THE SPECIES OF *HOPLOPHONEUS*

BY GEORGE GAYLORD SIMPSON

Recent expeditions in charge of Albert Thomson have added several fine specimens of *Hoplophoneus* to the American Museum collections from the "*Oreodon* beds," lower Brulé or Orella, of the Big Badlands of South Dakota. Routine identification of these specimens for cataloguing revealed that none of the supposed species of this genus has really been defined in a distinctive, valid way and led to extensive research on the literature and on our specimens. This study did not result in a definitive revision of the genus, but it does

clear away some of the existing confusion and has some aspects of general interest. A summary of its results is therefore presented in the following comments which are merely notes, omitting most of the detailed data on which they are based and making no pretense of monographic treatment or conclusive value.

The morphology of the genus has been so well described and illustrated in the studies cited at the end of this paper that no illustrations need be given here.

TAXONOMIC HISTORY

Taxonomy, especially that of fossil vertebrates, tends to go through four stages of increasing sophistication. In the first stage, now entirely past, taxonomic categories were used very broadly. Workers were more concerned with resemblances than with differences and tended to place together all animals that resembled each other to any noteworthy degree. Students then commonly failed to make real distinctions, but they seldom made unreal ones. In the history of *Hoplophoneus* this stage involves only Leidy's work. He described two very different species now referred to this genus, and these, incidentally, appear to me to be the only species of the six described before 1920 that are surely valid.

In the second stage of taxonomy, which still persists as a lively historical hangover, students are fascinated by differences, to which alone they pay much attention. They seem to assume that the taxonomic rank and reliability of the morphologic characters of a specimen are in direct proportion to the magnitude of their deviations from those of allied specimens. This leads to splitting in a special sense, not necessarily that of giving taxonomic groups

unduly high rank (although this may also be done), but that of recognizing too many groups. Under this system it is unlikely that two different groups will be falsely united, but it is inevitable that single groups will be falsely divided. Cope, Williston, Adams, and Thorpe attacked the taxonomy of *Hoplophoneus* while in this historical stage, adding to Leidy's two species seven others of which I believe only one to be (somewhat doubtfully) valid.

A third stage, now predominant in most paleontological work, is a natural reaction from the second, with a tendency to swing back toward the first, which, however, cannot now be reached again because of the great accumulation of impedimenta inherited from the second. The concept of variability here becomes basic in taxonomic work. Differences are noted, as before, but unless they are very pronounced or, especially, qualitative as well as quantitative, they are commonly denied taxonomic value, or it is believed that their taxonomic value cannot be determined. A defeatist attitude regarding the recognizability of real minor groups is common and it is often

felt and sometimes said that paleontological species have no particular value or cannot be recognized objectively and are convenient artifices rather than expressions of natural truths. In the history of *Hoplophoneus*, Sinclair, Scott, and Jepsen have exemplified this stage, Jepsen formerly suggesting that the Linnaean system may be hopelessly unsuited for use on such material and Scott and Jepsen virtually abandoning the attempt to revise species and considering only genera as really distinctive.

The fourth stage, which is perhaps now being reached in vertebrate paleontology, approaches the subject from a combination of these earlier points of view and takes an essentially new attitude in the interpretation of their data. Resemblances and differences are equally studied and stressed and the concept of range of variation within a group is accepted as basic. Minor natural groups, including species and even, at times, subspecies and races, are believed to be recognizable from paleontological materials and the method of their recognition and study are to consider the collected specimens as samples from which inferences as to the probable limits of the natural population are to be made by orderly methods. Objective estimates of population variation developed from the theory of probability and sampling are made. It is recognized that the differences between two real groups may be less than those within one of them and that it is not simply the magnitude of differences that determines their significance but the variability involved and the associations between different characters and different types of data. The present paper does not succeed in taking the taxonomy of *Hoplophoneus* fully into this stage, but it attempts to direct study toward it.

The first species now placed in *Hoplophoneus* was named by Leidy as *Machairodus primaevus* in 1851. He later placed it in *Drepanodon*, under the (mistaken) impression that this was the valid name for European saber-tooths.[1] In 1869

Leidy described a second, much larger species as *Drepanodon occidentalis*. In 1873 Cope described a species *Machaerodus oreodontis* and in the following year removed it to a new genus *Hoplophoneus*, of which it became the type. The original definitions of both species and genus were based on errors or misconceptions but in his definitive work of 1885 Cope gave an essentially correct description and placed Leidy's two species in his genus (along with a species from the John Day, not reviewed in the present paper). In 1895 Williston briefly described another Oligocene saber-tooth as *Dinotomius atrox*, making no comparison of his new genus with *Hoplophoneus* except to say that the coronoid process was much as in the latter.

The first general revision of the genus was that of Adams in 1896. He recognized five White River species: Leidy's two, Cope's one and two then described as new, *H. robustus* and *H. insolens*. He noted the unquestionable synonymy of *Dinotomius* with *Hoplophoneus* and placed *Dinotomius atrox* in the synonymy of *H. occidentalis*. This synonymy was accepted by Riggs (1896) in his detailed description of Williston's material and was also accepted by Williston, himself, and by all later students. The only valid characters used by Adams to define the five species were those of size. He also mentioned differences in the vertical or overhanging character of the occiput, but later study has shown that these differences, as far as real and not due to distortion, are simple functions of size. Adams also mentioned the presence or absence of P^2, but showed it to be variable and later students have found that it is not clearly associated with size or other characters and has no evident taxonomic value. Of *H. occidentalis* he added that it had no posterointernal cusp on the lower sectorial. Riggs (1896) noted that this was an error as regards "*D. atrox*" and that it might validate that species if confirmed in *H. occidentalis*. In fact this part of the tooth is broken away in both the other specimens known to Adams and the supposed character was simply a mistake.

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[1] Scott and Jepsen (1936) believed that Leidy's was the first use of this generic name and that he therefore validated it as antedating *Hoplophoneus* in this sense. They have since found (pers. com.) that

Drepanodon had previously been used at least once in a different sense and that *Hoplophoneus* is the valid name of the genus here under discussion.

In 1920 Thorpe studied the group and added three more species, *H. latidens, H. marshi,* and *H. molossus.* These are all well within the size range of the previously named species and were defined mainly on the basis of various supposedly distinctive proportions and indices in the type skulls and jaws.

The species so far mentioned were all from the lower Brulé or its equivalent. Some later forms (John Day) were referred, but these seem best placed in different genera and are not discussed here. The first *Hoplophoneus* found in the older Chadron was *H. mentalis,* described by Sinclair in 1921, and in 1926 Jepsen named another Chadron species, *H. oharrai.* This completed the list of supposed species of (Oligocene) *Hoplophoneus* so far proposed, which thus includes:

1.—*H. primaevus* (Leidy, 1851).
2.—*H. occidentalis* (Leidy, 1869).
3.—*H. oreodontis* (Cope, 1873).
4.—*H. atrox* (Williston, 1895).
5.—*H. robustus* Adams, 1896.
6.—*H. insolens* Adams, 1896.
7.—*H. latidens* Thorpe, 1920.
8.—*H. marshi* Thorpe, 1920.
9.—*H. molossus* Thorpe, 1920.
10.—*H. mentalis* Sinclair, 1921.
11.—*H. oharrai* Jepsen, 1926.

Sinclair (1924) expressed dissatisfaction with the large number of supposed species, most of them apparently living in the same region at the same time, and showed that most of these supposed species intergraded and that they did not differ more than do individuals of one species of living cats. He explicitly reduced *H. latidens* to the synonymy of *H. primaevus* but otherwise made no attempt at revision. Jepsen (1933) again emphasized the difficulty of specific definition in a thoughtful, pessimistic digression on the unsuitability of Linnacan taxonomy for paleontological use. He was then studying *Eusmilus* and did not discuss the species of *Hoplophoneus* except to say that too many species were currently recognized.

In their description of the genus, Scott and Jepsen (1936) did not attempt specific revision, but said that the number of proposed species was assuredly too large. They did list *H. robustus, insolens,* and *atrox* as synonyms of *H. occidentalis,* without discussion, and omitted mention of *H. latidens* and *marshi.*[1] The other proposed species were listed as if valid and *H. oreodontis, primaevus, occidentalis,* and *oharrai* were said to be "most distinctly marked as separate."

SIZE DISTRIBUTION AND VARIATION IN THE *H. OREODONTIS–INSOLENS* SERIES

The first step in attempting the determination of probable true specific limits is to bring together as large and as homogeneous a sample as possible. For this purpose specimens from the lower Brulé of the Big Badlands of South Dakota referred or referable to *H. oreodontis, H. primaevus, H. robustus,* and *H. insolens,* as these species have hitherto been distinguished, afford the best available basis for study. These form a nearly continuous sequence in size. The still larger *H. occidentalis* proved, in the course of this analysis, to be distinctly separable from this series and so is omitted from the analysis given here and is discussed on a later page. The type and two important referred specimens of *H. oreodontis* are likewise omitted here because, as will be shown later, they are not in growth

stages comparable with the other specimens in question and because the type and one of the referred specimens are not from South Dakota. Adult specimens from South Dakota referred to *H. oreodontis* are, however, included in the present section. Thorpe's three species are omitted from this basic sample for comparison, because they are not from South Dakota and because they are defined mainly by characters of proportion requiring separate discussion. *H. mentalis* and *oharrai* are from lower horizons and are therefore also kept separate.

The area covered by these specifications

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[1] It is probably a *lapsus* that they gave a copy of Thorpe's figure of the type of *H. latidens* over the legend "*Drepanodon molossus*" (their Fig. 7). This skull does not show the characters that they give as distinctive of *H. molossus* and so they probably did not mean to reduce *H. latidens* to the synonymy of the latter.

OBSERVED RANGES IN LOWER BRULÉ ADULT SPECIMENS OF *Hoplophoneus* FROM SOUTH DAKOTA, EXCEPT *H. occidentalis*

Variate	H. "oreodontis"		H. "primaevus"		H. "robustus"		H. "insolens"		Totals	
	N	R	N	R	N	R	N	R	N	R
Prosthion—basion	3	$130\frac{1}{2}$–137	8	142–156	5	163–179	2	177–179	18	$130\frac{1}{2}$–179
Prosthion—inion[1]	3	144–163	1	169	5	184–200	2	206–216	11	144–216
Prosthion—anterior edge of P³	3	36–41	6	41–47	7	49–55	2	51–55	18	36–55
Maximum diameter of upper canine alveolus	3	11.7–13.9	9	13.6–15.2	6	14–18.5	1	17.5	19	11.7–17.5
P³–M¹	2	29.6–30.5	10	30.5–37.5	7	34.5–41.5	2	37.3–43.5	21	29.6–43.5
Length P³	3	9.7–10.1	9	9.8–12	6	11–12.8	2	12–14	20	9.7–14
Length P⁴	2	17.3–17.6	9	17.7–20.9	7	17.5–21.5	2	20.5–21.3	20	17.3–21.5
Palatal length	3	62–75	8	72–77	7	78–90	2	86	20	62–86
Breadth on postorbital processes	2	56–$57\frac{1}{2}$	4	63–70	4	67–76	2	76–81	12	56–81
Breadth of postorbital constriction	2	28	8	23–34	5	31–36	2	35–36	17	23–36
Diastema, C–P³	1	11.5	7	11.5–14.5	4	13–16.3	0		12	11.5–16.3
Condylobasal length	2	135–145	6	149–165	4	172–182	1	190	13	135–190
Orbit to alveolar margin	1	23	5	$21\frac{1}{2}$–26	3	23–$26\frac{1}{2}$	0		9	$21\frac{1}{2}$–$26\frac{1}{2}$
Infraorbital foramen to posterior edge of zygomatic process of maxilla	1	21	5	22–27	3	$25\frac{1}{2}$–$29\frac{1}{2}$	0		9	21–$29\frac{1}{2}$
Length of face	1	47	5	47–58	5	53–58	1	67	12	47–67
Length of cranium[2]	1	98	4	102–105	4	111–125	1	123	10	98–123
Length of mandibular ramus	2	106–112	5	110–123	6	130–137	1	142	14	106–142
Depth of flange	1	38	4	39–47	5	41–50	1	57	11	38–57
Diastema C–P₄	2	28–29	5	29–37	5	34–39	1	$39\frac{1}{2}$	13	28–$39\frac{1}{2}$
Depth under P₄	2	19.4–21.5	5	20–24	5	23–26.6	1	26.2	13	19.4–26.6
Depth posterior to M₁	2	20–20.6	5	18–21	5	21.5–26	1	24.6	13	18–26
Coronoid height above condylar-alveolar level	2	17–$19\frac{1}{2}$	4	$16\frac{1}{2}$–20	4	15–20	1	$17\frac{1}{2}$	11	15–20
Length P₄	2	9–11.4	5	11–12.8	6	11–13.5	0		13	9–13.5
Length M₁	2	15.7–16	5	15–18	6	15.8–20.0	0		13	15–20

is only about 200 square miles, incomparably smaller than the average range of a single species of cats today and, indeed, far smaller than the average for a single subspecies or geographic race.[3] It is practically impossible that any geographic varieties were developed in such an area, and unlikely that any would be preserved in it. It is quite possible that different allied taxonomic groups might have occurred in different ecologic stations in the area, but this can only be inferred from the existence of such groups, not used as a basis for their separation and recognition.

The geologic time covered by the lower Brulé is considerable, since a thickness of as much as four hundred feet of sediments is apiece. Figures for the puma are still larger, and those for the medium-sized to large Old World cats have the same order of magnitude.

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[1] Or, maximum diameter of skull.

[2] The skull is taken in lateral projection, a line drawn from prosthion to most distant point of condyle and a vertical dropped to it from the most anterior point of the orbital rim. The length anterior to this vertical is the facial length and that posterior to it the cranial length. The measurement is difficult and subject to observational error, but it provides important data not as well shown by any other dimensions.

[3] For instance, a single species of jaguar, perhaps the most nearly comparable of recent American cats, ranges over more than five million square miles and its local races, even in the most split classification, average over three hundred thousand square miles

included. *A priori* there is no reason why distinct species may not have followed each other here at different times. In fact, however, there is now no evidence that this did occur and some evidence that it did not. All four of the supposed species here considered (and also *H. occidentalis*) have definitely been recorded within a vertical distance of less than forty feet of conformable strata and all the data suggest that they were absolutely contemporaneous. It is fairly well established that a succession of invading, sharply distinct species does not occur. It is probable that slow evolution *in situ* did occur, but if so the known facts almost preclude evolution of more than subspecific rank. This would be shown only by a secular shift in group means, and the material for its possible detection is not now in hand.

Twenty-eight different continuous variates of skull and jaws have been studied in detail. By combining trustworthy measurements in the literature (particularly Sinclair, 1924, and Jepsen, 1933) with others taken by myself and with one set (on the type of *H. robustus*) kindly taken for me by Dr. C. L. Gazin, I have been able to obtain from nine to twenty-one individual values for each of these variates. The fact that measurements have been taken by different hands introduces another element of variation, but this is clearly too insignificant to have affected materially the results based on these data. Some variates, such as breadth across the zygomata, were discarded because the material afforded too few reliable values, and others, like the distance from prosthion to bregma, were given little emphasis because they proved to have little practical significance or not to be comparable in different instances.[1]

The preceding table gives the observed ranges for most of the important variates considered. The "specific" determinations

follow either those published by competent authorities who recognized the four species as separate or were made by me using their criteria. It will later appear that they probably do not correspond with true taxonomic species.

These observed ranges give the most immediately comprehensible picture of the general situation for a practical worker. For the present purpose, however, they are of less value than are actual distributions, to be studied for evidences of bimodal or multimodal character, and statistical data providing valid means of comparison of the relative amounts of variation of each variate.

Of the various distributions, some have no very clear mode, some have one, some seem obscurely to have two, and some clearly have two. It would take many pages and it is not necessary to give all these in full. The following examples cover the sorts of patterns shown:

A.—Breadth at postorbital constriction
   (Mode obscure)

	Frequencies				
	H. "oreo-don-tis"	*H.* "pri-mae-vus"	*H.* "ro-bus-tus"	*H.* "in-sol-ens"	
Value					All
23.0–24.9		1[2]			1
25.0–26.9					0
27.0–28.9	2	1			3
29.0–30.9		1			1
31.0–32.9		3	2		5
33.0–34.9		2	2		4
35.0–36.9			1	2	3
					17

B.—P³–M¹
   (One well-defined mode)

	Frequencies				
	H. "o."	*H.* "p."	*H.* "r."	*H.* "i."	
Value					All
28.0–29.9	1				1
30.0–31.9	1	2			3
32.0–33.9		3			3
34.0–35.9		4	3		7
36.0–37.9		1	2	1	4
38.0–39.9			1		1
40.0–41.9			1		1
42.0–43.9				1	1
					21

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[1] The bregma, for instance, is the intersection of sagittal and coronal sutures. Its position is subject to great non-significant variation from unimportant fluctuations of these sutures. Moreover in adult specimens the coronal suture frequently cannot be exactly followed. In young individuals it crosses the midline near at the anterior end of the sagittal crest, but in old individuals it is commonly at some distance—and usually an indeterminable distance—posterior to this point.

[2] This remarkably small value, from Sinclair, may possibly be a misprint, although it is not definitely beyond the possible range. In either case it makes no important change in the general situation.

C.—Condylobasal length
(Two obscure modes)

Frequencies

Value	H. "o."	H. "p."	H. "r."	H. "i."	All
135–144	1				1
145–154	1	4			5
155–164		1			1
165–174		1	2		3
175–184			2		2
185–194				1	1
					13

D.—Length of mandibular ramus
(Two well-defined modes)

Frequencies

Value	H. "o."	H. "p."	H. "r."	H. "i."	All
105–109	1				1
110–114	1	1			2
115–119		3			3
120–124		1			1
125–129					0
130–134			1		1
135–139			4		4
140–144				1	1
					13

Comparison of these and of other distributions of linear dimensions (and also those of proportions and qualitative characters, studied with equal care) show the following facts beyond much question:

1.—The adult specimens referred to *H. oreodontis* are in no way clearly distinguished from the *H. primaevus* group, and they appear to be merely the two or three smallest individuals of *H. primaevus*.

2.—The specimens placed in *H. insolens* are similarly indistinguishable from the general sample identified as *H. robustus* and probably are merely the largest individuals of the latter.

3.—The *H. oreodontis–primaevus* group and the *H. robustus–insolens* group approach each other closely in all characters and their ranges widely overlap in many characters (including all tooth dimensions).

4.—These two groups tend, nevertheless, to have distinctly different modes in many characters, especially longitudinal bone dimensions (and in proportions or indices that can be shown to be correlated with these), and by comparing all of these and the positions of individual specimens in the different distributions it is possible to divide the whole series into these two groups, leaving only one or two specimens of somewhat doubtful position.

There are thus two, but not four, different groups included in this series of specimens. The next thing to consider is what these groups are in biologic and taxonomic terms. I think that they are simply the males and females of the same species, on the following grounds:

1.—From the field data it appears that these two groups lived for a considerable period in the same region at the same time. They are commonly found in close association. It is almost impossible for two species so closely similar in all characters, actually intergrading in most, to remain distinct when occupying the same area.

2.—The two groups are about equally abundant, such discrepancy in numbers as exists in collections being far within the probable limits for chance sampling of a population in which they did occur in equal numbers. Male and female cats of one species tend to be about equally abundant. When two distinct cat species occupy one area, one is generally much more abundant than the other in collections.

3.—The differences between the two groups are closely similar in kind and in degree to those between males and females of one species of cat in populations where the sex difference is known. They do not correspond, or are not so closely analogous, to differences usually existing between two species of cats occupying one area.[1]

4.—If these are distinct species, then one or both of these two groups presumably contains both males and females.[2] But if this were true, it would follow that these two species would show less sexual dimorphism and less variation within the species (sexes combined) than is yet known for homologous characters of any species of felids, recent or fossil.

These considerations are in themselves almost conclusive. In order to test whether the amount of variation shown by this species, on the hypothesis here expressed, is consistent with that normal for a single species of cats, I have compiled and analyzed a large number of data on recent lions, leopards, jaguars, and pumas and on the extinct species *Smilodon californicus* and *Panthera atrox*. The results show conclusively that the amount of variation shown by the whole *H. oreodontis–primaevus–robustus–insolens* series is of the same order of magnitude as in most single species of cats. It is, if anything, rather less than might be expected. These extensive and complex data are not here published in full. The following extract from

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[1] These statements are based on detailed study of many data on several species of recent and some of fossil cats.

[2] My records include about a dozen members of each group. The chances that each group would be all of one sex and yet that the two should not be the two sexes of one species are so small as to be quite negligible.

COMPARISON OF VARIABILITY IN *Hoplophoneus primaevus* (INCLUDING *H. oreodontis, H. robustus,* AND *H. insolens*) WITH TWO OTHER FELID SPECIES

	N	R	M	σ	V
1.—Condylobasal length of skull:					
a.—Mixed samples:					
H. primaevus	13	135–190	162.3 ± 4.4	15.9 ± 3.1	9.8 ± 1.9
Smilodon californicus	25	271–344	308.6 ± 4.7	23.4 ± 3.3	7.6 ± 1.1
Panthera pardus chui	8	179–245	206.0 ± 9.1	25.7 ± 6.4	12.5 ± 3.1
b.—Males only:					
H. primaevus	6	165–190	177.5 ± 3.3	8.1 ± 2.3	4.6 ± 1.3
P. p. chui	13	206–245	221.8 ± 3.7	13.5 ± 2.6	6.1 ± 1.2
c.—Females only:					
H. primaevus	7	135–157	149.4 ± 2.6	6.9 ± 1.8	4.6 ± 1.2
2.—Length P^4					
a.—Mixed samples:					
H. primaevus	20	17.3–21.5	19.53 ± .30	1.34 ± .21	6.9 ± 1.1
Smilodon californicus	22	33.4–46.0	40.15 ± .53	2.47 ± .37	6.1 ± .9
Panthera pardus chui	8	22.4–27.9	25.19 ± .64	1.82 ± .45	7.2 ± 1.8
b.—Males only:					
H. primaevus	9	19.0–21.5	20.43 ± .27	.82 ± .19	4.0 ± .9
P. p. chui	13	24.5–27.9	25.86 ± .30	1.07 ± .21	4.1 ± .8
c.—Females only:					
H. primaevus	11	17.3–20.9	18.78 ± .37	1.23 ± .26	6.6 ± 1.4

them is sufficiently typical of the whole, using one variate (skull length) in which sexual dimorphism is likely to be pronounced and one (length of upper carnassial) in which it is usually more obscure. The *H. primaevus* sample has been sexed as explained above, considering *H. "oreodontis"* and most *H. "primaevus"* (of authors) as females, and one *H. "primaevus"* (which according to its combined characters should probably have been identified as a small *"robustus"*) and *H. "robustus"* and *H. "insolens"* as males.

The *Smilodon californicus* sample is that of Merriam and Stock (1932). It is, on the whole, less variable than would be expected—there are several possible reasons for this, but it is not here important because, little variable as it is, the difference from the whole *Hoplophoneus* sample is not probably significant. The *Panthera pardus chui* sample comprises seventeen adult specimens from the Belgian Congo, classified and annotated by Allen (1924). On these and nineteen other recent leopard skulls and associated jaws, I have made all the measurements homologous with those

made on *Hoplophoneus.*[1] On the whole this recent group is actually more variable than the combined *Hoplophoneus* sample, although one would expect the greater heterogeneity and the varying preservation of the fossils to exaggerate their variability. The *P. p. chui* sample is very homogeneous, all belonging not merely to one species but also to one local, interbreeding geographic race living under almost completely uniform ecologic conditions. This leopard sample happens to include only four adult females and in order to test the hypothesis as to *H. primaevus* here advanced, a sample balanced as to sex was made by combining these with four males taken at random (by shuffling and drawing numbered cards) from the full series of thirteen adult males.

It is interesting that the pronounced dimorphism of most of the larger felids has

[1] An accidental result of the study of variation in the Congo leopards was to show that the supposed subspecies *Panthera pardus iturensis* J. A. Allen, 1924, is not demonstrably distinct from *P. p. chui* (Heller, 1913). Allen sorted his specimens by habitat into those of the rain forest (Ituri) and those of the adjacent savannah and brush country. The latter were referred to *chui* and the former were found to be smaller and darker, and to differ in various proportions. They were therefore distinguished as a sub-species. The procedure is, of course, entirely correct, but the series are highly variable and the mean differences are so slight that they are not statistically significant in any case. These series of specimens, which include all of Allen's hypodigms of both species and the type of *P. p. iturensis*, thus do not demonstrate that the forest population is really distinct. A larger series might show this or might obliterate the supposed difference. Incidentally, Allen exaggerated the difference by discarding the smallest old male of *P. p. chui* on the grounds that it is a dwarf. The specimen is not abnormal as far as any objective data show and is merely a normal small variant. His largest specimens of this series could with equal propriety have been discarded as "giants" making *P. p. iturensis* obviously the same as *chui.* Even his smallest *iturensis* adults are well within the probable range of *chui* as far as his material shows.

commonly led to the belief both popular and scientific that two distinct sorts or species usually occur in one area. Thus Allen (1924, p. 261) refers to what Pocock, who inclined to believe them correct, called "the oft-repeated statements of sportsmen that two kinds of Leopards, larger ones called Panthers and smaller ones called Leopards, occur in the same localities." Allen shows beyond much doubt that the "panthers" are males and the "leopards" females of the same race. Similarly Merriam and Stock (1932, pp. 165–167) have remarked on the supposed occurrence together of two species of Pleistocene felines, *Panthera atrox* and *Panthera imperialis*, over a large area including the Mexican plateau and California and they show that these, again, are probably based in large part on sexual differences in one species. The available evidence seems to me to point to the conclusion that the difference between *H. primaevus* and *H. robustus* is simply another example of this sort.

PROPORTIONS AND INDICES

The conclusions of the preceding section were reached after the characters of relative, rather than absolute, size had also been studied and they are in agreement with the results of the latter study, which will now be briefly mentioned. Fifteen different indices, each of which has been used in the taxonomy of this genus or of

OBSERVED RANGES OF INDICES IN SUPPOSED SPECIES OF *Hoplophoneus*

Index	H. "oreodontis" N	R	H. "primaevus" N	R	H. "robustus" N	R	H. "insolens" N	R	Total N	R
A. $\dfrac{\text{Prosthion–inion}}{\text{Prosthion–basion}}$	3	110–119	1	116	5	112–116	2	116–121	11	110–121
B. $\dfrac{\text{Face}}{\text{Cranium}}$	1	48	4	46–55	4	42–52	1	54	10	42–55
C. $\dfrac{\text{Breadth on Postorbital processes}}{\text{Prosthion–basion}}$	2	42–43	4	41–47	4	39–46	2	43–45	12	39–47
D. $\dfrac{\text{Breadth of Postorbital constriction}}{\text{Prosthion–basion}}$	2	20.4–21.3	7	18.1–23.2	5	18.6–21.1	2	19.8–20.1	16	18.1–23.2
E. $\dfrac{\text{Length C alveolus}}{\text{Prosthion–basion}}$	3	8.5–10.1	7	9.1–11.1	5	8.6–11.1	1	9.9	16	8.5–11.1
F. $\dfrac{\text{Length P}^4}{\text{Prosthion–basion}}$	3	12.9–13.3	7	12.1–14.1	5	10.7–12.6	2	7.4–11.6	17	7.4–14.1
G. $\dfrac{\text{Flange depth}}{\text{Ramus length}}$	1	33.9	4	31.6–40.2	5	31.3–36.8	1	40.1	11	31.3–40.2
H. $\dfrac{\text{Depth under P}_4}{\text{Ramus length}}$	2	17.3–20.3	5	18.1–20.5	6	16.9–19.8	1	18.5	14	16.9–20.5
I. $\dfrac{\text{Coronoid above condyle-alveolar level}}{\text{Ramus length}}$	2	15.2–18.4	4	14.7–16.2	4	11.2–14.7	1	12.3	11	11.2–18.4
J. $\dfrac{\text{Length M}_1}{\text{Ramus length}}$	2	14.3–14.8	4	12.6–14.9	6	12.2–14.6	0		12	12.2–14.9

related forms, were studied carefully and several others more summarily examined. The observed ranges of ten indices for the supposed species *H. oreodontis, primaevus, robustus,* and *insolens* are given in the accompanying table. (In each case the index is understood to be 100 times the ratio as labeled.)

It is evident that all these indices are highly variable and also that no one (or indeed no combination) of them would suffice to classify an individual specimen as belonging to one and only one of these supposed species or even to place it surely as male or female, assuming that the four "species" really represent two sexes of one species as concluded in the previous section. This is good confirmatory evidence that these specimens do really belong to one species. Groupings based on size, as these "species" were, cannot also be defined by proportions and groupings based on proportions cannot also be defined by size. In most cases there are no significant differences in indices between the various size groups and the group of which the most observations happen to be available often shows nearly or quite the whole observed range for all.

There are, however, indices for which there is a fairly regular change in the averages for smaller and for larger individuals, even though the great variation and the overlapping ranges make this obscure or undeterminable on the basis of a few specimens. For instance, index D of this list is really and definitely smaller for *H. "insolens"* (or for large males) than for *H. "oreodontis"* (or small females). Such changes may have taxonomic value or they may be correlated with size regardless of taxonomic differences. It is now a well established fact that proportions change during growth and that they may be correlated with size, even among adults, in such a way as to be determined by the size and not to be independent genetic characters. Thus a difference in index accompanied by a difference in size has no taxonomic significance unless it can be shown to be different in kind or degree from what normally occurs in a single species of the group under consideration.

To check this, the relations of proportions to size in *Hoplophoneus* have been examined in some detail and compared with growth changes in *Hoplophoneus* and with growth series and adult series in *Smilodon californicus, Panthera atrox, Panthera onca,* and *Panthera pardus.* Phleger (1940) in an important paper on this subject, has studied relative growth involved in several analogous indices of the first three of these species. For a rough determination of relative growth in *Hoplophoneus,* Amer. Mus. No. 9764, an immature animal with the permanent dentition just starting to be used, was compared with old individuals of comparable size as judged by the cheek teeth. From all these data the following conclusions were reached as to each of these ten indices:

A.—These two dimensions are closely correlated as would be expected from their close structural relationship and in all the series examined their index has relatively little variation, with no evidence of significant trend of change with growth or adult size. In *Hoplophoneus* one of the largest specimens happens to have the largest index, but this is probably a chance result. The series as a whole shows no significant correlation of this index with size or other characters.

B.—The facial: cranial index is highly variable but in *Panthera pardus* (both *chui* and the perhaps synonymous *iturensis*) there is a slight but real tendency for the index to increase with age and with size. This is, moreover, a widespread tendency among mammals (and even among many lower vertebrates). The face grows more rapidly than the cranium, so that older and larger animals have relatively longer faces. The young A.M. No. 9764 also has a slightly shorter face, relative to the cranium, than do the most nearly comparable adults. In the adult specimens the correlation is obscured by great variation and it is not statistically significant for the small available series of values (ten), but the visible trend is in the same direction. Its relatively short face has been given as a distinctive character of *H. "oreodontis,"* but in the first place the index is within the wide range of variation

for the larger supposed species, and in the second place the fact that it is below the average for the larger forms is just what would be expected within a single species.

C.—This index shows no clearly significant trend in any of the material examined. It is not correlated with size, as far as can be seen from small samples, and it fluctuates erratically. It is the resultant of two opposite factors and the ascendancy of one over the other is not definite or predictable. The general width of this part of the skull increases much more slowly than does the skull length, but on the other hand in middle stages of growth, at least, there is an acceleration of the development of the postorbital processes themselves since these are barely developed in young and small individuals and are prominent in old and large ones.

D.—In spite of the erratic overlap of the observed ranges, this index in every felid examined shows a strong, indubitably significant negative correlation with the gross size of the skull, or in other words the breadth of the postorbital construction has strong negative heterogony. Phleger found values of the heterogony coefficient, k, of .42 for *Panthera onca*, .55 for *Smilodon californicus*, and .56 for *Panthera atrox*. Between our immature *Hoplophoneus*, A.M. No. 9764, and the type of *H. robustus* k is .41 and between this immature animal and the likewise comparable Princeton No. 12957 k is .45. Larger growth series of *Panthera pardus* show that the interorbital breadth grows almost harmoniously for a short time after birth but that by the time the full deciduous dentition is well in use its growth slows down abruptly and that it thereafter grows very slowly or hardly at all. The same tendency has been observed in other mammals and it is probably general.

E.—The size of the canine tends to be positively, but only loosely, correlated with adult size. It would be expected to show strong negative heterogony with growth, on the principle that the canine does not, in fact, grow while the skull does. It is surprising that such a tendency is not really visible in our material of *Hoplophoneus*. Between Amer. Mus. No. 9764,

for instance, and comparable adults k is not significantly different from 1.0, which would imply either that the canine grows harmoniously with the skull or that this animal is not really comparable but belongs to a group with decidedly smaller canines. Even among the mature specimens the differences are not what would be expected and what occur with other tooth indices. The material of various growth stages is insufficient to explain the anomaly, but it suggests the possibility that the canine alveolus (which is what is measured, rather than positively homologous points on the canine itself) does indeed grow in this group. The canine perhaps continues to move downward for some time during adult life, so that the part at the alveolus changes and becomes progressively larger.

This peculiar situation, whatever its true cause, tends to obscure real and definitive differences between the size of the canine in different mature groups of *Hoplophoneus*. Thus young males may tend to have relatively smaller canines (or at least canine alveoli) than old females. There is, nevertheless, some difference, the average index (E) for five specimens regarded as males being 10.3 while for nine regarded as females it is 10.0, but this is a somewhat smaller difference than is usual in cats and is not clearly significant. Taking only individuals in late maturity or senility, in which further protrusion of canines is unlikely, would probably give higher averages for both males and females and probably show a greater mean difference between them, but I have only one probable male specimen in this condition (which does happen to have a very high index, 11.1). These data are consistent with the sexing of *Hoplophoneus* specimens as I have carried this out, but they do not strongly confirm its correctness or help in its performance.[1]

F.—The length of P⁴, measured on the tooth itself, certainly does not grow significantly after eruption. Its index against

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[1] Even in recent cats that show very strong sex dimorphism and decidedly different averages for this index in the two sexes, the ranges for the index often overlap so that sex cannot be surely determined from the index itself.

skull length therefore becomes rapidly smaller as the individuals become larger in a growth series, and the same decisively significant negative correlation with skull size is shown within the adult series not only in these *Hoplophoneus* specimens but also in *Panthera atrox* and *P. pardus*, in which I have measured the correlation, and probably in all cats. In these animals males and females and small and large individuals of the same sex differ less in the size of the cheek teeth than they do in skull dimensions. The situation in this *Hoplophoneus* series is what would be expected by analogy in a single species.

G.—The index for relative depth of flange, although highly variable, shows no evident trend in our material. As far as shown, the flange has great individual variation but grows more or less in harmony with the growth of the skull. This again suggests that the upper canine grows (or is progressively more protruded) throughout much of the animal's life, for the canine tip never projects beyond the flange and yet the flange is not relatively longer in young than in old animals.

H.—Contrary to expectation, this index shows a low, suggestive but not conclusive, negative correlation with length of ramus. There may thus be a tendency for larger animals to have relatively more slender jaws, although this is too variable to be certain on the basis of a small series of animals. *P. pardus* seems to show the same tendency, but here again the evidence is not fully conclusive.

I.—This index shows a statistically significant negative correlation with length of mandible. As in all cases, there is much variation, but large individuals of *Hoplophoneus* unquestionably tend to have relatively smaller coronoid processes. This may also be in part a sexual difference since the difference between presumable males and females may (doubtfully) be a little more pronounced than would be expected from size alone. Although it was not primarily used for that purpose, the index permits sexing most specimens, an index (for an adult) greater than 15 usually belonging to a female and one less than 14.5 usually to a male. The distributions

do overlap between these two values. The same tendency for large individuals to have relatively small coronoid processes is seen in *Smilodon californicus* but I do not detect it in *Panthera*. It is probably related to the great difference in jaw musculature between the machairodont and feline groups.

J.—This index is analogous with F and the remarks about the latter are also true of this.

Thorpe (1920) has used an index for the relationship of the anteroposterior dimension of the anterior zygomatic pedicle (from infraorbital foramen to posterior margin of the zygomatic process of the maxilla) to its vertical dimension (from the orbital rim to the alveolar margin). He says that this has considerable value in specific determination and uses it in defining *H. latidens*, said to have an index of 117 as against 162.5 for *H. robustus*[1] and 143 for *H. primaevus*. This implies that the index is relatively invariable within one species and is positively associated with other characters of possible taxonomic value, but grounds for these assumptions are not given. I have investigated the point in fourteen specimens of *Hoplophoneus* and in twenty-two of *Panthera*. The index is highly variable within any one species (no matter how narrow the species be made, beyond placing every specimen in a distinct species) and it does not show evident association with any other possibly significant characters. Thus for specimens referred by competent authorities (including Thorpe, himself) to *H. primaevus* and surely referable to that species even if *H. oreodontis*, *H. robustus*, etc., be kept distinct, the index varies in known specimens from 88.5 to 143. Instead of being distinctive in this respect, the type of *H. latidens* happens, by accident, to be almost exactly at the average for *H. primaevus*.

Nor is there in my data any clear trend or association of the values of this index, even in the loose way that the facial–cranial index is associated with size. It is possible that the index tends to become smaller

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[1] But there is a *lapsus* somewhere, because the dimensions that he gives would make the index 180.5, which is so much above other known indices as to be improbable. Even 162.5 is the highest known to me, although not outside the probable range.

with increasing size (or age), but if so the correlation is very low and many more specimens would be required to demonstrate its reality (i.e., statistical significance). As it is, the four smallest specimens for which I have data cover almost the entire known range for the genus, from 91 to 150. Their mean value, 120, happens to be greater than the mean for the four largest specimens, 103, but this could be a mere accident of sampling. Even if real, its taxonomic value would be more than doubtful, for the differences bear no relationship to the supposed species as determined by Adams, Thorpe, etc. For instance, the types of *latidens* and *molossus* and authoritatively identified, thoroughly representative specimens of *robustus*, *primaevus*, and *oreodontis* all show indices within the relatively narrow range 108–120. Moreover, indices in Pleistocene *Smilodon* and even in recent leopards also occur in this range. The index seems to have less taxonomic value than almost any other.

This is not said in criticism of Thorpe, but to emphasize a serious defect in most paleontological taxonomy, including much of my own. We often tacitly assume that any great, clear morphological distinction has taxonomic value. In fact, as this example shows and as could be shown by many more examples, this principle is thoroughly fallacious. A very slight morphological difference may have taxonomic value and a very great difference may have none. The valid criterion is not the greatness of the distinction, but its association with different samples defined on other grounds, taking into account some good

measure of the variability of the character.

The sizes and proportions of limb bones and other skeletal parts have not been studied in great detail. Although it is the rule rather than the exception for skulls of *Hoplophoneus* to be associated with skeletal material, the number of homologous post-cranial measurements available to me is not great enough to establish surely the significance of deviations and the trends of associations. It is, however, evident that the general size grouping is consistent with that of the skulls and can be interpreted in the same way. The characters sometimes considered of taxonomic value are those of length of limb bones relative to the skull and of the stoutness of the bones relative to length. In recent cats (and indeed in most mammals) these are both correlated with size within a species. Small individuals tend to have relatively more slender limb bones but these bones tend to be shorter relative to the skull, i.e., their width grows with positive heterogony relative to their length and the length with positive heterogony relative to the skull. What data are available for *Hoplophoneus* simply agree with this general trend and suggest no basis for specific distinction. For instance, in the smaller specimen Princeton No. 13628, referred to *H. "oreodontis,"* the index of distal width against length of femur is 17 and that of length of femur against condylobasal skull length is 113. In the larger Amer. Mus. No. 1406, referred by Matthew to *H. "robustus"* and by Scott and Jepsen to *H. "primaevus,"*[1] both indices are larger, as would be predicted, 22 and 118, respectively.

QUALITATIVE CHARACTERS

The only clear-cut qualitative differences observed within *Hoplophoneus* are the presence or absence of P^2 and of I_1. Although Adams suggested that the presence of P^2 had some significance, he showed that it was variable and later students have not given it taxonomic value. It is more often present than not, but its absence has no clear association with size or other possible taxonomic characters, or even, apparently,

with age since P^2 happens to be quite absent in one of the rare immature specimens and to be present in our most nearly senile individual. In specimens referred to each of the four supposed species here under consideration P^2 is present in some and

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[1] This is the specimen referred to in the first column of their table, 1936, p. 139. The number given there, 1405, is a misprint and should be 1406. I believe that this animal is a male.

absent in others. Moreover, in specimens referred to *H. primaevus* (*sensu stricto*) and to *H. robustus*, at least, it is present on one side and absent on the other. It also varies greatly in size and in position, sometimes a fairly large, two-rooted tooth, sometimes a one-rooted vestige, sometimes near the canine, and sometimes almost overlapping P^3.

Amer. Mus. No. 9764, an immature individual placed by Matthew in *H. oreodontis*, appears to have only two incisors. As regards the upper jaw (Matthew, 1910, Fig. 3A), this is an error. The side figured is restored, and further preparation and study of the other side shows three incisor alveoli. In the lower jaw only two incisor roots are present but (a) I_1 has a short root in this genus and its alveolus is possibly broken off in this specimen, (b) in some cats there is a stage of replacement when only two lower incisors are functioning and this is an immature animal, and (c) the otherwise very closely similar Amer. Mus. No. 5338 has three lower incisors and the most probable explanation of the present specimen is that it has an individual anomaly. Wood (1927) refers to the specimen and notes that I_1 may be absent in two known specimens of *H. mentalis*, but that this is somewhat doubtful as to fact and if true is of doubtful significance.

I_1 is relatively reduced in *Hoplophoneus* and there may have been some tendency toward its loss, but this is not established and has no present significance for taxonomy.

THE TYPES OF *H. ROBUSTUS* AND *H. INSOLENS*

Adams did not explicitly designate types of species and his descriptions, based on various specimens, are somewhat ambiguous in this respect. Although I believe both these species to be synonyms of *H. primaevus*, the designation of their types is important. Adams' description of *H. robustus* mentions Amer. Mus. No. 650 and Princeton No. 10647. He says that "the species is represented" by the latter but that the former, better specimen is "its most perfect type." Although he does not seem here to be using "type" in a technical sense, there is little doubt that Amer. Mus. No. 650 was essentially his type and it should be, and hereby is, designated lectotype if both of these specimens are considered syntypes. Dr. Matthew overlooked the fact that Amer. Mus. No. 650 was the type or the better syntype of *H. robustus* and he exchanged it with the U. S. National Museum, where it is now preserved.

Adams' description of *H. insolens* mentions three specimens and says that "either" (any?) of them are "typical": a skeleton determined by Osborn and Wortman as *H. occidentalis*, Princeton No. 11022, and Princeton No. 11372. Although not mentioned by number, either by Osborn and Wortman or by Adams, the first specimen mentioned is almost certainly Amer. Mus. No. 655. The three specimens are evidently syntypes in Adams' publication. Princeton No. 11372, which includes a good skull, appears to be the most exactly determinable specimen and is therefore designated as lectotype. There is some doubt whether Amer. Mus. No. 655 really belongs in the same group, but its skull is so poorly preserved that any conclusion based on it is shaky. The lectotype, as represented by measurements given by Jepsen (1933), is included in the preceding discussions of variation in the *H. primaevus* group. Amer. Mus. No. 655 is not, because it provides so few reliable measurements and is so uncertain in general.

H. OREODONTIS

The specimens discussed above and shown to be small females of *H. primaevus* do not include the type or two important referred specimens of *H. oreodontis*.

The type of this species, now Amer. Mus. No. 5337, is a fragment of the right lower jaw with two unerupted incisors, and with dm$_4$ in place. P$_4$ is forming in its crypt, but so little of it is yet calcified that its definitive form and size cannot be determined. Dm$_4$, the most characteristic part of the specimen, is not known to me in any other specimen of *Hoplophoneus*.

Cope's emended, indeed totally different, definitive description of *H. oreodontis* in 1885 was not based on the type but on another specimen, now Amer. Mus. No. 5338, which includes the lower jaws and the facial part of the skull, with the permanent dentition. The hypodigm of the species as Cope left it (1885) and as subsequent students have accepted it thus in reality excludes the type and for Cope was essentially this one referred specimen. Adams practically ignored both the type and Cope's hypodigm and used as his stated basis for comparison, i.e., as his hypodigm, Princeton No. 10515. The same specimen was apparently Sinclair's hypodigm (1924). Jepsen (1933) gave measurements of this specimen and another, Princeton No. 13628, and these two seem to have been the principal if not the only members of the hypodigm of Scott and Jepsen (1936).

To these specimens may be added another, Amer. No. 9764, which includes almost complete skull and jaws and is closely comparable with Cope's second specimen, Amer. Mus. No. 5338. Matthew identified this specimen as *H. oreodontis* and apparently based his concept of the species mostly on it, although he did not say so in print. He figured the palate of this specimen (1910, Fig. 3A), but he labeled it simply *Hoplophoneus*, without specific name. His measurement on a later page (p. 313) was probably of this specimen. It has the peculiarity that only two incisors seem to be present, as discussed above.

If one goes back to Cope's type, then *H. oreodontis* is now unrecognizable and must remain so until a series of specimens shows the specific association of dm$_4$ with the permanent dentition. The type does not warrant the conclusion that *H. oreodontis* is a small species, since its small size is purely juvenile.

It is extra-legal but is, I think, justified to accept Amer. Mus. No. 5338 as neotype of this species.[1] It was, Cope says, found at the same horizon and locality as the type, it cannot be shown to be of a different species, it was referred to this species by its original describer, and the definition that has ever since been accepted as actually basic for the species, even though it is not the earliest definition (which involved a thoroughgoing error), was based on this specimen and not on the type. If this is accepted as neotype, then the species can be shown beyond much doubt to be synonymous with *H. primaevus*.

It differs from representative specimens of *H. primaevus* as follows:

All bone dimensions are absolutely smaller.
The canine base or alveolus dimensions are absolutely smaller.
The diastemata are also relatively smaller.
The flange depth is smaller.
The ramus depth is smaller.
The ratios of cheek tooth dimensions to almost any bone dimension are larger.

If Amer. Mus. No. 9764 is considered to be the same as this specimen, whatever it may be—an almost unescapable conclusion—then the following can be added:

The diameter of the postorbital constriction is relatively larger.
The ratio of face to cranium length is smaller.
The index of the anterior zygomatic pedicle is smaller.

This is an impressive array of characters and without analysis might appear to validate the species beyond any question, but it does not really do so. It is demonstrable that most of these characters of proportion are correlated with gross bone size among the cats in general and, with little doubt, in *Hoplophoneus* in particular, regardless of species. Smaller and larger specimens referred to *H. primaevus* by authorities who recognized *H. oreodontis* as distinct

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[1] Using "neotype" broadly for any substitute type replacing either a lost type or, as in this case, a type that cannot be placed in any possible current hypodigm.

tend to show the same sort of differences, only less in the degree to which the size difference is less. Differences equal both in kind and in degree are demonstrated in a series of leopard skulls of a single local race.

It is necessary, then, either to show that these proportions are different from what they would be in a *H. primaevus* skull of THIS SIZE, or that the size itself is significantly different from *H. primaevus*. As far as one can extrapolate from the available specimens of *H. primaevus*, the proportions are within the probable range for that species at about this gross size. As for the size itself, Cope's 1885 hypodigm specimen or neotype and Amer. Mus. No. 9764 are the youngest specimens available (except the useless *H. oreodontis* type). Sutures closing or closed in all the other specimens are here completely open and the permanent teeth have just come into place and are barely beginning to wear. These are therefore small animals because they are young.

What size they would have when fully grown can best be judged from the only dimensions available on them that are not positively correlated with age, i.e., tooth dimensions. The table below affords a summary comparison.

Thus the cheek teeth are not only within the range of *H. primaevus, sensu stricto*, but are on the whole rather large for that "species" and are also within the range of (the probably synonymous) *H. "robustus."* On this basis there is every reason to believe that these specimens far from representing a separate, small species would, if they had lived to full maturity, have been rather large individuals of *H. "primaevus"* or rather small individuals of *H. "robustus."*

The canines are the only apparent argument against this conclusion. It is possible that they are really smaller than in most specimens of *H. primaevus*, and in such a case this could and, on the available data, probably would be merely a variation. There is, however, inconclusive but probable evidence that in *Hoplophoneus* the canines continued to move downward and hence that their alveoli continued to enlarge for some time after the permanent cheek teeth were in place. In that case, the small diameters of these alveoli are also simply characters of youth. In either case no reliable specific difference from *H. primaevus* is demonstrated.

There are specimens in the collections that as adults are distinctly below the size usually assigned to *H. primaevus* and that have been called *H. oreodontis*. These include Princeton Nos. 13628 and 10515 (Scott and Jepsen hypodigm of *H. oreodontis*) and our new specimen Amer. Mus. No. 38980, which is one of the oldest but one of the smallest specimens in the series. Combining my measurements with Jepsen's, the tooth dimensions homologous with those given below are for this group of three specimens:

LC	11.7–14.3
P^3–M^1	29.6–30.5
LP^3	9.7–10.2
LP^4	17.3–18
LP_4	ca. 9–11.4
LM_1	15.7–ca. 16

These specimens thus are really small, and not merely young. These are the specimens that I have considered to be small females of *H. primaevus*. The present data show that even if they are assigned to a distinct species, that species is not *H. oreodontis*.

	Amer. Mus. No. 5338	Amer. Mus. No. 9764	Referred to *H. primaevus* by Matthew and by Jepsen	Referred to *H. robustus* by Matthew and by Jepsen (including type)
LC	12 1/2	12	13.6–16.4	14–18.7
P^3–M^1		33.3	31.6–35.7	33.6–41.5
LP^3		11	9.8–12	11–13
LP^4	{ r. 20.2 { l. 19.8	19.7 } 19.7 }	18.2–19.9	17.5–21.5
LP_4	{ r. 11.7 { l. 11.9	12.2 } 12.0 }	11–12.8	11–13.5
LM_1	{ r. 17.7 { l. 17.8	17.9 } 17.7 }	16.1–18	15.8–20.0

H. MARSHI

Thorpe pointed out that this species is based on a submature individual and he compared it chiefly with *H. oreodontis* (i.e., presumably with Amer. Mus. No. 5338, not the type), which is also submature. The various skull proportions are near those of *H. oreodontis* if based on this specimen, in other words, near those of immature *H. primaevus*. Thorpe's type is perhaps somewhat older than A.M. 5338 and a somewhat larger individual, i.e., a male that would be referred to "*H. robustus*" when fully grown. Three of the characters on which Thorpe mainly based the species appear to be within the ob-

served or safely inferable range of large individuals of the *H. primaevus–robustus* group: large incisive alveoli, long pointed palate, and large molar alveoli. The fourth, peculiar shape of canines, appears to me to be wholly due to the fact that they are only partly protruded and would be far larger and more recurved in a fully adult animal. We do not have enough growth stages to judge the systematic position of an immature animal with entire confidence, but I do not see any clear-cut character that would exclude this from being a robust young male of *H. primaevus*.

H. LATIDENS

Sinclair (1924, p. 113) has already remarked that he saw no reason for referring *H. latidens* elsewhere than to *H. primaevus*. With this I entirely agree. Thorpe was, of course, quite correct in saying that his specimen is on the whole nearest to *H. robustus*, with some more *primaevus*-like characters and some between the two. It was doubtless this apparently equivocal mingling of the characters of two supposed species that led Thorpe to create a third, but the two species of reference intergrade and are (in my opinion) synonymous, making a group

into which Thorpe's specimen fits as a normal member not peculiar in any important way. The numerous small differences in absolute dimensions and in proportions noted by Thorpe are all well within the ranges now demonstrated for *H. primaevus*. It is entirely possible that a form like this, being from a different locality (in Colorado) and possibly a somewhat different horizon from typical *H. primaevus*, really does represent a different race, but the two known specimens do not show this to be the case.

H. MOLOSSUS

This species was described by Thorpe on the basis of a single specimen from Nebraska. Most of the dimensions are within the observed range of *H. primaevus* (defining that species to include *H. "oreodontis"* and *H. robustus*) and all are within the theoretical range (i.e., the range that the available sample shows to be probable for the whole population). Nevertheless the proportions are peculiar and are probably not those normal for *H. primaevus, sensu lato*. In general the bone dimensions of skull and jaws are small, about those of small females of *H. primaevus* (or of *H. "oreodontis"*) while the tooth dimensions are large, about those of aver-

age males of *H. primaevus* (or of *H. "robustus"*). This at once suggests that the animal is an immature male and some of its apparently distinctive indices are in fact closely approached by those of Amer. Mus. No. 9764 which is very probably an immature male of *H. primaevus*, but others are not and Thorpe's data plainly show that his type is not really immature. The facial : cranial index (B of the preceding discussion) has an observed range of 42–55 in *H. primaevus* and is 44 in No. 9764, but is 56 in *H. molossus*. This is not surely significant in itself, but it is striking in view of the fact that small individuals tend to have smaller indices while this,

one of the smallest known specimens of the genus, has the largest known index (except for *H. occidentalis*, an animal not far from twice this size).

A similar difference, not surely significant in itself but perhaps becoming so when related to the size of the skull, is seen in the index length of canine alveolus: prosthion–basion (E), which is 11.7 in the type of *H. molossus*. This is above the observed range in *H. primaevus* and is striking because in the latter species this index may be larger in large than in small individuals.

The postorbital constriction is somewhat below average diameter for *H. primaevus*, but does not differ noticeably from those of the skulls of that species most comparable in other dimensions, so that it is not really distinctive (nor is its index, D),

as was at first thought. Scott and Jepsen (1936, p. 135) add that the constriction is remarkably anterior in position. I cannot judge the significance of this rather subtle character from the data now available. Along with some of the other characters, it is made questionable by Thorpe's statement that the only known specimen shows some post-mortem deformation.

Thorpe's statement that *H. molossus* has heavy, massive skeletal bones also suggests a distinction since small specimens of *H. primaevus* tend to have relatively slender bones.

Given only one specimen and the absence of absolute distinctions, it is possible that *H. molossus* is based on an abnormal specimen of *H. primaevus*, but the evidence suggests that it is distinct.

H. OCCIDENTALIS

Only four specimens surely of this species have been recorded in the literature and I know of no others. The type is a lower jaw fragment, lacking both ends, with P_4. Williston's type of *Dinotomius atrox* is a nearly complete skull and skeleton, and another closely similar specimen was found with this. Amer. Mus. No. 1407 is a complete mandibular ramus with the crowns of P_4 and M_1, correctly referred to this species by Adams. These specimens are much larger in every dimension than are those of *H. primaevus*, with its probable synonyms, and equally distinctive from *H. molossus*, the third probably valid Brulé species. The difference in gross size is unquestionably significant and the addition of the *H. occidentalis* specimens to the *H. primaevus* series would indicate a species much more variable than is warranted by any valid analogy. The only possible question is whether, as Scott and Jepsen (1936) implied by placing them in the synonymy of *H. occidentalis*, the specimens called *H. robustus* and *H. insolens* might not be females of this species rather than males of *H. primaevus*. From the point of view of the sexual dimorphism and variability implied, this is not impossible and perhaps it cannot be quite disproved on

purely morphological grounds. It is, however, unlikely on the following grounds:

1.—If *H. "robustus"* and *H. "insolens"* do not belong to *H. primaevus* then that species (including the material referred to *H. "oreodontis"*) was much less variable and showed less sexual dimorphism than any comparable cats, machairodont or feline, as far as known.

2.—As demonstrated above, *H. primaevus* and "oreodontis," on one hand, and *H. "robustus"* and "insolens," on the other, nearly or quite intergrade in all their characters and show all the expected and probable resemblances and distinctions normal for the two sexes of a single species. It is highly improbable that the females of one species would so closely resemble and intergrade with another species living in the same region at the same time or that the morphological relationships of the females of one species to the males of another would so exactly correspond to the normal relationships of males to females of one species.

3.—It is very improbable that of two closely related species one would show great variation and extreme (even though not abnormal) sexual dimorphism, as would a species combining *H. occidentalis* with *H. "robustus"* and "insolens," while the other showed abnormally little variation and no evident dimorphism, as would a species including only *H. primaevus* and "oreodontis."

4.—The *H. occidentalis* specimens may be all of one sex, or may include three females and one male. This sex ratio in the sample and this degree of variation are well within limits of probability if these are the only specimens

known of the species. But if *robustus* and *insolens* are the females of the species, then all four specimens of *H. occidentalis* are males (and highly variable as such) and a sample of about twenty includes only four males. This is not impossible, but it is improbable.

Most of the proportions of these large specimens are about as in *H. primaevus*. Those that are more or less distinctive are, as a rule, correlated with size and show in *H. occidentalis* about what would be expected because of its large size. In other words, although the proportions are in some cases distinctive, give the species a characteristic appearance, and are aids in recognizing it, they may be merely consequences of its greater size and not separate genetic characters. Thus the facial–cranial index (B) is about 63 (calculated from Williston's apparently accurate figure), a very large figure well above the known range for *H. primaevus*, but in the latter this index is highly variable and apparently tends to be larger for larger individuals. The index of the postorbital constriction (D) is relatively small, but within the *H. primaevus* range and this index is generally smaller in larger animals. The canine index, E, is very large in Williston's specimen, 14.0, and probably does go beyond the limit of normal variation or of probable regression on size for *H. primaevus*, but the correlation in the latter is not close enough to show this beyond doubt. The proportions of the other teeth and of the lower jaw show no striking peculiarities. The small brain, high emarginate sagittal crest, produced inion, and other peculiarities of Williston's specimen are also about what would be expected either in a large variant individual or in a large species.

H. occidentalis thus appears to be the only species known in the lower Brulé of South Dakota that is surely distinct from *H. primaevus*. The occurrence together of these two sharply different allied species is entirely normal. A definite ecological distinction is suggested. *H. primaevus* is abundant, *H. occidentalis* rare, also a normal situation when two allied cats occur together. The area of deposition was apparently mostly inhabited by the smaller species. The larger species may have been everywhere less common, but may also have lived mostly in a somewhat different environment and be represented here only by strays. One possible analogy is afforded by the occurrence of leopards and tigers in Asia.

It will be recalled that this fauna also includes *Dinictis*, probably with two valid species, and *Eusmilus*, with one. These are adaptively quite distinct from *Hoplophoneus* and complete a picture of a normally varied cat assemblage with five or six different sorts each occupying its own place in the general regional fauna.

AN INTERESTING NEW SPECIMEN

Amer. Mus. No. 38804, found by Mr. Thomson in the lower Brulé in 1938, includes skull, jaws, and most of the skeleton of a *Hoplophoneus* smaller than *H. occidentalis* but well above the average for *H. primaevus*. The prosthion-basion length, 181 mm., is slightly above that recorded for any Brulé specimen except Williston's *"Dinotomius atrox"* (= *H. occidentalis*), although the difference of only 2 mm. from the largest specimens referred to *H. "insolens"* and *"robustus"* is hardly significant. Although an unusually big animal, with the development of crests, etc., that goes with size, almost all its dimensions and proportions are within the observed range for the largest individuals of *H. primaevus*, used in the broadest sense to include *"robustus"* and *"insolens,"* or so near it that the deviation has no clear significance. The only exception is that the upper canines appear to be abnormally large, both relatively and absolutely. Crushing and fissuring of the specimen with subsequent filling of cracks with matrix make this not exactly measurable, but the anteroposterior diameter of the canine alveoli was probably about 22 mm. and the index, E, about 12. The largest values in the *H. primaevus* series are 17.5 mm. and, for the index, 11.1. The difference is not clearly significant in view of the imperfect preservation of the specimen and it is, after all, most likely that this is merely an

extreme variant of *H. primaevus*, about the most robust male known. The very fragmentary skull of Amer. Mus. No. 655, a syntype but not the lectotype of *H. insolens*, also belongs to a very large animal for this group and is peculiar in various ways hard to evaluate on such imperfect material, among them the probable possession of upper canines absolutely and relatively very large, as in this new specimen.

CHADRON SPECIES

The described Chadron species are *H. mentalis* Sinclair and *H. oharrai* Jepsen. Their authors have described them fully and I have not re-examined any of the specimens so that I can add nothing except the suggestion that the two may be synonymous as already hinted but not definitely advanced by Wood (1927). The specimens rather closely resemble the most robust males of *H. primaevus*, but are probably correctly distinguished from that species. It is just possible that the dubious specimens mentioned above, Amer. Mus. Nos. 38804 and 655, represent a survival of this group, as a separate phylum, into the Brulé, but this is not probable.

Clark (1937) has reported the discovery of a specimen referred to *H. robustus* in the upper part of the Chadron, but has given no detailed description or measurements. A considerably larger sample of

Chadron specimens will be required to show the probable average distinctions corresponding with changes of level within this group.

A new specimen extending the geographic range is Amer. Mus. No. 27798, found by A. C. Silberling in beds of Chadron age on the west side of the Long Pine Hills in Carter Co., Montana. This consists of the cranium posterior to the postorbital constriction, part of the upper jaw with all six incisors and the left canine, and a fragment of the left lower jaw with P_4–M_1. These remains do not permit exact identification, but the large canine and the size of the cranium and production and shape of its crests suggest *H. oharrai*. The lower jaw fragment is perhaps closest to *H. primaevus*, but the parts preserved show no good distinction between the two species.

TAXONOMIC CONCLUSIONS

The data summarized in preceding pages suggest the following conclusions regarding the eleven proposed White River species of this genus:

1.—*H. primaevus* (Leidy, 1851). Surely valid. As hitherto used, in a strict sense, the name has probably included most of the females and one or two small or young males of a natural species.

2.—*H. occidentalis* (Leidy, 1869). Surely valid. A second, larger, ecologically different, less abundant species.

3.—*H. oreodontis* (Cope, 1873). Now indeterminate but possibly determinable at some future time on the basis of the type. Cope's hypodigm of 1885 or neotype is probably an immature *H. primaevus* and is above rather than below the average size for that species. The small mature specimens later referred to *H. oreodontis* are thus different. They are probably the smallest females of *H. primaevus*.

4.—*H. atrox* (Williston, 1895). A synonym of *H. occidentalis*.

5.—*H. robustus* Adams, 1896. Probably includes most of the males of *H. primaevus*, of which it is thus a probable synonym. Very unlikely to be a synonym of *H. occidentalis*.

6.—*H. insolens* Adams, 1896. One or two specimens so identified may just possibly, but not probably, be distinctive. Other specimens, including the lectotype, appear to be merely the largest males of *H. primaevus*. Unlikely to be synonymous with *H. occidentalis*.

7.—*H. latidens* Thorpe, 1920. Probably based on slight variants of *H. primaevus*. They could represent a different race from most of the material, but the available specimens do not establish this as probable.

8.—*H. marshi* Thorpe, 1920. Similarly a possible race, but not demonstrated to be such. At present not distinguishable from immature *H. primaevus*.

9.—*H. molossus* Thorpe, 1920. Apparently valid, but data do not yet quite preclude the possibility that the known specimen is a deviant or abnormal *H. primaevus*.

10.—*H. mentalis* Sinclair, 1921. Probably

valid and almost surely so if *H. oharrai* is a synonym.

11.—*H. oharrai* Jepsen, 1926. Distinct from any named Brulé species. Possibly synonymous with *H. mentalis* but this is not demonstrated.

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