaches the tail, which is almost black with a tip entirely black. Hind legs and tail viewed at a distance of six feet, look very dark, almost pure black. The fore legs are black, but not so deep. Tips of ears darkest. Two specimens, ... one from ... Maine, the other from ... Idaho [the latter note being referable to "columbiana"] seem to answer closely the above description. The light upper and forward portions of body are a grizzled grayish brown. The long hairs black tipped. The basal half of hairs of anterior back are hair brown. I can discover no color characters to separate the Idaho specimen from the one from Maine, nor do the skulls indicate any reliable differences. The Main skin ... has white patches on lower fore leg, breast and vent, and an immature pacifica has white on throat, arm pits and vent." Rhoads went on to say that these white spots may disappear with age.

Miller, in 1900, described it simply as "dark brown or blackish, darker on underparts; no throat patch." Rhoads, in 1903, describing Pennsylvania fishers, said "the color is variable but a general pattern and hue prevails. It is darker below than above; belly, legs and tail being almost black. The upper parts lighten more and more as the head is reached, from brownish-black

to grayish or even hoary-brown or tawny. The usual patches of lighter color (white) are found on chest, arm pits, or belly between thighs. Old specimens are the lightest colored, some become nearly white."

De Vos (1952) examined a larger series of winter skins from Ontario and described them thus: "the general coloration is dark brown, approaching blackish down the middle of the rump, the tail and the limbs. The nose is blackish also. The head, shoulders and back are often grizzled as a result of the broad whitish sub-terminal bands of the guard hairs. The ears have pale linings and are well covered with short buff-colored fur inside and out. The underparts are dark brown, slightly grizzled with occasional small white patches...."

Variability in the fisher's coat has long been recognized as being rather great. Richardson (1829) described as a new "form" "Mustela canadensis var. alba", which he said "has the nose and feet brown; the rest of the fur is white". This is near albinism, but Audubon and Bachman (1851-1854) wrote that "in some specimens, we have seen a white spot on the throat, and a line of the same colour on the belly; others ... have no white markings on the body; we have seen a specimen nearly white, with a brown head. Another, obtained in ... North Carolina was slightly hoary on the whole upper surface." Elliot (1901a) said they are "variable, but dark. Some specimens are glossy black, including the tail and under parts; others are gray or grayish white on the head and neck, and the base of the tail dark chestnut; the majority of examples have more or less white on the chin, chest and abdomen."

De Vos (1952) examined 200 winter skins from Ontario and concluded that "color variations between individuals are fairly striking. No such variation could be detected between local populations. The overall color of the dorsum varies from pale gray to practically black.... This is true for both sexes, although the gray color predominates in males. A reddish-brown tinge can be noticed occasionally. The texture of the fur is coarser in the male. On the ventral side there is not much variation between individuals, although light backed specimens are slightly paler than dark ones. No large throat patches such as are commonly seen in marten and mink were observed, although a few individuals had one or a few white spots on the throat. The largest white patch is usually found on the belly, anterior to the anus. In some animals white spots are present on the axillas of the front legs which may occasionally be fused on the mid-ventral line and extend anteriorly for a short distance."

Goldman (1935) in his description of "M. p. columbiana" said that the color of the skins were "about as in M. p. pennanti and M. p. columbiana." Rhoads, in 1898, however, when he described "pacifica", thought that skins of that "race" could be told from "pennanti" since they possessed Prout brown colouration on the basal half of the hairs of the anterior back. Grinnell reported, however (Grinnell 1933 and Grinnell, Dixon and Linsdale 1937), that he examined the U. S. National Museum and U. S. Biological Survey collections of skins, and found no means of distinguishing "pacifica" from "pennanti". Bachrach

(1946) assures us, however, that fisher skins from west of the Manitoba-Ontario border are coarser, browner, paler and that "fur fibres seem to be lacking ... because the guard hair is so very coarse."

I have examined a fairly large series of skins of all three "races" and while I find the above descriptions, especially that of de Vos, thoroughly adequate, I conclude that skins are so variable from any one locality as to include the variation shown between the "races". In actual fact I find myself completely unable to distinguish one "race" from another on the basis of skins and conclude that they cannot be used as a means of distinction.

Cranium: Skull described by Rhoads (1898) as "small; nasals relatively short, less elongate at basal apex. Posterior upper molar relatively small, its inner lobe not greatly developed longitudinally so as to only slightly exceed the breadth of outer lobe; neck of crown of same tooth but slightly constricted."

Since this "race" will be the standard for comparison of the remaining "subspecies" I add nothing more here than the statistics of a sample of fisher obtained from east of the Manitoba-Ontario boundary.

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	11.51	.30	2.63	21	9.77	.31	3.16	17
Upper tooth row	4.36	.12	2.82	16	3.74	.05	1.42	5
Mastoid width	5.43	.21	3.80	21	4.43	.13	2.96	15
Palate length	6.21	.22	3.56	16	5.22	.19	3.55	6
Canine width at base	2.21	.13	5.67	23	1.78	.09	4.78	19
Rostral width	2.26	.13	5.57	23	1.84	.10	5.22	19
Min. preorbital space width	2.65	.11	4.11	16	2.31	.21	8.98	6
Min. postorbital space width	1.91	.13	7.01	16	1.84	.03	1.52	5
Bulla length	2.19	.08	3.83	24	2.01	.08	3.83	19
Upper molar inner moiety length	.73	.04	4.93	25	.61	.03	4.96	18
Upper molar width	1.05	.04	3.89	24	.92	.03	3.49	18
Waist of upper molar	.56	.03	5.94	25	.46	.02	3.66	18
Palate width	1.12	.07	6.41	23	1.01	.06	5.75	18
Length of last upper PM	1.19	.06	4.72	25	1.05	.04	3.34	19
Total length	96.42	3.02	-	52	84.03	4.04	-	58
Tail length	36.26	1.47	-	52	34.40	1.68	-	32
Hind foot	12.02	.94	-	10	10.97	1.01	-	6

Geographic variation: Rhoads (1898) suspected that the fisher of the "Hudsonian zone" of Canada might be sufficiently distinct from typical Alleghenian "pennanti" to merit "subspecific" distinction, but had no specimens available to test his hypothesis. I have seen specimens from both regions and conclude that there is now little reason for considering Rhoad's suggestion significant. De Vos (1952) found that while individual variation in

Ontario was "fairly striking", "no ... variations could be detected between local populations". Bachrach (1946) said that fisher east of the Manitoba-Ontario border were much silkier and darker in fur, while further west had coarser, browner and paler fur, in which "fur fibres seem to be lacking ... because the guard hair is so very coarse". Of the eastern type, Bachrach said that those from Ontario were slightly better and more heavily furred than were those from Quebec and Labrador.

Goldman (1935), when describing "M. p. columbiana", said that that "race" extended through the Rocky Mountains and "east, mainly in southern Canada, grading towards Martes pennanti pennanti in Manitoba." Anderson and other writers have somewhat reinterpreted this distributional statement; Anderson (1946) described the distribution of "pennanti" as "west to the Rocky Mountains; ... from Manitoba northward it is considered after Goldman to intergrade with Mustela [sic] pennanti columbiana through northern Saskatchewan and northern Alberta...." The problem of distribution is considered subsequently but Goldman believed that "M. pennanti pennanti" in Manitoba began to increase in size, so that it intergraded imperceptibly into "M. p. columbiana" in the Rocky Mountains.

I have examined very few specimens of fisher from west of Manitoba to the Rocky Mountains, and find it difficult to test Goldman's theory of intergradation through the whole of the Prairie Provinces. Through the kindness of Mr. J. Bryant I have, however, been able to examine a series of 50 skulls from Norway House and Cross Lake, Manitoba, five skulls from Red Earth,

Saskatchewan and, through other sources, five specimens from the Peace River district, British Columbia, Fort Smith, Alberta, Peace River, Alberta, and Nelson River, Keewatin. The Manitoba specimens average about intermediate between "M. p. pennanti" from further east and "M. p. columbiana" from the Rocky Mountains. The Saskatchewan sample is almost identical to the Manitoba one. Oddly enough the Peace River, Alberta, and British Columbia specimens fall within the range of "pennanti", not "columbiana", while those from Fort Smith, Alberta, fall within the range shown by samples of "columbiana". Goldman was, then correct in assuming that Manitoba specimens are intermediate between "pennanti" and "columbiana". Two specimens from Alberta and British Columbia appear nearer to "pennanti", however, while a third does not. Until more specimens are obtained from Alberta and Saskatchewan, we can do nothing toward solving the problem of what kind of variation occurs within the fisher there. For the present, we must accept Goldman's hypothesis that the fisher of Alberta, Saskatchewan, Manitoba and Mackenzie are intermediate between "M. p. pennanti" and "M. p. columbiana", or that perhaps a cline exists between the two.

Cranial statistics for the Manitoba sample follow:

	Males				Females			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylbasal length	11.69	.21	1.78	15	10.01	.17	1.70	17
Upper tooth row	4.44	.11	2.46	7	3.77	.08	2.07	7
Mastoid width	5.56	.10	1.70	6	4.55	.06	1.36	3
Palate length	6.34	.15	2.37	7	5.15	.01	.27	2

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Canine width at base	2.27	.07	3.26	17	1.86	.04	2.36	17
Rostral width	2.36	.08	3.18	17	1.93	.09	4.51	17
Min. preorbital space width	2.63	.09	3.31	7	2.24	.08	3.58	7
Min. postorbital space width	1.85	.15	8.00	7	1.93	.12	6.02	7
Bulla length	2.21	.06	2.62	15	2.02	.06	3.02	17
Upper molar inner molety length	.73	.03	3.55	16	.60	.02	2.82	17
Upper molar width	1.07	.04	4.11	17	.92	.04	4.24	17
Waist of upper molar	.54	.02	3.68	17	.47	.03	6.28	12
Palate width	1.14	.07	6.40	17	1.04	.02	1.63	12
Length of last upper PM	1.24	.03	2.59	16	1.08	.03	2.78	12
Total length	94.27	3.26	3.46	10	82.90	2.99	-	19
Tail length	35.86	2.00	-	9	31.32	1.86	-	19
Hind foot	12.03	.80	-	8	10.73	.69	-	12

Distribution: Reported (often without reference to specimens) to be the "subspecies" present in the following states and provinces: Iowa (Scott 1937); North Dakota (Bailey 1926a); South Dakota (Over and Churchill 1945); Wisconsin (Barger 1951 and Shorger 1942); Ohio (Bole and Moulthrop 1942); Minnesota (Shorger 1942); Michigan (Shorger 1942); New Hampshire (Carpenter and Siegler 1945); Vermont (Osgood 1938); Maryland (Mansueti 1950); West Virginia (McKeever, Frum and Berard 1951); Wyoming (erroneously? by Thomas 1952b); New Brunswick (Morris 1948); Quebec (Anderson 1934b, 1938, 1946, Eidmann 1935, Cameron 1953); Ontario (Cross and Dymond 1929, Downing 1948, Anderson 1946); Northwest Territories (Anderson 1937 and 1946);

Manitoba (Anderson 1946). Until Goldman described "M. p. columbiana", the range of this "race" had been interpreted to include all of the species range except the Coast Mountains and Cascade Range of western North America. Goldman gave the range of his new "race", "columbiana", a distribution as follows: "Rocky Mountain region from northern British Columbia south, formerly, at least, to central Idaho; east mainly in southern Canada, grading towards Martes pennanti pennanti in Manitoba". Goldman did not say whether the Prairie Province specimens should be considered "pennanti" or "columbiana", or whether neither and rather pure intergrades, but I gather he meant them to be considered "columbiana"; this at least is the interpretation made by Anderson (1946), who considered "pennanti" to occur in the following Canadian provinces: Ontario, Quebec, Manitoba and Northwest Territories and considered "columbiana" to occur in British Columbia, Alberta, Saskatchewan, Yukon, Northwest Territories and Manitoba. Anderson, in 1937, said, however, that he considered the fisher of the southwestern part of the Northwest Territories (Slave River, Simpson and Liard River) to be represented by "pennanti". Miller and Kellogg (1955) give pennanti's range as extending west to the Rockies, and south to Yellowstone Park. Soper, in 1952, considered the fisher of Prince Albert National Park, Saskatchewan, to be "columbiana", however, although he saw no specimens.

Anderson (1946) considered the area of intergradation between the two forms to extend "from Manitoba westward ... through northern Saskatchewan and northern Alberta and north to

Great Slave Lake...." Cowan (1939) speaking of specimens from the Peace River region of British Columbia wrote that "they differ from topotypes of M. p. columbiana in slightly smaller size, smaller zygomatic width and shorter palate, in which features they may be approaching M. p. pennanti. However, our material is too scant for these apparent trends to be significant." I have been able to examine this material and conclude that these specimens lie within the range exhibited by "pennanti", and not that by "columbiana". Specimens from Alberta, Saskatchewan and Manitoba, however, average so much larger (being truly intermediate) that the smallness of the Peace River specimens must be attributed to either error of sampling, or to a greater degree of geographic variation than is known of at present, which latter conclusion is, I think, quite possible.

Since the Manitoba - Saskatchewan sample of skulls averages almost exactly intermediate between "columbiana" and "pennanti", perhaps tending slightly towards "columbiana", and since Ontario specimens are distinctly referable to "pennanti" it follows that somewhere between Ontario and Manitoba a relatively abrupt change occurs in fishers, and that from Manitoba to the Rocky Mountains, a relatively gradual one, extending over a broad geographic area occurs. This being so, it seems best to agree with Anderson in naming western Ontario or eastern Manitoba as the western limit of "pennanti" and central or western Manitoba, the eastern limit of "columbiana". How variation occurs to the south of Manitoba, in the United States, is not known, and so few specimens will likely be obtained from there in future, that the problem may never be solved.

I conclude then, that fisher from the following states and provinces might be considered as belonging to this "race": eastern Manitoba (?); Ontario; Quebec; New Brunswick; Nova Scotia; North Dakota (?); Wisconsin; Iowa; Minnesota; Illinois; Michigan; Indiana; Ohio; West Virginia; Virginia; Tennessee; North Carolina; Pennsylvania; New Jersey; New York; Connecticut; Massachusetts; New Hampshire; Vermont; Maine; and other states in the eastern United States where it might have occurred. Anderson (1946) considered those fisher of the Northwest Territories east of Great Slave Lake to belong to this "race", but I have seen no specimens to confirm this view.

Specimens examined: 118 specimens from Ontario, Quebec, Michigan, Pennsylvania, New York and New Hampshire.

Skull diagrams and photographs: de Blainville 1841, pl. G13; de Kay 1842, vol.1, pl. 13; Thomas 1886, pl. 11; Baird 1859, pl. 36; Coues 1877, pl. 2; Seton 1929, vol. 2, pt. 2, pl. 72; Hamilton 1943, figure 66; de Vos 1952, figures 14, 15 and 16.

"Martes pennanti columbiana" Goldman 1935.

Synonymy: I know of no synonyms for this race.

Type specimen: U. S. National Museum Collection no. 56953 (Goldman 1935, Poole and Schantz 1942).

Type locality: "From Stuart Lake near headwaters of Fraser River, British Columbia" (Goldman 1935).

Pelage: "Color about as in M. p. pennanti of eastern Canada and the northeastern United States, and Martes pennanti pacifica of central Washington", is all the description Goldman gives of the skins of this race. I have examined a good series of skins and find them indistinguishable from skins of either "pennanti" or "pacifica".

Cranium: Goldman, comparing the skull of this race to those of "M. p. pennanti" and "M. p. pacifica", said "Skull somewhat larger, more elongate than either; palate decidedly longer, usually extending farther posteriorly beyond molars, but relatively rather narrow at constriction; rostrum and maxillary tooth row usually longer; carnassials usually larger; premolars less closely crowded.... The skull of M. p. columbiana is larger and may usually be distinguished from those of the other forms by the greater length of the palate".

Rand (1945b) examined two skulls from the Liard River (within 50 miles of the Yukon-British Columbia border, just north of where the Alaska Highway crosses the river) and compared the measurements of these to those from Ontario, Quebec and Goldman's topotypes. He concluded that "the ... measurements show that western animals average slightly larger than do eastern ones, and it may be advisable to recognize this lightly characterized race" ["columbiana"].

I have pointed out elsewhere that Goldman considered this "race" to intergrade with "M. p. pennanti" between the eastern slopes of the Rocky Mountains and Manitoba. I have also pointed out that Rhoads in 1898 felt that he could not separate

an Idaho skull from skulls from the eastern United States.

Examination of a series of skulls referable to this "race" on geographic grounds, plus most of Goldman's rather large series of topotypes, indicates that his description is essentially sound, and that the animal is, when compared to "M. p. pennanti", significantly larger, longer skulled and with a longer palate, tooth row, and upper carnassial. It is significantly larger (to the 95% level) in condylobasal length; mastoid width, rostral width (males only), and length of last upper premolar (males only). Near significance is attained in palate length, canine width and palate width, these in males only and the last of which is smaller, not larger. When compared to "M. p. pacifica" it is likewise larger, being significantly distinct in condylobasal length (males only); upper tooth row (males only); mastoid width (males only); palate length (males only, approaching significance in females); bulla length (females only, but approaching it in males); larger palate width (females only); and oddly, a smaller upper molar width and inner moiety length (females only); the length of the last upper premolar (in males only), and canine and rostral width (females only) approaches but does not reach significance.

We may conclude, then, that Goldman was correct in considering "M. p. columbiana" distinctly larger than either "M. p. pennanti" or "M. p. pacifica". It has been pointed out elsewhere, too, that Goldman appears to have been correct in saying that his "race" intergrades with "pennanti" between the Rocky Mountains and Manitoba, a sample of Manitoba specimens lying about midway in cranial measurements between the two (see under

discussion of "M. p. pennanti"). Because some of the characteristics of the Manitoba sample lie closer to "columbiana" than "pennanti", they are, following Goldman, considered here to belong to the former "race". See measurements under discussion of "M. p. pennanti".

The cranial statistics obtained for this "race" follow. Statistics for the Manitoba specimens are given elsewhere, as described above.

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	11.78	.28	2.40	33	10.05	.16	1.56	35
Upper tooth row	4.44	.11	2.39	18	3.80	.11	2.92	7
Mastoid width	5.63	.17	2.97	19	4.62	.14	3.07	10
Palate width	6.38	.15	2.32	18	5.31	.10	1.96	6
Canine width at base	2.30	.11	4.66	36	1.82	.05	2.75	35
Rostral width	2.35	.09	2.61	36	1.88	.06	3.04	34
Min. preorbital space width	2.70	.12	4.52	18	2.23	.09	3.99	7
Min. postorbital space width	1.94	.17	8.66	18	1.90	.08	4.21	7
Bulla length	2.22	.07	3.25	33	2.04	.08	3.73	34
Upper molar inner molety length	.74	.04	5.03	36	.59	.03	4.42	35
Upper molar width	1.06	.05	4.53	36	.89	.02	2.48	35
Waist of upper molar	.55	.04	6.56	36	.46	.02	3.69	34
Palate width	1.10	.06	5.11	36	1.03	.04	3.99	34
Length of last upper PM	1.23	.04	2.92	36	1.07	.03	2.34	34
Total length	100.97	4.01	-	18	82.90	3.89	-	19
Tail length	39.38	2.04	-	18	31.32	1.97	-	19
Hind foot	12.64	.84	-	8	10.73	.80	-	12

Geographical variation: Specimens are so few that little other than the means of lumped subsamples, taken over wide geographic areas can be obtained. Specimens from Norway House, Manitoba, show a mean condylobasal length of 11.69 cm. in males and 10.01 cm. in females. This, plus other characters, lie about midway between equivalent measurements of "pennanti" and "columbiana" as outlined above. Since this marks the known eastern limit of what is by Goldman and here considered this "race", we may conclude with him that east of the Rocky Mountains the "race" decreases gradually in size, until in Manitoba it gives the measurements given above, and east of which in Ontario it relatively abruptly grows smaller to give the "form" names "pennanti". Several specimens in Alberta seem to confirm this view (see discussion under "M. p. pennanti"), but Cowan (1939) found Peace River, British Columbia, specimens to lie within the range shown by "pennanti" and not "pacifica". I have seen Cowan's material and agree with him that they are as small as "pennanti". As Cowan himself says, however, the two skulls are too few for these apparent trends to be significant.

Rand's (1945b) specimens from the Yukon - British Columbia boundary are no different in measurement from those further south.

Rhoads (1898) believed that fisher from the southern Rocky Mountains might some day be shown to be a "paler race", and found he could not distinguish an Idaho skull from eastern ones. The few Idaho skulls I have seen are, in my opinion, no different from typical "columbiana" to the north, and it is now known that

fisher do not occur in the southern Rocky Mountains, though it is believed to occur in the Wasatch and Uinta Ranges of Utah.

Distribution: Given by Goldman (1935) as "Rocky Mountain region from northern British Columbia south, formerly, at least, to central Idaho; east, mainly in southern Canada, grading toward Martes pennanti pennanti in Manitoba". Anderson (1946) and Rand (1945b and d) refer southern Yukon Territory specimens to this "race". Other references to this "race" are British Columbia east of the Coast Range (Anderson 1946, Quick 1953, Stanwell Fletcher 1943, Cowan 1939, Baker 1951); Alberta (Anderson 1946); Rand 1948a); Saskatchewan (Soper 1952, Anderson 1946); Manitoba (Anderson 1946); Idaho (Davis 1939, Rust 1946); and Utah (Durrant 1952). We may hypothesize that all of these designations are correct, and that they are also represented in eastern Washington and Oregon, Montana and Wyoming. Miller and Kellogg (1955) say that "M. p. pennanti" occur south in the Rocky Mountains to Yellowstone Park, but the western limit of the "race" is here considered to be Manitoba or Western Ontario.

Specimens examined: 163 specimens from British Columbia, Alberta, Manitoba, Saskatchewan, Northwest Territories and Idaho.

Skull diagrams and photographs: None that I know of.

"Martes pennanti pacifica" (Rhoads 1898).

Synonymy: Martes (or Mustela) canadensis pacifica, penanti pacifica; pennanti pacifica; pennanti.

Type specimen: S. N. Rhoads' Collection, Academy of Natural Sciences, Philadelphia, no. 1074 (Rhoads 1898, Anderson 1946).

Type locality: "Lake Kichelos, Kittitass County, Washington; altitude about 8000 feet" (Rhoads 1898); "Lake Keechelus, Kittitas county, Washington, altitude 8,000 feet" (Miller 1924).

Pelage: Described by Rhoads as follows: "Above, from between eyes to middle back, grizzled, grayish ochraceous heavily lined with black, becoming hazel black on hind back and dark black on rump, thighs and tail. Whole head behind eyes clove brown basally, strongly grizzled with dirty white. Snout to eyes blackish seal brown. Chin, throat, breast and belly between legs dark chestnut and hazel, obscured with black, legs and feet black, the fore legs showing the vandyke brown bases of hairs. Basal half of hairs of anterior back are Prout's brown as compared with the hair brown of canadensis [pennanti], the tawny suffusion so deeply marked in ... pacifica ... separates it at a glance from canadensis...."

Grinnell, Dixon and Linsdale (1937) described Californian specimens from the Sierra Nevada thus: "Adults (prime winter pelts from the Yosemite region); no sharply set-off color markings anywhere, save for occasional irregularly placed white spots on lower surface; a gradual change in color tone is apparent, from rather ashy grayish brown on head to nearly black on legs and tail. The muzzle, including the whiskers, is dark bister; nose pad, black; hair on rim and inside of ear, buffy white. Backs of ears, head from cheeks and between ears backward,

sides of neck and shoulders, a grizzled grayish or buffy white; this because overhairs are black terminally, white or buffy white subterminally, and dark mummy brown basally. This same pattern of hair color extends back along sides of body to flanks, but there the terminal black tips become longer and the subterminal light bands darken until they are cinnamon brown. The darkening of the overhairs is most pronounced down middle of back from between ears, progressively increasing to base of tail; a similar effect, as of dark band, is seen on lower surface from chin to belly, save as sometimes interrupted by the sporadic white spots already alluded to. The color of the underfur is everywhere dark, rather rich brown, varying from mummy brown on sides of neck, and dark sepia on throat, to deep mars brown on tail. The overhairs of rump, feet and tail are glossy black.... The variations in coloration, ... judging from the specimens at hand from California are slight. The pallor of the grizzling on the head and shoulders varies from ashy white to a rather buffy white. The extremes of dullness in this regard is shown in certain pelts from the Trinity region of northwestern California. However, a slight yellowing of the pelage of some skins may have resulted from the tanning process used.... The ventral spotting is usually restricted to two regions, the chest and the near vicinity of the genitalia. There may be simply a few scattering white hairs or small tufts of them, or there may be abrupt, solidly white spots as much as 2 inches in diameter, involving the entire depth of overhair and underfur. These spottings never accord with perfect bilateral symmetry, though there may be a divided

representation on the two sides of the chest. There is a median white spot on the throat, well marked or barely indicated, in 3 or 4 pelts. These white interruptions of the body color on the lower surface of the fisher remind one of the ventral orange markings in the marten."

I have little to add to these descriptions except to say again that I cannot distinguish any of the three named "races" of fisher on the basis of the pelts alone. Rhoads' statement that the basal half of the underfur on the back are differently coloured in "pacifica" and "pennanti", is not supported by the specimens I have examined, nor is degree of tawny suffusion distinctive.

Cranium: Skull described by Rhoads as "very large, with relatively long nasals. Posterior upper molar large, with spreading inner lobe much wider longitudinally than outer section of same tooth; the crown suddenly constricted at the middle.... The dimensions of the type skull, when we consider that it was a female, show that the fishers of the Cascade Mountains attain a much greater size than those of the Appalachian chain. Young adult skulls of the same age from western Washington and Main show the same distinctions."

Goldman, in 1935, said that "the skull of M. p. pacifica is similar in size to that of typical pennanti, but usually differs noticeably in the greater breadth of the rostrum and the more widely spreading zygomata. The skull of M. p. columbiana is larger and may usually be distinguished from those of the other forms by the greater length of the palate."

Grinnell (in Grinnell, Dixon and Linsdale 1937 and Grinnell 1933), without knowing of Goldman's work referred to above, and without knowing of his description of "M. p. columbiana", attempted to determine the validity of "M. p. pacifica", examining the U. S. National Museum and Biological Survey Collections in so doing. He says (1937): "Without looking up Rhoads' description at the time he [Grinnell] went over eastern and western specimens including skins and skulls from Maine, Quebec, Washington and California, but did not find any character of sufficient constancy to warrant recognition of a race 'pacifica'. There were 24 skulls from near Mount Adams, Washington, a place not far from the type locality of 'pacifica', and these showed such great age and individual as well as sexual variation as to convince the observer that any characters of geographic significance would have to be very well marked indeed to stand out as of practical diagnostic value. Turning now to Rhoads' descriptions of fishers We find that the characters given for his 'pacifica', based, be it noted, on very meagre material (a total of 2 skins and 5 skulls), are as follows: (1) darkness of general color; (2) large size; (3) large last upper molar, with a broad inner lobe. With respect to darkness of color, eastern and Washington skins average so closely alike that this supposed distinction fails. With respect to size, which Rhoads emphasizes as an outstanding character of 'pacifica', the only skull measurements he presents are of his type, said by the trapper from whom he obtained it to have been a female, but the dimensions given are those of a male! They fall within the

"figures we give for Californian specimens for that sex. Rhoads seemingly had no notion of the great amount of sexual variation in the fisher. Suffice to say that we find no grounds for ascribing to this animal any readily appreciable geographic variation in size. With reference to size and shape of last upper molar, again there is so much variation in the material now examined that we find nothing outstanding by which to distinguish a western from an eastern subspecies. However, in our Californian series of specimens, certain slight though inconstant peculiarities have become apparent. A prime skin ... from the Sierra Nevada is not duplicated in pallor (whiteness) about the head and shoulders by any other skin seen from any other place in the range of the fisher. Several other skins from the Sierra, though not quite so pale as this one, still are paler, less tawny, than Washington pelts, whereas some other Sierran ones are equally as tawny. It may be said that there is a mean tendency in the Sierran fishers to be paler-colored than northern or eastern fishers. But in our opinion, this tendency is not strong enough to warrant recognition in nomenclature." These authors then go on to name all Californian fisher "Martes pennanti", giving no subspecific determination, and thus denying the validity of Rhoads' "pacifica". To the best of my knowledge, Dalquest (1948) in his catalogue of Washington mammals, has been the only subsequent worker to follow Grinnell's nomenclature. Scheffer (1938), Hall (1946) and Anderson (1946) among others, have not done so."

I have pointed out that I believe that Grinnell was unaware of Goldman's work when he came to the above conclusion, and one wonders what interpretation he made when he learned that

"pacifica" and "pennanti", although essentially similar, were separated by a considerably larger "race", "columbiana". It is likely Goldman's work which caused Scheffer, Hall and Anderson among others to uphold the status of the "race" "pacifica".

Concerning Grinnell's criticism of Rhoads' supposed "race", Grinnell concluded that its essence lay in darkness of general colour, large size, and the largeness and broadness of the upper molar. Grinnell said the skins of "pennanti" and "pacifica" averaged too similar to each other to merit distinction. To this I agree, adding that individual variation is rather more, perhaps, in both than Grinnell implied. I have found myself completely unable to separate skins referable to both "subspecies". Concerning size, Grinnell says that the measurements of Rhoads' supposed female type indicate that it really was a male, and that it falls within the range shown by California specimens. Comparison of Rhoads' measurements to my own indicates that Grinnell was correct, and that Rhoads described a male, believing it to be a female, and that further the specimen could as well be referred to "pennanti" as to a new "race". Regarding the third point, Grinnell said that so much variation was to be found in the size of the upper molar that it could not be used as a means to distinguish "pacifica". Examination of the statistics obtained from the samples I have studied, while suggesting a smaller molar in "columbiana" than in "pennanti" or "pacifica", indicates that the means obtained for the latter two "races" cannot be distinguished at the 95%

level, though there is suggestion in the figures that upper molar inner moiety length averages slightly larger in "pacifica" than in any other "race". It follows then that Grinnell, insofar as present material allows conclusion, was essentially correct, and that Rhoads' diagnostic characters for "pacifica" are inadequate.

This leaves us with the distinctions made by Goldman, who, I am led to believe, was unaware of the work done by Grinnell. He said, in brief, that "pacifica", though cranially of the same size as "pennanti", possessed a wider rostrum, and more wide spreading zygomata. My statistics indicate that in making this distinction with regard to rostral width, Goldman was correct. "M. p. pacifica" samples are distinguishable at the 95% level of probability from samples of "pennanti", by the larger rostral width of the former, which averages 1 mm. wider in both male and female in the "pacifica" "form". I made no measurements of zygomatic breadth, so am unable to test Goldman's other distinction. Casual examination of skulls, however, leads me to conclude that it may be a valid means of distinction.

Since "pacifica" and "pennanti" are geographically separated from each other by "M. p. columbiana", one might expect to find other means of distinction. Statistical comparison of samples shows them to be distinctive at the 95% level in the following characteristics: smaller palate length (males only); greater rostral width; greater mastoid width (females only); greater canine width (females only). Statistical significance is approached but not reached in greater

condylobasal length (females only); lesser bulla length (males only); larger upper molar inner moiety length (males only); greater length of last upper premolar (males only).

Comparison to "M. p. columbiana" was made under the discussion of "columbiana", where "pacifica" was shown to be distinctively smaller than that "race" in most characteristics, but equalling it in canine and rostral width, and slightly exceeding it in size of upper molar.

Cranial statistics for the "race" follow.

	<u>Males</u>				<u>Females</u>			
	\bar{x}	SD	CV	n	\bar{x}	SD	CV	n
Condylobasal length	11.43	.26	2.27	24	9.99	.21	2.05	10
Upper tooth row	4.28	.09	2.17	20	3.85	.25	6.42	9
Mastoid width	5.41	.15	2.74	24	4.63	.18	3.84	9
Palate length	6.02	.12	2.00	20	5.18	.08	1.58	8
Canine width at base	2.27	.08	3.70	26	1.85	.05	2.75	11
Rostral width	2.36	.10	4.37	26	1.93	.07	3.68	10
Min. preorbital space width	2.67	.11	4.11	20	2.35	.12	5.03	6
Min. postorbital space width	1.97	.14	6.97	20	1.89	.06	3.29	6
Bulla length	2.16	.09	4.35	26	1.97	.06	2.84	10
Upper molar inner moiety length	.76	.04	4.52	26	.63	.03	4.48	11
Upper molar width	1.07	.04	3.65	26	.93	.04	4.43	11
Waist of upper molar	.57	.03	5.72	26	.48	.03	5.47	11
Palate width	1.11	.06	5.22	25	.99	.03	2.64	11
Length of last upper PM	1.21	.03	2.31	26	1.09	.04	3.41	11
Total length	101.57	4.15	-	6	86.40	-	-	5
Tail length	37.73	2.20	-	6	36.13	-	-	5
Hind foot	12.28	.91	-	5	9.88	-	-	5

Geographic variation: The specimens examined are insufficient to determine anything of this. They intergrade presumably with "M. p. columbiana" on the east slopes of the Coast Mountains of British Columbia, and Grinnell, Dixon and Linsdale (1937) say that fisher of the Sierra Nevada of California show a "mean tendency ... to be paler-colored than northern or eastern fishers" (see above). I am unable to determine variation of any other sort, although it doubtless exists.

Distribution: Range described by Rhoads as "Pacific slope of America, from Alaska to California". Bailey (1936) gives the range as "British Columbia south through Washington and Oregon to northern California...." Anderson (1946) gives it as "Pacific coast and mountain region from California to southern Alaska Panhandle." This subspecific designation has been given to the fisher of the Coast Range of British Columbia (Anderson 1946), Washington Coast Mountains and Cascades (Scheffer 1938, but not Dalquest 1948), the Sierra Nevadas of Nevada (and hence by extension of California) (Hall 1946), and Oregon (Bailey 1936). Bailey said that "no specimens have been seen from the Blue Mountain section [of Oregon], but provisionally the records are included under this name". The fisher of the Blue Mountain region should likely be considered representative of "M. p. columbiana" rather than "pacifica".

A more specific delimitation of the distribution of this "race" might be made as follows: Coast Mountains of British Columbia, the Olympics, Coast and Cascade Ranges of

Washington and the Coast Mountains and Sierra Nevada of California and very western Nevada.

Specimens examined: 71 specimens from British Columbia, Washington, Oregon and California.

Skull diagrams and photographs: Elliot 1899, p. 267; Grinnell, Dixon and Linsdale 1937, vol. 1, figure 74.

CLASSIFICATION OF NORTH AMERICAN MARTEN AND FISHER

To the present I have employed the classical conception of marten fisher classification, naming thirteen (reduced to seven) subspecies of marten and three of fisher, and pointing out that a much simpler and more accurate classification was available. I employed the older scheme as I realize there will be many who will want to retain it, and without providing an account of their terms little of value would be available to them. I believe, however, that the simplified scheme referred to in the introduction to this paper has many virtues.

It seems to me that it is apparent that whatever classification one chooses is one of opinion and convention only. Thus I do not attribute any degree of actual reality (aside from logical reality) to any of the categories of species or subspecies. Much has been made in the past concerning the supposed reality of the species. Admitting logical reality in the species (see Gregg 1950 and 1954), I believe that Gilmour (1940) and Burma (1954) (restated by Smith 1955), have shown that this category, and all others in the hierarchy, have no

actual reality whatsoever. For this reason, whatever classification is selected is wholly a matter of opinion. There is, however, so much usefulness in employing the degree of logical reality to be found in the concept of the "biological" species of Huxley, Mayr, and others that the choice made must be founded on this.

We admit, then, that in the martens of the New World, only one species exists, these being divisible into two basic "subtypes", americana and caurina. The problem is this: are these two basic subtypes to be recognized in the trinomial (i.e. as Martes a. americana and M. a. caurina), or will we, as Wright (1953) suggests, subjugate this basic distinction by considering the two divisions "subspecies groups" and instead emphasizing trivial distinctions, naming thirteen or more subspecies as they are currently accepted. Another way of stating the problem is this: given three grades of distinction, but only two categories in which to fit them, which will be emphasized in the trinomial, the grade of higher, or of lower magnitude? I conclude that the logical procedure is to emphasize the grade of higher magnitude by endowing the trinomial with it, rather than by so doing to the lower. Before asking the reader to agree with me, however, it would be well to point out some of the advantages and disadvantages that would result from the change.

Of disadvantages, three come to mind immediately. The first is that it makes one more change to be held in the memory of scientists; changes in classification are made far too often for retention in the memory of anyone not a specialist in the

group. However, I think that if this change were to be accepted it would offer far more permanence than does the old scheme, which allows for the naming in future of any number of new "subspecies", all based on trivial or nonexistent distinctions of little or no worth. The second disadvantage is that it places the degree of magnitude involved in the distinction between subspecies on quite a different plane than is usually accepted. Thus the subspecies in *Martens* would be the equivalent of about the "subspecies group", "species", or even "species group" of other mammalian genera. This would cause a great deal of inconvenience to "practical" workers in the science, comparative physiologists, ecologists, zoogeographers and others, all of whom depend on the systematist for a sound interpretation of the geographic distribution of phenotypes. On the other hand, I offer that the subspecies, as currently accepted, is of little use to any of these groups anyhow (see Lack 1946, Hubbell 1954, Tucker 1946, Sibley 1954, Wilson and Brown 1953, Brown and Wilson 1954, Burt 1954, Gosline 1954). If the trinomial system is to be maintained, I believe that the lowest level involved, the subspecies and its nomenclatural epithet, will have to be of much more real nature and of a higher level of magnitude than is currently accepted. By naming only two subspecies of *Martens* I believe I am predicting the level of the subspecies as future workers will conceive of it. I do not think that Wright's use of the grade "subspecies group" is justified, because then it is ignored in the trinomial. It has

been suggested earlier that Martes zibellina, americana, martes and melampus may possibly be all one biological species. If this proves to be the case, we should have to name thirty-five subspecies of the one species M. martes (divided into four subspecies groups, of course). It would have been much simpler to name only four subspecies of the species.

I have come to the conclusion that the currently accepted subspecies of martens have been isolated from each other at various times during the Pleistocene, and hence have had somewhat different histories which have resulted in the nature of geographic variation they exhibit. These historical populations do, I believe, approximate some of the subspecies as now accepted and should be given some means of succinct reference. It is my opinion that they do not merit subspecific distinction, this belonging to the higher grade of distinction I employ. For this reason I am obliged to give these populations vernacular names. This is the third disadvantage. The reader may feel that I am only substituting vernacular names for good, sound, sensible trinomials; this is in part precisely what I am doing. For those who disagree I have given elsewhere detailed descriptions of "subspecies".

The disadvantages of maintaining the old scheme of classification seem to me to outweigh those of changing to the new. Not only is the new scheme simpler, once accepted, and an insurance of future stability, but I believe it offers a far truer picture of reality as it exists in nature. Criticism has recently been directed toward the subspecies concept by such

writers as Wilson and Brown (1953), Brown and Wilson (1954), Burt (1954), Gosline (1954) and others listed earlier in this discussion, and their criticisms are largely mine. These authors show that the concept is unsatisfactory for the following reasons: (1) The capacity for genetically independent characters to show independent geographical variation. Thus the number of recognizably distinctive populations increases as a function of the number of characters studied, the rate of increase being slightly greater than an arithmetical one. (Wilson and Brown 1953). I cannot show this relationship in *Martens* although I suspect that it occurs. Were we to employ Womble's method in summing groups of differences geographically, the number of definable geographic "races" would increase in a calculable ratio. (2) The common occurrence of the micro-geographic race, each distinct, but occupying only a restricted geographic range. If these are formally recognized the list of trinomials will become very large, obscuring rather than clarifying the nature of geographic variation (Wilson and Brown 1953). Durrant (1946) lists 35 races of Thomomys bottae and T. talpoides from Utah alone. Burt (1954) says that more than 150 subspecies of T. bottae are now listed for North America with more to come. In the *Martens*, if we are to accept most or all of the subspecies now named, it would be necessary to name several more at least, if all equal variation is to be described. Employing condylo-basal length alone, new races should be named from southern Alaska and Yukon, southern Ontario, northern coastal British Columbia, Utah and elsewhere, and even then no real picture of

variation in condylobasal length would be attained. (3) The arbitrary lower limit of the subspecies; there is no limit to the minute distinctions that may be used to differentiate subsamples (Wilson and Brown 1953). Austin (1952) found he was unable to name subspecies in petrels using the "97% rule", and was obliged instead to use the "84% rule" in comparing his subsamples. Were I to use the "84% rule" in martens, I believe I could show almost any subsample I chose to be distinct from any other, in one or another character.

(4) Minor geographic variation may often be environmental rather than genetic, and we have no way of distinguishing the two (Edwards 1954). Goldschmidt (1940) recognized some of these and called them "phenocopies". Allee and Lutherman (1940) have shown how extremely these "phenocopies" may deviate from the normal when artificially induced, and since martens tend apparently to follow Bergmann's and Gloger's rules, at least some geographic variation now rated worth subspecific designation is open to question.

(5) The most severe criticism that has been directed against the concept has been stated many times (see Womble 1951, Wilson and Brown 1953), but is usually ignored by systematists. It is this: systematists work in a completely non-objective fashion. Rather than studying variation first, and from it devising a classification, they arbitrarily select type localities, build up subsamples by additions, and from this attempt to describe variation. In other words they work deductively, presuming a case is so and then proving it. Burt

(1954) shows how three completely different pictures of variation in Neotoma alleni were obtained by three different workers using the same material. I have no doubt that a completely different picture of marten variation and named subspecies in marten would have resulted if the mammalogists of the early 1900's had selected different locations to travel into for their types.

In my opinion we can avoid the difficulties listed above by ignoring the subspecies as it is currently accepted. We have a basic distinction in the martens between americana and caurina, and I offer that these be accepted as subspecies. The advantages gained are many. There is stability and a true picture of basic variation. The units involved can be limited geographically and morphologically and are founded on genetic distinction. They have had distinctive histories and, all things considered, have far more reason to merit emphasis in the trinomial than the minor distinctions of the current subspecies.

Wilson and Brown (1953) suggest that the subspecies concept be disposed of completely, rather than maintained as I have suggested above. I sympathize with their view and would prefer it rather than the maintenance of subspecies, as presently conceived of. Smith (1955) suggests that the stage of differentiation reached by americana and caurina, is intermediate between what are generally named species and subspecies. This degree of differentiation marks what he calls "hypospecies". Using his scheme, caurina and americana would be described as being macroparapatric hypospecies.

If, for the time being, the subspecies concept as I use it is maintained, similar changes need to be made elsewhere. In fisher geographic variation is less, if anything, than in martens, therefore I would dispose of the "subspecies" of fisher too, naming them all one species with no subspecies. The subspecies of Eurasian marten fall into the same category, and I would likewise advocate their removal. For example, according to Bobrinskoy et al. (1944), geographic variation in M. martes is "expressed chiefly in size and colour"; in M. foina "individual variation is great, geographic variation very slight". Kozhantshikov (1930) says that the characters assigned to the continental races of M. zibellina are variable and insignificant. My own examination of small numbers of Eurasian specimens had led me to the same conclusions.

If the simpler classification is used, a means of distinguishing populations of different historical origin is necessary. Various methods have been suggested, and the simplest is the use of vernacular names, these having no nomenclatural value whatsoever. The populations so designated have been named variously by different authors. Some of the terms used include "microsubspecies" (Huxley 1942), "subspecies" (Goldschmidt 1940), "microrace" (Dobzhansky 1937), "ecotype" (Valentine 1949), and "morph" (Edwards 1954). It does not matter what term is used so long as it is realized that the names applied to them are meant to have no nomenclatural significance, that no geographic limits other than very general ones are placed on them, and that no implication is made that the distinctions they may show

are genetic and not environmental. For convenience I will use the Edwards term "morph", although he explicitly denies the use of the word for environmentally distinctive animals.

The classification of marten and fisher used in the remainder of this paper is as follows.

Martes americana americana (Kerr 1792). Including all those forms named under "M. americana" in the preceding synopsis. It is considered to be made up of the following morphs:

Alaskan-Yukonian morph: Large and generally pale. Includes what generally has been heretofore named as the "subspecies" "actuosa" and "kenaiensis".

British Columbian morph: Small and dark coloured. Includes, essentially, the "subspecies" "abietinoides".

Saskatchewan-Manitobian morph: Large and, generally, dark. Includes the onetime "subspecies" "abieticola". It is so similar to the Alaska - Yukonian morph that were it not for its supposedly distinctive history, it would not be separated from it.

New England-Ontarian morph: Small and pale. Essentially equivalent to the "subspecies" "americana" in the classical sense.

Newfoundland-Labradorian morph: Large and dark. Includes the range of the "subspecies" "brumalis" and "atrata".

Martes americana caurina (Merriam 1890). Including all "forms" named under "M. caurina" in the preceding synopsis. Although considerable geographic variation occurs, there is no need in

the account following, to subdivide it into "morphs", the history of the subspecies being essentially the same. On purely morphological grounds, it is possible to distinguish the large Queen Charlotte Island - Alaskan Panhandle morph, the small northwest Californian morph, and the deviant Utah morph, among others.

Martes pennanti (Erxleben 1777). Here considered of three "morphs", essentially equivalent to the classically accepted "subspecies". Eastern american morph: Essentially the "subspecies" "pennanti". Montane morph: Essentially the "subspecies" "columbiana". Coastal morph: Essentially the "subspecies" "pacifica".

These "morphs", so called, are named here only for the sake of convenience in presenting the historical account which follows. No other significance should be attributed to them whatsoever. A concept of variation should be based on the maps and accounts given and not on the erroneous one of discreet, named populations.

PHYLOGENY

PALAEONTOLOGY

It would be valuable to the solving of the problem of marten if a detailed survey of the fossil record were to be made. Lack of time and the required facilities having made this impossible, only a fragmentary account is given here. From this an attempt is made to derive something of the evolution of marten.

Fossil marten present difficulties for several reasons. References of fossil specimens to the genus have often been loosely made. Simpson (1945) wrote that "all pre-Pleistocene records may be viewed with doubt since they almost always use the generic name in a broader sense than among recent mammals and often prove to be erroneous when the species became better known." Many writers, for example, believe the genus Mustela to have appeared in the late Miocene, but Hall (1951) considers that all specimens dated earlier than the Pleistocene and referred to this genus, should properly be placed elsewhere.

Another difficulty is that, as Simpson (1945) points out, very few of the fossil species appear to be ancestors of later one. For this reason it is very difficult to discern phyletic lines within the genus.

The greatest difficulty arises from the scarcity of the fossil material available. Various reasons are given for this situation. The most plausible one is that throughout its history it has been an upland form, living in the boreal parts of the continents which are poorly represented paleontologically. The bones being small and fragile were less likely to be preserved than more robust forms, and being carnivores were likely less abundant than the herbivores (Scott 1937, Romer 1945).

Almost all authors consider the Mustelidae to be among the most primitive living carnivores and nearest to the basic Creodont stock. Among the Mustelids the genus Martes is generally considered the most primitive (Weber 1927-28,

Pilgrim 1932, Winge 1941, Gregory 1951).

The origin of the genus is usually ascribed to the Old World (Simpson 1945, Gordon 1947, Scott 1937, Takai 1952), but Romer (1945) apparently believes it to have originated in the New. Simpson (1947a and b) wrote that "appearance of ... all the musteline genera common to North America and Eurasia is essentially simultaneous on the two land masses.... It is possible, but very uncertain, that most of the migration was from the Old World to the New". The date of the origin of the genus has been variously placed at upper Oligocene (Gregory 1951), lower Miocene (Pilgrim 1932), upper Miocene (Takai, 1952), Miocene (Scott 1937, Romer 1945) and upper Miocene or lower Pliocene (Simpson 1945). The genus is supposed to have first appeared in the New World in the Miocene according to Romer (1945) and the upper Pliocene according to Simpson (1945).

My own survey of the literature of fossil martens leads me to conclude that no specimen of age earlier than Miocene has been permanently referred to the genus Martes. Correlation of the deposits with standard sections are often extremely difficult, but I presume most or all of them are referable to the upper Miocene. As far as I have been able to determine, fossils of the genus from the upper Miocene have been found in deposits in Europe, Asia and North America, so that it is impossible to say where the genus originated.

A catalogue of the species of marten represented in the fossil record follows. Detailed accounts of North American Pleistocene forms may be found in Hall (1936). What follows is

complete insofar as I have been able to make it so. Details are given only for those near to Recent species. I have unfortunately been unable to examine any of the specimens discussed below. Synonymies are given in Appendix B.

Martes americana americana (Kerr 1792). Pleistocene of Pennsylvania. See also Baird (1857), Allen (1876b), Coues (1877), Trouessart (1897), Hay (1902), Osborn (1909), Sinclair (1915), Hay (1930) and Hall (1936). Hall, in 1936, wrote that the sole ascription of this subspecies to the Pleistocene seems to be Allen's (1876b) statement relative to Mephitis frontata that it had been found by Baird in the Port Kennedy, Pennsylvania, bone caves. Whether they were truly Pleistocene or not Hall was unable to determine. He did conclude that they were relatively old, and Brown (1908) dated them "lower Middle Pleistocene". Hay 1909 and Baker 1920 considered them Pliocene, Osborn (1909 mid-Pleistocene, and Hay 1902 Aftonian. Hay (1930) dated them Late Pleistocene. I know of no other references to the species. Late pre-European specimens have been found in southern Ontario by Wittemburg (1919, 1939, 1948) and in Maine (Norton 1930).

Martes americana caurina (Merriam 1890). Pleistocene of California. See also Hall (1926c), Hay (1927), Hall (1936). This form was described by Hall in 1926 (c) as M. caurina nobilis and later redesignated by the same author (1936) as M. caurina sierrae Grinnell and Storer. The simplification of classification favoured in this paper leads me to refer it

to the latter designation, or to M. a. caurina. The fossil material consists of seven partial or complete jaws (all but one lower jaws) from Samwell and Potter Creek Caves, California. Hall considered these specimens to be of Pleistocene origin, but younger than those from the Port Kennedy deposits referred to above. Brown (1908) dated them as "late phase of the Middle Pleistocene". Hall (1936) dated them as Middle Pleistocene or later.

Martes anderssoni Schlosser 1924. Pliocene of Chiton Gol, China and Mongolia. See also Teilhard de Chardin (1926) and Teilhard de Chardin and Leroy (1945).

Martes arzilla (Gregorio 1886). Pleistocene of Sicily. Described originally under the genus Mustela, and never changed to Martes so far as I know.

Martes crassa Teilhard de Chardin and Leroy 1945. Pliocene of Yushe, China.

Martes diluviana (Cope 1899). Pleistocene of Port Kennedy, Pennsylvania and Cumberland Cave, Maryland; see also Schlosser 1902, Rhoads 1903, Baker 1920, Hay 1923, and Hall 1936. Gidley and Gazin 1933 and 1938. Hall, in 1936, synonymized

M. parapennanti Gidley and Gazin 1933 with this species, finding no essential difference between the two. The species resembles M. pennanti, according to Hall (1936) but with teeth averaging an eighth less in linear dimension, and with other minor differences. The age of the Port Kennedy deposit has been discussed

above. Hall (1936) believed the Cumberland Cave fauna to be about the same age.

Martes filholi (Deperet 1887). Miocene of France and Germany. See also de Blainville 1841, Deperet 1892, Schlosser 1888, Filhol 1891, Gaillard 1899, Helbing 1936, Viret and Mazenot 1948. This species has been synonymized with the species Mustela genetoides, and Viverra macrorhyncha by some of the above named authors (see synonymy).

Martes flavigula (Boddaert 1785). Pliocene of North India and Yenkingchon Pits, China; Pliocene or Pleistocene of Java. See also Lydekker 1885, Flower and Lydekker 1891, Colbert 1933, Brongersma 1941, and Colbert and Hooijer 1953. Simpson (1945) dates the origin of this species (as the genus Charronia) as Recent, but I presume the above designations to be correct. Brongersma found the Javan specimens identical to the forms now living there. Colbert and Hooijer considered the Chinese specimens sufficiently larger to merit naming as a new subspecies "Charronia flavigula tyrannus".

Martes foina (Erxleben 1777). The sole fossil ascription to this species, are specimens of "diluvial age" from near Liege, Belgium, referred to by de Blainville (1841). These, he said, were notably larger and with heavier skulls than those of Recent representatives of the same species from the same locality.

Martes fœxi Hibbard and Riggs 1949. Pliocene of Meade County, Kansas.

Martes gamlitensis "von Meyer" (according to Thenius 1949).
Miocene of Bavaria.

Martes gazini Hall 1931. Tertiary of Oregon.

Martes kinseyi Gidley 1927. Miocene of Madison Valley of Montana. See also Hay 1930.

Martes laevidens Dehm 1950. Miocene of Bavaria.

Martes lydekkeri Colbert 1933. Lower Pliocene of northern Punjab, India. See also Colbert (1935). Is considered by Colbert (1935) a precursor of M. martes.

Martes martes (Linnaeus 1758). Pleistocene of England, Ireland, French Alps, southern France, Germany, Denmark and possibly Palestine. See also Trouessart 1897, Reynolds 1912, Hormann 1933, Garrod and Bate 1937, de Bois 1928, and Degerbol 1933. Reynolds (1912) says some British specimens "may come from the late Pliocene".

Martes majori (Weithofer 1889). Pliocene of Italy. Described originally under the genus Mustela, and not, so far as I know, ever placed in Martes.

Martes nambianus Cope 1874. Miocene of Loup Fork, New Mexico. See also Cope 1874, 1875, Coues 1877, Matthew 1899, Roger 1896, Trouessart 1897, Hall 1930.

Martes pachygnatha (Teilhard de Chardin and Piveteau 1930). Pleistocene of Nihowan, China. See also Teilhard de Chardin and Leroy 1945.

Martes palaesyriaca (Nehring 1902). Athlit Caves, Mount Lebanon (date ?) of Syria. See also Bate 1932. Are likely pre-historic, but scarcely Pleistocene.

Martes pennanti (Erxleben 1777). Pleistocene of Pennsylvania and Arkansas. See also Allen 1876b, Baird 1857 and 1859, Coues 1877, Trouessart 1897, Hay 1902, Brown 1908, Haug 1911, Hay 1914 and 1921, Lockwood 1884, Matthew 1915b, Osborn 1910, Hall 1936. The Pennsylvania skulls were first described from the Carlysle bone cave by Baird in 1857, who described among them one larger than any other he had seen. Brown (1908) described the Arkansas specimens from the Conard Fissure. These, he said, differed somewhat from Recent pennanti by its smaller PM_4 and M_1 . Hall (1936) did not examine Brown's material, but concluded, on reading his description that he was possibly dealing with specimens of M. diluviana rather than M. pennanti. Hall has also pointed out that the fisher no longer ranges nearly so far south as Arkansas. Hay (1930) considered these deposits as likely late Pleistocene. Brown (1908) however, considered the Port Kennedy deposit "lower middle Pleistocene", the Conard Fissure deposit very late Pleistocene. Hay (1912) dated the latter fauna Saugamon, but in 1908 had considered it Illinoian. Hall (1936) dated it intermediate in age between those of Port Kennedy and Potter and Samwell caves. Supposedly late pre-European specimens of fisher have been found in southern Ontario (Wittemburg 1919, 1939, 1948), Lake Michigan shore in Indiana (Rand and Rand 1951) and Ohio County, Indiana

(Kirkpatrick and Conoway 1948). Scott (1937) erroneously or otherwise, considers the origin of the species M. pennanti to have occurred early in the Recent.

Martes pusilla Viret 1951. Miocene of southern France.

Martes sainjoni Maget 1908. Miocene of southern France.

Martes ten Shikama 1949. Pleistocene of Kuzun, Japan.

Martes transitoria (Gaillard 1899). Miocene of southern France. Originally described under the genus Mustela and not, so far as I know, changed to Martes.

Martes vetus Kretzoi 1947. Upper tertiary of Germany. See also Heller 1933. Considered by Kretzoi to be synonymous with M. intermedia Heller.

Martes woodwardi Pilgrim 1931. Lower Pliocene of Asia; specific locality not known to me.

Martes zdanskyi Teilhard de Chardin and Leroy 1945. Pliocene of Yushe, China.

Martes zorilloides (Lartet 1851). Miocene of southern France. Named originally as Mustela. Never, so far as I know, determined to be Martes.

Other non-specific references to marten, other than those that may be synonymized with references given above, or that have not later been shown to represent the genus Mustela

follow: Gidley 1920 - Pleistocene of Maryland; Stock 1925 - Pliocene of California; Merriam 1917 - Pliocene of Oregon; Merriam, Stock and Moody 1925 - Pliocene of Oregon (here called Mustela); Osborn 1925 - La Brea of California; Stock 1925 - La Brea of California; Hofman 1893 (Abh. Geol. Reichs 15 : 34) - Miocene of Austria; Schlosser 1888 - Miocene of Suevia; Takai 1952 - Lower Miocene of eastern Asia.

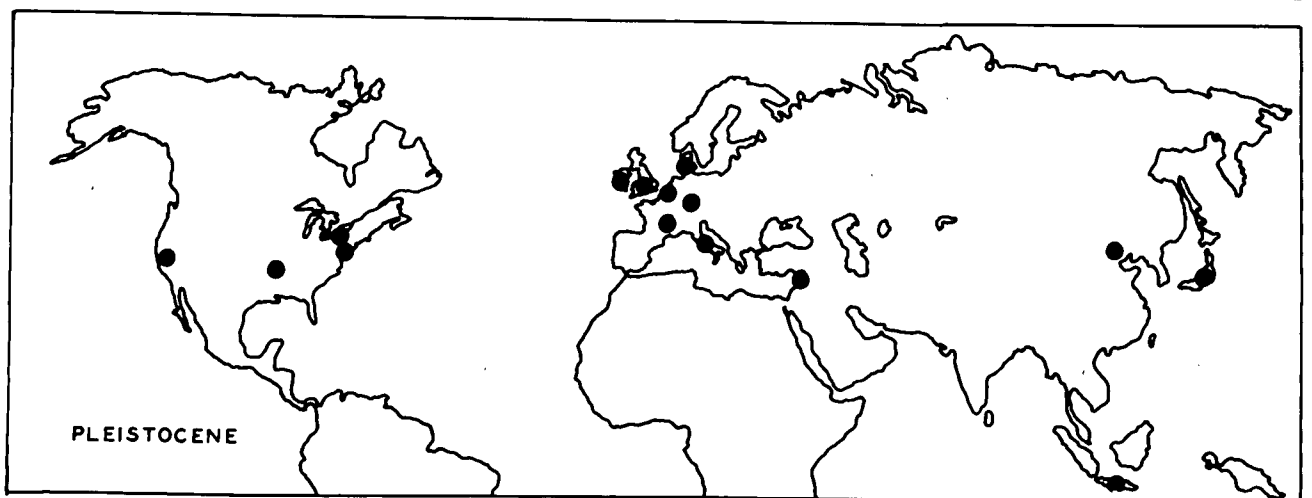
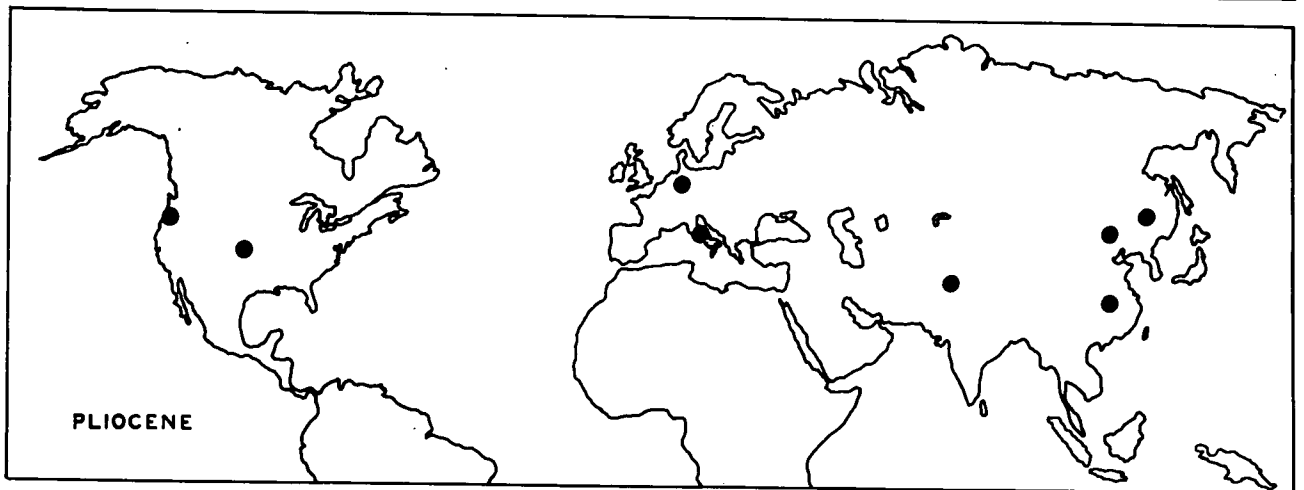
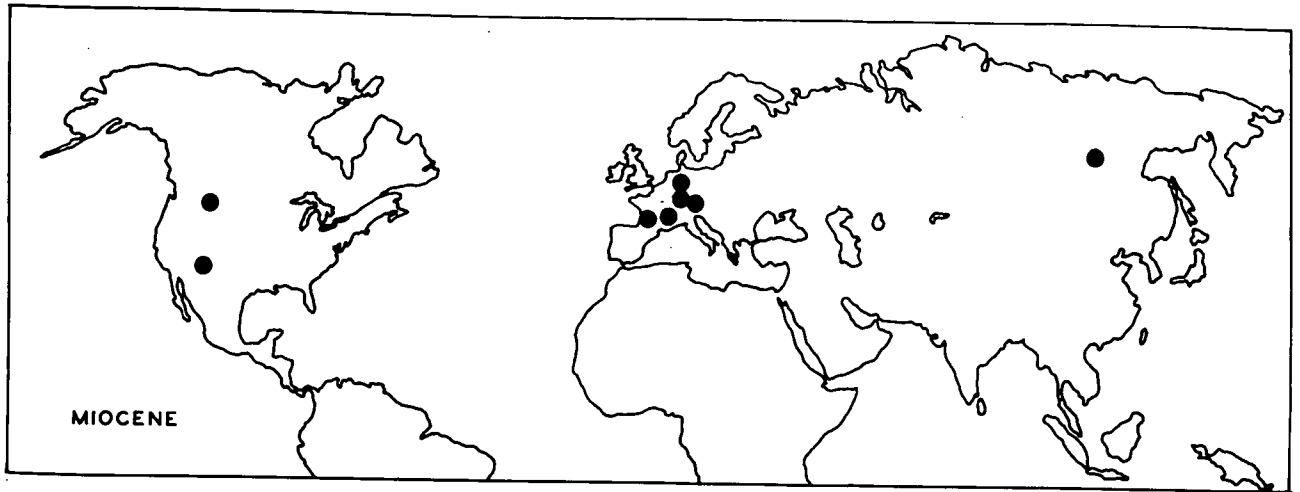
Hall (1936) considered references to the Rancho La Brea specimens as being misidentifications of material properly referable to Mustela frenata.

If the records of fossil marten are mapped (Figure 12), certain conclusions may be obtained, as follows. The distribution of all fossil specimens fall within the range of the present day distribution of the genus. Minor exceptions to this are shown by M. nambianus, M. foxi, and M. pennanti in central North America. No fossil species that is living today has been found far beyond its present day range, with two exceptions. One is the pleistocene location of M. pennanti in Arkansas, a considerable distance from its present limit. The second is more instructive, This is the location of M. lydekkeri, allied by Colbert (1935) to M. martes, in northern India, far from its present range in west central Russia.

The genus apparently appears in the Miocene simultaneously in Europe and North America. Takai (1952) assures us that it has been recorded from the lower Pliocene of eastern Asia.

Figure 12.
(To face page 308)

Figure 12. The distribution of the fossil species of marten.



It appears then, that the fossil record tells us little more than that the genus arose during the Miocene and appeared essentially simultaneously in Eurasia and the New World, and that little in the way of intercontinental migration of either the genus, or its component species can be demonstrated.

It is a general practice with palaeontologists to name all fossils earlier than the Pleistocene distinct species. Not having surveyed the literature in detail, it is hard to determine when the Recent species originated, but from the above material, the following tentative scheme may be drawn up.

Martes flavigula: First known from the Pliocene of China, northern India and possibly Java.

Martes pennanti: First known, along with its relative M. diluviana, from the Pleistocene of the eastern United States.

Martes foina: Known first from the Pleistocene of Belgium.

Martes martes, and the martes, zibellina, melampus, americana complex: (grouped together because, as previously pointed out, morphological and distributional evidence closely allies them). The first of this complex to appear, so far as I have been able to determine, is M. lydekkeri from the lower Pliocene of northern India. This is said by Colbert (1935) to be "almost identical in size and structure with the modern Martes martes." It is followed in the late Pliocene or early Pleistocene by M. martes in Europe and western Asia, and in the Pleistocene by M. americana in eastern and western United States. I know of no fossils

of M. zibellina or of M. melampus, although they are likely at least as old as the Pleistocene, and even the Pliocene, M. ten has been described from the Pleistocene of Japan, but placed in a distinctive subgenus, so that it is not likely a forerunner of M. melampus.

In attempting to devise a phylogeny, I must make use of what knowledge may be obtained from the fossil material here considered, and the morphological interpretations dealt with in the preceding pages. Maslin (1952) has attempted to list and discuss those morphological characters in a group that imply primitive or advanced condition, and thus to treat objectively the criteria used in determining phylogenies. I do not know enough about martens to be able to comply with his principles, and have been obliged to resort to a single rule of thumb: that a greater degree of morphological distinction between the two species means that a longer period of time has elapsed since the two became genetically isolated. In other words, degree of morphological distinction is a measure of time of isolation. This rule may be applied only very generally, however, because Simpson (1944) has shown that rates of evolution need nowhere be near the same in different species, and Mayr (1942) has pointed out that populations genetically isolated may be very similar morphologically (sibling species) and that on the other hand very closely related forms may show quite different morphologies. I have no means of determining the situation in martens, and am obliged therefore to accept the rule as I have stated it.

Martes flavigula is first known from the middle Pliocene. It is so distinctive, however, when distinguished from the Martes martes complex, which is first known through M. lydekkeri in the lower Pliocene, that I conclude the division between the two must have occurred very early in the Pliocene or in the Miocene. The same situation holds for M. foina and M. pennanti. These forms are, however, more similar to the Martes martes complex than is M. flavigula, hence I conclude that their phyletic lines evolved some time between the evolution of the M. flavigula lineage and the time of M. lydekkeri (lower Pliocene). Of the two, M. pennanti is the more distinctive, hence it is hypothesized that it appeared before M. foina. According to Simpson (1947 a and b), most migration across the Bering land bridge occurred in late Miocene time; hence I hypothesize the origin of the M. pennanti line in North America to have occurred at this time.

M. americana americana is as distinct from the M. martes complex as M. foina. However, unlike M. foina, it is still capable of interbreeding with one of the complex (M. a. caurina). I conclude that it evolved later than did M. foina, but before the remainder of the M. martes complex had broken up into its present day species. Most Bering land bridge migration of the time occurred in the middle and upper Pliocene, according to Simpson (1947a and b), so that I place the origin of the stock of M. a. americana in North America in the middle Pliocene.

The M. martes complex is represented in the fossil record only by specimens of two of its species from the late Pliocene, possibly, and the middle Pleistocene of North America

and Europe. I presume that the species now comprising it evolved before the beginning of the Pleistocene, perhaps as Reynolds (1912) suggests, in the late Pliocene. I hypothesize that M. a. caurina crossed to North America in the upper Pliocene, at the peak of the Pliocene Bering land bridge migration (Simpson 1947a and b). Even greater migrations occurred in the Pleistocene, so that it is not impossible that the migration occurred during the early Pleistocene. Romer (1945) and Colbert (1942) point out that it is becoming increasingly clear that most mammals characteristic of the North American Pleistocene arrived here at or near the beginning of the epoch.

The conclusions are diagrammed as a formal phylogeny on Figure 13. It should be regarded as only tentative.

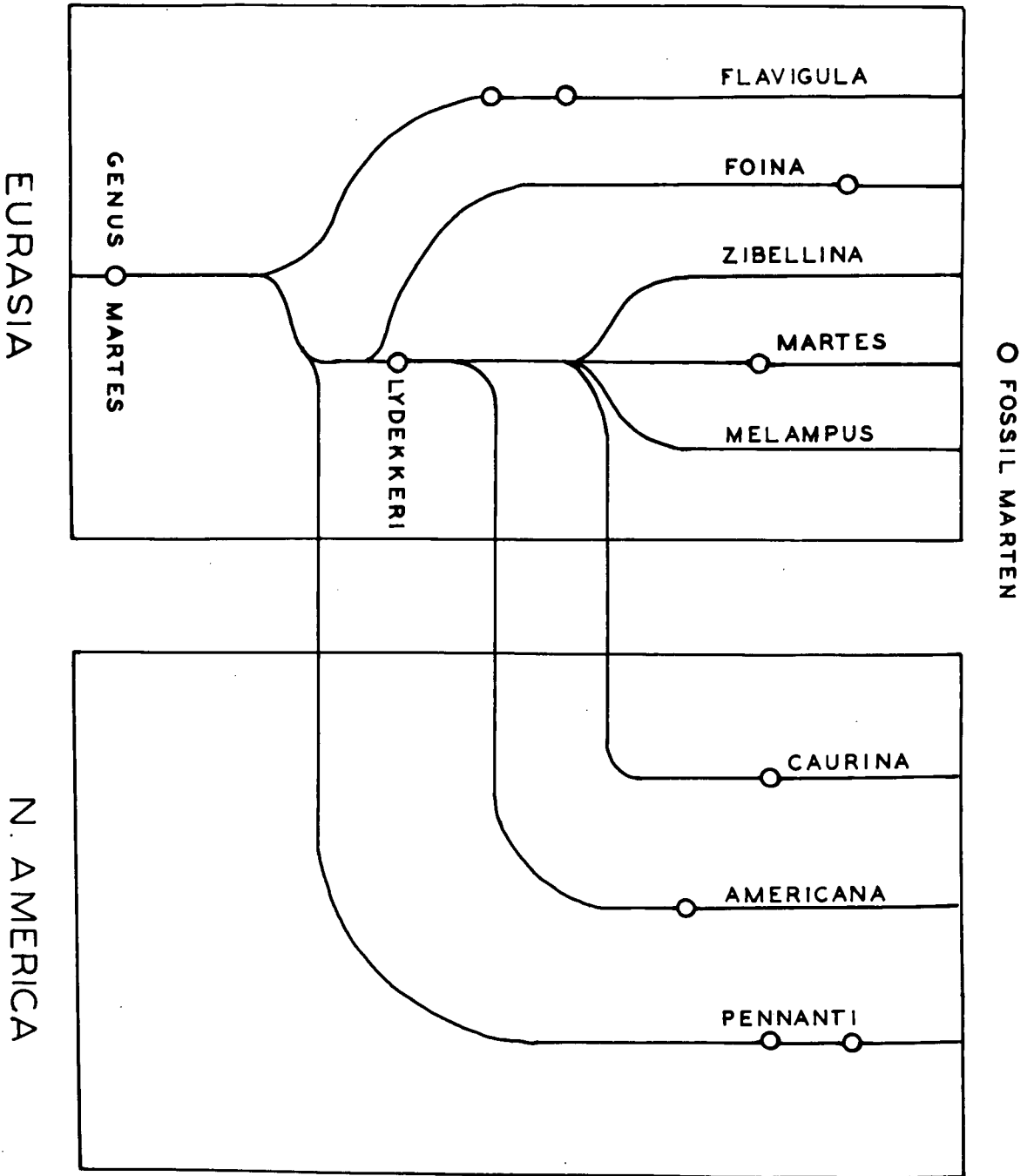
It will be noticed that I consider the origin of the genus Martes to have occurred in the Old World. This is done as a matter of convention, following the pattern set by earlier authors. I tentatively attribute the origin of the M. martes complex to Eurasia, because of the early date of the material referred to M. lydekkeri, and because of the greater number of species of the complex in the Old World. This latter point may only be a result of the greater expanse of land available to the marten of Eurasia with the result that there was greater likelihood of secondary speciation.

In North America today, Martes americana americana exists as far northwest as Alaska, much nearer to the former Bering land bridge than does M. a. caurina. This suggests that M. a. caurina and not M. a. americana was the first to arrive

Figure 13.
(To face page 312)

Figure 13. A hypothesized phylogeny of the Recent species of marten.

MIOCENE			PLIOCENE			PLEISTOCENE					REC.
						N		K		I	
										W	



in North America. I do not agree with this, and as both Davis (1939) and Dalquest (1948) suggest, offer that this peculiarity of distribution is a result of shifting of distribution due to the advance and retreat of the ice front during the Pleistocene.

BIOGEOGRAPHY

INTRODUCTION

During the Pleistocene, continental and mountain glaciers, growing out of the mountains of the northeast and west coast, covered most of what today constitutes the range of the marten and fisher in North America. There is reason to believe (as pointed out below) that the range of these animals at the beginning of the Pleistocene was much as it is today. It becomes obvious then that the advance of the Pleistocene ice front must have had extreme effects on the marten and fisher populations that it displaced.

A survey of the fossil record shows us that we can learn little of the Pleistocene history of these animals from it. We know that M. a. americana or less likely M. a. caurina, and M. pennanti existed on the east coast, and M. a. caurina on the west coast during middle or late Pleistocene time, but little more. If anything more of the histories of these animals is to be hypothesized, other approaches to the problem must be taken.

There are various means of attacking such problems, three of which immediately come to mind. They are all zoogeographic, or rather biogeographic in nature. One is a

comparison of distribution maps, in a simpler or more complex fashion. Van Dyke (1939) and Linsley (1939) have done this recently for insects, Mayr (1946) for birds, and Dalquest (1948) for mammals. The second method is the application of criteria for the determination of centers of origin, as outlined by Adams (1902 and 1908), Matthew (1915a), Cain (1944), Darlington (1948), Hulten (1937) and Halliday and Brown (1943). The third means is the application of palaeoecological methods, an interpretation of the history of an animal through the history of its environment. This has been done recently by Voous (1947 and 1949) for the European bullfinch and the woodpecker, genus Dandrocopus, and by Howell (1952) for the sapsucker. There are, of course, other approaches, but these three, especially the last two, are the ones with which I will spend the most time.

The basic dictum around which this account will be built is this: that the history of the vegetation in which an organism lives is the key to the history of the organism itself. Since this will be important in the account following, some evidence in support of it must be given.

Not all mammals are restricted to a given vegetation type. Some of the bats, the raccoon, striped skunk, cougar, coyote, bobcat, deer mouse, meadow mouse and white tailed deer among others, seem to have distributions not strictly related to the distribution of vegetation types. In marten and fisher, however, this is not the case. They occur, in a general sense, wherever boreal evergreen forests occur, and not elsewhere. This general rule may be accepted, although it is more applicable to marten than to fisher.

The close relationship of plant and animal distribution and evolution, although often stated (Adams 1902 and 1908, Clements and Shelford 1939, Camp 1947, Clements 1916, Hulten 1937, Gunderson and Hastings 1944), is often ignored. Clements (1916), Axelrod (1952b) and Simpson (1952) point out that the controls of both are different. Plants are controlled by climate, edaphic factors, biotic factors and land connections, in that order, while animals are controlled chiefly by land connections and plants in that order.

I hypothesize that the history of the genus Martes and its predecessors are closely associated with the Arcto-tertiary flora as outlined by Chaney (1925, 1936 and 1940), Cain (1944) Mason (1947), Axelrod (1949 and 1952a) and others listed by these authors. As evidence of this, I suggest that the distribution of fossil marten never lies outside the known range of this flora, and that Martes is still extremely primitive and close to its Tertiary ancestry. This flora originated in the Cretaceous or earlier, and with the increasing continuity of climate resulting from late Tertiary mountain building, moved southwards approximately 10° latitude during the Tertiary to about its present position by the Pliocene. It became isolated from its Eurasian counterpart during the Pliocene and Pleistocene and gave rise during the same period to the eastern hardwood forest, the Cascade, Montane, Sierra Nevada forests of the west and presumably the boreal forest to the north. The relationship of this last named forest is largely assumed. The genera Pinus, Picea, Thuja and Populus

are known from the Cretaceous, and Abies, Taxodium and Chamaecyparis are known from the Miocene or earlier, but fossils are rare (Arnold 1947). Daubenmire (1947) says that the modern taiga has arisen since the Oligocene, but it is likely much older, not extending its distribution to its present range until mountain building of the later tertiary occurred. The segregation and isolation of the present day vegetations of the coastal mountains likely occurred at about the same time.

By the end of the Pliocene, the vegetation derived from the Arcto-Tertiary flora had a distribution and composition much as it has today (Clements 1916, Axelrod 1952a). Presumably both Martes americana americana and M. a. caurina had evolved by then, and had distributions somewhat similar to that of today.

Our knowledge of the Pleistocene is not detailed because so little evolution occurred within that epoch. No dating by index fossils is possible and chronologies outside the drift border are exceedingly difficult to obtain. Only in the post-Mankato has any sort of reasonable picture of events been obtained and even here the picture is still fragmentary.

There is reason to believe that this situation will not always hold. New methods of accurate correlation (Lougee 1953), the absolute correlation and chronology provided by the use of radioactive techniques (Libby 1952, Urry, in Hough 1953), and current refinements of pollen analysis, as carried out by such workers as Deevey, Frey, Potzger, Hansen and others, will eventually provide a means by which vegetation maps for various stages of the post-Mankato will be prepared. Attempts have

already been made in this direction in Europe (see Hare 1953), but it will likely be some time before their equivalents are produced in North America. If such charts were available now, a reasonable interpretation of the late Pleistocene history of marten and fisher might be devised. Until they are, only a sketch of such an interpretation can be attempted.

The most recent and important accounts of the Pleistocene are to be found in Flint (1947) and Deevey (1949). Much of what follows is drawn from these.

How long the Pleistocene lasted can only be guessed at. Flint (1947) estimates its length as about a million or a million and a half years. Hough (1953) dates the Kansan ice advance as being 845,000 years old (using Urry's percentage equilibrium method on ocean cores). To my knowledge, this is the oldest absolute date obtained for the Pleistocene. The Aftonian interglacial is estimated to have lasted about 200,000 years based on weathering; at least it is considered to have lasted quite considerably longer than the subsequent Yarmouth interglacial, so that it seems likely that Flint's original estimate of the length of the Pleistocene was not far wrong. At any rate, it appears likely that while great changes in the compositions of faunas occurred during the Pleistocene, not nearly so much in the way of evolution occurred. The average extent in time of genera of land carnivores is said to be about six and a half million years (Simpson 1944, Zeuner 1950, see also Nicol 1953). Species distinctions in mammals have not

evolved since the middle Pleistocene (about 500,000 years ago) according to Zeuner (1950) and they may not occur after twice as great a length of time. "Good" subspecies take about 500,000 years to evolve according to the same author.

There are some cases of supposed very rapid evolution. Cain (1944) says that the genus of hawthorns (Crataegus) has produced many species in historic time. Durrant (1952) believes that mammal subspecies have evolved on the islands in Great Salt Lake in only 2,000 years and Huxley (1940) says that adaptive colour changes in insular house mice have occurred in 100-200 years. McCabe and Cowan (1945) give other examples of relatively rapid evolution.

I conclude that even though the length of the Pleistocene is not yet known exactly, it could not have been so long as to have allowed very much evolution within the martens and fishers, and that they are basically as they were in the early Pleistocene. I have pointed out that this decision had been reached earlier, on the fragmentary fossil evidence, but restate it here because some workers have interpreted the two subspecies of marten to have evolved during the Pleistocene, not before. The evidence is not conclusive, however, and it may be considered hypothetical, and not unreasonable.

Four major advances and retreats of ice are known from the Pleistocene. These have been dated by various means, most usually in the past by depth of leaching of till (Kay 1931, Thornbury 1940), or by counting of varves (Antevs 1953 and earlier papers). Recent developments in techniques employing

rate of radioactive decay promise absolute chronology, and Hough (1953), using Urry's work on ocean cores, arrives at the following scheme:

Wisconsin glacial	10,000 to 65,000 years ago
Sangamon interglacial	65,000 to 270,000 years ago
Illinoian glacial	270,000 to 340,000 years ago
Yarmouthian interglacial	340,000 to 720,000 years ago
Kansan glacial	720,000 to 845,000 years ago.
Aftonian interglacial and Nebraskan glacial	No dates available.

Within the Wisconsin, four sub-ages are known (sometimes considered five). Their dates are also uncertain. Nelson (1954), by correlating glaciations in the mountains of Colorado with the standard section, arrived at the following dates of glaciation: 11,500, 17,000, 46,000 and 63,000 years ago. The first of these (for the last glaciation) was obtained by radio-carbon dating of the Two Creek bed in Minnesota and of the Mankato maximum by Libby (Flint and Deevey 1951, Arnold and Libby 1951), which give an average for the latter of 10,000 years. Other measurements show the Cary to be at least 18,000 years old (Flint 1953), and $19,200 \pm 1,000$ years (Urry 1948, p. 697). These do not appear to coincide with Urry's findings for Hough's (1953) ocean core, for within the Wisconsin he finds glaciations at 11,000, 15,000, 26,000, 38,000, 51,000 and 64,000 years ago. Although he attempts to correlate these to the known Wisconsin chronology, the fit appears poor.

Even though the chronology seems discordant, the

evidence of multiple glaciation is accepted today as fact (Flint 1947). It is known that its effect on boreal biota was extreme, but lack of dating makes the details obscure. The four major glaciations in North America had an extent of the same magnitude as the last glaciation, as maps of the drift border (Flint et al. 1945) indicate, but not much more is known. Flint (1947) concludes that the facts at hand indicate the likelihood that the pre-Wisconsin sheets originated in the same districts, developed and retreated in the same manner and had the same approximate outer edge as did the Wisconsin. Flint also points out the possibility that the Nebraskan was preceded by one or more glaciations whose drift has not been identified, or which has been subsequently lost.

The floras and faunas of the pre-Wisconsin are summarized by Hay (1923, 1924 and 1927), Baker (1920), Flint (1947) and others. See also Hansen (1935), Rosendahl (1937), Lane (1941), Schulta, Wenighoener and Frankforter (1951), Leonard (1950), Voss (1939), Hough (1953), Hibbard (1952b), Flint and Deevey (1951), McLearn (1927), Coleman (1933), Coleman (1941), Frey (1952). The only general conclusion that may be drawn is that not only were the glaciations similar, but that the interglacials were as warm or warmer than the present, and that the distribution of boreal biota at glacial maxima may have been essentially as it was in the Wisconsin maxima, although it has not been shown to be so.

The Wisconsin age is broken into four sub-ages, Mankato, Cary, Tazewell and Iowan. Each of these is marked by

readvance in the Lake States and midwest after a phase of ablation of unknown extent (Flint 1947).

It appears that the longest break in the glaciation of the Wisconsin was made between the Tazewell and the Cary advances (Ruhe 1950 and 1952, Hough 1953, Schultz, Wenighoener and Frankforter 1951). Ruhe (1952) proposes calling this the Bradyan interval. Flint (1947) believed that the ice sheet did not retreat more than a few hundred miles in the Iowan-Tazewell interval, and that the Two Creeks interval could likewise not have been long. Murray (1953), working on the Valders red till, concluded, however, that the ice must have retreated to a point north at least of the Straits of Mackinac. Flint (1953) says it may have shrunk north of all of the Great Lakes, and north of the St. Lawrence River.

The most recent and detailed papers concerned with ice retreat in the late Wisconsin are those of Lougee (1953), Flint (1953) and Antevs (1953). Most of what follows is based on Flint's paper. Currently it appears the Binghampton, Newburgh, New Britain, Valparaiso, younger Catskill, upper New England, Cary and Boston drifts are considered to be Cary in age (Flint 1945, 1947, and 1953, Antevs 1953), but MacClintock (1954) believes drift in the Gaspé to be also Cary, which Flint considers more likely Mankato. During Two Creeks time ice retreated to the points given above, advancing shortly thereafter to the Mankato drift border. This is currently described as including the Altamont, Max, Rolling River, Des Moines, Mankato, Valders, Port Huron, Manistee, Syracuse, Glens Falls, Fort Edward,

Fifteen Miles Falls, Coveville, St. Johnsbury, Gorham, Aroostook County, and Gaspe moraines and other drifts and deposits, according to Flint (1953), and correlating his conclusions with those of Antevs (1953), Flint (1947), MacClintock (1954), Denny (1952), Bretz (1943), Horberg (1952) and Allison (1947).

Not all writers agree. In the above, all correlations east of the Adirondacks are those of Flint (1953). Port Huron time is considered by some to predate Two Creeks time, but likely approximates if nothing more, the general position of the Mankato ice front. MacClintock (1954), as pointed out above, believes the Gaspe drift to be Cary, and Flint (1953) admits the possibility that the Mankato ice may have passed through Cape Breton Island.

Townsend and Jenke (1951) are not certain that the Altamont moraine is the chronological equivalent of the Max and Mankato systems, though most other authors assume they are. Halliday and Brown (1943) and Raup (1946) correlate the Altamont with ice fronts about Great Slave and Great Bear Lakes as mapped by Cameron (1922), but there seems to be no real evidence for this. Flint (1953) correlates Tolleston Lake Chicago and Lake Warren with the Mankato maximum. Not all have agreed with this in the past.

The possible biogeographic significance of the Altamont system to biogeographers was first pointed out by Halliday and Brown (1943) as far as I know. It has been mapped by Bretz (1943), Flint et al. (1945), Hansen (1949b), Horberg (1951 and 1952) and others. Townsend and Jenke (1951) have shown that

the term Altamont should be restricted to the type locality in South Dakota, and propose the name Max moraine for the system to the northwest. These authors are not sure that the two are equivalent in time; further they are not sure that the Max is a true terminal moraine, although it is accepted as such here.

Bretz, in 1943, considered the whole "Altamont" to be Mankato in age. Those lying to the southwest he considered older. Some of these showed signs of readvance, he concluded, so that the region was not one of constant ice retreat. Horberg (1952) came to the same conclusion on somewhat different grounds. He indicates that the Altamont corridor must have been nearly, if not completely, obliterated during either or both of the Tazewell and the Cary. Flint (1947, figure 57) came to the same conclusion apparently. Horberg (1951) has also mapped a series of moraines lying between the Max-Altamont system and Lake Winnipeg, lying parallel to it, and presumably younger than it.

The northern limit of the ice free corridor is not known, although the cool nature of the climate of the present day Mackenzie mountains suggests that it did not extend beyond these. Denny (1952) suggests that relict signs of congeliturbation between Fort Nelson and Dawson Creek indicate that the area may have been in part ice free, but marked by a rigorous Arctic climate.

The first stage of ice retreat in Mankato time was presumably in the Altamont sector. Ice retreat, as it is concerned with the Great Lakes, is complex and detailed in Leverett

and Taylor (1915). The first major moraines to the north are the Le Pas, Sioux Lookout and Pembroke, all of which are correlated by Antevs (1953). Flint (1947, p. 265) tentatively correlates the ice marginal lakes now marked by Lakes Athabaska, Great Slave and Great Bear with Lake Agassix, which presumably was present at the time. It is quite possible that these should also be correlated with the morainic system southwest of Cree Lake.

The next advance, the Cochrane, is believed by Schultz, Wenighoener and Frankforter (1951) to have been sufficient to affect stream regimen as far away as Nebraska. No correlations, which seem positive, have been made elsewhere, but the steady succession of eskers in Mackenzie and Keewatin suggests that they might be found somewhere about the Keewatin Mackenzie boundary. The ice sheet, then, presumably shrank into the region of Hundon's Bay.

It is assumed by Flint in his various papers that the final site of deglaciation was in Ungava and Labrador, because it was the source of the Laurentide sheet. The pattern of eskers shows there was a gradual retreat of ice on all sides into a center somewhere near the middle reaches of the Kaniapiskin River.

The pattern of glacial retreat in the Cordilleran sheet is not yet known. Flint (1947) and most other authors now agree to the synchronous nature of glaciation throughout the northern hemisphere. For this reason it is likely that the basic pattern known from the Lake States and Europe will

be shown to hold here too. However, in most localities no more than two glaciations are recorded, although four are recorded from the Sierra Nevadas (Blackwelder 1931), the Sawatch Range (Nelson 1954) and elsewhere. In Washington and British Columbia two are recorded and there is some evidence for a third. The two recorded ones are called the Vashon and the Admiralty in western Washington, the Wisconsin and the Spokane in eastern Washington. The Vashon and Wisconsin are considered equivalents of the Wisconsin in the east by Bretz (1923). See also Flint (1947).

Johnston (1926), Kerr (1936), Davis and Matthews (1944) all indicate that the interior plateau of British Columbia shows only slight evidence of glaciation. Flint (1947) concludes that the glaciers grew out of the mountains of the east and the coast, flowing later into the intermontane region. It is to be assumed that with post-Vashon retreat, ice first left the intermontane region while it persisted in the mountains, leaving the mountains perhaps only in the climatic optimum (Matthes 1939). It is likely too, that within the intermontane plateau, deglaciation was initiated in the Okanagan region, and at its northern edge, in Yukon territory (Flint 1947, p. 217). Matthews (1951) believed that ice last left the Garibaldi Park region about 8,000 years ago, and the same worker has told me that a radiocarbon date of 10,000 years has been obtained for material in the Hope-Princeton area. Hansen (1947) concludes that postglacial climates in the west were similar to those recorded from the eastern United States.

Besides the evidence provided by the Altamont moraine, there are good theoretical reasons for believing that the first ice free area in formerly glaciated regions was in the Altamont corridor of Alberta.

Most evidence of ice advance indicates that the Laurentide sheet grew outward from the James Bay, Labrador Ungava region. See Flint et al. (1945) for striae, grooves, boulder trains, drumlins and other evidences of ice advance, and Flint (1947) for evidence from erratics. Flint (1943, 1947 and 1953) and Flint and Dorsey (1945) have advanced the theory that, contrary to earlier opinion, only one ice center occurred east of the Rocky Mountains, this centering in the mountains of Quebec, Labrador, Greenland and other highlands of the northeast. The reasons for this conclusion are as follows. Regions with continental climates maintain glaciers at higher altitudes because of reduced snowfall, and lack of cloudiness (Flint 1947). The work of Sanderson (1948) and Hare (1951) gives added proof of the correctness of this view. A second reason is that the area from James Bay and the Great Lakes to the Rocky Mountains is one of gradually increasing altitude (Flint 1947). A third reason is that the pattern of known hingelines as mapped by Flint (1947, figure 81) and Lougee (1953) indicate concentricity around the hypothesized center, with early ice retreat in Alberta and the Prairies. A fourth reason is that James and Hudson's Bay and the Thelon Basin are recognized as depressions not yet arisen from the load of ice they once bore (Flint 1947, Bird 1953 and 1954). It follows that the last great mass of

ice centered in this region, since it is still depressed. The region was likely freed of ice, however, before Labrador and northern Quebec were (Flint 1943 and 1953, Osborne 1951). It might be argued that, except for the effects of hinging, the topographic isopleths south and west of Hudson Bay likely approximate the position of the ice front at various stages of retreat. An added reason is that the known sequence of drainage changes in the Great Lakes (Leverett and Taylor 1915), Lakes Ojibway, Barlow and Agassiz (Nikiforoff 1947) and Athabasca and Great Slave (Cameron 1922) all suggest a pattern of glacial retreat as outlined by Flint. A further reason is that Moraines younger than the Altamont, which have been correlated at various times in the past by Antevs, all suggest an easterly or northeasterly retreat from the Altamont sector. And lastly the eskers, deposits of supra and sub-glacial streams which presumably ran at right angles to decaying ice margins, are almost certainly Wisconsin in origin (Flint 1947 and 1952 and W. H. Mathews, verbal information). These when plotted (figure 14) give a picture of ice retreat at no variance with the theorized retreat of Flint and the evidence listed above.

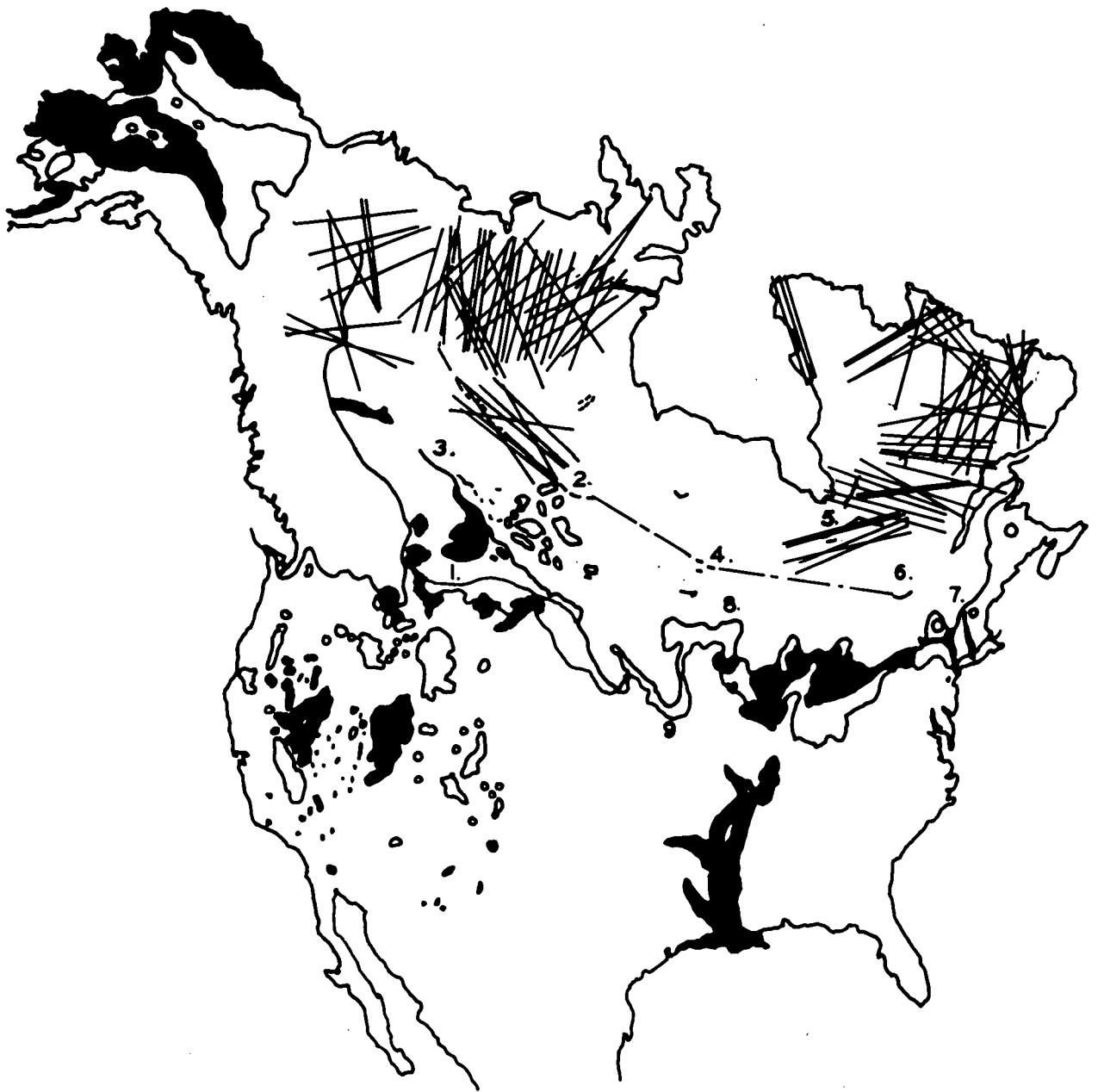
Some of the above information has been mapped on figures 14, 15, and 16. These indicate the evidence for an ice free corridor in the Altamont sector while much of Ontario and Quebec were still glaciated. Figure 17 depicts a general sketch of the ice limits at about Lake Algonquin time during the climatic optimum approximately 5,000 years ago.

Figure 14.
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Figure 14. North America in Mankato time.

1. marks the early Mankato ice front;
2. the le Pas moraine;
3. the Max-Altamont system;
4. the Sioux Lookout moraine.
5. the Cochrane deposits;
6. the Pembroke moraine;
7. the St. Johnsbury moraine;
8. the Mankato system;
9. the limits of Cary drift.

The dotted lines mark an assumed late stage correlation between the Cree Lake, le Pas, Sioux Lookout and Pembroke moraines. Fluvial and lacustrine deposits are shown in solid black. The series of straight lines about the Canadian Shield are lines drawn at right angles to eskers, and are assumed to approximate positions of late Mankato ice fronts at various stages of retreat. Compiled from many sources, but especially from Bretz 1943, Horberg 1951 and 1952, Flint and others 1945, Flint 1947 and 1953, Meinzer 1922, Kellogg 1936, Denny 1952, Baker 1920, Wilson 1945, Bird 1953, Canada Dept. of Mines and Resources map series, Antevs 1953 and Lougee 1953.



Figures 15,
16 and 17.

(To face page 327)

Figures 15, North America during the Pleistocene.
16 and 17.

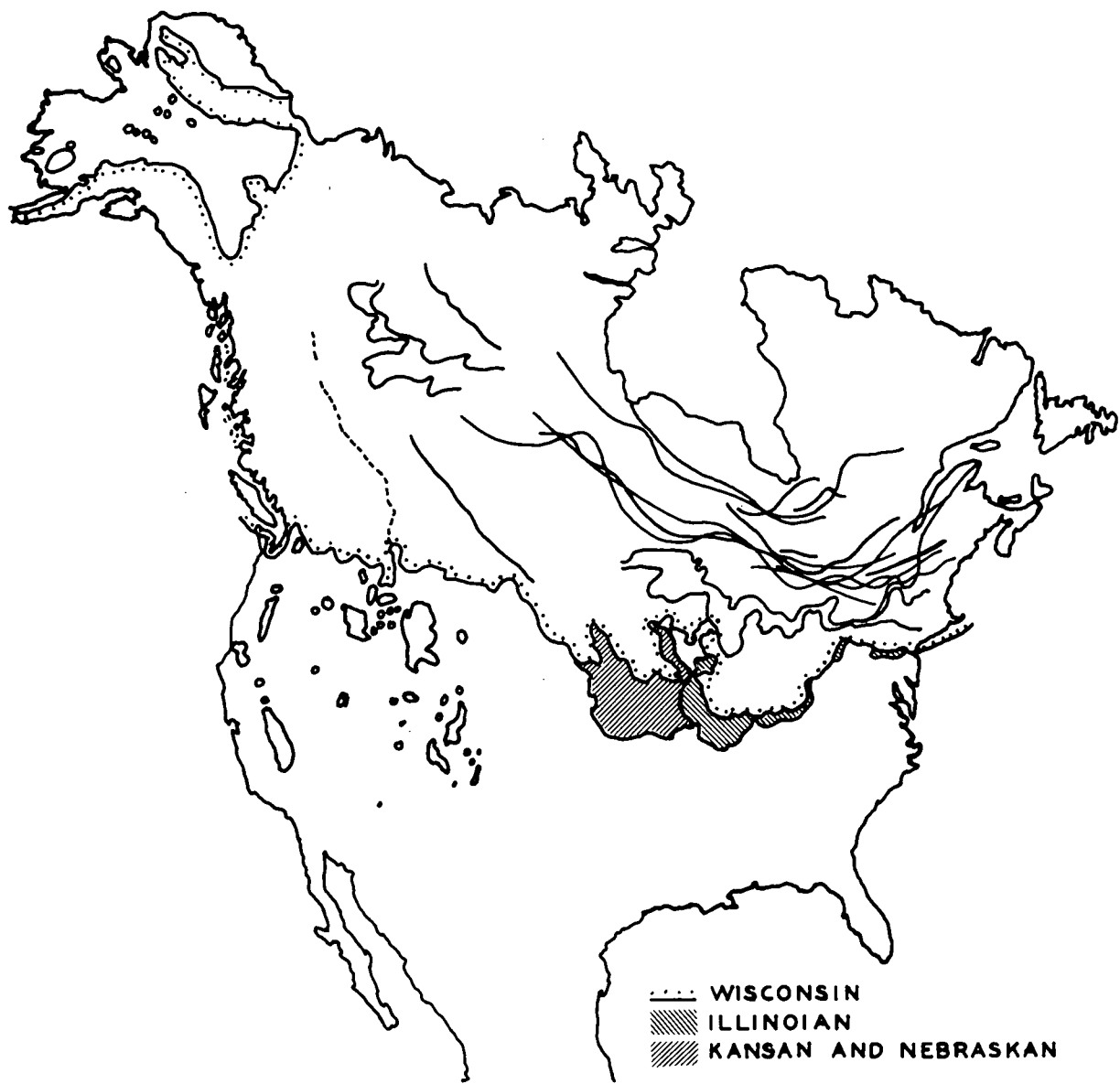
Figure 15 maps the extent of the drift borders, together with assumed lines of glacial retreat as they have been mapped by various authors. The dotted line marks the separation of the Cordilleran and Laurentide ice sheets. From Flint and others 1945, Flint 1947 and 1953, Leverett and Taylor 1915, Antevs 1925, 1928, 1929, 1931 and 1953, Cameron 1922, Norman 1938, Rutherford 1941, and Denny 1952.

Figure 16 maps the distribution of pluvial and postglacial lakes and maximum incursions of the sea; the dotted line bounds the principal areas of loess deposition. From Flint and others 1945, Flint 1947, Meinzer 1922, Wolfe 1942, Kellogg 1936. The former presence of the lake in the Peace River region was pointed out to me by Dr. W. H. Mathews.

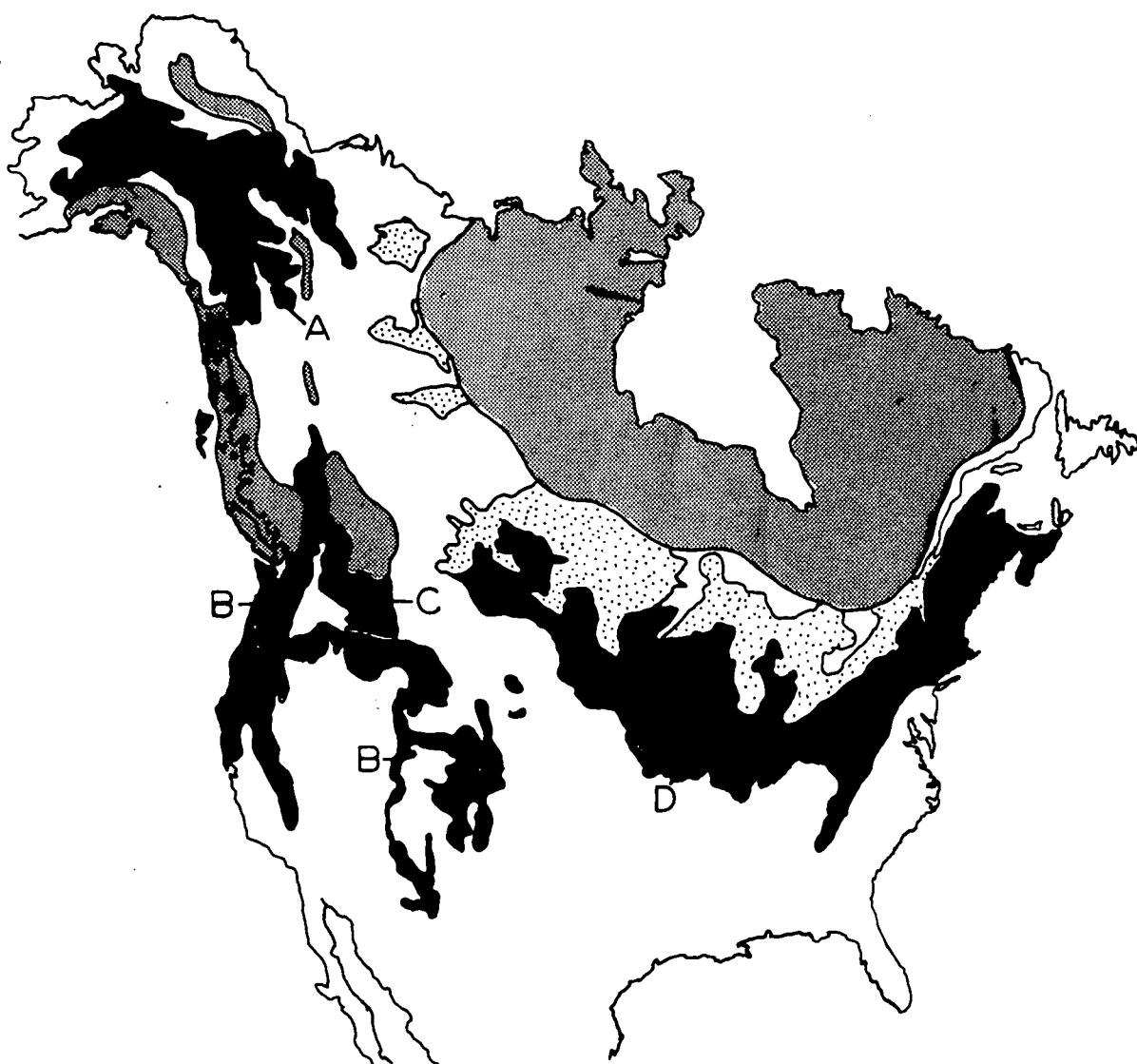
Figure 17 maps my conception of the distribution of ice and of martens and fishers at about the time of late Lake Algonquin and the climatic optimum (approximately 5,000 years ago.




The symbols on Figure 17 denote the following:

- A. Alaskan-Yukonian morph of M. a. americana, M. pennanti absent.
- B. M. a. caurina, and coastal and montane morphs of M. pennanti.
- C. British Columbian morph of M. a. americana, and possibly montane morph of M. pennanti.
- D. Eastern American morph of M. pennanti, and the following morphs of M. a. americana: to the west, Saskatchewan - Manitobian; to the east, Newfoundland - Labradorian, and in between and to the south, New England - Ontarian.







-  BOREAL FOREST, MARTEN & FISHER
-  LAKES
-  GLACIAL ICE

REFUGIA OF THE WISCONSIN

The following are the important refugia of the boreal biota during, and possibly preceding, the Wisconsin maxima, according to most authors writing on the subject. The first in the United States east of the great plains (Transeau 1903, Adams 1905, Harshberger 1911, Baker 1920, Gleason 1923, Hulten 1937, Halliday and Brown 1943, Raup 1946, de Beaufort 1951, Rand 1954 and many others). Most of the more recent workers tend to subdivide this into four major units, the driftless area, the area remaining west of the Appalachian mountains, the Appalachian mountains, and the coastal plain and now submerged coastal shelf. The second is unglaciated Yukon and Alaska (Adams 1905, Baker 1920, Hulten 1937, Halliday and Brown 1943, Raup 1946, Dalquest 1948, de Beaufort 1951, Rand 1954). A third refugium is the Coast and Cascade Mountains south of the ice sheet (Adams 1905, Harshberger 1911, Baker 1920, Swarth 1936, Orr 1943, Halliday and Brown 1943, Dalquest 1948, de Beaufort 1951, Rand 1954). And the fourth is the Rocky Mountains south of the ice sheet (Transeau 1903, Adams 1905, Baker 1920, Swarth 1936b, Orr 1943, Halliday and Brown 1943, Dalquest 1948, de Beaufort 1951, Rand 1954). Other minor refugia are sometimes named. These include the Arctic islands and nunatacks, neither of which are considered important here, the latter on the authority of Wynne-Edwards (1937) and other workers.

Biogeographers have determined the refugia listed above by various means, the most important of which follow. The first means to be discussed are objective and based on palaeontologic grounds.

The distribution of Pleistocene fossils and the known data of pollen analyses have often been used. On figure 18 a large proportion of these have been mapped. Ideally these would all be referred to the late Wisconsin. Some at least are known to be considerably older. This mapping shows clearly that the eastern United States and the Coast and Cascade Mountains were important refugia. The supposed Alaskan refugium is not so well documented but is accepted here. The Rocky Mountain refugium is marked by very few fossils and its status appears to be unsatisfactory. Some workers have doubted its existence as a refuge of any importance (Harshberger 1911), while others have maintained it on floristic or faunistic grounds (Orr 1943 and others). I accept it here but with less conviction than I do the others. Its chief claim, I think, lies in the distinctive nature of the present day biota of the Rocky Mountains and the Intermontane Plateau.

Examination of this map leads to the question of whether the three refugia south of the ice were isolated from each other. The biota of all three are distinctive, but other evidence is less convincing. The whole Great Basin area was, according to Meinzer (1922) as moist as southern Oregon is today, and about 8° C. warmer. Parts of southern Oregon are today essentially unforested (after Dayton 1949). However, the possibility is good that at least parts of the Coastal and Intermontane refugia were united during the glacial maxima.

There is reason for believing that the mountain refugium was separated from that in the eastern United States. Fossil

Figure 18.
(To face page 329)

Figure 18. The distribution of Pleistocene forest fossils.

The boreal forest is assumed to be represented by the following fossil species:

Abies balsamea, Larix laricina, Larix spp., Picea glauca, P. mariana, Pinus banksiana, Populus balsamifera, P. tremuloides and Betula neoalaska.

Lake forest:

Betula lutea, Pinus strobus, Thuja occidentalis, Tsuga canadensis.

Also mapped are boreal animal, diatom and moss fossils, and pollen profiles with boreal conifers at their bases. Hardwood and southeastern pine forest:

various extinct and living species of the genera Acer, Carya, Castanea, Celtis, Fagus, Fraxinus, Gleditsia, Juglans, Juniperus, Liquidamber, Liriodendron, Magnolia, Nyssa, Platanus, Quercus, Robinia, Tilia, Ulmus, Carpinus, Ostrya, Sassafras, and Betula nigra, Pinus echinata, P. serotina, P. virginiana, P. cariboea, P. taeda, P. distichum, P. serotina, P. glabra and Chamaecyparis thyoides. Also pollen profiles with hardwood species at their bases.

Coast and Rocky Mountain forests:

Pseudotsuga spp., Tsuga mertensiana, T. heterophylla, Pinus radiata, P. muricata, P. contorta, P. monticola, P. ponderosa, P. albicaulis, Acer macrophyllum, Picea sitchensis, P. engelmanni, Sequoia spp., Larix occidentalis, and pollen profiles with bases of these.

Based on many sources, but chiefly Lamotte (1952), Frey (1953), Hansen (1947, 1948, 1949a and b, 1950a and b, 1952 and 1953), Hansen and Mackin (1949), Hansen and Packard (1949), Heusser (1952 and 1954b), Cain (1940), Potzger (1951 and 1953), Potzger and Tharp (1947), Sears (1948) and Deevey (1951).



- BOREAL FOREST
- LAKE FOREST
- X HARDWOOD AND S.E. PINE
- COAST AND ROCKY MOUNTAIN

grasses of Pleistocene date are known from Nevada, Arizona, New Mexico, Alabama, Louisiana and elsewhere (Lamotte 1952), and loess deposits occur through the eastern plains (Flint 1945 and 1947), Schulta, Wenighoener and Frankforter 1951), indicating that while some reduction in the extent of the grasslands occurred, it was not extensive (see figure 16). Halliday and Brown (1943) present evidence that aspen parkland occurred north of the grassland during glaciation and it is possible that conifers also occurred here, as Transeau (1905) believed. The Black Hills are still forested with conifers today, and fossil conifers are known from Nebraska (Bessey 1888, Transeau 1903).

Fossil marten and fisher are known from the Pleistocene of the southeastern refugium and fossil marten from the southwestern, as pointed out earlier.

The second means of determining refugia is subjective and based on biogeographic grounds. Detailed accounts of the biogeographic method and its results are given by Adams (1902 and 1908), Hulten (1937), Halliday and Brown (1943), Cain (1944) and Deevey (1949). We are concerned chiefly with those methods used to determine centre of emigration, here interpreted as refugia.

If the present day distribution of the Coast, Montane, Boreal and Lake Forests are mapped with the Wisconsin maximum, it is found that they still extend into the areas named above as refugia. Marten today still follow this same pattern of distribution, extending into all four refugia, with one possible exception, the southeastern one. The range extends clearly

beyond the Mankato maximum, but scarcely south of other of the more extensive advances. This refugium is of such extent, however, that taken with the fossil marten known from the area leads to the conclusion that it occurred here during the maxima.

Fisher occur today in all refugia except the Alaska Yukon one. It is suggested elsewhere that fisher did not survive the Wisconsin, or at least the Mankato, there, and that this in part explains its absence today.

Transeau in 1905 mapped the distribution of boreal conifers and concluded that they showed concentricity in distribution with a center in the eastern United States. He concluded that this was an important refugium and that, with glacial ablation, various species of conifers have moved out varying distances from this center, some as far as Alaska. This method, with modifications, has been used by Hulten (1937) and Raup (1947) with results indicating the reality of the remaining refugia. Hustich (1949a) says that the number of plant species in northern Labrador is 172, while on the north shore of the St. Lawrence it is 622 species and varieties, a situation which has presumably resulted in part from the same cause.

Halliday and Brown (1943) have plotted the distribution of percentage density of Canadian forest trees, and they conclude that regions of greatest density mark the general region of former refugia. They conclude that the above named refugia are well documented, and suggest the possible existence of several others not considered here. Rostlund (1952) has done somewhat the same thing with fishes and has arrived at an essentially

similar map. Other factors than those discussed here may have been at work and Rostlund attaches no biogeographic significance to the distributions mapped.

Marten and fisher, when mapped to show the number trapped per year per 1,000 square miles of forest (figure 19 for marten), show again that greatest densities occur near, or in, former refugia, with the exception that fisher does not occur in the Alaska-Yukon refugium. The catch of marten and fisher has been reduced so much in the past several centuries, however, as pointed out elsewhere, that not too much significance can be attached to it.

Faunistic and floristic studies tend to indicate that the areas considered former refugia are marked by greater or lesser degrees of endemism (Harshberger 1920, Hulten 1937, Van Dyke 1939, Cain 1944, Deevey 1949 and others). These are generally, but by no means always, interpreted as marking isolation in refugia.

Rand (1954) concluded, on faunistic grounds, that M. a. americana wintered the Wisconsin in the southeastern refugium, M. a. caurina in the two southwestern refugia.

Having indicated the likely refugia of the boreal biota, including marten and fisher, they are now discussed in somewhat greater detail.

The southeastern refugium is far better known than any other, and it is from the northern limits of this region that the Pleistocene sequence and biotic succession were first known and set up as a standard for the continent. Deevey (1949)

has reviewed what is known biotically of this area and what follows is in part a sketch of his account.

The map of Pleistocene fossils and macrofossils (figure 18) indicates that at various times in the Pleistocene the boreal biota has extended as far east as the coastal plain, as far south as Florida and the Gulf coast and as far west as Minnesota, Nebraska, and eastern Texas. Miranda and Sharp (1950) point out that eastern Mexico, as far south as the Guatemalan border, supports outliers of the hardwood forest, presumably Pleistocene relicts.

It is unfortunate that so few of the records mapped can be dated within the Pleistocene; it is thus impossible to map the distribution of boreal biota at any given time. This together with the peculiar mixtures of hardwood and boreal species often present in deposits and the scarcity of pollen profiles from outside the drift border, has led sometimes to disagreement concerning the extent of the boreal refugium.

It is an odd fact that tundra pollen or fossils had until recently only rarely been recorded from the region, as tundra records are common in Europe. The situation led earlier workers, and many recent ones, to believe that it was not widespread in North America. This may be so, but recent findings (Potzger and Friesner 1948, Deevey 1951, Hibbard 1952a, Kitts 1953) indicate its presence, and Deevey concludes that it has been missed only because of certain analytic techniques. Denny (1951) says that signs of solifluction in Pennsylvania and the Appalachians likewise indicate a former tundra climate.

Figure 19.
(To face page 333)

Figure 19. The relative densities of marten in North America. Mapped is the average number of marten trapped per 1,000 square miles of forested area per year by states and provinces. Figures obtained from various sources, in part from Anon. (1927-50), Minville (1946) and Yeager (1950).



Russell (1901) has pointed out, however, that present day forests grow on top of the moraine covering the base of Malaspina glacier in Alaska. This suggests that during periods of ablation tundra might have been very much reduced.

The area covered by the boreal and lake forests during late Wisconsin time has also been a subject of disagreement. Earlier workers concluded that the belt of conifers south of the ice in the east was relatively narrow (see Potzger 1946 for a resume of earlier views, also Transeau 1903, Adams 1902, Harshberger 1911, Gleason 1923; Braun 1947, 1950 and 1951 and Wolfe 1951 are more recent proponents of the hypothesis). The current view of many workers is that the conifers had a much more extensive range (Potszger 1946, Deevey 1949 and subsequent papers). This founded largely on the distribution of known boreal fossils, and the fact that nearly all pollen profiles from the eastern United States show spruce pollen at their bases (Deevey 1949, Frey 1951 and others). Odum (1952) believes, however, that the prevailing winds of the Wisconsin blew out of the northwest, and that caution is necessary until it is shown that the coniferous pollen, found in profiles, was not carried by wind from further north.

The presence of hardwood forests is found at one time or another in nearly every profile lying outside the present day boreal forest limits. Since marten and fisher are not common in the hardwood forest today, it need not be considered further.

Post-glacial migration of forests within the refugium is beginning to be understood only now. Recent and important interpretations of pollen data and chronologies derived from them are to be found in Flint (1947), Sears (1948), Deevey (1949 and 1951), Frey (1951 and 1953) and Potzger (1953), but the total literature is voluminous. In essence, however, each profile shows three important horizons, according to Deevey (1949 and subsequent papers). At the bottom of the profiles the pollen of supposed tundra species predominates. Higher in the profile these are replaced by pollen of spruce and fir, then pine (Pinus banksiana ?) and then the present day climax species. Westward the climatic optimum is marked by grass pollens (Lane 1941). Not all phases recorded in the profiles occurred simultaneously, the sequence occurring later nearer the drift border. The pine zone is radiocarbon dated as 9,500 years ago in West Virginia and 6,000 years ago in northern Maine.

The migration of vegetation in eastern Canada is not as yet well understood. Potzger (1953) believes that the presence of the Champlain and Ottawa seas in the St. Lawrence valley did not allow colonization until late in Lake Algonquin time (3,500 to 2,500 years ago). The Canadian Shield in Quebec was not forested until the persisting glaciers in the area north of Montreal had disappeared (Osborne 1951).

Wenner (1947) has shown that in Labrador the forest advanced into the tundra in late post-glacial time, and has since retreated. He believed that the area was not freed of ice until the time of the pine zone further south, or later.

Migration of vegetation west of Hudson Bay is discussed elsewhere.

The eastern coast is believed by Antevs (1947) and Lougee (1953) to have been exposed in post-Mankato time to form a series of islands. The date of the subsequent rise in sea level is given as shortly after the climatic optimum. The tree species that found refuge in this refugium are presumably all those of the southeastern pine forest, the eastern hardwood forest, the lake forest and the eastern boreal forest, and do not need to be discussed here. I believe that marten and fisher both occurred here during all of the glacial maxima.

The Coast refugium extended south of the ice sheet in the Coast and Cascade Mountains and Sierra Nevadas of Washington, Oregon and California at least. Chaney and Mason (1930), working on fossil floras, say that it extended at least 440 miles south of its present southern limit, and the same authors (1933), on other grounds, put the figure at 200 miles. Van Dyke (1939), using relict populations of beetles, says that the refugium extended to Los Angeles and Riverside Counties, California, on the coast and to northern Lower California in the Sierra Nevadas. Not only was the biota moved southward, but it likely was shifted to lower altitudes in the mountains (Flint 1947, pl. 5). The fossil evidence for this refugium is good (figure 18). It is made up wholly of species referred to as the "coastal biota".

Dalquest (1948) believes that with climatic amelioration little of the fauna moved north of the Fraser River; most of the present biota north of this region, he believes, was

derived from the Rocky Mountain refugium. There does not appear to be much outside evidence to support this view, and the interpretation is here made that the coast fauna moved north along the Coast Range into the Alaskan panhandle. Hansen's (1947) pollen profiles indicate that the Coast Mountains of Washington and Oregon were first vegetated by sitka spruce, douglas fir and western hemlock which has persisted, while the Cascades were first colonized by Pinus contorta, later changing to western larch and western white pine.

Profiles from the Alaskan panhandle (Heusser 1952, 1954b) indicate an early dominance of Pinus contorta, this being later replaced by sitka spruce and western hemlock. The source of these is uncertain, but has been suggested to be any of coastal and Rocky Mountain refugia, the Alaska-Yukon refugium or the ice free corridor west of the Max-Altamont system. The Coast refugium or Alaska-Yukon refugium appear to be the most likely sources, but the question remains unsettled.

McCabe and Cowan (1945) and Osgood (1901) present evidence indicating that the Queen Charlotte Islands were not glaciated, at least during the Late Wisconsin. Heusser (1955) has taken pollen profiles from here, and concludes that since climax tree pollen occurs at the very bottom of the deepest cores, the region was unglaciated and forested during the Mankato, at the very least.

The following are the important tree species presumed to have persisted in this refugium (Lamotte 1952, Hulten 1937, Halliday and Brown 1943) Picea sitchensis, Abies amabilis,

Abies grandis, Tsuga heterophylla, Pseudotsuga taxifolia,
Populus trichocarpa, Betula papyrifera, Tsuga mertensiana,
Pinus monticola, P. ponderosa, Picea engelmanni, Larix occiden-
talis, and many others.

The Rocky Mountain refugium is the least well documented. Its southern limit is not known, though Miranda and Sharp (1950) thought they had found relict traces of it in Mexico. Through plotting the lowest level of cirques (Stearns 1942, Louis 1926-1927, Flint 1947, Leopold 1951), it is known that Pleistocene snowlines were about 5,000 feet lower at 50° N latitude and about 4,000 feet lower at 35° than at present, and the biota were doubtless comparably depressed. The present fragmentation of its range in the northern, middle and southern Rocky Mountains of the United States is doubtless due to post-glacial amelioration of climate, its ranges being originally contiguous.

The ice at the northern limit of the refugium was thick; so thick that at its maximum, according to Alden (1954) it nearly or entirely submerged the Purcell and Selkirk Mountains near the 49th parallel. Williams (1948) says that some nunatacks projected above the ice in British Columbia, but Denny (1952) says that evidences of solifluction indicate that no forests could have survived in the northern part of the province.

There is almost no fossil record for this refugium (figure 18). The few profiles available (Hansen 1947 and 1948) show tree pollen at their very bases, and Hansen concluded that forests were present and lay very near to the ice sheet. All profiles start with a dominance of Pinus contorta, and lesser

amounts of P. monticola, the former being later replaced in many places by P. ponderosa. Harshberger (1911) considered this a relatively unimportant refugium, and supposed that the area derived most of its biota from the coastal refugium in post-Wisconsin time. There is no evidence available yet to indicate that Harshberger was wrong in this conclusion.

Hansen (1947) found that his profiles show the whole of Washington and northern Oregon east of the Pacific coastal slope to have been vegetated initially with Pinus contorta. The non-forested Great Basin vegetation did not reach north into Washington, isolating the two refugia until the time of the climatic optimum. Dalquest (1948) has, as pointed out, believed that the two refugia were isolated.

It is presumed that the montane biota, with glacial recession, moved north to its present location (Dalquest 1948 and others). Some of Alaska's vegetation may have come from it (Hansen 1953). Raup (1946) believed that the "Park-like white spruce" forest (Picea glauca var. albertiana) that now marks most of the area just inside the tree line in Manitoba and the Northwest Territories reached the area from the Rocky Mountain refugium. This view is at variance with most other interpretations, though it appears a well founded conclusion.

The tree species believed by Hulten (1937) and Halliday and Brown (1943) to have persisted in this refugium are, among others: Picea glauca, P. engelmanni, Pinus contorta, Abies lasiocarpa, Tsuga heterophylla, Pseudotsuga taxifolia, and Populus trichocarpa.

The fourth and last refugium to be discussed is the Alaska-Yukon refugium. The absence of glaciation in Alaska was due to low precipitation during the Pleistocene, according to Flint (1947). The same author states that nearly all evidences of glaciation here appear to refer to the Wisconsin. Recent work indicates the likelihood of at least two Wisconsin and two pre-Wisconsin glaciations (Goldthwaite 1954).

Chaney (1937) says that the fossil vegetation of the Fairbanks area indicates that the climate was much as it is today. However, Taber (1953) concludes that silts and permafrost indicate that during maximum glaciation trees likely disappeared from central Alaska, though they may have persisted on the sunny slopes of protected valleys on the Yukon plateau. Except for the Arctic slope, the ground was about as well covered by vegetation as it now is, as indicated by lack of Pleistocene wind erosion.

Hansen (1953) thinks there is every reason to believe that most of Alaska supported luxuriant tundra vegetation, at the very least. He says that Pauly (1952, not seen by me) has suggested that the climate during maximum glaciation was often warmer than at present, and at no time colder. According to Hansen, the deepest cores in Alaska and the Yukon bear no tree pollen, although they appear very early after deglaciation, suggesting a nearby source of supply. Heusser (1954a) thinks that Alpine fir came to Alaska from unglaciated Yukon. The Bering Sea region, on geological grounds, is believed to have been exposed by lowered sea levels during Pleistocene maxima

(Flint 1947). How much migration of biota between Siberia and Alaska occurred is not known, but it may have been considerable.

POST-WISCONSIN MIGRATION

The evidence available indicates that, as the glaciers retreated, the biota of the four main refugia had their major place of meeting in the region of the Mackenzie River. The primary evidence is biogeographic. Porsild (1951) considered the Mackenzie River mouth to be the chief point of division between the eastern and western vegetation of the tundra. Rostlund (1952) considers the area the least densely populated by fishes within forested North America, and Halliday and Brown (1943) show the area to be the least densely occupied by the transcontinental genera of forest trees, with the exception of the genus Populus.

The most important studies have been those of Raup. In 1946 and 1947, he published detailed phytogeographic studies of the Mackenzie-Athabaska region and concluded that this was the area in which the biota of the southeastern and Alaska-Yukon, and to a lesser extent the Rocky Mountain refugia, had met and intermingled in post-Mankato time. Some species from the southeastern refugium have apparently migrated all the way to Alaska (Transeau 1905), while certain fishes have moved from Alaska into Ontario (Radforth 1944). These are extreme cases, however, and the bulk of the biota do not appear to have extended far beyond the place of meeting.

The sequence by which post-Mankato vegetation reached

the area is not nearly so clear, however. Raup (1946) saw a long period of extreme cold in post-Altamont time, during which the ice free area about Great Slave Lake and Lake Athabaska were covered with tundra, but unforested. He concluded that it was not until the time of the climatic optimum that forest first entered the area. The first vegetation to arrive was a forest of Picea glauca var. albertiana, from the Rocky Mountain sector. This was replaced later by a jack pine forest from the southeast, these in turn being replaced later by the present climax of mesophytic white spruce from Alaska and the southeast. The earlier white spruce and pine forests are now restricted to the area inside of the tree line to the northeast, the spruce forest forming the outer strip of forest.

Raup's conclusions, apparently sound in their interpretation of migration, have not been completely supported in their chronology. Raup believed that forest invasion of the area was delayed due to the coldness of the adjacent glacial lakes. He inferred this from the lack of driftwood in the earlier sediments of Lake Athabaska, Slave Lake and Lake Agassiz, together with its frequent occurrence in later and recent deposits.

Horberg (1951) has interpreted certain ridges on the floor of Lake Agassiz as being periglacial, and concluded that they supported Raup's thesis. Nikiforoff (1952) disagreed with Horberg's conclusion. He believed the features in question to be a result of wave action only.

Other evidence tends to discredit Raup's argument. Flint (1953) believed that Lake Agassiz was likely refilled and

drained several times; each draining, one might argue, should have resulted in a degree of climatic amelioration. Much more important, however, are the conclusions obtained from pollen profile studies made in the Yukon and Alaska (Hansen 1949a and b, 1950b, 1952 and 1953, Heusser 1954a). The profiles obtained show tree pollens at their very bases, and have led both Hansen and Heusser to conclude that the ice free area in Alberta was forested as early as Mankato time.

MARTEN AND FISHER

I conclude from the material presented in the preceding that there is good reason for hypothesizing the following about marten and fisher.

The Pleistocene has extended over a long period of time, but not long enough to allow evolution to the specific level to occur. Marten and fisher have not evolved so much from their parental stock that the forest they live in cannot be used to interpret something of their history. Four major glaciations occurred in North America, but little is known about their effect on marten and fisher, except that marten and fisher are known from the mid-Pleistocene of the east and marten (M. a. caurina) from the west. It is not inconsistent to argue that the effects of pre-Wisconsin glaciations on marten and fisher were little different from the effects of the Wisconsin. There is no evidence to suggest that an east-west shifting of distribution occurred. In some cases inter-glacial periods are known to have been warmer than the present, and presumably marten and fisher then ranged

farther north than they do now, in the same way that they once ranged farther south.

Four or five glaciations are known from the Wisconsin. The major break in the sequence of glaciation occurred during the second and third. During the third and fourth (Cary-Mankato) glaciations at least, marten found refuge in forested areas southwest of the ice sheet, in the Rocky Mountains, the Coast and Cascade Mountains, southeast of the ice sheet and in unglaciated Alaska and Yukon. Fisher does not occur today near the Alaska-Yukon refugium, and I hypothesize that it was absent from the region during the late Wisconsin.

With post-Mankato ice retreat, the first ice free area appeared in the Altamont sector, and the region east of the Cordillera and west of the Canadian Shield was likely ice free long before the Shield area and Labrador-Quebec were deglaciated (figure 17). Presumably marten and fisher occupied the area west of Hudson's and James Bay considerably before the area east.

I suggest that during the Cary-Mankato glaciations the eastern American morph of Martes pennanti and the Saskatchewan-Manitoban, New England-Ontarioan and Newfoundland-Labradorian morphs of Martes americana americana persisted in the southeastern refugium. I believe the largest group of these three lay most northerly, the other more southerly. Thus the Saskatchewan-Manitoban morph occurred in the area about the western Great Lakes, and the Altamont corridor, the Newfoundland-Labradorian in the region of the eastern Great Lakes and the St. Lawrence Valley, while the New England-Ontario morph lay

somewhere to the south. Like Hooijer (1950), I believe that the effects of Bergmann's rule are likely older than the last 6,000 years, and here consider them of glacial origin. With climatic amelioration I presume these morphs migrated to their present ranges. During the climatic optimum, they may at one time have ranged considerably further north than they now do.

The Alaskan-Yukon morph of M. a. americana persisted through the Cary-Mankato in the Alaska-Yukon refugium. With glacial retreat it migrated south to the Peace River in British Columbia, and east to its point of contact with the Saskatchewan-Manitoban morph in the region about Great Slave Lake. No fisher occurred in this refugium, hence their present absence north of Great Slave Lake.

The British Columbian morph of M. a. americana may have occurred in the Rocky Mountain refugium or in the southwestern portion of the southeastern refugium. Here I accept the first alternative, with no evidence that it is the case. I believe that the montane morph of M. pennanti also occurred here, migrating north and east to its present range. The similarity of its range to that of the Saskatchewan-Manitoban morph in some respects suggests that it may actually have spent the Wisconsin in the southeastern refugium. Its present day scarcity in the Rocky Mountains of the United States lends support to this suggestion.

Martes americana caurina probably spent the late Wisconsin glacial maxima in the Pacific Coastal refugium. The Queen Charlotte Island morph of caurina may easily have spent

the late Wisconsin on unglaciated Queen Charlotte Islands, migrating subsequently to the Alexander Archipelago. It may also have occurred in the Rocky Mountain refugium south of the British Columbian morph of M. a. americana. The Coastal morph of M. pennanti likely also spent the late Wisconsin in the Coastal refugium.

The migrations discussed here are mapped on Figures 17 and 20. It is possible that the differences in magnitude of the migrations of marten and fisher from their various refugia may be explained by Hulten's (1937) theory of biotype depauperization (see also Stebbins 1942).

I have suggested above that fisher did not exist in the Alaska-Yukon refugium because it does not now occur near there. This is not a wholly satisfactory explanation for, while it does not occur there, it also does not now occur in Quebec much north of Mistassini where it should, if the historical factor were the only important one in effect. In actual fact the distribution of fisher when compared to a life zone map (Muesebeck and Krombein 1952 is one example of such a map) is seen to correspond closely to that of the Canadian life zone while marten occur in both the Canadian and Hudsonian zones. This same relationship is shown in a comparison of marten and fisher range to vegetation maps (for example Halliday 1952). Here fisher are seen to be absent from the northern "transition forest". Raup (1946) described this forest as with "trees ... widely spaced and branched all the way to the ground. There is little or no shrubbery, but the soil is frequently covered

Figure 20.

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Figure 20. Post-Mankato migration of marten and
fisher in North America. The assumptions
on which the map is based are discussed in
the text.



KEY

- M.A. AMERICANA
- 1. ALASKAN-YUKONIAN
- 2. BRITISH COLUMBIAN
- 3. SASK.-MANITOBIAN
- 4. NEW ENGL.-ONTARIAN
- 5. NEWF.-LABRADORIAN
- M.A. CAURINA
- M. PENNANTI
- A. EASTERN AMERICAN
- B. MONTANE
- C. COASTAL

with a dense growth of bunch lichens and mat-forming shrubs." Hare (1950) says that it is characterized by a precipitation-evaporation value of about 14 to 17. Why Marten should occur here and fisher not, is unknown, and is likely connected in some way with the tendency of fisher to stay at lower altitudes in the mountains further south.

Whatever the reason, it is quite possible that the fact that the fisher does not occur in this forest in Quebec as well as in the northwest, means that much of my argument concerning the presence of marten in the Alaska-Yukon refugium may not be valid. Marten may not have spent the late Wisconsin in the Alaska-Yukon refugium, but rather it may have migrated there from the southeastern one in post-Monkato time.

It has been suggested elsewhere that much of the variation in marten that has been to the present considered worthy of subspecific mention may be due to environmental rather than purely genetic or historic causes. In Martes americana americana this possibility is worth consideration.

Within M. a. americana, two basic types of geographic variants may be noted, namely larger ones to the north (Alaskan-Yukonian, Saskatchewan-Manitoban and Newfoundland-Labradorian morphs) and smaller ones to the south. In this respect the subspecies may be said to approximate the situation predicted by Bergmann's Rule.

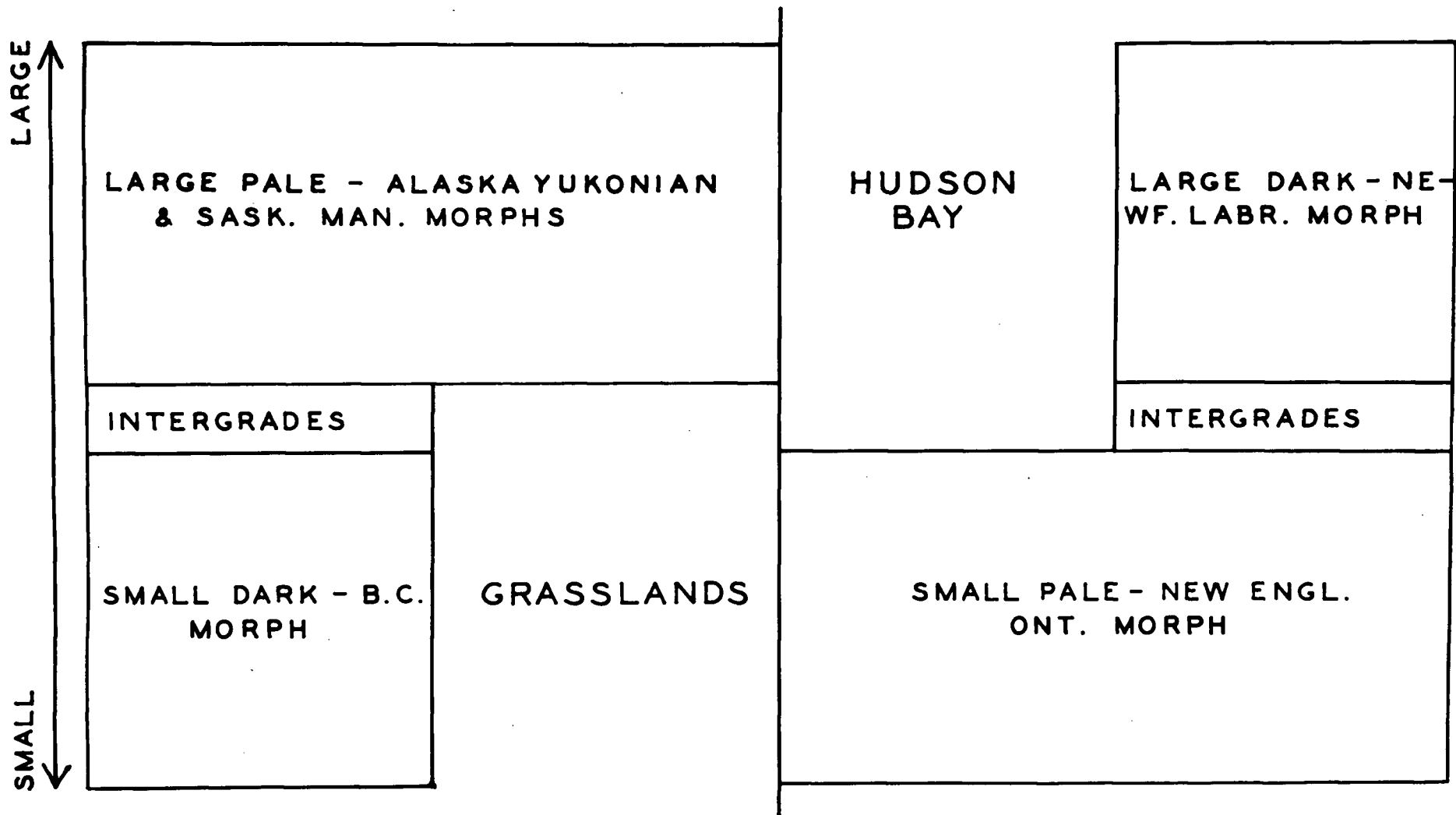
The larger type is split by Hudson's Bay into two groups, an eastern and a western one. To the east, marten are darker (Newfoundland-Labradorian morph), to the west, paler (Alaskan-Yukonian and Saskatchewan-Albertan morphs). It

might be suggested that the darkness of the northeastern morph is due to higher precipitation, the paleness of the northwestern one to moisture deficit (Sanderson 1948) as implied by Gloger's Rule.

The small type of marten to the south is broken into two east - west groups by the Prairies, resulting in the isolation of the British Columbian and New England-Ontarioan morphs. The western morph is darker than the eastern, again possibly an example of Gloger's Rule. The suggested relationship of marten to climate is diagrammed on Figure 21. If in the future it is found to be real, it may be possible that this relationship will be shown to hold in M. a. caurina and M. pennanti.

Figure 21
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Figure 21. Diagram illustrating the possible relationship of Martes americana americana to climate, as stipulated by Bergmann's and Gloger's Rules.



SUMMARY

The genus of marten (Martes), although given various interpretations in the past, is now a relatively stable unit generally considered to be made up of three subgenera and seven or eight Recent species. Of the three subgenera, only one (Charronia) is distinctively different.

Martes martes and M. foina were possibly recognized as distinct species by the ancient Greeks. The sable (M. zibellina) may have been recognized as early as this as well, but more likely considerably later. Martes flavigula and M. melampus were not known until the end of the eighteenth and the beginning of the nineteenth centuries.

The American martens, although likely known soon after the discovery of the New World, were not described carefully until the time of Buffon. The number of species described has varied from one to about six.

The species of the world's marten have not been compared to each other for nearly one hundred years. Martes foina, M. flavigula and M. pennanti appear distinctive enough, but the remaining species M. americana (including caurina), M. martes, M. zibellina and M. melampus show morphological and distributional characteristics that suggest they may be a single biological species. Morphologically, M. caurina is far more similar to M. martes, M. zibellina, and M. melampus than it is to M. americana, yet M. americana and M. caurina are known to interbreed freely in nature. Since the ranges of these species

are nowhere sympatric, their specific status is therefore considered open to question.

Life histories of all the species of marten are so similar that, with the exception of M. foina and M. flavigula, they cannot be used to distinguish them.

Nongeographic variation in marten and fisher is more extreme than many workers have believed. Males are heavier and larger than females (skull measurements being 1.10 times larger in males). Changes also occur with maturity and season of the year. These variations are sufficient to make the value of skins in systematic work uncertain.

The techniques used currently in the study of geographic variation are inferior to the one devised by Womble, and a simplification of his method is used to map distribution of condylobasal length in male marten.

The distribution of marten in North America is governed closely by the distribution of northern evergreen forest. In almost every instance where the forest is present, the presence, or former presence, of marten may be assumed.

The current scheme of marten classification has been to divide North American forms into two species or subspecies groups. Martes americana is usually considered to be made up of seven subspecies, Martes caurina of six. Samples of crania of these allow all subspecies to be distinguished statistically, although the degree of distinction varies a good deal. Within each "species" all variation is clinal, and many more subspecies of the magnitude of those now accepted could be named. At

least some of the variations may be described in terms of Bergmann's and Gloger's Rules. The "subspecies" brumalis, abieticola, boria, kenaiensis, origenes, sierrae and vancouverensis are considered to be synonyms of other "races".

There is no longer any reason, as P. L. Wright has shown, for believing that M. americana and M. caurina are distinct species. He has shown that they intergrade over a front extending through northern Idaho and western Montana, and also, there is reason to believe, in British Columbia. He shows that both are to be considered subspecies or subspecies groups of M. americana.

The distribution of fisher approximates that of marten, but is less closely related to the distribution of northern evergreen forest. Compared to the distribution of marten, it is absent from all islands, from Alaska and much of Yukon, Mackenzie, northern Quebec and Labrador and from much of the Rocky Mountains in the United States. In the eastern United States, on the other hand, it appears to have now, and to have had in the past, a considerably greater range than the marten. In the mountains it never ranges so high as the marten.

Three subspecies of the one species Martes pennanti are currently accepted. These may be distinguished by statistical means, but available specimens are so few that only general variation can be determined. In magnitude, the subspecies of fisher are about the equivalents of the accepted subspecies of marten.

An examination of the concept of the subspecies, as it is accepted at the present, leads to the conclusion that it is unsatisfactory as a means of describing geographic variation. Its weaknesses include the following: it has no actual reality; the number of definable subspecies are a function of the number of characters studied; it has no lower limit; the variation described is rarely known to be genetic; subspecies are usually determined by deductive, rather than inductive, methods; and gradient phenomena (including subspecies) cannot be partitioned internally. These considerations, together with the unsatisfactory subjugation of the basic division of caurina and americana in the trinomial, leads to the conclusion that only two subspecies of marten should be named, Martes americana americana and Martes americana caurina. All other variation is best described by the use of maps, vernacular names, etc.

Since variation in fisher is of the same sort as in marten, it is suggested that subspecies designations be disposed of there also.

Fossil specimens referable to the genus are not common. Twenty-eight fossil species are known, when synonyms are disposed of, of which five are still living, two of them in North America. Although the origin of the genus is usually ascribed to the Old World, specimens referred to Martes appear simultaneously in the late Miocene in Europe, Asia, and North America. No fossils are known from any distance outside the present day range of the genus. From the evidence available it appears that the genus appeared in the Miocene, and by the late Miocene

had evolved into two stocks, one leading to Martes flavigula, the other to the remaining Recent species. Martes pennanti is perhaps as old as the very late Miocene. In the lower Pliocene Martes foina may first have appeared, by the middle Pliocene Martes americana americana, and by the upper Pliocene or very early Pleistocene the remaining forms, M. zibellina, M. martes, M. melampus and M. americana caurina. This hypothesized phylogeny places the origin of the Recent forms further into the past than most workers have believed, but it does not seem inconsistent with the few facts available.

Marten are so closely related in distribution to the distribution of vegetation, and are sufficiently old and primitive that it is suggested that their history is closely correlated with the history of vegetation. If this is so, their history is likely related to that of the Arcto Tertiary forest of the late Tertiary and the northern evergreen forest of the Pleistocene.

The Pleistocene lasted for about a million years, and four ice advances occurred, but little in the way of evolution is believed to have taken place in marten and fisher. On paleontologic and biogeographic grounds it appears that in the Wisconsin the boreal forest persisted in four major refugia, one in Alaska and the Yukon, one in the Coast Mountains south of the ice and on Queen Charlotte Islands, one in the Rocky Mountains south of the ice, and one in the United States east of the Mississippi.

In post-Mankato time the first area freed of ice was

in the sector to the west of the Max-Altamont system. Current evidence indicates that it was forested very early. Subsequent deglaciation was to their centers in the Coast Mountains and Labrador, with forest moving in and re-establishing itself as terrain was made available.

It is suggested that marten persisted in all of the above named refugia, M. a. americana in the Alaska-Yukon and the southeastern ones, and M. a. caurina in the two southwestern ones.

Variation in size, according to Bergmann's Rule, evolved at this time, and not later as has often been assumed. With glacial ablation, marten migrated with the forest they lived in to their present pattern of distribution.

It is believed that fisher were absent from the Alaska-Yukon refugium, but present in the others. Their post-glacial history is assumed to be much that of marten.

There is reason for believing that at least some geographic variation in marten and fisher may be environmentally, and not necessarily genetically, induced.

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APPENDICES

APPENDIX A

Indices devised by Brongersma (1941) and expanded during the present study.

The measurements given below by number are the following:

1. Width of inner lobe of P^4 x 100 / width of trenchant part of P^4 ;
2. Width of inner lobe of P^4 x 100 / length of P^4 ;
3. Breadth of M^1 x 100 / length of P^4 ;
4. Lateral length of M^1 x 100 / mesial length of M^1 ;
5. Mesial length of M^1 x 100 / breadth of M^1 ;
6. Breadth of P^4 (across inner lobe) x 100 / length of P^4 ;
7. Canine width at base / bulla length.

Martes martes

	n	\bar{x}	SD
1	8	84.11	7.70
2	8	30.29	2.40
3	79	97.34	5.30
4	18	73.61	5.90
5	71	73.92	5.00
6	18	67.67	4.20
7	6	.994	.019

Martes foina

	n	\bar{x}	SD
1	12	57.17	5.10
2	12	21.66	2.40
3	71	91.60	5.30
4	28	82.78	7.40
5	70	66.43	4.30
6	28	59.68	3.50
7	19	1.045	.150

Martes zibellina

	n	\bar{x}	SD
1	5	77.60	10.58
2	5	26.60	3.80
3	100	98.56	5.19
4	5	69.80	4.24
5	100	72.77	4.36
6	5	65.80	4.58
7	20	.949	.012

Martes flavigula

	n	\bar{x}	SD
1	15	78.07	5.38
2	14	26.79	1.73
3	22	92.55	5.19
4	15	95.73	4.79
5	22	51.04	2.44
6	14	60.14	4.12
7	2	1.012	.044

Martes melampus

1	2	80.00	2.82
2	2	29.50	.70
3	3	93.00	5.29
4	2	79.00	11.31
5	3	68.00	2.64
6	2	65.00	2.82
7	2	1.18	.31

Martes americana

1	20	69.40	1.35
2	20	24.85	.50
3	55	95.11	3.87
4	20	82.75	1.44
5	61	61.98	3.74
6	20	60.85	1.37
7	185	.87	.05

Martes caurina

1	20	71.10	1.57
2	20	26.65	.55
3	51	100.39	5.19
4	20	71.65	1.62
5	64	64.09	3.74
6	20	66.25	1.08
7	69	1.01	.05

Martes pennanti

1	20	60.05	1.17
2	20	20.90	.52
3	58	86.60	3.00
4	20	83.15	1.35
5	68	69.84	2.83
6	20	56.35	.86
7	52	1.05	.08

APPENDIX B

Synonymy of the fossil and Recent martens of the world.

This synonymy attempts to list alphabetically all the epithets used to apply to forms referred now, or in the past, to the fossil and Recent martens of the world. It is most complete for New World martens; for the Old World and fossil forms it is less extensive. I have borrowed a great deal from the works of Ellermann, Morrison-Scott (1951), Brongersma (1941), Chasen (1940), Pocock (1936) and the several excellent fossil mammal bibliographies of Trouessart, the U. S. Geological Survey and the Geological Society of America (Camp, Taylor and Welles 1942, Camp and Vanderhoof 1940, Camp, Welles and Green 1949 and 1953, Hay 1902 and 1930, Trouessart 1897 and 1904), the Zoological Record and other bibliographic aids.

In the list below, only the epithets and their combinations are given. These must be used with the lists of synonyms given elsewhere under specific and subspecific descriptions in order to obtain all of the names and name variants that have been applied to given forms. Synonymization is made to the older scheme of classification, not the new one offered in this paper. Reference here is made only to the first use, to the best of my knowledge, of a given name or name combination. Subsequent usages are not included, unless they differ from the original one, other than by restriction through the naming of new forms.

Fossil forms described originally as belonging to the genus Martes, and subsequently removed from it, are included

below, together with a citation of change. Forms named prior to 1912, which were referred to the genus Mustela and not since either denied entry or admitted into the more restricted limits of Martes, are included and followed by a question mark.

In a few cases I have not been able to provide a full citation for the sources referred to. In these cases, rather than listing them in the "Literature cited" of this paper, I provide as much information as I can in the text following. All other references are given in the section "Literature cited".

The use of an asterisk (*) indicates that the form named is extinct.

abieticola: Mustela americana abieticola Preble 1902: 68 = "Martes americana abieticola" Miller 1912b:92; Cumberland House, Saskatchewan.

abietinoides: Martes americana var. abietinoides Gray 1865: 106; Mustela americana abietinoides Rhoads 1902:451; = "Martes americana abietinoides" Miller 1912b; between Kicking Horse Pass and Columbia River, presumably British Columbia.

abietum: Martes abietum Fleming 1824:14; = Martes martes martes Miller 1912a; 372.

actuosa: Mustela americana actuosa Osgood 1900:43; Mustela caurina actuosa Elliot 1901c: 510; Martes actuosa Anderson 1937:106; = "Martes americana actuosa" Miller 1912:93; Fort Yukon, Alaska.

alba (1): Mustela canadensis var. alba Richardson 1829:54;

= "Martes pennanti pennanti" Miller 1912b:94.

(2): Mustela foina alba Bechstein 1801, 1:759; = Martes foina foina Miller 1912a:375.

(3): Mustela zibellina var. alba Kerr 1792:178;
probably = Martes zibellina zibellina Ognev 1925:276.

altaica: Mustela altaica Pallas 1811:pl. 2; Martes abietum
var. altaica Gray 1865:104; Martes foina altaica Satunin
1914,1:111; = Martes foina intermedia Bobrinskoy et al.
1944:121.

americana: Mustela zibellina americana Kerr 1792:178;

Mustela zibellina var. americana Brandt 1855:16; Martes americana Gray 1865:106; Mustela americana True 1884:610;
Mustela americana americana Rhoads 1902:445; = "Martes americana americana" Miller 1912b:92; eastern North America.

americanus: Mustela americanus Turton 1802, 1:60; Martes americanus americanus Dice 1927:30; = "Martes americana americana" Miller 1912b:92.

amurensis: Mustela zibellina var. amurensis Dybowski 1922:349;
= Martes zibellina schantarica Ellerman, Morrison-Scott
1951:249.

anderssoni: *Martes anderssoni Schlosser 1924:13; Pliocene
of Chiton Gol, China and Mongolia.

angustifrons: *Mustela angustifrons Gervais 1859:248; =
*Palaeogale angustifrons Filhol 1879:177 (according to
Cintract 1950).

ardea: *Mustela ardea Gervais 1859:252; = Pannonictis pilgrimi Kormos (according to Cintract 1950).

arsenjevi: Martes zibellina arsenjevi "Kuznetzov 1941"

(according to Bobrinskoy et al. 1944:122); Ussuri basin, eastern Siberia.

arzilla: *Mustela arzilla Gregorio 1886:241; = *Martes arzilla? Pleistocene of Sicily.

asiatica: Mustela zibellina var. asiatica Brandt 1855:6; = Martes zibellina zibellina Ognev 1925:276.

asiatica-rupestris: Mustela zibellina asiatica-rupestris Brandt 1855:2; = Martes zibellina zibellina Ognev 1925:276.

aterrima: Viverra aterrima Pallas 1811, 1:81; Charronia flavigula aterrima Heptner 1934:24; = Martes flavigula aterrima Ellerman, Morrison-Scott 1951:250; Between Uth and Amur Rivers, eastern Siberia.

atrata: Mustela atrata Bangs 1897:62; Mustela caurina atrata Elliot 1901c:510; Martes atrata Miller 1912b:93; = "Martes americana atrata" Allen 1942:166; Bay Saint George, Newfoundland.

averini: Martes zibellina averini Bashanov 1943:53 (according to Ellerman, Morrison Scott 1953 but dated 1942 by Bannikov 1953); Katon Karagai region, southern Altai.

baicalensis: Mustela zibellina var. baicalensis Dybowski 1922: 349 (In Arch. Tow. Nauk Lwow.); = Martes zibellina princeps Ognev 1925:278.

bedfordi: Mustela melampus bedfordi Thomas 1905a:103; = Martes melampus melampus Ellerman, Morrison-Scott 1951:247.

borealis (1): Mustela flavigula var. borealis Radde 1862, 1:;9; Martes flavigula borealis Thomas 1908:967; Charronia flavigula borealis Howell 1929:24; = Martes flavigula aterrima Ellerman, Morrison-Scott 1951:250.

(2): Martes martes borealis "Kuznetzov 1941" (according to Bobrinskoy et al. 1944:121); northern area of European Russia, excluding the Kola Peninsula.

boria: Mustela boria Elliot 1905a:139; Martes boria Miller 1912b:93; Martes americana boria Allen 1942:167; = "Martes americana actuosa" Miller 1912b:93.

bosnia: Martes foina bosnia Brass 1911: XII (in Aus der Reiche der Pelze); = Martes foina bosniaca Brass 1911:468.

bosniaca: Martes foina bosniaca Brass 1911:468 (in Aus der Reiche der Pelze); Bosnia, Yugoslavia.

brachyura: Mustela brachyura Temminck 1844:33; Martes brachyura Gray 1865:105; = Martes zibellina brachyura Harper 1945:237; Hokkaido and Kurile Islands, Japan.

brumalis: Mustela brumalis Bangs 1898:502; Mustela americana brumalis Osgood 1900: pl. 7; Mustela caurina brumalis Elliot 1901c:510; Mustela atrata brumalis Elliot 1901a: 336; Martes brumalis Miller 1912b: 93; = "Martes americana brumalis" Anderson 1930:99; Okkak, Labrador.

bunites: Mustela foina bunites Bates 1906:318; Martes bunites Miller 1912a:380; = Martes foina bunites Ellerman, Morrison-Scott 1951:247; Kontopalo, Kania, Crete.

- campestris: *Martes campestris Gregory 1942: = *Lutra pristina Matthew and Gidley 1904: (Gregory, verbal communication, February, 1954).
- canadensis: Mustela canadensis Schreber 1778, 3:492; Viverra canadensis Shaw 1800, 1:429; Martes canadensis Swainson 1835: 154; = "Martes pennanti pennanti" Miller 1912b:94.
- castaneus: Gulo castaneus "H. Smith" (according to Gray 1865: 108); = "Martes pennanti pennanti" Miller 1912b:94.
- caurina: Mustela caurina Merriam 1890:27; Mustela americana caurina Rhoads 1898:423; Mustela atrata caurina Elliot 1901a:335; Martes caurina caurina Miller 1912b:93; "Martes americana caurina" Bailey and Bailey 1918:88; Grays Harbour Chehalis County, Washington.
- chrysogaster: Galidictis chrysogaster Smith 1843, 1:167; = Martes flavigula flavigula Chasen 1940:90.
- chrysospila: Martes chrysospila Swinhoe 1866:286; = Martes flavigula chrysospila Ellerman, Morrison-Scott 1951:250; Mountain forests of central Formosa.
- columbiana: "Martes pennanti columbiana" Goldman 1935:176; Stuart Lake, British Columbia.
- coreensis (1); Martes melampus coreensis Kuroda and Mori 1923: 27; Tenan, southern Chusei district, Korea.
- (2) Martes zibellina coreensis Kishida 1927:130 (In Choju Chosahokoku 4:); = Martes zibellina hamgyenensis Kishida 1927b:509.

crassa: *Martes crassa Teilhard de Chardin and Leroy 1945:6;
Pliocene of Yushe, north China.

delphinensis: *Martes delphinensis Deperet 1892:26; = *Mustela delphinensis Villalta and Crusafont 1943.

diluviana: *Mustela diluviana Cope 1899:229; = *Martes diluviana Hall 1936: early Pleistocene of Pennsylvania.

dissimilis: *Mustela dissimilis Maget 1908; *Herpestes dissimilis Villalta and Crusafont 1943: = *Mustela dissimilis Cintract 1950:31.

domestica: Martes domestica Frisch 1775:11, and Pinel 1792, 1:55; = Martes foina foina Miller 1912a:375.

elliottii: Mustela elliottii Gray 1865:109, incorrectly citing Horsfield 1851:99, = Martes flavigula flavigula Wroughton 1919: 343.

elongata: *Mustela elongata Gervais 1848-1852:118; = *Trochictis elongata Schlosser 1888:128.

fagorum: Mustela martes var. fagorum Linnaeus 1758, 1:67; = Martes martes martes Miller 1912a:372.

felina: *Mustela felina Filhol 1877:259 (according to Cintract 1950); = *Mustela felina Teilhard de Chardin 1915:73; = *Palaeogale felina Cintract 1950:30.

ferruginea: Mustela zibellina ferruginea Brandt 1855:8; = Martes zibellina zibellina Ognev 1925:276.

- ferrugineus: Gulo ferrugineus "H. Smith" (according to Gray 1865:108; = "Martes pennanti pennanti" Miller 1912b:94.
- filholi: *Mustela filholi Deperet 1887:129; = *Martes filholi Schlosser 1888:138; Miocene of France and Germany.
- flarigula: Mustela flarigula Fulton 1903:750 (in the Journal of the Bombay Natural History Society, vol. 14); = Martes flavigula flavigula Wroughton 1919:343.
- flavigula: Mustela flavigula Boddaert 1785:88; Martes flavigula Bonhote 1837:560 (In Journal of the Asiatic Society of Bengal 6:); Mustella flavigula Millard 1907:218; Pustella flavigula Millard 1907b:1040 (in the Journal of the Bombay Natural History Society, vol. 17); Charronia flavigula Pocock 1918:309; Lamprogale flavigula Ognev 1928:26; Charronia flavigula flavigula Allen 1929:1; Lamprogale flavigula flavigula Pocock 1936b:352; Charionia flavigula Thom 1937:317 (in the Journal of the Bombay Natural History Society, vol. 39); = Martes flavigula flavigula Wroughton 1919:343; locality uncertain, but fixed by Pocock as Nepal.
- foina: Mustela foina Brisson 1762:178 and Erxleben 1777, 1:458; Martes foina Nilsson 1820:38; = Martes foina foina Miller 1912a: 375; Germany.
- foxi: *Martes foxi Hibbard and Riggs 1949:836; Pliocene of Kansas.
- fusco-flavescens: Mustela zibellina var. fusco-flavescens Brandt 1855: pl. 2; = Martes zibellina zibellina Ognev 1925:276.

- gamlitensis: *Martes gamlitensis "H. von Meyer" (according to Thenius 1949); Miocene of Austria.
- gazini: *Martes gazini Hall 1931; tertiary of Oregon.
- genetoides: *Mustela genetoides de Blainville 1841:61 and pl. 14; = *Martes filholi Schlosser 1888:138.
- glareae: *Martes glareae Sinclair 1915:76; = *Plionictis glareae Matthew 1924:65.
- godmani: Mustela godmani Fischer 1829:217; = "Martes pennanti pennanti" Miller 1912b:94.
- goodmanii: Mustela goodmanii Gray 1865:108, incorrectly citing Fischer 1829:217.
- guatkinsi: Martes guatkinsi Ellerman, Morrison-Scott 1951:250 = Martes flavigula guatkinsi; Madras, India.
- guatkinsii: Martes guatkinsii Horsfield 1851:99; Mustela guatkinsii Bonhote 1901:349; = Martes flavigula guatkinsi Ellerman, Morrison-Scott 1951:250.
- hamgyenensis: Martes zibellina hamgyenensis Kishida 1927:509 (In Dobuts Zasshi Tokyo 39:); Korea.
- hangiengensis: Martes zibellina hangiengensis Kishida and Mori 1931:380 = Martes zibellina hamgyenensis Kishida 1927:509.
- hardwickii: Mustela hardwickii Horsfield 1829:239; Martes hardwickii Smith 1843:273; Putorius hardwickii Boitard 1847, 8:12 (in the Dictionnaire Universale d'Histoire Naturelle, vol 8); = Martes flavigula flavigula Wroughton 1919:343.

henrici: Mustela henrici Schinz 1845,2:36; Mustela flavigula henrici Dammerman 1929:35 (in Treubia vol. 11); Lamprogale flavigula henrici Sody 1937:243 (in Temminckia, vol. 2); = Martes flavigula henrici Chasen 1940:90; Sumatra.

henricii: Mustela henricii Westermann 1849:13 (In Bijdragen tot de Dierkunde); Mustela flavigula henricii Bonhote 1901:346; Martes flavigula henricii Robinson and Kloss 1919:304, Martes henricii Raven 1935:258; Lamprogale flavigula henricii Pocock 1936a:558; = Martes flavigula henrici Chasen 1940:90.

hudsonius: Mustela hudsonius Ord 1815:291; = "Martes pennanti pennanti" Miller 1912b:94.

humboldtensis: Martes caurina humboldtensis Grinnell and Dixon 1926:411; "Martes americana humboldtensis" Wright 1953:85; Humboldt County, California.

huro (1); Mustela huro Cuvier 1823, 29:256; Martes americana var. huro Gray 1865:106; = "Martes americana actuosa" Miller 1912b:93.

(2); Martes huro Smith 1843:188; = "Martes americana americana" Miller 1912b:92.

hydrocyon: *Mustela hydrocyon Gervais 1859:248; = *Trochictis hydrocyon Lartet 1892 (in Deperet 1892):5.

indochinensis: Martes flavigula indochinensis Kloss 1916:35; Klong Menao, south eastern Siam.

intermedia: (1) Mustela intermedia Severtzov 1873:61; = Martes foina intermedia Bobrinskoy et al. 1944:121; basin of the

Chu, Tallas and Naryu Rivers, eastern Turkestan.

(2): *Martes intermedia Heller 1933:286; = *Martes
vetus Kretzoi 1947:596.

intermedius: *Martes intermedius Brunner 1933: = *Martes
vetus Kretzoi 1947:596?

japonica: Martes japonica Gray 1865:104; = Martes melampus
melampus Ellerman, Morrison-Scott 1951:247.

japonicus: Mustela japonicus Thomas 1897:161; = Martes
melampus melampus Ellerman, Morrison-Scott 1951:247.

jeniseensis: Martes zibellina jeniseensis Ognev 1931, 2:
= Martes zibellina yeniseensis Ognev 1925:277.

kamtschadica: Mustela zibellina var. kamtschadica Dybowski
1922:349 (In Arch. Tow. Nauk. Lwowi:); = Martes zibellina
kamtshadalica Ognev 1925:279.

kamtshadalica: Mustela zibellina kamtshadalica Birula 1918:
82. (In C. R. Mus. Zool. Acad. Sci. Petrograd 1918:);
= Martes zibellina kamtshadalica Ognev 1925:279; Kamts-
chadka Peninsula, Russia.

kansuensis: Martes melampus kansuensis Pocock 1941:322;
noted by Pocock, but apparently never described (Ellerman,
Morrison-Scott 1951:246), hence = Martes melampus melampus
Ellerman, Morrison-Scott 1951:247.

kardwickii: Mustela kardwickii Pechuel-Loesche 1893, 1:601
(in Brehm's Tierleben, 3rd edition, vol. 1 of Säugetiere);
= Martes flavigula flavigula Wroughton 1919:343.

- kenaiensis: Mustela americana kenaiensis Elliot 1903a:151;
Mustela kenaiensis Elliot 1905b:421; = "Martes americana kenaiensis" Miller 1912b:93; Kenai Peninsula, Alaska.
- kinseyi: *Martes kinseyi Gidley 1927:239; Miocene of Montana
- koreana: Charronia flavigula koreana Mori 1922:610; = Martes flavigula chrysospila Ellerman, Morrison-Scott 1951:250.
- kozlovi: Martes foina kozlovi Ognev 1931, 2:631; Kam (in the valley of the Mekong River) eastern Tibet.
- kuatunensis: Mustela flavigula kuatunensis Bonhote 1901:348;
Charronia flavigula kuatunensis Cabrera 1922:164; = Martes flavigula flavigula Wroughton 1919:343.
- laevidens: *Martes laevidens Dehm 1950:65; Miocene of Bavaria.
- larteti: *Mustela larteti Filhol 1888:25, and Villalta and Crusafont 1944.
- lasiotis: Mustela lasiotis Gray 1843:64, and Jentink 1892:140;
Martes flavigula lasiotis Brongersma 1941:126; = Martes flavigula henrici Chasen 1940:90.
- latinorum: Mustela martes latinorum Barrett-Hamilton 1904:389;
 = Martes martes latinorum Miller 1912a:373; Nurri Mountains, Sardinia.
- leporinum: *Mustela leporinum Khomenko 1915:1; = *Martes leporinum?
- leporium: *Mustela leporium Pilgrim 1931: = *Martes leporium?

- leptorhyncha: *Mustela leptorhyncha Filhol 1891:105; =
Viverra leptorhyncha Thenius 1948:121.
- leucholachnaea: Mustela foina leucholachnaea Barrett-Hamilton
 1899:383; = Martes foina intermedia Bobrinskoy et al 1944:121.
- leucholachnea: Mustela foina leucholachnea Bate 1906:318; =
Martes foina intermedia Bobrinskoy et al. 1944:121.
- leucolachnaea: Martes leucolachnaea Blanford 1879:26; = Martes
foina intermedia Bobrinskoy et al. 1944:121.
- leucopus: Mustela leucopus Kuhl 1820:74; Martes leucopus Gray
 1843,1:63; Martes americana var. leucopus Gray 1865:106; =
 "Martes americana americana" Miller 1912b:92.
- leucotis (1): Mustela leucotis Bechstein 1800; Mustela henrici
leucotis Trouessart 1897, 1:273; Martes henricii leucotis
 Raven 1935:258; = Martes flavigula henrici Chasen 1940:90.
- (2): Mustela leucotis Griffith, Smith and Pidgeon
 1827, 2:297 and plate facing; Martes leucotis Smith 1843:188;
 = "Martes americana americana" Miller 1912b:92.
- lorenzi: Martes martes lorenzi Ognev 1926:47; Storojevaia,
 Kuban District, Caucasus.
- lutreola: Mustela lutreola Godman 1860, 1:149; = "Martes
pennanti pennanti" Miller 1912b:94.
- lydekkeri: *Mustela lydekkeri Colbert 1933:1; = *Martes
lydekkeri Colbert 1935:94; Siwaliks (lower Pliocene) of
 northern India.
- macrorhyncha: *Viverra macrorhyncha Filhol 1891:96; *Martes
filholi Schlosser 1888:138.

maculata: Mustela zibellina var. maculata Brandt 1855:pl.3;
= Martes zibellina zibellina Ognev 1925:276.

martes: Mustela martes Linnaeus 1758, 1:46; Viverra martes
Shaw 1800, 1, 2,:410; Mustela martes var. martes Brandt
1855: = Martes martes martes Miller 1912a:372; Upsala,
Sweden.

martinus: Mustela martinus Ames 1874:69; = "Martes americana
americana" Miller 1912b:92.

martis: Mustela martis Gesner 1847:356; = Martes martes martes
Miller 1912a:372.

majori: *Mustela majori Weithofer 1889:62; = *Martes majori?
Pliocene of Italy.

mediterranea: Mustela mediterranea Barrett-Hamilton 1898:442;
Mustela foina mediterranea Bate 1906:319; = Martes foina
mediterranea Miller 1912a:380; Sierra de Jerez, Cadiz,
Spain.

melampus: Mustela melampus Wagner 1841; = Martes melampus
melampus Ellerman, Morrison-Scott 1951:247; Japan.

melanopus: Martes melanopus Gray 1843:63; Mustela melanopus
Temminck 1844; 31; = Martes melampus melampus Ellerman,
Morrison-Scott 1951:247.

melanorhyncha: Mustela melanorhyncha Boddaert 1785:88; =
"Martes pennanti pennanti" Miller 1912b:94.

melina: Mustela melina Kerr 1792:183; = Martes flavigula
flavigula Wroughton 1919:343.

melli: Charronia melli Matschie 1922:17; = Martes flavigula
flavigula Wroughton 1919:343.

- milleri: Martes foina milleri Festa 1914:7; Aghios Isidoros, Island of Rhodes.
- munki: *Martes munki Viret 1933:15; = *Mustela munki Villalta and Crusafont 1943:
- mustelina: *Mustela mustelina Coues 1877:16; *Palaeogale minuta Cintract 1950:31; = *Ischyrictis mustelinus Viret 1951:48.
- mustelinus: *Aelurodon mustelinus Cope 1873:1, *Martes mustelinus Cope 1874:520; *Laphyctis mustelinus Viret 1933:pl.1; = Ischyrictis mustelinus Viret 1951:48.
- nambianus: *Martes nambianus Cope 1874, 1:147; *Mustela nambianus Cope 1875:68; *Putorius nambianus Cope 1877:305; = *Martes nambianus Hall 1930: Miocene of New Mexico.
- nehringi: Mustela foina nehringi Satunin 1906:120 (In Mitt. Kauk. Mus. Tiflis 2:); = Martes foina nehringi Ellerman, Morrison-Scott 1951:247; Tiflis, Transcaucasia.
- nesophila: Mustela nesophila Osgood 1901:33; Martes nesophila Miller 1912b:94; Martes caurina nesophila Grinnell and Dixon 1926:417; = "Martes americana nesophila" Wright 1953:85; Massett, Graham Island, Queen Charlotte Islands.
- nigra: Mustela zibellina nigra Kerr 1792:179; Mustela nigra Turton 1802; 1:60; Martes nigra Smith 1843:189; = "Martes pennanti pennanti" Miller 1912b:94.
- nobilis: *Martes caurina nobilis Hall 1926c:127; = "Martes americana sierrae" Wright 1953:85.

notialis: Mustela martes var. notialis Cavazza 1912:181; =
Martes martes notialis Ellerman, Morrison-Scott 1951:245;
 south of Abruzzi, southern Italy.

ochracea: Mustela zibellina var. ochracea Brandt 1855:pl. 3;
 = Martes zibellina zibellina Ognev 1925:276.

ogygia: *Mustela ogygia Matthew 1901:358; *Martes ogygia
 Sinclair 1915:80; = *Plionictis ogygia Matthew 1924:21.

origenes: Mustela caurina origenes Rhoads 1902:458; Martes
caurina.origenes Miller 1912b:93; = "Martes americana
origenes" Wright 1953:84; Garfield or Rio Blanco County,
 Colorado.

pachygnatha: *Mustela pachygnatha Teilhard de Chardin and
 Piveteau 1930:107; = *Martes pachygnatha Teilhard de
 Chardin and Leroy 1945: lower Pleistocene, Nihowan,
 China.

pacifica: Mustela canadensis pacifica Rhoads 1898:423;
Mustela penanti pacifica Elliot 1899:266; Mustela pennanti
pacifica Miller and Rehn 1901:227, and Elliot 1901a:337; =
 "Martes pennanti pacifica" Miller 1912b:94; Kittitas
 County, Washington.

palaeosinensis: *Mustela palaeosinensis Zdansky 1924:33;
 *Martes palaeosinensis Orlov 1941: = *Mustela palaeo-
sinensis Teilhard de Chardin and Leroy 1945; = Sinictis
palaeosinensis Pilgrim and Hopwood (1931) according to
 Colbert (1935).

- palaesyriaca: *Mustela palaesyriaca Nehring 1902:145; =
 *Martes palaesyriaca Bate 1932:183. Prehistoric of Antelias
 Cave, Palestine.
- parapennanti: *Martes parapennanti Gidley and Gazin 1933:347;
 = *Martes diluviana Hall 1936:88.
- parviloba: *Mustela parviloba Scott and Osborn 1890:71;
 *Martes parviloba Sinclair 1915:81; *Plionictis parviloba
 Matthew 1924:65; = *Ischyriictis mustelinus Viret 1951:48.
- peninsularis: Mustela flavigula peninsularis Bonhote 1901:
 346; = Martes flavigula peninsularis Chasen 1940:90;
 Bankasun, Tenasserim.
- penanti: Mustela penanti Elliot 1899:267; = "Martes pennanti
pennanti" Miller 1912b:94.
- pennanti: Mustela pennanti Griffith, Smith and Pidgeon 1827,
 2:297; Mustela pennanti pennanti Miller 1900:73; = "Martes
pennanti pennanti" Miller 1912b:94; eastern Canada.
- pennantii: Mustela pennantii Erxleben 1777:470 or 479; Martes
pennantii Smith 1843:190; Mustela pennantii pennantii Bangs
 1910:492; = "Martes pennanti pennanti" Miller 1912b:94.
- pentelici: *Mustela pentelici Gaudry 1862:527; *Martes
pentelici Deperet 1892:27; = Mustela pentelici Nafiz and
 Malik 1933.
- piscator: Viverra piscator Shaw 1800,1:414 = "Martes pennanti
pennanti" Miller 1912b:94.
- piscatoria: Mustela piscatoria Lesson 1827:150; = "Martes
pennanti pennanti" Miller 1912b:94.

plesictis: *Mustela plesictis de Laizer and de Parieu (according to Cintract 1950); = *Plesictis lemanensis Pomel (also according to Cintract).

princeps: Mustela zibellina princeps Birula 1922:8 (In Ann. Mus. Zool. Acad. Sc. St. Petersburg. 22:); = Martes zibellina princeps Ognev 1925:278; Bargusin Mountains, Transbaikalia.

pusilla: *Martes pusilla Viret 1951:58; Miocene of southern France.

putorioides: *Mustela putorioides Gervais 1848-52:27 and pl. 27, fig. 9; and Cintract 1950; Oligocene of France.

quadricolor: Viverra quadricolor Shaw 1800, 1:429; = Martes flavigula flavigula Wroughton 1919:343.

quadricolus: Mustela quadricolus Chenu and Desmarest 1853, 1:273; = Martes flavigula flavigula Wroughton 1919:343.

robinsoni: Lamprogale flavigula robinsoni Pocock 1936a:403; = Martes flavigula robinsoni Chasen 1940:90; Tjibodas, Java.

robusta: *Mustela robusta Newton 1894:200, and Viret 1929.

rosanovi: Martes foina rosanovi Ognev 1931, 2: = Martes foina rosanovi Ellerman, Morrison-Scott 1951:247.

rosanowi: Martes rosanowi Martino 1917:1; = Martes foina rosanovi Ellerman, Morrison-Scott 1951:247; northwestern slope of Chadyr dag Mountains, Crimea.

rossica: Mustela zibellina var. rossica Brandt 1855: = Martes zibellina zibellina Ognev 1925:276.

rufa: Mustela rufa Desmarest 1820-22:184; = "Martes pennanti pennanti" Miller 1912b:94.

rupestris: Mustela zibellina var. rupestris Brandt 1855: pl. 2; = Martes zibellina zibellina Ognev 1925:276.

ruthena: Martes martes ruthena Ognev 1926:49; Dmitrovsk subdistrict, Moscow Government, Russia.

saba: Lamprogale flavigula saba Pocock 1936b:549; = Martes flavigula saba Chasen and Kloss 1932:13; near Sandakan, British North Borneo.

sahalinensis: Martes zibellina sahalinensis Ognev 1925:279; Wedernikovo, Sakhalin Island.

sainjoni: *Martes sainjoni Maget 1908:225; Miocene of France.

sajanensis: Martes zibellina sajanensis Ognev 1925:278; Orsyba River, northern Sayan Mountains, middle Siberia.

schantarica: Martes zibellina schantarica Ellerman, Morrison-Scott 1951:249; Shantar Islands, lower Amur, eastern Siberia.

schantaricus: Martes zibellina schantaricus "Kuznetzov 1941" (according to Bobrinskoy et al. 1944:120); = Martes zibellina schantarica Ellerman, Morrison-Scott 1951:249.

schmerlingi: Martes Schmerlini Pomel; = Martes martes Linnaeus 1758, 1:56 (all according to Trouessart 1897).

sierrae: Martes caurina sierrae Grinnell and Storer 1916:2; = "Martes americana sierrae" Wright 1953:85; Yosemite National Park, California.

sinuensis: Mustela sinuensis Griffith, Smith and Pidgeon 1827, 2:297; = Martes americana americana" Miller 1912b:92.

sylvatica: Martes sylvatica Nilsson 1820, 1:41; = Martes martes martes Miller 1912a:372.

sylvestris (1): Martes sylvestris Frisch 1775:11; Mustela sylvestris Oken 1816, 3, 2:1029; = Martes martes martes Miller 1912a: 372.

(2): Mustela zibellina var. sylvestris Brandt 1855: pl. 2; = Martes zibellina zibellina Ognev 1925:276.

syriaca: Mustela foina syriaca Nehring 1902:145; = Martes foina syriaca Ellerman, Morrison-Scott 1951:247; Wadi Syr, Syria.

szetchuensis: Mustela flavigula szetchuensis Hilzheimer 1910: 310; = Martes flavigula flavigula Wroughton 1919:343.

taxodon: *Mustela taxodon Gervais 1848-52:118; = *Trochictis taxodon Schlosser 1888:127.

ten: *Martes ten Shikama 1949: Pleistocene of Kuzon, Japan.

toufoeus (1): Mustela toufoeus Hodgson 1842:281 (In the Journal of the Asiatic Society of Bengal, 11:); Martes foina toufoeus Ellerman, Morrison-Scott 1951:246; Llasa, Tibet.

(2): Martes toufoeus Wroughton 1919:343; = Martes foina intermedia Bobrinskoy et al. 1944:121.

transitoria: *Mustela transitoria Gaillard 1899:56; = *Martes transitoria? Miocene of southern France.

tsuensis: Mustela melampus tsuensis Thomas 1897:161; = Martes melampus tsuensis Ellerman, Morrison-Scott 1951:247; Kamoze, Tsushima Islands, Japan.

tungusensis: Martes zibellina tungusensis "Kuznetzov 1941"

(according to Bobrinskoy et al. 1944:120); Basins of the Nizhnaya and Podkamennaya Tungusha, middle Siberia.

typica: Mustela flavigula typica Bonhote 1901:343; = Martes flavigula flavigula Wroughton 1919:343.

typicus: Mustela melampus typicus Thomas 1897:161; = Martes melampus melampus Ellerman, Morrison-Scott 1951:247.

tyrannus: *Charronia flavigula tyrannus Colbert and Hooijer 1953:50; = *Martes flavigula tyrannus; middle Pliocene of China.

uralensis: Martes martes uralensis "Kuznetzov 1941" (according to Bobrinskoy et al. 1944:121); whole of the Ural Range.

vancouverensis: Martes caurina vancouverensis Grinnell and Dixon 1926:414; = "Martes americana vancouverensis" Wright 1953:85; Vancouver Island, British Columbia.

vetus: *Martes vetus Kretzoi 1947:596.

vison (1): Mustela vison Harlan 1825:67; = "Martes americana americana" Miller 1912b:92.

(2): Mustela vison Godman 1826 (fide Cuvier?), 1:149; = "Martes pennanti pennanti" Miller 1912b:94.

vulgaris: Martes vulgaris Griffith, Smith and Pidgeon 1827, 5:123; Martes abietum var. vulgaris Gray 1865:104; = Martes martes martes Miller 1912a:372.

vulpina: Mustela vulpina Rafinesque 1819a:82, and 1819b:411; presumably = "Martes americana americana" Miller 1912b:92,

but possibly "Martes caurina caurina" Miller 1912b:93 or
"Martes americana abietinoides" Miller 1912b:93.

waterhousi: *Mustela waterhousi Pomel(?); = Palaeogale water-
housi Trouessart 1904:201.

woodwardi: *Martes woodwardi Pilgrim 1931: Lower Pliocene of
 Asia.

xanthospila: Martes flavigula xanthospila Swinhoe 1870:623;
Mustela flavigula xanthospila Bonhote 1901:347; = Martes
flavigula chrysospila Ellerman, Morrison-Scott 1951:250.

yeniseensis: Martes zibellina yeniseensis Ognev 1925:277;
 forest along Yenesei River, Krasnoarsk district, eastern
 Siberia.

yuenshanensis: Charronia yuanshanensis Shih 1930:3; = Martes
flavigula flavigula Wroughton 1919:343.

zdanskyi: *Martes zdanskyi Teilhard de Chardin and Leroy
 1945:9; Pliocene of Yushe, north China.

zibellina: Mustela zibellina Linnaeus 1758, 1:46; Viverra
zibellina Shaw 1800,1: Martes zibellina Smith 1843:187;
Martes zibellina zibellina Ognev 1925:276; Fixed by Ognev
 as surroundings of Tobolsk, Tomsk Government, Siberia.

zibethoides: *Viverra zibethoides de Blainville 1841:pl.13;
 *Mustela zibethoides Filhol 1891:98; = *Ischyriictis zibeth-
oides Helbing 1930:637.

zorilloides: *Mustela zorilloides Lartet 1851:17; = Martes
zorilloides? Miocene of southern France.

APPENDIX C

Cranial measurements

The following is an alphabetical listing of the cranial measurements used in the preceding, together with definitions where they are needed.

Breadth of M^1 . Greatest mesial-labial width or breadth of upper molar; it is the same as "upper molar width".

Breadth of P^4 across inner lobe. The greatest width of the last upper premolar, taken so as to include the inner flange of the tooth.

Bulla length. Unfortunately has two different meanings as used in this paper: (a) Where used in the key to the marten species (p. 40) and in others of Brongersma's indices (Appendix A and Figure 8), and where used in all cases that concern fisher (M. pennanti), it means the greatest length of the bulla, measured from the external carotid foramen to the hind surface of the jugular process. (b) Where used in conjunction with all accounts of North American marten (except under those topics above) it means the greatest length of the bulla measured from the external carotid foramen to the midpoint of the suture located on the surface of the jugular process.

Canine width at base. Width separating the outer sides of upper canines, measured at alveoli.

Condylbasal length. Linear anter-posterior distance from the most anterior point of the premaxillae to the midpoint of a line connecting the most posterior surfaces of the occipital condyles.

Height of skull at bulla. The greatest dorso ventral height of the cranium, taken at and including the deepest part of the bullae, but exclusive of the sagittal crest if present.

Lateral length of M^1 . The greatest antero-posterior length of the lateral (labial) lobe of the upper molar.

Length of last upper premolar.

Length of P^4 . As above, being the same as the length of the last upper premolar.

Mastoid width. The greatest width separating the outer surfaces of the mastoid processes.

Mesial length of M^1 . Greatest antero-posterior length of the inner (lingual) lobe of the upper molar. Is identical to the measurement termed elsewhere as "upper molar inner moiety length".

Minimum preorbital space width. Least width separating the outer surfaces of the preorbital concavities.

Minimum postorbital space width. Least width separating the outer surfaces of the postorbital concavities

Narrowest palatal width.

Palatilar length. Least antero-posterior length of palate measured from the anterior surface of the suture of the two premaxillae to the posterior surface of the palate, on the azygos notch.

Rostral width. Greatest width of rostrum at the point of greatest constriction behind the canines.

Upper molar inner moiety length. The same as "Mesial length of M^1 ".

Upper tooth row. The least distance in a straight line from the anterior surface (at the alveolus) of the upper canine to the posterior surface of the inner lobe of the upper molar on the same side.

"Waist" of upper molar. The least antero-posterior width of the isthmus connecting the outer and inner lobes of the upper molar.

Width of inner lobe of P⁴.

Width of trenchant part of P⁴.

APPENDIX D

The sources used in determination of distribution of marten and fisher.

The following, together with all sources listed under the topics marten and fisher distribution constitute a complete list of the material used in the preparation of those discussions, and the distribution maps.

Adams (1909), Adams, Burns, Hankinson, Moore and Taylor (1920), Allen (1894a, 1894b and 1910), Allin (1940), Anderson (1913 and 1946), Anon. (1943), Bailey and McInnes (1886), Banfield (1947), Bangs (1896 and 1910), Buchanan (1920), Cahalane (1948), Cahn (1921 and 1937), Carl (1944), Carl and Hardy (1943 and 1945), Christian (1951), Clarke (1942), Colvin (1880), Cowan (1944), Cowan and Mackay (1950), Cowan and Munro (1946), Coventry (1931), Dice (1919), Dixon (1938), Dutcher (1903), Dymond, Snyder and Logier (1928), Edson (1930), Elliot (1903b), Elsey (1950), Faribault, Guillim and Barlow (1911), Felger (1910), Forster (1772), Gifford and Whitebread (1951), Good (1880), Goodwin (1929), Gosling (1910), Gray (1865), Grimm and Whitebread (1952), Grinnell, Dixon and Linsdale (1930), Hall (1934), Hardy (1949), Hatt (1924), Hawbecker (1945), Hayward (1952), Herrick (1892), Hesse (1946), Holland (1949), Hollister (1912), Hosie (1938), Howell (1924), Hubbard (1943 and 1947), Jackson (1922), Johnson (1922 and 1930), Keele (1910), Lett (1890), Linsdale (1937), Low (1890), MacLulich (1936), Marshall (1946), McEwen (letter), Merriam (1890 and 1899), Merriam and Stejneger (1891), Miller (1897), Munro (1945, 1947 and 1950), Munro and Cowan

(1944), Orr (1943), Osgood (1901 and 1909), Palmer (1949), Parker (1952), Patch (1922), Plamondon (1938), Porsild (1945), Racey (1936 and card file), Racey and Cowan (1935), Rand (1944a), Remington (1952 and 1953), Rhoads (1902), Roberts and Early (1952), Robinson and Robinson (1946), Roest (1951), Roslund (1950), Rousseau (1949), Schoonmaker (1929 and 1938), Selwyn (1891), Sheldon (1925, 1930 and 1932), Snyder (1928 and 1938), Snyder, Logier and Kurata (1942), Soper (1920, 1923, 1942 and 1947), Stanwell-Fletcher (1943), Swarth (1912 and 1936a), Thomas (1952a), Toner (1946), Townsend (1887), Ulke (1923), Wilber (1946), Williams (1922, 1925, 1933 and 1946), Wood and Dice (1924), Wright (1953), Wright and Simpson (1920).

ABSTRACT

Three subgenera of the genus Martes exist in the world today. The first, Martes, consists of the following species: M. americana, M. foina, M. martes, M. melampus and M. zibellina; the second, Pekania, of only one, M. pennanti; and the third, Charronia, of one, M. flavigula, with sometimes a second, M. guatkinsi.

Of the subgenus of Martes, M. americana, M. martes, M. zibellina and possibly M. melampus are so closely related morphologically that there appears good reason to believe that they all belong to one species.

Two species occur in North America, namely M. americana and M. pennanti. Until recently M. americana was considered to be made of two species, M. americana and M. caurina, and thirteen or so subspecies. The recent work of P. L. Wright indicates that while the two "species" are distinctive morphologically, they intergrade at the point where their ranges meet and must be considered a single species. Martes pennanti has been considered one species, made up of three subspecies.

The concept of the subspecies proves in many respects to be unsatisfactory. It lacks reality, it involves the arbitrary partitioning of continua, it possesses no lower limit, and it is determined deductively, among other failings. This, together with the clinal nature of variation in the marten and fisher leads to the conclusion that marten of the New World should be considered represented by only two subspecies (M. a.

americana and M. a. caurina), the fisher by one species, and no named subspecies.

The distribution of marten and fisher corresponds closely to the distribution of the northern evergreen forests. The distribution is less precise in fisher than in marten.

Fossils referable to the genus Martes are first recorded from the Miocene of both the Old and New Worlds. Twenty-eight fossil species are known (when synonyms are disposed of) of which five are still living, two of them in North America. It appears that modern martens and fishers arrived in the New World (or evolved there) late in the Pliocene or early in the Pleistocene.

During the Pleistocene marten found habitable environments in the forest refugia of southeastern United States, the Rocky Mountains south of the ice sheet, the Coast and Cascade Mountains south of the ice sheet, and in Alaska and Yukon. Fisher presumably occurred in all of these except the Alaska - Yukon one. With post-glacial climatic amelioration they migrated to the regions of their present occurrence.
