

A CONTRIBUTION TO THE CLASSIFICATION AND PHYLOGENY OF  
THE MARTEN (SUBGENUS MARTES PINEL) OF NORTH AMERICA  
WITH SPECIAL REFERENCE TO THOSE OF BRITISH COLUMBIA.

by

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# ABSTRACT

Statistical study of 418 marten skulls gives evidence for the subspecific status of brumalis, americana, actuosa, caurina and nesophila. Abietinoides is probably separable from americana. Vancouverensis, caurina and origenes cannot however be separated. Geographic distribution of the latter three suggests that for the time being their status should not be changed.

Only one species occurs in North America, according to the unpublished work of Wright. This is divided into two groups, referable to the formerly conceived species americana and caurina.

The genus Martes arose in the lower Pliocene and segregated into the subgenera of martens and fisher during the Pliocene. The americana group preceded caurina to North America, both arriving sometime before the Kansan. Between the Kansan and the Illinoian the americana group divided into two branches, and by the Wisconsin or earlier, origenes had separated from caurina.

During the Wisconsin ice advance marten found refuge in four regions: the lake states, the Rocky Mountains, the Coast Range and Alaska. Repopulation of North America with the ice retreat occurred from these refugia, during which time or later final subspeciation took place.

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INTRODUCTION

The present study has been carried out for the purpose of increasing knowledge concerning (1) the classification and (2) the phylogeny of the Martens (subgenus Martes Pinel) of North America, with emphasis on those of British Columbia.

Past studies which have been made on the subgenus, as far as it occurs in North America have been few. Rhoads (1902) has published the only paper concerned solely with this group and is the source of most subsequent references to it. Other authors of importance are referred to throughout the paper following.

Sincere appreciation for assistance in this study is due Dr. I. McT. Cowan under whom it was made, for advice given and for help in obtaining the specimens studied; to Dr. W. A. Clemens for advice and encouragement; and to Mr. Y. Edwards, Mr. W. Cottle and Mr. R. Webb who put specimens at my disposal. Thanks are also due the custodians of the various museums who have made specimens available

to me. Dr. P. L. Wright has kindly made unpublished findings of his own available to me, for which I am indebted. I wish to thank my wife as well for continued assistance and encouragement.

## METHODS

The present study has been divided into two parts, as described above: (I) classification and (II) phylogeny.

Classification in this paper is concerned mainly with skull characteristics. Four hundred and eighteen skulls, from the collection of the University of British Columbia Museum, the British Columbia Provincial Museum, the National Museum of Canada, the Royal Ontario Museum, the Museum of the University of Michigan, the Carnegie Museum and the Museum of Vertebrate Zoology, were studied, employing the statistical methods presented by Simpson and Roe (1939).

Originally a series of 32 standardized measurements, ratios and sums were made on each skull from British Columbia. Parameters for these were calculated and compared. Those which did not show significant differences between samples or were possessed of a high coefficient of variability were discarded. Eventually six skull characteristics were found to be of use. These are used throughout this study, and include (1) condylobasal length (2) rostral width (3) upper tooth row (4) bulla length (5) ratio of canine width divided by bulla length and (6) the sum of the width plus the length of the upper molar. The precise definitions of these are given in the Appendix. The first and third measurements, because of their variability could be taken only on adult skulls. Immature specimens were separated from mature ones

using the methods described by Rhoads (1902) and Marshall (1951). Because the characters used in obtaining the ratio in measurement (5) and the sum in measurement (6) showed a small coefficient of variability themselves, it was assumed that differential growth rates did not affect their use together. For each sample measured, the mean, standard deviation, coefficient of variability and their standard errors, were calculated and the samples compared statistically. All measurements are given in centimeters.

The conclusions concerning phylogeny presented in the second part of this paper were arrived at after (1) examination and comparison of the skulls mentioned above and (2) a careful review of the pertinent literature.

A bibliography of about eight hundred titles concerned with the classification, phylogeny and ecology of the marten has been prepared during this study. It is expected that this will be deposited in the library of the University of British Columbia.

#### PART A. CLASSIFICATION:

##### Results:

Samples of skulls (sometimes discouragingly small) referable to the following supposed populations (subspecies) were examined: nesophila, vancouverensis, caurina, origenes, sierrae, humboldtensis, actuosa, horia, abieticola, abietinoides, americana and brumalis. No specimens representative of supposed atrata or kenaiensis were observed.



GENUS Martes PINEL 1792

1758	<u>Mustela</u>	Linnaeus, vol. 1, p. 45; type <u>Mustela Martes</u> Linnaeus
1798	<u>Zibeline</u>	Buffon and D'Aubenton, vol. 7, p. 309
1765	<u>Fouine</u>	Buffon and D'Aubenton, vol. 13, p. 161
1775	<u>Martes</u>	Frisch, p. 11
1777	<u>Mustella</u>	Scopoli, p. 491
1792	<u>Martes</u> ,	Pinel, vol. 1, p. 55; type, <u>Martes domestica</u> Pinel
1800	<u>Viverra</u>	Shaw, vol. 1, p.
1820	<u>Martes</u> ,	Nilsson, vol. 1, p. 38
1829	<u>Zibellina</u>	Kaup, p. 31
1848	<u>Charonia</u>	Gistel, p. 559
1865	<u>Pekania</u>	Gray, p. 107
1865	<u>Charronia</u>	Gray, p. 108
1865	<u>Foina</u>	Gray, p. 108
1911	<u>Martes</u>	Thomas, p. 139
1928	<u>Lamprogale</u>	Ognev, p. 26

The genus Martes has been recognized under different names as an entity since Linnaeus' 10th edition. These authors formerly giving it the name Mustela called weasels Putorius. Mustela is now reserved for the weasels and Putorius for the polecats.

The authority for the name Martes is at present in some doubt. Buffon's terminology has never been considered Linnaean and for that reason illegitimate. Thomas (1911) and Brongersma (1941) likewise

invalidate Linnaeus' Mustela as the name, the former stating that "the ermine was clearly the Mustela of both Gesner and Linnaeus and should therefore be treated as the type species".

Alton (1879) states that "several systematists ... have assigned the Linnaean title Mustela to the martens ... on the ground that the ... name was only employed ... to mark sous-genres, and was not used binomially to indicate genera. The first definite separation was made three years later by Nilsson, who gave the generic name Martes to the present group...."

Palmer (1904) however, gives credit for the name to Frisch (1775). Thomas and Miller (1905) reported that Frisch had not been sufficiently pure in his usage of binomials, and was thus invalidated. Hershkovitz (1948) discredited Frisch for the same reason.

Pinel (1792) is the next authority to use the name Martes. There is however, even here, some question as to Pinel's absolute purity. Thus we arrive at Nilsson (1820) again. If Nilsson should not pass then the name Martes would be lost, for the next to employ the name used it for a group of viverrids. (Wagler 1830).

Until final judgment is passed by the International Commission, authority for the name must remain open to question. For the purpose of this paper, however, it seems best to consider Pinel the authority for the name Martes as do most current students.

Most systematists consider the genus to be comprised of three subgenera: Pekania Gray 1865, Tomictis Hall 1931, and Martes Pinel 1792.

SUBGENUS MARTES PINEL 1792

1792 Martes Pinel, vol. 1, p. 55.

The subgenus Martes is constituted of the true martens. The present study recognizes one species as existing in North America. Schmidt (1943) lists three species (foina, martes and zibellina) from Eurasia (Fig.1). Of interest in this respect is Ponomarev's (1946) successful hybridization of martes and zibellina. Thus probably between two and four species (in the modern sense) of marten exist in the world to-day. However, future taxonomic work will possibly result in a lowering of this number. Mayr (1942) points out that Miller in 1912 considered 76% of his species monotypic. While Okland in 1937 listed only 55% monotypic. There appear to be far fewer monotypic species of mammals than has formerly been recognized and this doubtless holds in the case of the Eurasian marten, as it has in those of America.

In the past, from one to half a dozen species of marten have been considered to occupy North America (Table I). Fourteen subspecies have been described as occurring but never all at any one time or by any one author.

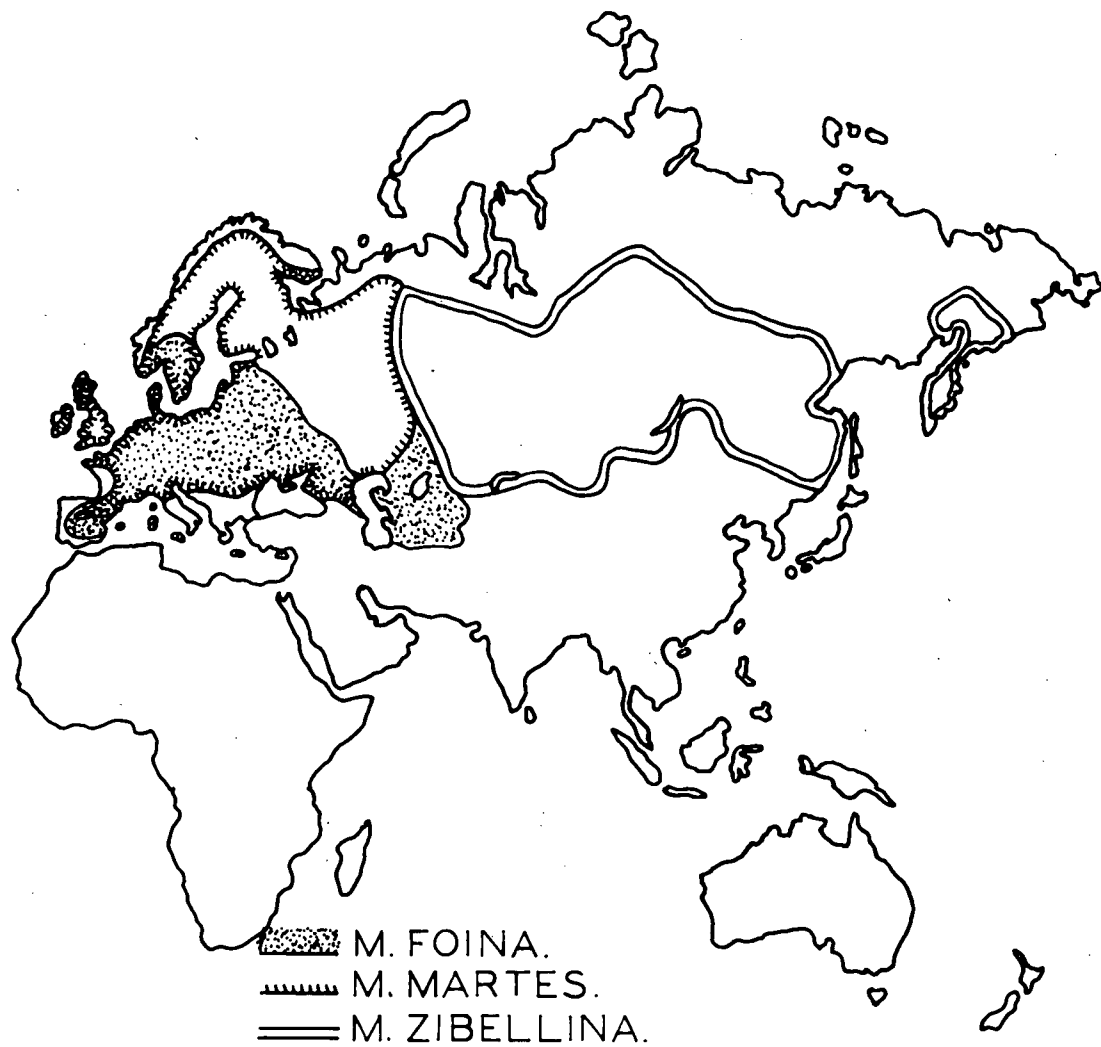
Rafinesque (1819) considered the New World marten a distinct species as did DeKay (1842). Richardson (1829) considered it only a variety of the European Mustela martes and Brandt (1855) a variety of the Asiatic Mustela zibellina

Baird in 1857 and 1859 named one species M. americana as occurring in North America, and this distinct from Old World forms.

Fig. I

(To follow page 6)

Fig. 1., Original distribution of Eurasian Marten. Not shown  
is the subspecies of Zibellina inhabiting Sakhalin Island.  
From Stirton (1939) after Ognev (1928), and from Schmidt  
(1943).



That he was in some doubt as to its exact status is revealed by his statement (1859) that "I am ... inclined to the belief that we have two species, one representing the pine marten ... the other similar to the sable ... both probably distinct from the corresponding Old World species."

Gray in 1865 distinguished between old and new world forms by the small size and peculiar shape of the upper molar in the latter. He separated the one species, americana, into three "varieties": abietinoides whose "habitat" was the "Rocky Mountains," huro of "Fort Franklin" and leucopus whose habitat is not named. I have found it difficult to relate Gray's varieties to the forms designated by more recent workers.

In 1874 Ames listed but did not describe two American species.

M. americana and M. martinus

Allen in 1869 refused to accept the presence of an American marten distinct from the Eurasian. He believed "beyond reasonable doubt that ... all thus far described belong to a single circumpolar species, with possibly one or two ... continental races." He called the American form Mustela martes Linnaeus. In 1876 Allen acknowledged the new world form as a distinct species on the basis of the lack of an "inner cusp on the second lower molar," and named it Mustela americana. At the same time he pointed out the increase in size of the skulls of marten taken from more northern latitudes.

Coues (1877) and True (1884) named only one species, M. americana.

Table I

(To follow page 7)



Table I. Former interpretations of the numbers of species and subspecies of North American marten. The bracketed numbers represent the number of subspecies listed under that particular species. In the two columns at the right are the total number of species and subspecies named by each author. Note that Anderson (1946) considered only Canadian forms.

								spp.	spp.
Richardson 1829	Mustela martes							1	
Brandt 1855	Mustela zibellina var. americana							1	
Baird 1857 & 59	Mustela americana							1	
Gray 1865	Martes americana (3)							1	3
Allen 1869	Mustela martes							1	
Ames 1874	Mustela americana. M. martinus							2	
Allen 1876	Mustela americana							1	
Coues 1877	Mustela americana							1	
True 1884	Mustela americana							1	
Elliot 1901	Mustela americana		M. atrata (4)					2	5
Miller & Rehn 1901	Mustela americana (2)	M. caurina	M. atrata	M. brumalis				4	5
Rhoads 1902	Mustela americana (4)	M. caurina (2)	M. atrata					3	7
Elliot 1905	Mustela americana (5)	M. caurina (2)	M. atrata		M. boria		M. kenaiensis	5	10
Miller 1912	Martes americana (5)	M. caurina (2)	M. atrata	M. brumalis	M. boria	M. nesophila		6	11
Miller 1924	Martes americana (5)	M. caurina (3)	M. atrata	M. brumalis	M. boria	M. nesophila		6	12
Anthony 1928	Martes americana (5)	M. caurina (3)	M. atrata	M. brumalis		M. nesophila		5	11
Allen 1942	Martes americana (7)	M. caurina (6)						2	13
Anderson 1946	Martes americana (5)	M. caurina (3)	M. atrata					3	9

With Elliot in 1901 the new era of taxonomic splitting had begun, probably originating with Merriam's (1890) description of caurina. This trend was continued through Miller and Rehn (1901) to Rhoads (1902) the first and last monographer of the groups. Working on 129 American and several foreign skulls, Rhoads divided the new world marten into three species and seven subspecies.

Elliot in 1905 listed six species and eleven subspecies. In 1912 Miller on the basis of Thomas' (1911) findings, changed the generic name from Mustela to Martes.

Miller's (1924) catalogue is to-day considered the standard in systematics. He lists six species and twelve subspecies. Anthony in 1928, Allen in 1942 and Anderson in 1946 all made minor changes in the classification of the group, Allen listing only two species.

At present it appears likely that only one species of marten exists in North America, as was suggested as early as 1946 by Hall. Dr. P. L. Wright (letter of July 9th 1951) informs me that statistical treatment of 250 skulls from Idaho and Montana shows complete intergradation between the two primary subspecies groups of American marten, thus indicating that they are probably conspecific. If these two major subdivisions fail to show genetic isolation it is very likely that none exists in the remaining less differentiated groups. Wright's work, as well as other signs of intergradation noted in this study, lead to the conclusion that in all probability only one species inhabits the continent.

The present study shows that all American marten fall into two main subspecies groups, namely the americana group (formerly Martes

americana) and the caurina group (formerly M. caurina).

The original distribution of marten kept "very close to the Canadian Faunal Region" (Seton 1929). That its distribution corresponds very closely to that of the narrow-leaved evergreen life form of tree is well known. (See Seton's 1929 map) Jurgenson (1939) reported that marten correlate well with the distribution of fir forests of the European U. S. S. R., but that preferred even to this is a mixed deciduous-coniferous forest ("Piceatum composition"). Emmons (1840), Rhoads (1903), Allen (1904) and Morris (1948) however remark that marten are partial to hardwood as well as coniferous forests.

The distribution of the marten, as it is assumed to have existed in North America prior to the advent of the white man, is mapped in Fig. 2. All faunal lists known and available to me have been used in its compilation. The mappings of the distribution of the Boreal and West Coast coniferous floras have been used in delimiting much of the periphery of the range, however. Earlier maps have been prepared by Seton (1929) and Anderson (1934) for North America, and by Cory (1912) and Hamilton (1943) for the eastern half of the continent. Fig. 3 maps in analogous fashion the distribution limits as understood at present in British Columbia. It is well known that the present range of marten is far different from what it was prior to the coming of the white man to the New World (See Allen 1942, Seton 1929). Huxley (1940) has mapped the present range of the Asiatic marten (after Ognev, 1928-30) as has de Vos (1951) for those of Ontario. Both show the populations of their respective regions to be broken into many (forty in Ontario) small isolated groups, none in contact with the other, and to possess a

Fig. 2.

(To follow page 9.)

Fig. 2. Hypothetical distribution of marten in North America prior to the advent of white men; based on faunal lists, state and continental range maps, and where these are inadequate, on the forest maps of Bowman (1911), Brown (1950), Halliday (1937), and Shantz and Zon (1924). Circles mark type localities of the subspecies named as occurring in that area (from Anderson 1934b). The numbers represent the following subspecies: 1 Martes americana atrata; 2 M. A. brumalis; 3 M. a. americana; 4 M. a. abieticola; 5 M. a. actiosa; 6 M.a. Kenaiensis; 7 M.a. nesophila; 8 M.a. caurina; 9 M. A. vancouverensis; 10 M.a. abietinoides; 11 M. a. origenes; 12 M.a. humboldtensis; 13 M.a. sierrae. Stippled areas represent supposed regions of intergradation.



southern limit far north of what it originally was. The range maps presented with this study are meant to be only approximations of the original distribution of the animal concerned. The method of mapping areas of intergradation in these is described in the discussions of subspecies.

#### SUBSPECIES GROUP 1., AMERICANA

Nomenclature and classification: Formerly the species americana and its subspecies.

Characteristics: Ratio of canine width at base - / -  
hullae length nearer to .90 than to 1.50 in  
males, .85 than .95 in females. Upper molar  
length width nearer to 1.20 cm. than to 1.35 cm.  
in males, 1.05 cm. than to 1.20 cm. in females.

Distribution: All marten east of the Coast Range,  
excluding those of the Rocky Mountain Chain  
south of the 49th parallel and those of the  
Sierra Nevadas, are of this group.

#### MARTES AMERICANA AMERICANA (KERR 1792)

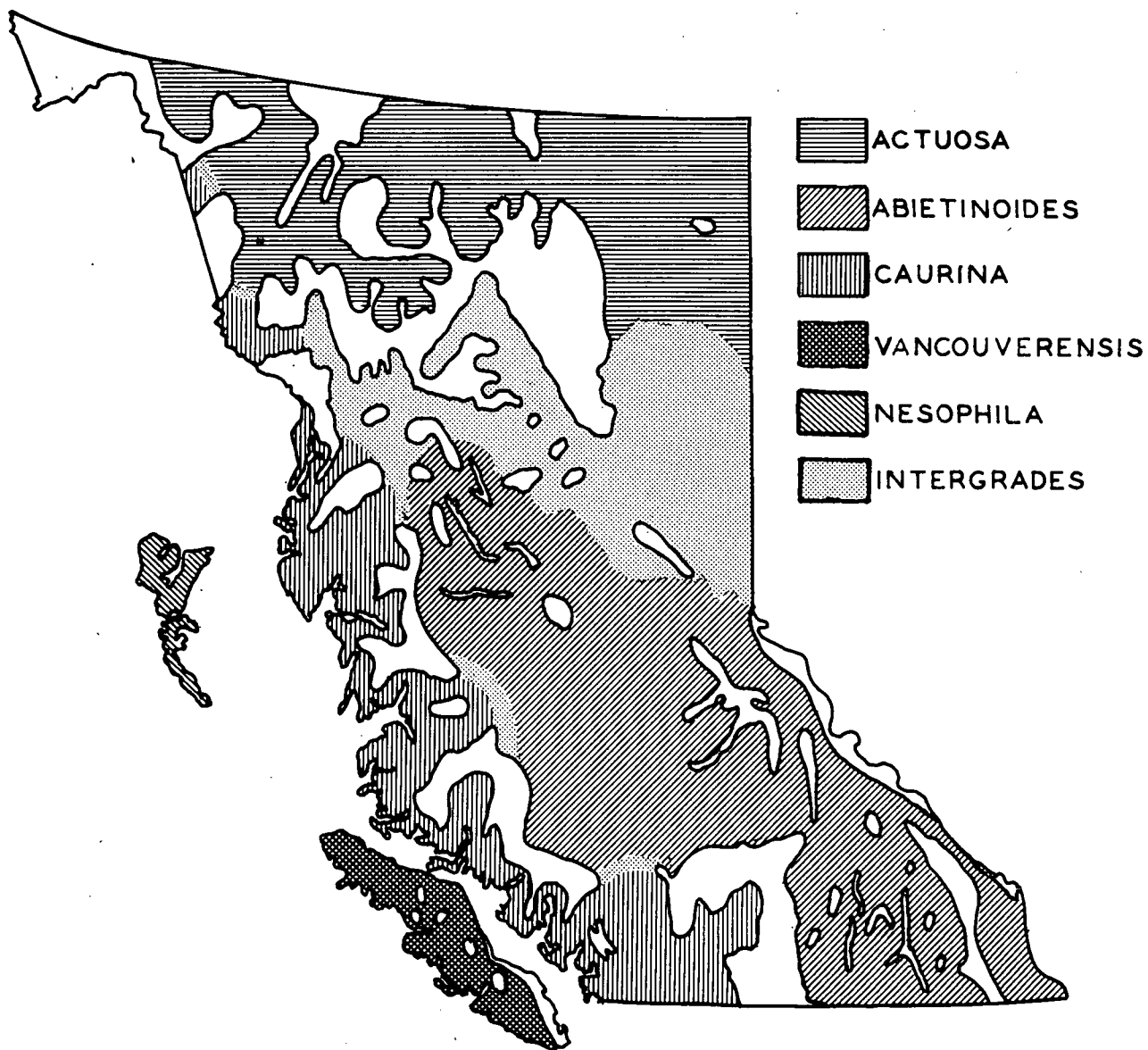
- |         |  |
|---------|--|
| 1772    | <u>Mustela martes</u> , Forster, p. 372 (after Linnaeus) |
| 1776-80 | <u>Mustela zibellina</u> Pallas, vol. 2, p. 57.          |
| 1792    | <u>Mustela zibellina americana</u> Kerr p.               |
| 1802    | <u>Mustela americanus</u> , Turton, vol. 1, p. 60.       |
| 1819    | <u>Mustela vulpina</u> Rafinesque, p. 82                 |
| 1820    | <u>Mustela leucopus</u> Kuhl, p. 74                      |
| 1823    | <u>Mustela huro</u> Cuvier, vol. 29, p. 256              |



Fig. 3.

(To follow page 10.)

Fig. 3. Hypothetical distribution of marten in British Columbia prior to the advent of white men; based largely on the faunal maps of Edwards (1950) and Munro and Cowan (1947). Stippled areas represent regions of supposed intergradation.



- 1827 Mustela Leucotis Griffith, Smith and Pidgeon,  
vol. 2, p. 297 and plate facing.
- 1827 Mustela sinuensis Griffith, Smith and Pidgeon, vol. 2, p. 297.
- 1843 Martes leucopus, Gray, p. 63
- 1844 Mustela (Martes) huro Schintz, p. 337.
- 1844 Mustela (Martes) leucopus, Schintz, p. 337.
- 1844 Mustela (Martes) vulpina, Schintz, p. 377.
- 1855 Mustela zibellina var. americana Brandt p. 16.
- 1865 Martes americana vars. abietinoides, huro and leucopus  
Gray, p. 106.
- 1874 Mustela martinus Ames, p. 69.
- 1885 Mustela americana, True, p. 610
- 1912 Martes americana americana, Miller, p. 92.

Type locality: "North America" (Turton 1802); "Eastern North America"  
(Miller 1900 and most authors); "Upper Missouri ?" (Elliot  
1901); "The region occupied by the small pale martens of  
southern Canada and the northern United States" (Rhoads 1902).

Type specimen: None, to my knowledge, unless it is that of Mustela  
martes described by Forster (1772) after Linnaeus' description.

Nomenclature: The authority for the name M. a. americana has generally  
been attributed to Turton (1806). Rhoads (1902) however  
pointed out that Turton's 1802 edition just contained the name,  
and my examination of Turton's earlier edition confirms his  
conclusion.

Allen (1895) stated that Kerr (1792), while not strictly

Linnaean, was sufficiently so to make his terminology legitimate. He stated that Turton copied many of his names, including "Mustela americana", from Kerr and that it is only due to the scarcity of Kerr's book that these have been attributed to Turton. Although I have not examined Kerr, the authority for the name, on Allen's statement, must rest with him until otherwise is shown.

Classification: Although Baird, as has been pointed out earlier, was the first to accept Turton's designation, Gray (1865) was the first to base the separation on skull morphology - "the small size of the last tubercular molar" in americana. Merriam in his description of caurina (1890) listed many characteristics peculiar to americana. However, credit goes to Rhoads (1902) for the first, and last, thorough analysis of the species. He found Coues', Gray's and Allen's separation of americana from martes, foina and zibellina on the basis of "the slight constriction with resulting rectangular shape" of the upper molar was fully warranted. Further he affirmed Allen's statement that americana almost always lacked the inner cusp of the second lower molar.

Rhoads found that marten from the Cascades and Pacific coast resembled foina however, far more than americana or Rocky Mountain forms, in the characteristics of the upper molar, flat cranium and broad zygomatic breadth. Great dissimilarity with zibellina was noted. On the other hand he found caurina

and foina similar in the small size of the bulla, and breadth and flatness of the brain case. In respect to sagittal crest, frontal constriction and teeth, he found closer relationship between caurina and zibellina.

He concluded that the caurina subspecies group is connected "far more closely with Eurasian than with the American type of marten ..." and are isolated members of the "martes-zibellina group".

Characteristics: Next to abietinoides, from which it is separated with difficulty, it is probably the smallest marten of the americana group. The two, however, are geographically isolated by intermediate populations of abieticola and actuosa.

#### MALES

	M		S D		C V		N
C L	7.982	.045	.223	.032	2.8	.4	24
R W	1.479	.007	.063	.005	4.3	.4	68
U T R	2.930	.021	.101	.014	3.4	.5	23
B L	1.677	.004	.035	.003	2.1	.2	67
CW/BL	.847	.003	.032	.002	3.8	.3	67
MW L	1.215	.007	.062	.005	5.1	.4	67

#### FEMALES

C L	7.252	.086	.258	.060	3.6	.8	9
R W	1.300	.010	.064	.007	4.9	.6	39
U T R	2.683	.036	.109	.025	4.1	.9	9
B L	1.564	.010	.068	.007	4.3	.5	39
CW/BL	.805	.006	.038	.004	4.7	.5	39
MW L	1.077	.008	.056	.006	5.2	.6	39

The symbols in the preceding table represent the following characters: C L = Condylbasal Length; R W = Rostral Width; U T R = Upper Tooth Row; B L = Bulla Length; CW/BL = Canine Width = / - Bulla Length; M W L = Upper Molar Width Length. These symbols are used in all descriptive tables following.

Statistical difference of significance (to the .05 level throughout this paper) is shown between the means of the samples of americana and brumalis in the ratio of canine to bulla length (males and females), condylbasal length (males only), rostral width (males only), upper tooth row (males only), bulla length (males only) and upper molar length plus width (males only).

A similar significant difference between the means of abieticola and americana is shown in rostral width and upper molar width plus length (males only).

Abietinoides shows a significant difference from americana only in the ratio canine width - / - bulla length (males only).

Distribution: Original range, as far as known, as mapped. Four specimens from Lake Mistassini show characteristics intermediate between americana and brumalis. Five specimens from Sioux Lookout District show none of the characteristics of abieticola. The boundaries of the range americana mapped in Fig. 2, since they do not disagree with the facts presented in this study, are taken from Cory (1912). Formerly it probably ranged as far south as northern Virginia (Audubon and Bachman 1856). Its southern limit is now probably Algonquin Park (Downing 1948) or possibly the Berkshire Mountains of Massachusetts (Hamilton 1943) De Vos (1951) has mapped its present range in Ontario.

Specimens examined: Gaspé Peninsula, five (N M C); Abitibi District Quebec, three (N M C); Kapuskasing, Ont.: one (N M C); Presque Isle Co., Mich. one (U.M); Sioux Lookout Distr. Ont. five (R O M Z); Kenora Distr., Ont. two (R O M Z); Algoma Distr., Ont. 12 (R O M Z); Sudbury Distr., Ont. 59 (R O M Z); Nipissing Distr., Ont. five (R O M Z); Thunder Bay Distr., Ont. seven (R O M Z); Cochrane Distr., Ont. four (R O M Z); Renfrew Distr., Ont. one (R O M Z); Lake Mistassini, Que. four (N M C); Muskoka Twp., Ont. one (R O M Z);

In the above, and in all future discussions, the following abbreviations are used in naming the collections studied:

N M C	National Museum of Canada;
U M	University of Michigan Museum;
R O M Z	Royal Ontario Museum of Zoology;
C M	Carnegie Museum;
U B C	University of British Columbia Museum;
B C P M	British Columbia Provincial Museum;
M V Z	Museum of Vertebrate Zoology.

#### MARTES AMERICANA BRUMALIS (BANGS 1898)

1898	<u>Mustela brumalis</u>	Bangs, p. 502
1901	<u>Mustela atrata brumalis</u> ,	Elliot, p. 336.
1902	<u>Mustela americana brumalis</u> ,	Rhoads, p. 448
1909	<u>Mustela caurina brumalis</u> ,	Hantzsch, vol. 9, p. 254.
1912	<u>Martes brumalis</u> ,	Miller, p. 93.
1934	<u>Martes americana brumalis</u> ,	Anderson, p. 95

Type locality: "Okkak, Labrador" (Bangs 1898); "Okak, Labrador" (Miller 1900).

Type specimen: Museum of Comparative Zoology, Bangs' Collection No. 7417, Cambridge, Mass. (Bangs 1898, Anderson 1946).



Characteristics: "when compared with skulls of true americana ...

show very striking differences; their large size, short wide rostrums and enormous teeth at once distinguish them" (Bangs 1898)

Rhoads (1902) considered the skulls of brumalis "surprisingly identical in size and proportion to those of actuosa" and the present study bears out his conclusion.

On the basis of the small sample studied it is the largest North American marten, being most similar to actuosa.

#### MALES

	M		S D	C V	N
C L	8.643	.118	.204	2.4	3
R W	1.619	.017	.045	2.8	7
U T R	3.190	.026	.046	1.4	3
B L	1.749	.019	.051	2.9	7
CW/BL	.906	.012	.033	3.6	7
MW L	1.363	.018	.048	3.5	7

#### FEMALES

C L	1.550	.149	.212	2.8	2
R W	1.475	.074	.106	7.2	2
U T R	2.795	.016	.023	.8	2
B L	1.560	.060	.085	5.4	2
CW/BL	.900	.009	.014	1.6	2
MW L	1.150	.029	.042	3.7	2

Statistical comparison with americana has been made under that subspecies discussion. Compared with actuosa (the only one similar to it) statistical significance of difference between means is shown in upper molar length plus width (males only). On the basis of the samples at hand no other differences have been detected.

Distribution: Labrador probably as mapped, north to the tree limit, intergrading with americana in the region about Lake Mistassini at least. Newsom (1937) records the presence of marten on Anticosti Island, but that they differ from the mainland form in having the "fore-paws and end of tail ... tipped with white hair."

Specimens examined: Fort Chimo, Ungava four (N M C); Grand Falls, Hamilton R., Lab. two (C M); vicinity Northwest R., Lab. three (CM)

MARTES AMERICANA ATRATA (BANGS 1897)

1897 Mustela atrata Bangs, p. 162.

1912 Martes atrata, Miller, p. 93

1942 Martes americana atrata, Allen, p. 166.

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

Type specimen: Museum of Comparative Zoology, Bangs' Collection No. 5752, Cambridge, Mass. (Anderson 1946).

No specimens of atrata have been examined in this study.

Bangs (1897) states however: "Size about that of M. americana (probably somewhat larger); colour very different ... skull slightly different ...

about the same size or larger ... ; rostrum narrow, audital bullae much larger and deeper ... and with a more marked 'bottle-nose' projection; dentition rather weaker throughout, with greater spaces between premolar teeth."

Rhoads (1902) stated that Bangs considered this a species on geographic rather than morphologic grounds, and that it is cranially much closer to americana than to brumalis. Most authors consider atrata to be a full species however.

Gilpin (1860) remarked that pelages of marten from Newfoundland were much more similar to those of Labrador (brumalis) than to those of Nova Scotia (americana).

Since Vancouver and Queen Charlotte Islands both bear separate subspecies of marten it is quite possible that examination of Newfoundland specimens will show them to be subspecifically different from mainland forms as well. On the basis of Bangs' description however, atrata cannot be given specific status and on the basis of its geographic position and in the interests of parsimony it must be considered a subspecies of the americana subspecies group until shown to be otherwise.

Distribution: Newfoundland.

Specimens examined: None.

MARTES AMERICANA ABIETICOLA (PREBLE 1902)

1902 Mustela americana abieticola Preble, p. 68.

1912 Martes americana abieticola, Miller, p. 92

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

Type specimen: U. S. National Museum, No. 19256/34962 (Poole and Schantz 1942)

Characteristics: Described by Preble (1902) as "much longer than Mustela americanus ... the sagittal crest being more highly developed ... dentition much heavier except last upper molar which is usually about the same size.... Approaches Mustela a. actuosa but though smaller has heavier dentition."

The several specimens examined during this study show characteristics intermediate between those of americana and actuosa.

#### MALES

	M		S D		C V	N
C L	8.27		.....		.....	1
R W	1.625	.015	.022	.011	1.4 .6	2
U T R	3.05		.....		.....	1
B L	1.690	.069	.098	.049	5.8 2.9	2
CW/BL	.962		.....		.....	1
MW L	1.390	.019	.028	.014	2.0 1.0	2

Statistical comparison with americana has been made under the description of that subspecies.

Significant differences in the comparison of means of actuosa with abieticola were found in upper molar length plus width (males only).

Specimens from Fort Vermilion and Wood Buffalo Park, Alberta and Thelon Game Sanctuary, N. W. T. appear much nearer to actuosa than abieticola. It is quite probable that abieticola should be considered

an intergrading form separating actuosa from americana. Because of the smallness of the sample studied, it is best to maintain its full subspecific standing until proven otherwise.

Distribution: Western Northern Ontario (?), Manitoba, Saskatchewan, and possibly extreme eastern Alberta and Mackenzie district.

Specimens examined: Herchmer, Man. two, (N.M.C).

MARTES AMERICANA ACTUOSA (OSGOOD 1900)

- 1900 Mustela americana actuosa Osgood, p. 43
- 1901 Mustela atrata actuosa, Elliot, p. 336.
- 1905 Mustela americana actuosa, Elliot, p. 139.
- 1908 Mustela americana actuosa, Preble, pp. 236-237
- 1912 Martes americana actuosa, Miller, p. 93.
- 1912 Martes boria Miller, p. 93
- 1937 Martes actuosa, Anderson, p.
- 1942 Martes americana boria, Allen, p. 167

Type locality: "Fort Yukon, Alaska" (Osgood 1900)

Type specimen: U. S. National Museum No. 6043 (Poole and Schantz 1942).

Classification: Three specimens from Mackenzie River district, the approximate type locality of boria, show no significant difference from those from Alaska, and constitute justification for accepting Preble's (1908) conclusion that boria and actuosa represent different colour phases of the same subspecies.

Characteristics: "Similar to M. brumalis but larger; ... skull somewhat larger, longer; dentition relatively much weaker; last upper molar decidedly the largest of the subspecies of Mustela americana. M. brumalis is also large but does not equal actuosa ... and has heavier dentition." (Osgood 1900).

Rhoads (1902) found that he could not distinguish brumalis from actuosa according to Osgood's diagnosis and the present study bears him out. Brumalis, further, on the basis of the small sample studied, appears the larger of the two. Further comparison is given under the description of that subspecies

#### MALES

	M		S D		C V		N
C L	8.325	.076	.255	.054	3.1	.7	11
R W	1.626	.014	.060	.010	3.7	.6	17
U T R	3.041	.027	.104	.019	3.4	.6	14
B L	1.753	.014	.056	.009	3.2	.6	16
CW/BL	.821	.012	.048	.008	5.2	.9	16
MW L	1.249	.015	.064	.010	5.1	.9	17

#### FEMALES

C L	7.677	.074	.166	.052	2.2	.7	5
R W	1.434	.016	.043	.011	3.0	.8	7
U T R	2.780	.020	.045	.014	1.6	.5	5
B L	1.619	.020	.053	.014	3.3	.9	7
CW/BL	.869	.009	.026	.006	3.0	.8	7
MW L	1.136	.013	.037	.009	3.3	.9	7

Statistical comparison with subspecies whose ranges lie to the east of actuosa has been made. Compared with abietinoides to the south, significance between means was found in condylobasal length (males), rostral width (males and females), bullae length (males and females), upper molar width plus length (females), and upper tooth row (females).

Twenty-seven specimens from north central British Columbia show characteristics intermediate between actuosa and abietinoides. Even though these show an average coefficient of variability no higher than the latter and the former do (3.7 compared to 4.5 and 3.3), they are probably best classed as intergrades. One skin from Bulkely House, British Columbia (B C P M) was quite different from five actuosa skins from Yukon (M V Z) and from six abietinoides skins (U B C) from south eastern British Columbia. The Bulkely House specimen was grayer, and with a whiter throat patch than in those of either actuosa or abietinoides, but in other characteristics showed greater similarity to actuosa. Twenty skulls from Fort Nelson B. C. are, however, typical actuosa.

In a similar fashion, eight skulls from Fort Vermilion, Alta. and Wood Buffalo Park, Alta. show characteristics intermediate between actuosa and abietinoides.

Distribution: All of timbered Alaska, excepting the Kenai Peninsula (supposedly), Yukon and the Northwest Territories, apparently intergrading with abieticola at about the 110th parallel longitude, and with abietinoides in the area ranging from about the 60th parallel latitude south to about the region of the continental divide. Absent from the Rocky

Mountains south of 55° and from the Coast Ranges.

Specimens examined: Fort Vermillion, Alta. five (N M C); Wood Buffalo Park, Alta. three (N M C); Thelon Game Sanctuary, N W T. one (N M C); Fort Nelson B.C. twenty (U M); lower Iskut R., B.C. one (B C P M); British Columbia four (N M C, U B C); Fort Graham, B.C. seven (NMC); Takla landing, B.C. three (B C P M); Driftwood R., B.C. three (B C P M); Omineca R., B.C. two (U B C); Bulkely House, B.C. two (B C P M); Charley Creek, Yukon R., Alaska five (M V Z); White R., Y.T. two (R O M Z); Mackenzie Delta, N.W.T. one (N M C); Kanto Rashke ?, Alaska two (M V Z); Chicton Mt., Alaska one (M V Z); Swanson Creek, Alaska three (M.V Z); 30 miles up Willow R., N W.T. two (N.M.C); Nekukah, Alaska one (M V Z); Alaska six (M V Z, U M); Mackenzie Distr. N.W.T. one (N M C)

MARTES AMERICANA KENAIENSIS (ELLIOT 1903)

- 1903 Mustela americana kenaiensis Elliot, p. 151  
1905 Mustela kenaiensis, Elliot, p. 421.  
1912 Martes americana kenaiensis, Miller, p. 93

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

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

Classification: No specimens of kenaiensis have been examined during this study. Elliot (1903) describes it as "smaller than M. a. actiosa, with longer tail, shorter feet, and general color darker; audital



bullae large, ridged, rectangular, longitudinally produced. Molars heavy; sagittal crest prominent; no gular or abdominal patches ... Skull smaller than those of either actuosa or brumalis."

Elliot's measurements are: condylobasallength 7.95 cm.; upper tooth row 2.5; length of bulla 1.7.

Osgood (1901) considered skulls of kenaiensis far more similar to M.a. americana than to actuosa. Elliot's measurements do not allow accurate comparison with those of actuosa. From the description given of the large bulla however, it is likely that kenaiensis represents the americana subspecies group. On the basis of Elliot's statement that the animal lacks gular or abdominal patches, it is probably best to keep it as a distinct subspecies for the time being.

Distribution: Kenai Peninsula, Alaska.

Specimens examined: None.

MARTES AMERICANA ABIETINOIDES GRAY 1865

- 1865 Martes americana variety 1, abietinoides Gray, p. 106.
- 1902 Mustela americana abietinoides, Rhoads, p. 451.
- 1912 Martes americana abietinoides, Miller, p. 93.

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

Type specimen: None, to my knowledge. Rhoads pointed out that Gray's abietinoides included the range of origenes and on the basis of Richardson's (1829) descriptions, that all of Gray's specimens were true abietinoides: hence Rhoads change of type locality.

Characteristics: "Black-brown; ears pale; head grizzled with white hairs, more or less gray; throat yellow or yellow spotted; throat spot large or broken up into small spots; the head sometimes with only a few gray hairs, and the throat with only a few distinct small spots" (Gray 1865)

Rhoads (1902) described it as possessed of a skull specifically identical with actuosa, and only slightly smaller in size, being intermediate in this respect between americana and actuosa, teeth bullae and skull proportions precisely as in americana.

The present study disagrees with Rhoads' description in that it finds abietinoides the smallest marten of the americana group, but agrees with his statement about the general similarity of proportion and size between abietenoides and M. a. americana. It is most like americana from which it is difficult or impossible to separate on the basis of skull characteristics.

#### MALES

	M		S D		C V		N
C L	7.858	.035	.206	.024	2.6	.3	34
R W	1.514	.007	.057	.005	3.8	.3	58
U T R	2.869	.038	.223	.027	7.8	.9	34
B L	1.648	.007	.059	.005	3.6	.3	60
CW/BL	.882	.005	.040	.003	4.5	.4	59
MW L	1.195	.006	.050	.004	4.2	.4	60

FEMALES

	M		S D		C V		N
C L	7.094	.091	.491	.064	6.9	.9	29
R W	1.342	.009	.060	.006	4.5	.5	42
U T R	2.555	.020	.108	.014	4.2	.6	29
B L	1.537	.007	.050	.005	3.3	.4	42
CW/BL	.835	.006	.040	.004	4.8	.5	42
MW L	1.057	.006	.045	.004	4.3	.5	42

Statistical comparison with actuosa and americana has been made under the descriptions of these two subspecies. Thirteen specimens taken from the periphery of abietinoides range (Wisteria P.O., B.C., Tatuk Lake, B.C. and Tahtsa Lake, B.C.) are typical of the subspecies;

Distribution: British Columbia south of the continental divide, intergrading with actuosa to the north; east to the eastern slopes of the Rocky Mountains, intergrading with actuosa and possibly abieticola; west to the eastern slopes of the coast range, probably intergrading with caurina and south into northern Idaho and Montana, intergrading with origenes.

Specimens examined: Tahtsa L., B.C. one (Collection of Robert Webb); Tatuk L., B.C. one (N.M C); Wisteria P.O., B.C. eleven (B C P M); Okanagan L., B.C. two (U B C); Jasper, Alta. one (N M C); Yahk, B.C. two (N M C); Eagle R., B.C. eighteen (U B C); Akalkolex R., B.C. four (B C P M); Banff Park, Alta. sixteen (U B C); Rocky Mts. west of Banff eight (U B C); Akamina R., B.C. fourteen (U B C); Blue R., B.C. seven (U B C); Quesnel L., B. C. one (U B C); Little Prairie, B.C. two (B C P M); Golden, B.C. one (U.B.C); Fatigue Creek, Alta. one

(U B C); Simpson Pass, Alta. twenty-one (U B C); Lempriere, B.C. one (U B C); Murtle L., B.C. one (U B C); Cranbrook, B.C. one (R O M Z); Morrissey, B.C. one (N M C); Nelson, B.C. one (N M C); Jasper Park, Alta. two (U B C); Vermillion Pass, B.C. two (U B C).

SUBSPECIES GROUP II, CAURINA.

Nomenclature and classification: Formerly the species Martes caurina and its subspecies.

Characteristics: Ratio of canine width at base - / -  
bulla length nearer to 1.50 cm. than .90 cm.  
in males, .95 than .85 in females. Upper  
molar length plus width nearer to 1.35 cm.  
than to 1.20 cm. in males, 1.20 than 1.05 in  
females.

Distribution: The coast ranges and Sierra Nevadas  
together with the Rocky mountains south of the  
49th parallel; Vancouver and Queen Charlotte  
Islands and elsewhere as described below.

MARTES AMERICANA CAURINA. (MERRIAM 1890).

- 1890 Mustela caurina Merriam, p. 27
- 1901 Mustela americana caurina, Osgood, p. 70.
- 1901 Mustela atrata caurina, Elliot, p. 335
- 1912 Martes caurina caurina, Miller, p. 93.
- 1951 Martes americana caurina, Wright, unpublished MS.

Type locality: "Chehalis County, Washington (coast near Gray's harbor)"  
(Merriam 1890).

Type specimen: U. S. National Museum Collection No. 186,450 (Poole and

Schantz 1942).

Characteristics: "In external appearance ... differs little from

M. americana ... except that the irregular markings of the throat and under surface generally are orange-red instead of whitish or yellowish.... The skull ... differs ... in the following particulars: the rostral portion is broader and shorter; the audital bullae are shorter and less inflated; the frontals are broader both interorbitally and post-orbitally; the shelf of the palate is less produced behind the plane of the last molar; the first upper pre-molar is smaller and more crowded; the upper molars are larger; the upper sectorial in addition to its larger size, has the inner lobe very much larger and longer, projecting anteriorly beyond the plane of the anterior lobe, the reverse being the case in M. americana; the last upper molar is not only larger, but has a much broader saddle; the transverse diameter of the tooth is about one-third greater than in M. americana, and the antero-posterior diameter of the inner lobe is both relatively and absolutely much greater; the distance between the outer alveoli of the upper canines equals the greatest length of the audital bullae instead of being much less; the transverse diameter of the upper molar is greater instead of less than the length of the upper sectorial ... the underjaw is heavier." (Merriam 1890).

The present study finds that caurina, as well as all the other subspecies of the group, are in general well characterized by the above description.

MALES

		M		S D		C V	N
C L	7.863	.066	.230	.046	2.9	.6	12
R W	1.639	.016	.072	.011	4.4	.7	19
U T R	2.920	.028	.099	.020	4.4	.9	12
B L	1.471	.018	.080	.012	5.4	.9	19
CW/BL	1.041	.016	.070	.011	6.7	1.1	19
MW L	1.337	.011	.052	.008	3.9	.6	19

FEMALES

C L	7.251	.071	.227	.050	3.1	.1	10
R W	1.479	.021	.082	.015	5.5	1.0	14
U T R	2.670	.026	.083	.018	3.1	.7	10
B L	1.427	.015	.059	.011	4.1	.8	14
CW/BL	.981	.017	.063	.012	6.4	1.3	13
MW L	1.227	.019	.072	.013	5.9	1.1	14

One specimen from Yakutat, Alaska shows greater similarity to actuosa than to caurina in bulla length and the ratio of canine width to bulla length. Greater similarity to caurina is present in rostral width and upper molar length plus width. Another specimen from Hole-in-the-wall, B.C. shows characteristics intermediate between those of caurina and actuosa.

Distribution: The coast range of North America; exact northern and southern limits unknown, but supposedly as far north as the base of the Alaska

pan-handle (Anderson 1946) and as far south as southern Oregon. (Grinnell, Dixon and Linsdale 1937).

Specimens examined: Hole-in-the-wall, B. C. one (U B C); Yakutat, Alaska one (M V Z); Anahim L., B.C. six (M V Z); Manning Park, B.C. twelve (U B C); Rainbow Mts, Mt. Brilliant, B.C. one (N M C); Bella Coola, B.C. one (B C P M); Stuie, Cariboo Mt., B.C. one (N M C); Atnarko, B.C. one (B C P M); Lillooet distr., B.C. five (N M C, B C P M); One-eye L., B.C. one (M V Z); Mason Co., Wash. one (U M); Chilliwack Valley, B.C. one (N M C); Kimsquit, B.C. one (N M C); Taliho, B.C. one (N M C); Kleena Kleena, B.C. one (M V Z); coast of northern B.C. one (U B C); Kynoch Inlet, B.C. one (U B C).

MARTES AMERICANA ORIGINES. (RHOADS 1902)

- 1902 Mustele caurina origenes Rhoads, p. 458
- 1912 Martes caurina origenes, Miller, p. 93
- 1951 Martes americana origenes, Wright, unpublished MS.

Type locality: " 'Marvine Mountain' (Garfield County?) Colorado" (Rhoads 1902)

Type specimen: U.S. National Museum Collection No. 112, 170 (Poole and Schantz 1942)

Characteristics: "Strikingly different from all other American martens except caurina in the absence of the light coloured cheek patches. Head relatively darker ... than in caurina, ears lacking a white border.... Viewed from above shows an even greater uniformity of colour than does caurina" (Rhoads 1902).

MALES

	M		S D		C V		N
C L	8.017	.074	.149	.052	1.9	.7	4
R W	1.643	.026	.076	.019	4.6	1.2	8
U T R	3.000	.036	.072	.025	2.4	.8	4
B L	1.531	.020	.057	.014	3.7	.9	8
CW/BL	1.015	.006	.017	.004	1.7	.4	8
MW L	1.426	.024	.070	.017	4.9	1.2	8

FEMALES

C L	7.260	.084	.147	.060	2.0	.8	3
R W	1.428	.020	.061	.014	4.3	1.0	9
U T R	2.636	.011	.020	.008	.8	.3	3
B L	1.418	.014	.043	.010	3.0	.7	9
CW/BL	.930	.009	.026	.006	2.8	.7	8
MW L	1.231	.026	.076	.019	6.2	1.5	8

The present study shows no statistically significant differences between the skulls of origenes and caurina; it appears that Rhoads' determination of the subspecies was made wholly on pelage characteristics. Three skins of caurina (M V Z, U B C) and six of origenes (M V Z) have been examined and Rhoads' distinction between the two on the basis of these appears to be only doubtfully valid. Because origenes is completely isolated geographically, and because of the supposed differences in coloration separating the two, it seems best to maintain the



subspecies until a larger sample of skulls and skins can be examined.

Distribution: The Rocky Mountains of the United States, formerly south as far as Taos, New Mexico (Seton 1929). According to Wright (letter of July 9, 1951) it extends as far north as Ravalli County, Montana, and central Idaho, where it intergrades with abietinoides (of the americana subspecies group), marten from Glacier National Park and extreme northern Idaho being typical abietinoides.

Dalquest (1948) identifies the marten of far eastern Washington as origenes; Rust (1946) and Davis (1939) call those of western Idaho caurina. In view of Wright's findings however, concerning the northern limit of origenes, and the fact that all of south western British Columbian marten are abietinoides, it is more likely that those of eastern Washington and north western Idaho are abietinoides, or abietinoides-origenes intergrades.

M.a. origenes appears to be geographically isolated from caurina being separated from it by the interior dry belt of western North America.

Specimens examined: Idaho eleven (M V Z, U M); Oregon one (M V Z); Wyoming two (U M); Montana three (M V Z).

MARTES AMERICANA HUMBOLDTENSIS GRINNELL AND DIXON 1926

1926 Martes caurina humboldtensis Grinnell and Dixon,  
p. 411.

1951 Martes americana humboldtensis, Wright, unpublished MS.

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

Type specimen: Museum of Vertebrate Zoology, Collection No. 19158, Berkeley (Grinnell and Dixon 1926)

Characteristics: Has been described by Grinnell and Dixon as follows: externally "resembles Martes caurina caurina; decidedly darker, of richer golden brown tone than M. c. sierrae.... Skull smaller than in either ... with rostrum slender, distinctly constricted behind roots 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 anteroposteriorly, as much so, relative to transverse diameter... as in sierrae, and hence more than in caurina"

Three skulls of humboldtensis that arrived too late for full consideration in this study are considerably smaller than the skulls of any other of the caurina subspecies group. No statistical difference between the means of the condylobasal lengths was found, however.

Until more specimens are made available, and until the ones available are more carefully analyzed, it is best to maintain it as a distinct subspecies.

Distribution: The Cascade Range of California, south of about 38° latitude. According to Grinnell, Dixon and Linsdale (1937) it intergrades

with caurina "to the north of California". Bailey (1936) lists Oregon martens as caurina however; if the two represent distinct subspecies, it must be admitted that the region separating them is unknown.

Specimens examined: Humboldt Co., Calif. two (M V Z); Del Norte Co. Calif. one (M V Z).

MARTES AMERICANA SIERRAE GRINNELL AND STORER 1916.

1916 Martes caurina sierrae Grinnell and Storer, p. 2.

1926 Martes caurina nobilis Hall, p. 127

1951 Martes americana sierrae, Wright, unpublished MS.

Type locality: "Head of Lyell Canon, 9800 feet altitude, Yosemite National Park, California" (Grinnell and Storer 1916)

Type specimen: Museum of Vertebrate Zoology No. 22112, Berkeley, California Grinnell and Storer 1916).

Hall in 1936 placed nobilis, a Pleistocene subspecies described by him in 1926, in the synonymy of sierrae (p. 87). ( = extinct)

Characteristics: Is described by Grinnell and Storer as "similar to Martes caurina caurina, but general coloration paler both above and below ..., sides of face decidedly pale ..., orange of chest very extensive.... Cranium with rostrum short as in caurina but extremely narrow; whole cranium narrower and brain-case relatively higher; sagittal crest very weak; auditory bullae even smaller than in caurina"

Five skulls of sierrae arrived too late for full consideration in the present study. Qualitative examination shows them to be larger than those of humboldtensis, (but not significantly so), and to lie within the range exhibited by caurina and origenes. One skin (M V Z) shows a summer pelage far paler, and acquired earlier, than do three of humboldtensis (M V Z).

As in the case of humboldtensis the subspecies must be allowed to stand.

Distribution: The Sierra Nevada Range of California and extreme western Nevada.

Specimens examined: Kern Co. Calif. one (M V Z); Emerald Co. Calif. one (M V Z); Fresno Co. Calif. two (M V Z); Madera Co. Calif. one (M V Z).

MARTES AMERICANA VANCOUVERENSIS GRINNELL AND DIXON 1926.

1926 Martes caurina vancouverensis Grinnell and  
Dixon p. 414.

1951 Martes americana vancouverensis, Wright, unpublished  
MS.

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

Type specimen: Museum of Vertebrate Zoology, No. 12, 474, Berkeley (Grinnell and Dixon 1926).

Characteristics: Described originally as "externally like Martes caurina caurina but ... rostrum shorter, frontal region and indeed whole cranium

broader; 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 like that of Mustela nesophila Osgood but smaller, and with weaker dentition; last upper molar much smaller and heel even less expanded....." (Grinnell and Dixon 1926).

#### MALES

	M		S D		C V		N
C L	7.968	.051	.154	.036	1.9	.5	9
R W	1.654	.020	.064	.014	3.9	.9	10
U T R	2.902	.020	.060	.014	2.1	.5	9
B L	1.519	.015	.050	.011	3.3	.7	10
CW/BL	1.029	.012	.040	.008	3.9	.9	10
MW L	1.329	.008	.028	.006	2.1	.5	10

#### FEMALES

C L	7.225	.038	.094	.027	1.3	.4	6
R W	1.468	.017	.045	.012	3.1	.8	7
U T R	2.605	.015	.037	.010	1.4	.4	6
B L	1.441	.014	.038	.010	2.6	.7	7
CW/BL	.964	.015	.040	.010	4.1	1.1	7
MW L	1.127	.018	.048	.012	4.3	1.1	7

Vancouverensis is not, on the basis of the above samples, statistically separable from caurina. On a purely geographic basis

at least, and until more skins of marten from Vancouver Island can be compared with those from the mainland, no change in its status seems to be warranted.

Comparison with nesophila is made under the description of that subspecies.

Description: Vancouver Island, excluding a narrow strip supposedly along the eastern and southern shores.

Specimens examined: Vancouver Island seventeen (B C P M, N M C, U B C).

MARTES AMERICANA NESOPHILA (OSGOOD 1901).

1901 Mustela nesophila Osgood, p. 33.

1912 Martes nesophila, Miller, p. 94

1926 Martes caurina nesophila, Grinnell and Dixon,  
p. 417.

1951 Martes americana nesophila, Wright, unpublished  
MS.

Type locality: "Masset, Graham Island, Queen Charlotte Islands, British Columbia" (Osgood 1901).

Type specimen: U. S. National Museum, Biological Survey Collection, No. 78066 (Poole and Schantz 1942).

Characteristics: "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.... Especially separable by thick rostrum" (Osgood 1901).

	M		MALES		C V		N
			S	D			
C L	8.140	.084	.147	.060	1.8	.7	3
R W	1.863	.017	.030	.012	1.6	.7	3
U T R	2.983	.043	.075	.030	2.5	1.0	3
B L	1.496	.023	.040	.016	2.7	1.1	3
CW/BL	1.163	.025	.044	.017	3.8	1.5	3
MW L	1.353	.005	.010	.004	.7	.3	3

FEMALES

C L	7.44						1
R W	1.60						1
U T R	2.70						1
B L	1.40						1
CW/BL	1.092						1
MW L	1.26						1

The above sample is statistically separable from vancouverensis on the basis of rostral width (males), canine width - / - bulla length (males and females) and upper molar length plus width (females). Similarly it is separable from caurina on the basis of rostral width (males) and canine width - / - bulla length (males).

Swarth (1911 and 1912) after examining specimens from Admiralty Island and Kuiu Island, Alaska concluded that they might represent a distinct species. I have examined Swarth's material however, and it is, for the characters studied, statistically

comparable to nesophila and must for the present be considered representative of that subspecies.

Distribution: Known beyond doubt only on Graham and Moresby Islands, Q.C.I., Admiralty Island and Kuiu Island, Alaska; mapped by Seton as occurring on all of the Queen Charlotte Islands and all of the Alexander Archipelago; it is not however listed as present on the coastal islands between 51 and 54 degrees by McCabe and Cowan (1945).

Specimens examined: Graham Island, Q.C.I. four (B C P M, U B C); Admiralty Island five (M V Z); Kuiu Island one (M V Z).

#### Conclusions:

On the basis of the statistical separability (to the .05 level or better) of the samples just described, there is probably sound evidence for the existence of the following subspecies: americana, actuosa, abietinoides, caurina, nesophila and brumalis. Vancouverensis and origenes, though represented by fairly adequate samples cannot be separated from caurina. Boria is likely best considered a variant of actuosa. The samples of abieticola sierrae and humboldtensis are too small for adequate analysis. No specimens of atrata or kensiensis were examined.

As a final check to the above conclusions, all samples were pooled, and treated with an analysis of variance. Significance beyond the .01 level was obtained for all measurements except condylo-basal length in females, and the ratio canine width divided by bulla



length, which was not tested.

Wright's work (1951) indicated that all North American marten are conspecific. As a result of his work and the conclusions arrived at during the present study, the following classification of marten has been prepared. This classification is as natural (phylogenetic) as present knowledge permits. The basis for the decisions invalued in its organization are discussed in Part II. The presence of a question name indicates doubt concerning the actuality of a subspecies.

Subspecies group americana

Martes americana americana (Kerr 1792)

Martes americana abietinoides Gray 1865

Martes americana atrata ? (Bangs 1897)

Martes americana abieticola ? (Preble 1902)

Martes americana brumalis (Bangs 1898)

Martes americana actiosa (Osgood 1900)

Martes americana kenaiensis ? (Elliot 1903)

Subspecies group caurina

Martes americana caurina (Merriam 1890)

Martes americana origenes ? (Rhoads 1902)

Martes americana humboldtensis ? Grinnell and Dixon 1926

Martes americana sierrae ? Grinnell and Storer 1916

Martes americana vancouverensis ? Grinnell and Dixon 1926

Martes americana nesophila (Osgood 1901)

Marten appear to follow certain of the rules of geographic distribution listed by Mayr (1942). The caurina group of the humid western coast is darker in colouration than is the americana group of the drier east (Gloger's Rule). Northern subspecies of the americana group (actuosa and brumalis) are larger than those to the south (Bergmann's Rule). I am unable to tell to what degree these size relationships are phylogenetic, and to what degree a result of convergent adaptation. The following discussion (Part II) assumes the relationship to be largely phylogenetic. This assumption is made with the knowledge that it is fully untested, and open to criticism. Only future work will tell how well founded it, and the following discussion based on it, is.

An artificial key to marten skulls is presented in Appendix B.

## PART II PHYLOGENY

### Discussion:

The literature pertaining to the phylogeny of the mustelids and the genus Martes is sparse, scattered and often lacking in general agreement. As an indication of this lack of interest in the group, Yeager (1941) points out that of the fur animals he considered only badger, otter and raccoon have received less attention than the wolverine, fisher and marten together.

Two approaches have been used in this study in an attempt to determine something of the racial history of marten. These are: (1) an examination of current interpretation of classification and of palaeontological data and (2) an interpretation of certain palaeocological

data.

(1) Classificatory and palaeontological data:

Mustelids have in the past been divided into from two (Cope 1882) to fifteen (Pocock 1921) subfamilies, with from four to eight being most usual. The subfamily Mustelinae, along with Lutrinae and Melinae however, have in almost all cases been considered an objective entity. In a similar fashion, the genus martes has been long recognized as representing a unit separable from most others.

The origin of the genus Martes is not well understood.

The situation is the usual one of having innumerable small branches given off near the base of the major splitting of a mammalian group.... In the Mustelidae the situation is further complicated ... by the fact that numerous known Miocene and Pliocene Mustelids are seldom real forerunners of the living genera, but in almost every genus appear to be all that is known of a distinct phylum.... (Simpson 1945)

The same author also remarks 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.

Another difficulty encountered is that palaeontologists have made the Mustelidae, and especially the genus Martes, a repository for all doubtful arctoid carnivores. Schlosser (1923) suggested grouping all of these into the subfamily Stenoplesictinae, but it has not been acted upon to any great extent. To make one problem more confusing still, not only is the origin of the group obscure, but it is poorly represented in the fossil record (Scott 1937).

The Mustelinids (the oldest of the Mustelids) first appeared

in the lower Oligocene, while the genus Martes (in the conservative sense) is first recorded from the lower Pliocene of the old world, and the upper Pliocene of the new (Simpson 1945).

Simpson (1947) believed that migration across the Bering land bridge occurred with varying degrees of intensity through all the Cenozoic subsequent to the Oligocene, excepting for the Recent. He states

the appearance of the Mustelidae, Mustelinae and all of 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.

He added that Martes probably crossed first in the upper Pliocene, but that the direction is very much in doubt. Pleistocene migrations were very extensive, and interglacial in the main. (Fig. 4)

The following genera have been suggested by various authors to lie in the direct phylogeny of the genus Martes: Palaeogale, Bunaelurus (Schlosser 1877-90), Sinictis, Plionictis, Plesiogulo, Oligobunis, Amphictis (Pilgrim 1932) Mustelavus (Scott 1937).

Species of Martes suggested as lying close to modern forms include Martes kinseyi (Gidley 1927), Martes gazini (Hall 1931), Martes diluviana (Hall 1936).

Pilgrim (1932) considered that Martes and Mustela have been distinct since about the Stampian (middle Oligocene). "Martes is, on the whole a survival of a primitive lineage -- it being most similar of all Recent forms to the hypothetical ancestor of the Mustelids."

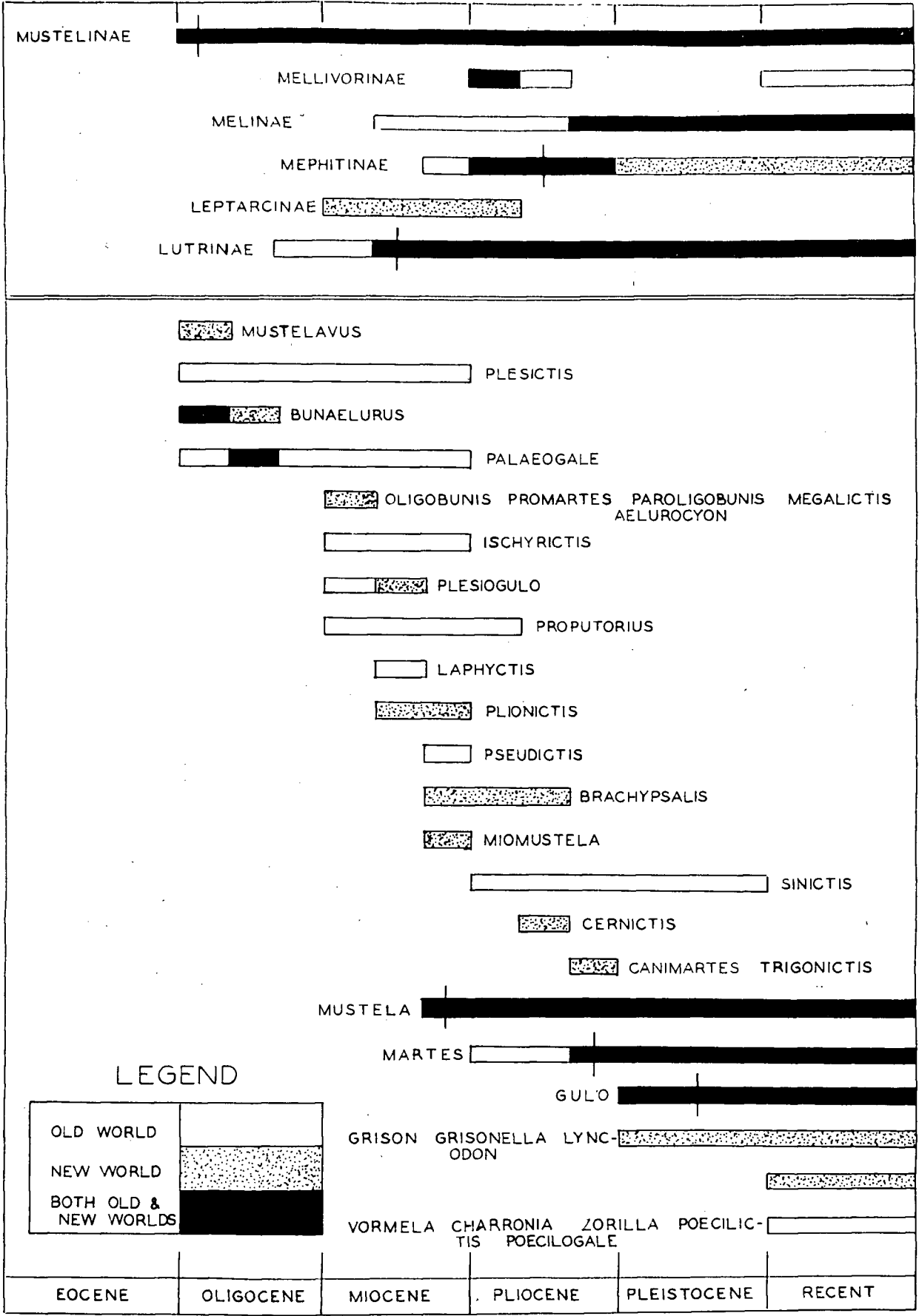
Little is known regarding Pleistocene Mustelids, either in Britain (Reynolds 1912), Eurasia (Dubois 1928) or America. Hall (1936)

Fig. 4.

(to follow page 43.)

Fig. 4. Distribution in time of the subfamilies (upper) and musteline genera (lower) of mustelidae.

Cross bars represent probable time of inter-continental migration. Largely after Simpson (1945) and Simpson (1947).



has presented the most recent survey of American Pleistocene Mustelids, and almost all that immediately follows is from his publication.

Nine genera of Mustelids (so called) are known from Pleistocene deposits, two are extinct and Enhydra and Conepatus are not recorded, while Spilogale, Mustela, Mephitis, Lutra, Taxidea, Gulo, and Martes are. The following then are the known Pleistocene recordings of marten, as listed by Hall.

Martes americana: The sole ascription to this subspecies appears to be Allen's (1876) reference to that found in Baird's collection from Pennsylvania. It may or may not be in reality a Recent deposit.

Martes americana sierrae: Hall in this (1936) paper placed his previously described (1926) M. caurina nobilis, a Pleistocene recovery from California in the synonymy of sierrae. He still considered it to be of Pleistocene origin.

Martes pennanti: Described by Allen (1876) and Brown (1908) from Pennsylvania and Arkansas. The latter reference is the only one known to me of a recovery of a still living Pleistocene Martes lying outside its Recent range.

Martes diluviana: Known from four specimens. Hall ascribed Gidley and Gazin's (1933) description of M. parapennanti to this species.

Hall concludes that Osborne's (1925) reference to a marten from Rancho la Brea was an erroneous identification of a weasel (Mustela).

I have nowhere found an opinion as to when the separation of the genus Martes into the subgenera Pekania (fishers) and Martes (martens)



occurred. Since the genus arose during the lower Pliocene, and both subgenera are known from the Pleistocene, it follows that the separation must have occurred some time during the Pliocene.

In summary then it appears that the origin of the genus Martes is not at all well understood; that it arose sometime about the lower Pliocene, possibly in Eurasia, having been distinct from Mustela from the Oligocene; that migration back and forth between the old and new world took place from the time of its origin to the Pleistocene; that the separation into its two component subgenera occurred about the Pliocene and that by the Pleistocene both subspecies groups of marten (americana and caurina) were present in North America.

(2) Palaeoecological data:

Zoologists have generally been slow to realize that there exist certain palaeoecological methods useful in the determination of biotic histories. It is well recognized that animal distribution in the present is largely governed by the responses of plants to climate (Shelford 1935, Clements and Shelford 1939). That the same has held in the past has not been so clearly understood. Nevertheless "the outline of the history of animals must coincide with that of the plants on which all animals ultimately subsist" (Hulten 1937).

Cain's (1944) text is the most recent exposition of the subject and the student desiring more detail should turn to that book.

Since so little is known about the former distribution of the marten, and since so much more is known about the former distribution of floras, and if marten have in the past been restricted to one of

those floras, it follows that much of the history of the marten is to be found in the history of that flora. It is upon this hypothesis that the following discussion is based.

It is well recognized that marten, and indeed almost all members of the subfamily Mustelinae are found only within communities of plants dominated by boreal conifers. If one plots the distribution of the coniferous west coast floras, the boreal forest and the lake forest together with that of the marten in North American, the close relationship between the two is apparent. It is equally apparent when the same is done for Asia, but somewhat more obscure in the case of Europe.

It is less easy to demonstrate that marten have, since their origin in the Pliocene, been possessed of the same relationship. It is known, however, that marten are not recognized to have shown specific changes since the Pleistocene, and all fossil recoveries are known from within their present range. Further, Pliocene Charronia from India are not known to be different from the forms now living there. (Flower and Lydeker 1891). In opposition to this, however, is the fact that not all fossil Martes are known to have come from regions contemporaneously boreal in nature, although at the same time the reverse has not yet been demonstrated. It is probably quite safe to conclude that for the Pleistocene at least, and very likely for much or all of the Pliocene, the demands, in terms of environment, of the martens ancestral to those now living, were not very different from what they are today. It seems unlikely that the tolerances of the components of animal communities

would change more than their vegetational substrata, and these it is known have changed very little (Arnold 1949, Cain 1944). Hooper (1949) has, for example, pointed out that all genera of North American rodents can be divided into three groups, each referable to the three major tertiary floras of the continent.

The present vegetation of North America is derived chiefly from three major floras: the so-called Arcto-tertiary Flora, the Madro-tertiary or Sierra Madrean Flora and the Neotropical-tertiary or Caribbean Flora. Marten today, and in all probability in the past, inhabited the whole of the Arcto-tertiary Flora. This flora appeared sometime between Cretaceous and Eocene times at high latitudes, migrating southward with climatic deterioration until during Miocene and Pliocene times it reached its approximate present position, forming the west coast coniferous forests the boreal forest, the Lake forest and the eastern hardwood forest (Axelrod 1937 and 1939, Berry 1923, Braun 1947 and 1950, Chaney 1936, 1940, 1947, Chaney, Condit and Axelrod 1944, Mason 1947, Simpson 1943, Scharff 1911).

While the large proportion of Mustelinids and the ancestors of marten probably migrated south with the Arcto-tertiary Flora in North America and Eurasia, the true martens (subgenus Martes) are believed to have evolved in Eurasia (Rhoads 1902, Davis 1939, Dalquest 1948) and to have arrived in North America near the beginning of the Pleistocene by crossing the Bering land bridge, as did most characteristic American Pleistocene animals (Colbert 1942, Romer 1945). Rhoads (1902) implied an earlier migration for the americana subgroup than for the caurina,

on the basis of the latter's close cranial relationship to Eurasian species. Davis (1939) likewise hypothesized an earlier migration for the americana group. There is some slight evidence besides Rhoads' comparative work that this sequence actually occurred. No true marten are known from North America prior to the Pleistocene. The caurina group is known from the Pleistocene of the west, and the americana from that of the east; primitive forms are assumed to lie farther from the point of origin than more recent forms (Matthew 1915, Taylor 1937). It seems likely then on the basis of the somewhat tenuous evidence now at hand that Martes americana arrived in North America from Eurasia early in the Pleistocene, and that the americana group preceded the caurina.

The glaciation of the Pleistocene, especially the last (Wisconsin) advance, has been the primary factor determining present day subspeciation and distribution (Deevey 1949).

It appears from analysis of pollen deposits and from geographic data that during the maximum of the last (Wisconsin-Vashon) glaciation, the forests occupied by the marten found refuge in (1) nunataks (2) south of the ice sheet, east of the Driftless area (3) south of the ice sheet in the Rocky Mountains (4) south of the ice sheet in the Coast, Cascade and Sierra Nevada Ranges and (5) in the unglaciated regions of Alaska. With the retreat of the Wisconsin-Vashon sheet, little or no migration occurred from nunataks; the boreal and lake forests moved north from the southeastern refuge, the former north to Labrador and west to near the Mackenzie River region; the Rocky Mountain forests moved north to

about northern British Columbia; the Pacific Coast floras moved north into Alaska; and the Alaskan boreal forest moved east to beyond the Mackenzie and south into British Columbia (Adams 1902 and 1905, Artist 1939, Braun 1928, 1947 and 1950, Brown 1938, Buell 1946, Cain 1944, Clements and Chaney 1937, Cooper 1931 and 1942, Darlington 1943, Davis 1946, Deevey 1943, Flint 1947, Fuller 1935, Gleason 1923, Halliday and Brown 1943, Hansen 1938, 1939, 1940, 1941, 1943 and 1947, Hansen and Packard 1949, Harshberger 1911, Hay 1902 and 1923, Hulten 1937, Krauss and Kent 1944, Mason 1947, Nichols 1935, Potzger 1946, Potzger and Wilson 1941, Raup 1941 and 1947, Rosendahl 1948, Sears 1935 a and b, 1938, 1942 and 1948, Transeau 1903 and 1905, Voss 1934, 1937 and 1939, Wilson 1938, Wynne-Edwards 1937).

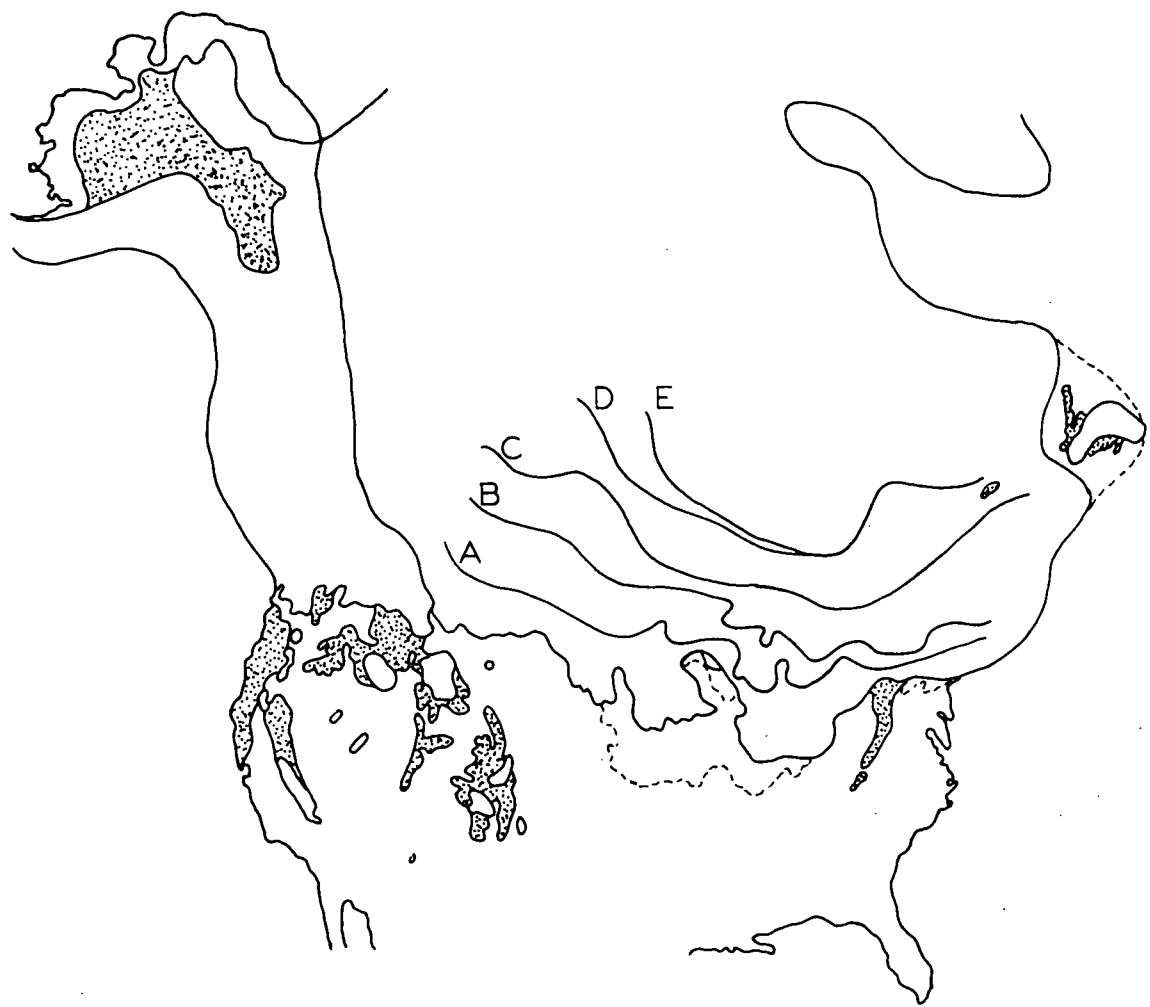
It is undoubtedly true that marten likewise spent the Wisconsin-Vashon glaciation in all of the above listed refugia, and followed the migrations of their forest environment to their present position. Evidence for this conclusion is as follows:

- (a) In both the old and the new world marten have adapted themselves to the whole of the range of coniferous life form. This indicates that the glacial refugia of marten must have been many and large (since little depauperization of "biotypes" has occurred) and in fact must have been precisely those of the forest it now lives in.
- (b) Marten today still have parts of their range extending into all of the several glacial refugia supposedly occupied by the forest they now live in. (Fig. 5).
- (c) There is some slight indication that greatest densities of marten are found near the regions of former glacial refugia. One would expect this to be the case if these refugia had in

Fig. 5.

(to follow page 49.)

Fig. 5. Areas of the present day distribution of marten lying outside the range of Pleistocene glaciation. Dotted areas mark marten distribution; solid line represents the boundary of maximum Wisconsin glaciation; dotted lines indicate older glaciations; lines A to E represent trend of post-Wisconsin glacial retreat. It is now believed that Newfoundland underwent complete glaciation during the Wisconsin. After Antevs (1928, 1929, and 1931), Flint (1945 and 1947), and Thwaites (1934).





the past been centers of postglacial dispersal, and if the subsequently acquired areas were still in the process of being populated. This same relationship has been found to occur in the density of forest trees in Canada (Halliday and Brown 1937). See Fig. 6.

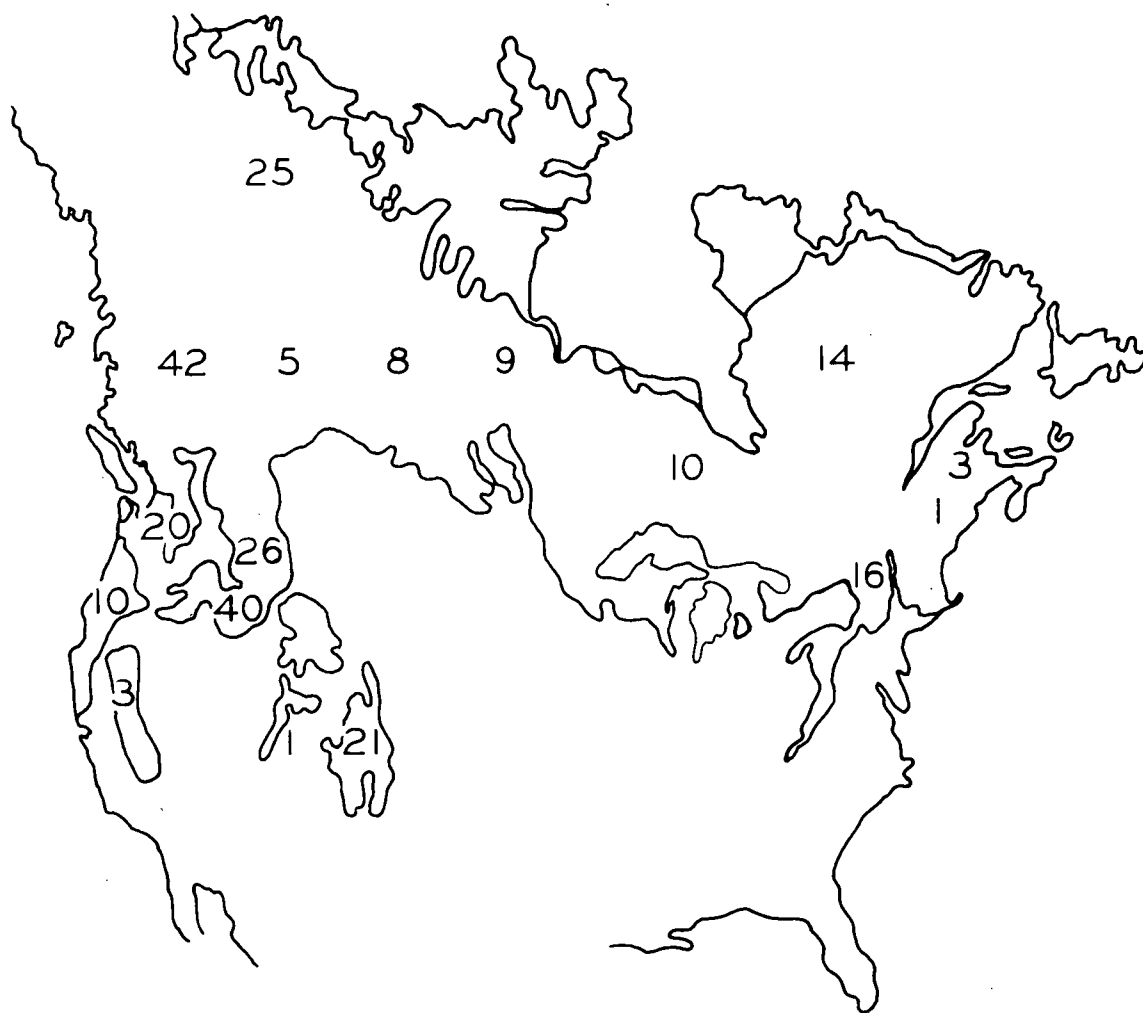
We are now in a position to speculate upon the postglacial history of the marten. Since Martes americana americana still ranges south into south eastern refugia, it doubtless spent the Wisconsin Ice Age there as did brumalis, and subsequently extended its range north to its present range limit. Abietinoides and origenes still exist in part in the Rocky Mountain refugium, and have since moved north to form their present distribution. Origenes has not arrived north of the glacial boundary, and has not yet made contact with caurina from which it was previously isolated. Caurina, humboldtensis and sierrae still range into the coastal refugium. Of these only caurina moved north with the retreat of the Vashon sheet. Actuosa and kenaiensis still occur in the Yukon refugium, only actuosa has migrated eastward, extending its range beyond the Mackenzie and into British Columbia. Abieticola, whose distribution lies in the center of the boreal forest, does not range into any of the glacial refugia, and its relationship to these is more difficult to determine. It seems likely, however, that abieticola represents an intergradation between actuosa and americana which has resulted from mixing of two strains on meeting after postglacial migration. The migrations described above are mapped on Fig. 7.

It is important here to take careful notice of the fact that all of the marten migrations described above correspond very closely

Fig. 6.

(To follow page 50.)

Fig. 6. Average number of marten trapped per 1000 square miles of forested land per state or province per year. Figures derived from Anon. (1927-1950). Anon (1950), Minville (1946), Ullman (1949) and Yeager (1950) . The number of years considered varies from two (Maine) to thirty-two (Quebec).



in terms of direction and distance travelled, with the migrations of coniferous forest species moving out of the same refugia, as determined by areographic and pollen analytical methods described by the students listed above. Insofar as these studies are accurate, the above doubtless represents a fairly precise picture of the postglacial migration of the marten in north America, and probably of certain other boreal animals as well.

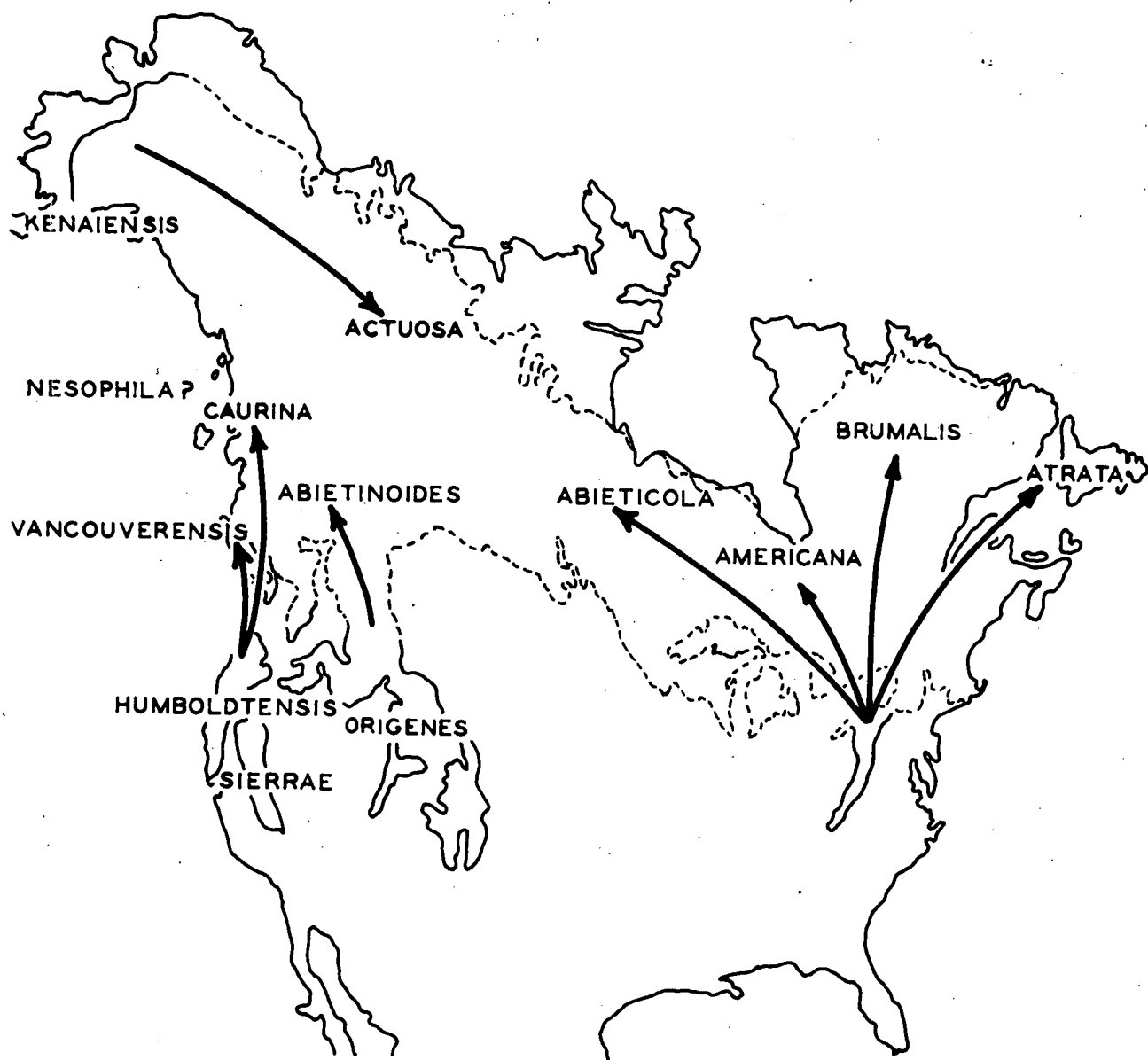
Assuming the above hypotheses to be reasonably sound, there are certain other phylogenetic relationships that can be considered. It will be noticed that all marten of the south eastern and Yukon refugia are of the americana group, while those of the Pacific Coast refugium are caurina. In the Rocky Mountain refuge however, both groups are represented (abietinoides and origenes). It follows that origenes and caurina were separated prior to or by the Vashon (Wisconsin) sheet and that the separation into americana and caurina subspecies groups must have occurred long before Vashon time, probably, as has been suggested, very early in the Pleistocene and in Eurasia.

It will have likewise been observed from the data presented in Part I of this study that M. a. actuosa and M. a. brumalis were more similar to each other than they were to any others, and that abietinoides and americana were also similar. If these similarities can be considered to possess a phylogenetic relationship, it implies that: (1) the separation of brumalis from actuosa occurred during Wisconsin time at the latest, while they were isolated from each other; that (2) the same is true for americana and abietinoides; that (3) abieticola has arisen

Fig. 7.

(To follow page 51.)

Fig. 7. Assumed post-Wisconsin marten migrations. Those subspecies not marked by an arrow are believed to have moved little or not at all from their location during the Wisconsin maximum.





since Wisconsin time through the interbreeding of actuosa and americana; and that (4) actuosa-brumalis must have been separated from abietinoides-americana sometime between the early Pleistocene at the earliest and the Illinoian glacial advance at the latest.

The insular subspecies of marten have yet to be considered. Atrata has not been examined but is said by Rhoads (1902) to be closer to americana than to brumalis; atrata probably arose from americana either during or subsequent to the Wisconsin. Vancouverensis and nesophila have doubtless sprung from caurina. Vancouver Island is considered to have been glaciated (Flint 1947) and doubtless migration to the island and subspeciation has occurred since Vashon-Wisconsin time. Nesophila shows far greater differences from caurina than does vancouverensis and this may be due to any or all of several facts. It has been suggested that the Queen Charlotte Islands have escaped glaciation (McCabe and Cowan 1945). This would mean that nesophila has been isolated for a much longer time than has vancouverensis. Small insular populations undergo a change in the frequency of their gene distribution such as to result in a homogenous population with phenotypes nonadaptively different from those of the parent stock (Huxley 1940). Whatever the factor at work is, it is not possible to determine more of the origin of nesophila than to ally it with caurina.

The foregoing may be summarized as follows: there is a certain amount of evidence to show that pre-americana crossed to the new world sometime between the late Pliocene and the Kansan, while pre-caurina probably followed at a later date, but also not later than Kansan.

Between the Kansan and the Illinoian americana had divided into abietinoides-americana and brumalis actuosa. Prior to the Wisconsin, origenes and caurina were separated. The advance of the Wisconsin sheet saw a segregation of marten in four refugia, each isolated from the other, during which time or subsequently subspeciation occurred. Of these refugia the south eastern repopulated most of Canada east of the Rockies (brumalis, americana, probably atrata and abieticola in part); the Pacific and Rocky mountain refugia Canada west of the Rockies (caurina, origenes, vancouverensis and abietinoides together with humboldtensis and sierrae); and the Alaska refuge the Alaskan and Canadian northwest (actuosa, kenaiensis and abieticola in part). M. nesophila is of a caurina origin, but its history is poorly understood.

#### Conclusions:

On the basis of the comparison of skulls described in Part I, and of the discussion of probable history of the marten in Part II, a provisional phylogeny of the subgenus has been prepared, and is presented in Fig. 8. This phylogeny assumes that all subspecies of marten discussed in this paper are valid ones, which is of course, not necessarily the case.

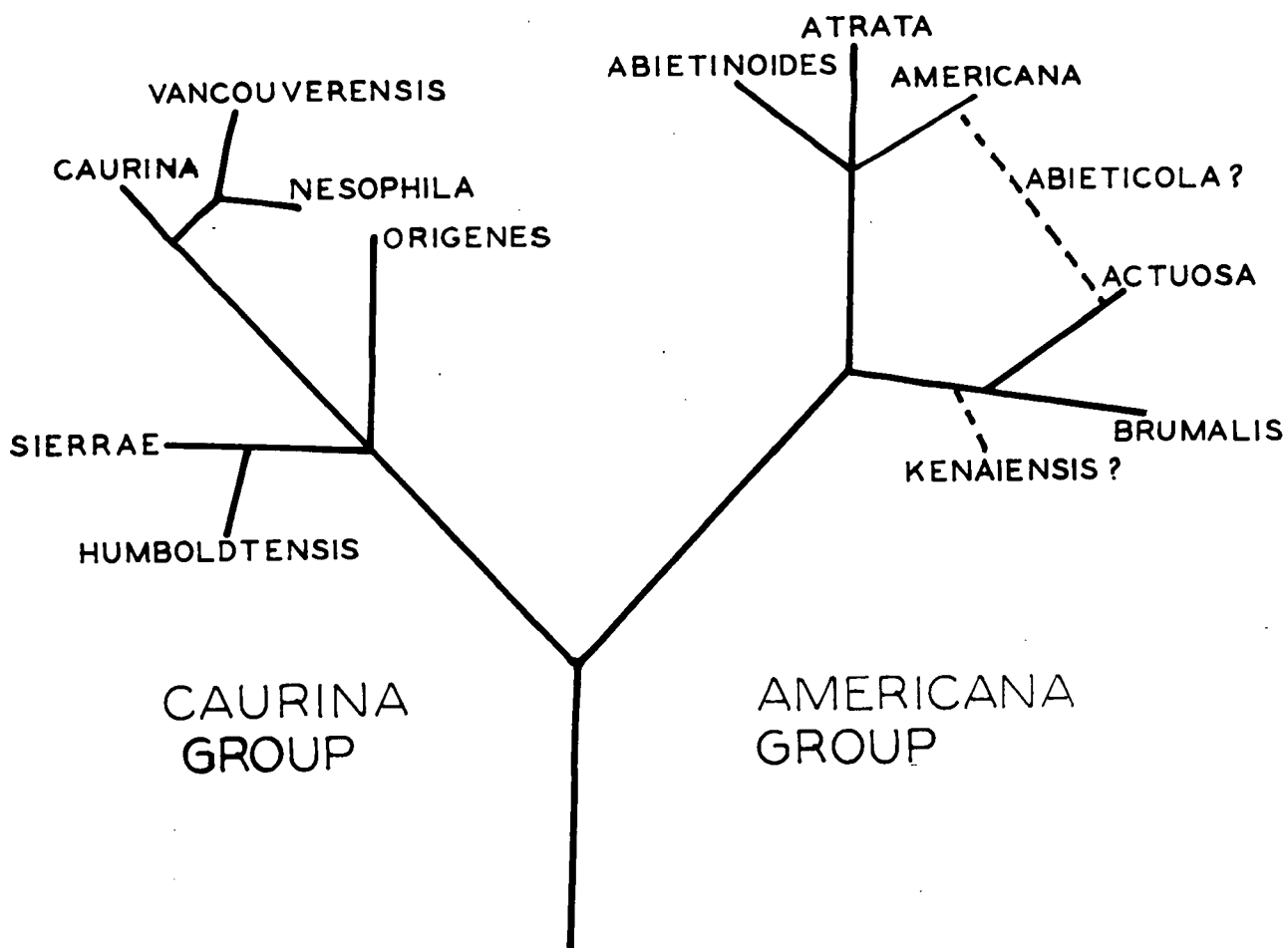
#### SUMMARY

1. A statistical analysis of 418 skulls of North American marten of the subspecies brumalis, americana, abieticola, actuosa,

Fig. 8.

(To follow page 53.)

Fig. 8. A hypothetical phylogeny of the martens of  
North America.



abietinoides, caurina, origenes, sierrae, humboldtensis, vancouverensis, and nesophila indicates that these, plus probably those not studied (atrata and kenaiensis) fall into two natural groups, the americana group (formerly the species americana) and the caurina group (formerly the species caurina). The unpublished work of Wright indicates that these two groups are conspecific, and that only one species, comprised of these two groups, exists on the continent.

2. What is probably adequate evidence for the subspecific status of brumalis, americana, actuosa, caurina and nesophila is presented. Abietinoides is, on the basis of the characters studied, probably separable from americana, while vancouverensis, caurina and origenes are inseparable. All three must for the time being be considered distinct however, until further examination of them is made on the basis of their geographic distribution. Abieticola is not well represented in the samples studied. It possibly represents a population of intergrades of actuosa and americana. Sierrae and humboldtensis are represented by samples too small for analysis.

3. An artificial key to the skulls of marten of North America is presented.

4. The history of martens is not well known. The genus Martes probably arose in the lower Pliocene, possibly in Eurasia, having been distinct from Mustela since the Oligocene. Migration between the old and new world occurred from the time of its origin to the Pleistocene. Separation into the subgenera of fishers and martens probably occurred during the Pliocene.

5. Pre-americana and pre-caurina both appear to have had their origin in the old world, the former preceding the latter in its migration to the new, both arriving sometime between the late Pliocene and the Kansan. Between the Kansan and the Illinoian pre-americana had segregated into abietinoides-americana and brumalis-actuosa. Prior to the Wisconsin origenes and caurina were separated. The advance of the Wisconsin ice sheet resulted in a gathering of marten into four refugia, during which time or subsequently, final subspeciation occurred. Repopulation of North America following the final ice retreat originated by migration from these refugia: atrata, brumalis, americana and abieticola in part from a south eastern refuge, origenes and abietinoides from one in the southern Rocky Mountains, humboldtensis, sierrae and caurina from one in the southern coast range, and actuosa and kenaiensis from an Alaskan refuge. Nesophila and vancouverensis are related to caurina, the former much less closely than the latter.

6. A hypothetical phylogeny of North America is diagrammed.

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## APPENDICES

### A Definitions of measurements used:

1. Condylobasal length: the greatest antero-posterior distance between the anterior end of the premaxillae and the posterior ends of the condyles.
2. Rostral width: the narrowest width of the rostrum behind the canines.
3. Upper tooth row: the shortest distance separating the anterior surface of the upper canine base from the posterior surface of the hypocone of the upper molar.
4. Canine width: the greatest width separating the upper canines at their bases.
5. Bullae length: the shortest length of the auditory bulla, taken from the medial and posterior surface of the foramen lacerum canal to the midpoint of the suture on the jugular process.
6. Upper molar width: the greatest width of the upper molar, when taken in a lateral plane.
7. Upper molar length: the greatest length of the inner moiety of the upper molar, taken in an antero-posterior plane.

Characters 4 and 5 were calculated as a ratio (canine width divided by bulla length)

APPENDICES

continued

B. Provisional artificial key to the skulls of the North American marten.

This key has been designed for skulls and uses skull characteristics insofar as specimens from which to devise them have been available. Where these have been lacking, the key reverts to a purely distributional one.

Many specimens will not be identifiable using this key. This is to be expected since it will be usable only if they are representative of what at present appears typical for that subspecies.

A Canine width - / - bulla length nearer .90 than 1.50 in males, and nearer .85 than .95 in females ..... americana group

(a) From continental North America, excluding the Kenai Peninsula, Alaska.

1. Condylbasal length nearer 8.5 than 8.0 cm. in males, and nearer 7.6 than 7.3 in females.

a Upper molar length plus width nearer 1.35 than 1.20 cm. in males, and nearer 1.20 than 1.05 cm. in females.

(1) From east of Hudsons Bay ..... brumalis

(2) From west of Hudsons Bay ..... abieticola

b Other than above; from west of

Hudsons Bay ..... actuosa

APPENDICES

continued

2. Other than above

- a Canine width - / - bulla length nearer .94 than  
.98 in males, and nearer .80 than .84 in females.

From east or south of Hudsons Bay .....americana

- b Other than above; from west of

Hudsons Bay .....abietinoides

(b) From Newfoundland, or the Kenai Peninsula

1. From Newfoundland .....atrata

2. From the Kenai Peninsula .....kenaiensis

B Other than above .....caurina  
group

(a) Not from California

1. Rostral width nearer 1.90 than 1.65 cm. in males,  
and nearer 1.60 than 1.45 in females. From Queen

Charlotte Islands or islands to the north.....nesophila

2. Other than above

a. From the mainland

(1) From the Coast range north of California caurina

(2) From the Rocky Mountains south of the  
49th parallel .....origenes

b. From Vancouver Island .....vancouver-  
ensis

(b) From California or extreme western Nevada

1. From the Coast Range .....humboldtensis

2. From the Sierra Nevadas .....sierrae