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VARIATION AND EVOLUTION IN THE PREMOLAR TEETH
OF *OSTEOBORUS* AND *BOROPHAGUS* (CANIDAE)

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Seven graphs analyze the important dimensions and proportions of the premolars in the described species of *Osteoborus* and *Borophagus*. Grids or scales of standard deviation multiples for a standard population (Coffee Ranch) are superimposed on the graphs. A graph of the relative width of P/4 plotted against the absolute width of M/1 shows, among other things, that *Aelurodon validus* does not belong in *Osteoborus*. The graphs show exactly the relations of isolated specimens and types to each other but do not resolve completely the fundamental uncertainties regarding their species or biostratigraphic positions. Species, as presently constituted, may differ less than extreme variants of the standard population. A probable new "missing link" between *Osteoborus* and *Borophagus* was found in the Christian Ranch local fauna of Texas. Both *Osteoborus* and *Borophagus* seem to have produced aberrant species. The early evolution of *Osteoborus* may be deciphered only by further study involving both *Aelurodon* and *Tomarctus*.

† † †

INTRODUCTION

It has long been recognized that *Borophagus* was the direct descendant of *Osteoborus*. *Borophagus* succeeded *Osteoborus* in time, and species representing the two stages of development are never found together. The structures which have undergone the most significant modification appear to have been the premolar teeth, especially the fourth lower premolar (P/4, Fig. 1). The principal tendencies were toward enlargement or broadening of the fourth lower premolar and reduction in size of the other premolars, upper and lower. These changes in the dentition appear to have been gradual and progressive. There were also significant changes in overall size, with increase in size being apparently the most general tendency. As jaws of these dogs are among the most common carnivore fossils of the Pliocene, they have been of some importance as index fossils through employment of the method of stage-of-evolution.

At the beginning of this study it seemed that if these striking and progressive modifications could be shown graph-

ically, such diagrams might be of great usefulness in determining the stage of evolution, and, hence, the relative geologic age, of isolated lower jaws of these animals. At the same time, it seemed desirable to determine how much variation in these same features might be ascribed to individual variation within a "species" from a single fossil locality. The large collections of *Osteoborus cyonoides* (referred) from the Coffee Ranch, or Miami Quarry of Hemphill County, Texas, were available for a statistical standard. Dalquest (1969) had published the basic statistics on this population of *Osteoborus* based on samples of up to 18 specimens from the Midwestern University collection. In gathering data for my graphs at the various institutions, I had access to a much larger sample. My original intention was only to show graphically the development of the fourth lower premolar plotted against a dimension of the lower carnassial as a measure of overall size. To satisfy some critics, the study was extended to cover all of the premolar teeth, including one graph of upper teeth. The Coffee

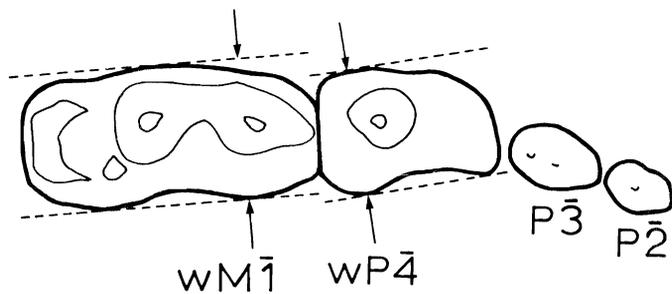


Figure 1. Diagram of the lower dentition of *Osteoborus* from Coffee Ranch, showing outstanding characters of the osteoborine dogs and the manner of taking measurements on the P4 and M1. Drawn from Matthew and Stirton (1930, Pl. 30), specimen UCMP 30120. Natural size.

Ranch population figures as the standard on all graphs. This study is limited, for the most part, to the specimens named or described in the literature. In some cases, however, I have given data on unpublished specimens in order to elucidate epochs in the evolution where adequate data were lacking in the literature.

Basic statistics of the standard population computed for this study are given in Table I. It will be noted that for a number of the variates considered, the size of the sample is many times as large as that treated by Dalquest.

On most of the graphs presented herewith two variates are plotted on each diagram, thus utilizing both ordinate and abscissa. The primary reason for doing so is to condense the presentation as much as possible. The correlations resulting

are generally of minor interest, although certain correlations proved to be of considerable value in interpreting the graphs involving ratios. It is assumed in what follows that the reader is familiar with the basic principles of biostatistics and also with those sections of Simpson, Roe, and Lewontin (1960) dealing with single specimens.

As the names used in this paper refer mostly to holotypes, I have generally used species names in the shortest form possible consistent with clarity. Generic names used are, with a few exceptions, those in current or recent use. For the benefit of readers less familiar with the group, and for purposes of reference, I give a partial synonymy in Table II, together with information on the provenance and the nature of the type specimen. In Table II all names are given in complete systematic citation form.

TABLE I
 Statistics, Dimensions of Lower and Upper Teeth of *Osteoborus cyonoides*, Referred from the Coffee Ranch Locality, Hemphill County, Texas *

Variate	N	\bar{X}	$s\bar{X}$ mm.	s mm.	V
w P /2	26	5.027	.085	.432	8.58
1 P /2	26	6.977	.099	.504	7.22
w P /3	55	5.826	.056	.416	7.14
1 P /3	54	8.621	.088	.646	7.50
w M /1	55	12.15	.084	.622	5.12
w P /3 ÷ w M /1	55	.478			
w P /4	99	10.828	.057	.567	5.24
w M /1	99	12.121	.056	.560	4.65
w P /4 ÷ w M /1	99	0.894			
w P /4 (R)	54	10.806	.079	.579	5.35
w M /1 (R)	54	12.049	.075	.552	4.58
w P 1/	6	4.477	.151	.507	11.32
1 P 1/	6	6.15	.123	.302	4.91
w P 2/	22	5.407	.070	.327	6.04
1 P 2/	22	9.266	.160	.751	8.10
w P 3/	11	6.11	.186	.615	10.07
w P 4/	11	11.61	.232	.769	6.62

*Means (\bar{X}) are in millimeters, except the ratios, which are pure numbers. R - right rami only (each from different individual).

TABLE II

Species Names Considered in this Paper, with Original Designations, Provenances, and Nature of Types

SPECIES NAME (Used in this Report)	SYNONYMS (Original and Early Designations)	PROVENANCE (Local Fauna)	TYPES (Upper or Lower)
<i>Aelurodon ricardoensis</i> (Stirton & VanderHoof)	<i>Aelurodon aphobus</i> , Stock 1928 <i>Osteoborus ricardoensis</i> Stirton & VanderHoof 1933	Red Rock Canyon, Ricardo, California	Lower
<i>Aelurodon validus</i> (Matthew & Cook)	<i>Aelurodon haydeni validus</i> Matthew & Cook 1909 <i>Osteoborus validus</i> , VanderHoof & Gregory 1940	Aphelops Draw l.f. = "Upper Snake Creek" *	Lower
<i>Borophagus crassapineatus</i> (Olsen)	<i>Osteoborus crassapineatus</i> Olsen 1956 <i>Osteoborus dudleyi</i> (White), Webb 1969	Phosphate Pits, Pierce, Polk County, Florida	Lower
<i>Borophagus diversidens</i> Cope 1892 (Type Species)		Blanco l.f., Crosby County, Texas	Lower
<i>Borophagus dubious</i> (Merriam)	<i>Hyaenognathus dubious</i> Merriam 1903	Pittsburg, Contra Costa County, California	Upper (P/4 only)
<i>Borophagus matthewi</i> , VanderHoof & Gregory 1940	<i>Hyaenognathus matthewi</i> Freudenberg 1910	Tequixquiac Marls, Valley of Mexico	Upper
<i>Borophagus pachyodon</i> , VanderHoof & Gregory 1940	<i>Hyaenognathus pachyodon</i> Merriam 1906	Asphalto, Kern County, California	Lower
<i>Borophagus solus</i> , VanderHoof & Gregory 1940	<i>Hyaenognathus solus</i> Stock 1932	Coso Mountains, Inyo County, California	Upper
<i>Osteoborus cyonoides</i> , Stirton & VanderHoof 1933	<i>Hyaenognathus cyonoides</i> Martin 1928	Edson, Sherman County, Kansas	Lower
<i>Osteoborus diabloensis</i> Richey 1938		Black Hawk Ranch, Mt. Diablo, California	Lower (+ Upper)
<i>Osteoborus direptor</i> Stirton & VanderHoof 1933	<i>Hyaenognathus direptor</i> Matthew 1924	ZX Bar l.f. = "Upper Snake Creek," Nebraska *	Lower
<i>Osteoborus gabushai</i> Webb 1969		Mixson's Loc., Alachua Clay, Florida	Lower
<i>Osteoborus hilli</i> Johnston 1939		Axtel l.f., Randall County, Texas	Lower (+ Upper)
<i>Osteoborus littoralis</i> , Stirton & VanderHoof 1933	<i>Borophagus littoralis</i> VanderHoof 1931	Crocker Spring, Kern County, California	Upper
<i>Osteoborus ore</i> Webb 1969		Withlacooche River, Florida	Lower
<i>Osteoborus progressus</i> Hibbard 1944		U.K. Loc. 6, Seward County, Kansas	Lower
<i>Osteoborus pugnator</i> , Stirton & VanderHoof 1933	<i>Porthocyon pugnator</i> Cook 1922	Beecher Island, Wray, Yuma County, Colorado	Upper (+ Lower)
<i>Osteoborus secundus</i> , Stirton & VanderHoof 1933	<i>Aelurodon saevus secundus</i> Matthew & Cook 1909	(Site unknown), Snake Creek area, Nebraska*	

* = data from Skinner, Skinner, and Gooris, 1977

DISTINGUISHING *OSTEOBORUS* AND *AELURODON*

The Aelurodon validus Problem. This paper deals mainly with *Osteoborus* and *Borophagus*. However, two species are treated here which, although they have been classified with *Osteoborus* in most recent literature, are now considered as belonging to *Aelurodon*. These are *Aelurodon ricardoensis* (Stirton and VanderHoof, 1933) and *Aelurodon validus* (Matthew and Cook; see VanderHoof and Gregory, 1940). Rather early in this study (Fig. 8) it became evident that these very large species were phylogenetically distinct from the main *Osteoborus-Borophagus* lineage. Yet they are obviously closer to *Osteoborus* than to a good many specimens which have been identified as *Aelurodon*. As the solution to this dilemma involves a good deal more than the results of my own research, I feel obliged to go into the problem of *Aelurodon* in some detail. Very recently the species *validus* has been cited as *Aelurodon validus* in a paper by Skinner, Skinner, and Gooris (1977), but without explanation as to the reason for the switch back to the old generic designation. The solution to this nomenclatural problem is due in large part to Richard H. Tedford, to whom I am most grateful for several helpful suggestions.

The best known genera of the subfamily Borophaginae (Simpson, 1945) are *Aelurodon*, *Osteoborus*, and *Borophagus*. (Five other "genera" included in the subfamily by Simpson are controversial and will not be discussed here.) The three genera named above have in common: rather heavy molar and carnassial teeth, and a parastyle on the upper carnassial. Two of these genera, *Osteoborus* and *Borophagus*, have reduced premolar dentition, a shortened face, and an enlarged and modified fourth lower premolar (Fig. 1). There are a few other characters which distinguish *Borophagus*, such as antero-posterior shortening of P/2 and P/3, and absences of the metaconid and parastyle.

The case of *Aelurodon* is not so simple. *Aelurodon* has long been poorly understood because of the inadequacy of the holotype of the type species, *Aelurodon ferox* Leidy, based solely on a single upper carnassial. McGrew pointed out as long ago as 1944 that the species which had been classified with *Aelurodon* fell "into two quite distinct groups." One of these groups McGrew called "the *Aelurodon saevus* group," the other the "taxoides group." The latter included by implication *Aelurodon wheelerianus* Cope. McGrew pointed out several differences in the lower dentition and suggested that "the differences here are so great that there seems to be sufficient justification for the separation of the taxoides group as a distinct genus." One of the characters of the taxoides group recognized by McGrew was that the premolars were "little reduced." Galiano and Frailey (1977:13) have recently pointed out that the P/1 in this group is in fact "exceptionally large." Oddly enough, Schlosser had many years before (1890) proposed the generic name *Prohyaena* for this group, with *Aelurodon wheelerianus* Cope as the type. The name

Prohyaena has been very largely ignored in subsequent literature, probably because of both the obscurity of Schlosser's reference and the battered condition of the holotype of *Aelurodon wheelerianus* Cope. I would point out as additional characters of this group that the P/4 is relatively small, and that all of the premolars, upper and lower, tend to have multiple cusps of a characteristic, discrete type.

The principal question remaining, odd as it may seem, is this: To which of McGrew's groups does the type species *Aelurodon ferox* belong? In examining a number of skulls with the "taxoides" type of premolars, I find that, in the P4/ (upper carnassial), there tends to be a small sharp crest connecting the protocone with the anterior blade (paracone). This crest is not in evidence in the holotype of *Aelurodon ferox*. I therefore conclude that *A. ferox* probably belongs to the *A. saevus* group of McGrew, and, hence, the generic name should remain with that group. I am therefore willing to accept tentatively *Prohyaena* Schlosser as an appropriate name for the other, or "taxoides" group.

Aelurodon, thus disembarassed of the taxoides group, is now seen as a group of true borophagines, although one which throughout its history remained more primitive than *Osteoborus* and *Borophagus*. In *Aelurodon* only the P/1 is greatly reduced; but it is never lost, so far as is known. P/2 and P/3 are less reduced. P/4 is large, but not widened posteriorly, and it never loses the posterior accessory cusp. There is little crowding of the premolar teeth in the row. Both upper and lower premolars tend to have reduced accessory cusps, especially on the front of the teeth. The face tends to be dishd and the forehead bulging, at least in the most advanced forms, such as *A. validus* from Sebits Ranch, Texas (see Johnston, 1939, Fig. 3). Some smaller species of *Aelurodon* will probably prove very difficult to distinguish from primitive species of *Osteoborus*. In truth it might be asked if the "paratype" lower jaw of *Osteoborus pugnator* (Cook) is not really that of a small *Aelurodon*.

THE LOWER ANTERIOR PREMOLAR TEETH—P/1-3

First Lower Premolar—P/1

It has long been known that in *Osteoborus cyonoides* from Coffee Ranch the first lower premolar is present in only a small number of rami. The task of determining the percentage of rami erupting this tooth is not as simple as might be expected. In some specimens the ramus is broken off anterior to P/2, or the border of the dentary is otherwise so damaged as to make it impossible to determine whether or not the tooth was present. In some jaws there is clear evidence that the tooth was once present but later broken off during life, or shed. In some cases the alveolus for the missing tooth had partially or wholly closed up. In this part of the study, therefore, only those specimens were considered which showed the upper border of the dentary intact between /C and P/2.

If there was "no trace" of the tooth ever having been present, it was considered that the tooth had never been erupted. It is possible that in a few of these cases an alveolus for P/1 might have healed over so perfectly as to give the impression that it had never been present. Nevertheless, I believe that the figures obtained on the incidence of this tooth afford a fairly close approximation of the probability of any particular ramus showing the tooth. From the 74 rami thus selected, only twelve showed evidence of having actually erupted P/1. This amounts to about 16 percent. Of these, the tooth itself was actually in place in only one. In this specimen, F:AMNH 23357, the tooth measured 3.40 x 4.25 mm.

On the other hand, P/1 may be present even in *Borophagus*. Specimen UNSM 2687 from the Lisco Quarry, Broadwater Formation, shows this tooth in the left ramus but not in the right. (The width and length are 6.9 and 7.3 millimeters, respectively.) This is the only specimen I know which shows evidence of having an erupted P/1. But because rather few lower jaws of *Borophagus* have been found, we must admit that the incidence of P/1 in *Borophagus* may not be very different from that in *Osteoborus cyonoides*.

It follows from the above that the presence of P 1/ (or its alveolus) in an isolated find of a jaw of one of these animals would constitute a strong indication of the presence of a species more primitive than that of Coffee Ranch. Some species in which this is the case are: *Osteoborus diabloensis* Richey, *O. galushai* Webb, *O. orc* Webb, and *O. pugnator* (Cook). This character is probably significant also in the case of *Osteoborus* from the famous Ft-40 Quarry of Nebraska, previously discussed (Richey, 1973). Later in 1973 a mandibular fragment with an alveolus for P/1 was found at this site. This indicates (but does not prove) that Ft-40 is older than Coffee Ranch. There is a possibility that we are dealing here with a small species of *Aelurodon* (not very different from a primitive *Osteoborus*), in which case the application of the above-mentioned rule could be very misleading.

Second Lower Premolar—P/2

P/2 is apparently not erupted in a small number of well-preserved lower jaws of *Osteoborus cyonoides* from Coffee Ranch. It may be that a certain number of jaws lost the P/2 soon after it was erupted and that the alveolus subsequently closed so as to leave no trace. In some cases (Col:AMNH 1325 and 1329; UCMP 30112 and 30115; and PPHM-JWT 1988-1) alveoli were observed which were only partly healed over. But in surveying a large number of specimens, certain rami were noticed which lacked the P/2 and showed no indication of ever having erupted it. An attempt was made to estimate the proportion of jaws in this category. Out of 94 jaws which had the pertinent portions preserved, nine were observed to show "no trace" of P/2. This works out at about 9.6 percent. Conversely expressed, the figures show that P/2 was erupted in at least 90.4 percent of the rami.

Dalquest (1969) has published statistics on length and breadth of eight P/2's from Coffee Ranch. For the sake of the completeness of my own study, I recomputed the statistics (Table I) on the somewhat larger number of measurements which were available in my records. These new statistics were used in Figure 2, which is a graph of the width of P/2 plotted against its length. It was feasible to use the figures for the lengths in this case, because the length can be measured accurately more often on P/2 than on other premolars, upper or lower. A further reason for plotting the length is to show the decreasing length of this tooth in the transition from *Osteoborus* to *Borophagus*. This is indicated on Figure 2 by the steepness of an imaginary line connecting *O. cyonoides* with the two occurrences of *Borophagus* shown.

The plus and minus 2-standard deviation limits of the standard population in Figure 2 were obtained by computation and superimposed on the plot of the various species and specimens. The reader is reminded that, in the normal distribution, $\pm 2s$ should include 95.5 percent of the individuals in the population. For practical purposes, then, $\pm 2s$ of the two variates are near the limits of the theoretical ranges of that species. The fact that *Osteoborus orc* falls within these "2s limits" does not prevent *O. orc* from being a perfectly good and useful species. Otherwise, to one unfamiliar with the evolution of *Osteoborus* and *Borophagus*, Figure 2 may appear quite difficult to interpret. The graph does not show a very distinct linearity, especially as regards the primitive species *O. diabloensis* and *O. galushai*. This is because the P/2 at first becomes smaller in the stages leading up to *O. cyonoides*, after which it becomes slightly larger in forms leading to *Borophagus*. On the other hand, the very large forms, *Aelurodon validus*, and especially *A. ricardoensis*, may be confused with *Borophagus*. In reality, these large species have other characters which distinguish them easily from *Borophagus*, and their lineage became extinct long before the appearance of *Borophagus*.

Third Lower Premolar—P/3

P/3 may be broken off or shed during life, in which case the alveoli may be nearly completely healed over. P/3 is often very little larger than P/2, thus being relatively more highly reduced than that tooth. P/3 is quite variable in size and shape, as is attested by the rather high coefficients of variation (Table I). This is especially true in the more advanced species of *Osteoborus* and in *Borophagus*.

Figure 3 is a simple plot of the width of P/3 against its breadth. The purpose of this figure is to show antero-posterior shortening of the P/3 in the transition from *Osteoborus* to *Borophagus*. This is indicated by the steepness of the trend in the upper right-hand corner of the graph. Because the length is by definition greater than the width, the normal trend in such a graph would be considerably less than 45°. Otherwise, Figure 3 is somewhat difficult to interpret. The large number

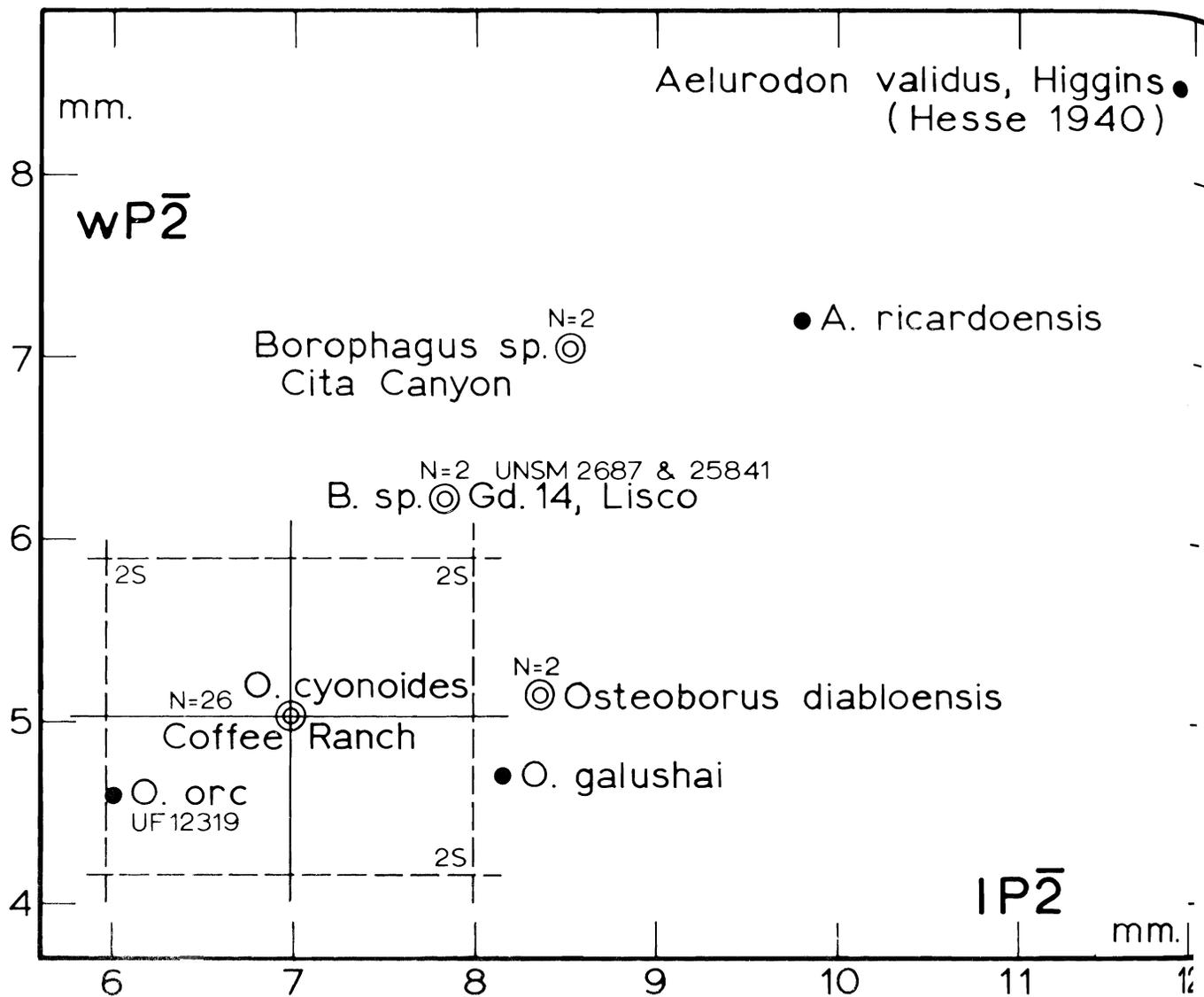


Figure 2. Comparison of widths and lengths of the second lower premolar in various species of *Osteoborus*, *Borophagus*, and *Aelurodon*; with grid of standard-deviation multiples of the Coffee Ranch population of *O. cyonoides* superimposed as standard of variability. Dots represent individual specimens, which are holotypes if the name only appears opposite. If specimen number or locality data only are given, dots represent referred or undetermined specimens. Double circles indicate means.

of types of species and other specimens which fall within the "2s limits" of *Osteoborus cyonoides*, Coffee Ranch, and the great variation in different specimens of *Borophagus*, indicate the difficulty of using the size of P/3 as a criterion in taxonomy or biostratigraphy.

Figure 4 gives the width of P/3 plotted against a measure of absolute size, the width of M/1. M/1 is chosen for this purpose because it is a conservative structure apparently little affected by the evolutionary changes involving the other teeth. The expected range of variation in a species is shown by the "2s limits" of *Osteoborus cyonoides* from Coffee Ranch. The reader is reminded that, the standard deviation's being a func-

tion of the overall size of the species, the "2s limits" would be a little greater for the larger species in the upper right-hand corner of the graph than for the Coffee Ranch species.

The general distribution of species in Figure 4 is in agreement with what is known of the evolution. But there are a number of anomalies in detail. Thus, in looking for a possible ancestor for the Coffee Ranch *Osteoborus*, we note that the species which has the most primitive teeth (in form) *diabloensis*, is not the smallest. Turning to the larger forms we note quite a number of *Borophagus* specimens in the lower right-hand part of the chart which have a P/3 larger than the Coffee Ranch *Osteoborus*. Yet there are ap-

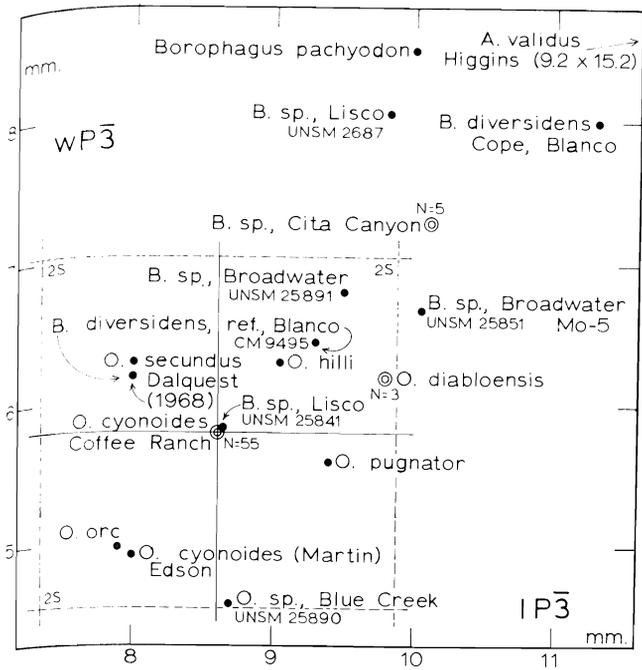


Figure 3. Comparison of widths and lengths of third lower premolar in various species of *Osteoborus*, *Borophagus*, and *Aelurodon*. For explanation of conventions and symbols, see Figure 2 and list of abbreviations.

to be a gap in the series of forms between *O. hilli* and *Borophagus*. It is difficult to tell whether this apparent gap is due to a spurt in evolution or to a fortuitous effect of the fossil record. The large species *Aelurodon ricardoensis* and *Aelurodon validus* in the upper right-hand corner of the chart also require explanation. In size of P/3 they seem to be confused with large species of *Borophagus*. But these very large forms formerly classed with *Osteoborus* show several characters which indicate that they belong to a lineage separate from the main *Osteoborus-Borophagus* line. The principal difference in the anterior premolar teeth is their graded size and open spacing (absence of crowding).

Figure 4. Comparison of the widths of the third lower premolar and the first lower molar (carnassial) in various species of *Osteoborus*, *Borophagus*, and *Aelurodon*. For explanation of conventions and symbols, see Figure 2 and list of abbreviations.

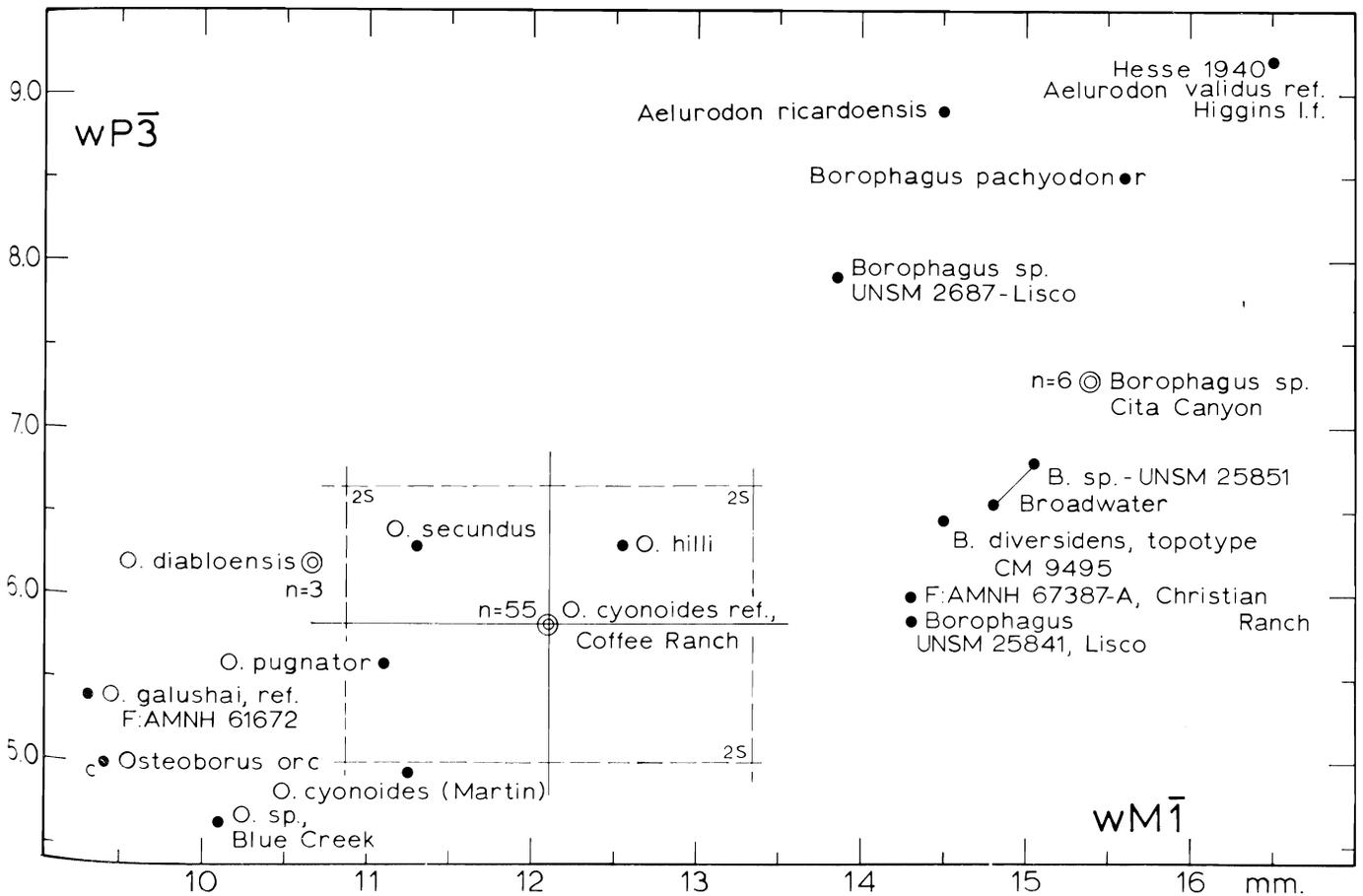


Figure 5 is an attempt to show the decreasing relative size of P/3 with evolution. This is not very apparent in charts such as Figure 4, because in the main lineage the relative size is decreasing while the overall size of the animals is increasing. In Figure 5 the width of P/3 appears on the ordinate as the quotient obtained by dividing the width of P/3 by the width of M/1. On the abscissa, in place of the species' names or specimen numbers, the faunas from which they come, arranged in presumed stratigraphic order, appear instead. The species and specimens are the same as those appearing in Figure 6.

THE SPECIALIZED FOURTH LOWER PREMOLAR—P/4

P/4 is the most characteristic tooth in the Borophaginae. It should be possible to distinguish the three genera, *Aelurodon*, *Osteoborus*, and *Borophagus*, by this tooth alone. In this study I have considered the dividing line between *Osteoborus* and *Borophagus* to be the point at which the width of P/4 becomes greater than that of M/1. Some writers have used the disappearance of the posterior accessory cusp of P/4 as the critical point in the classification. As for *Aelurodon*, probably only the members of the so-called "*Aelurodon saevus* group" of McGrew (1944) are true borophagines. In these the P/4, while remaining large, is not widened at the posterior end or noticeably pitched backward, and it retains a good-sized accessory cusp. These contrast noticeably with the asymmetrical P/4s of medium-sized species of *Osteoborus* and with *Borophagus*. They are not very different in form,

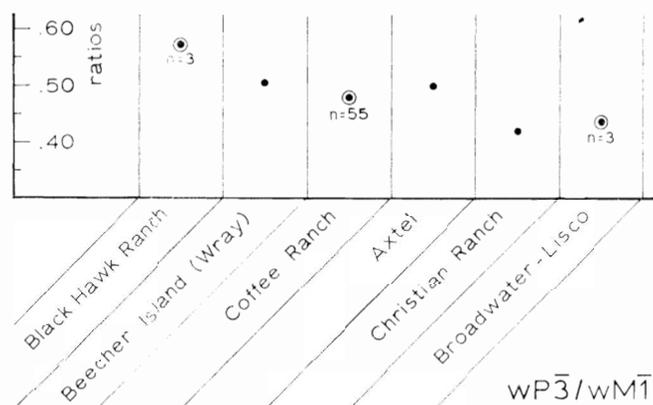


Figure 5. Diagram showing decreasing size of the third lower premolar relative to size of first lower molar with time. Widths of teeth only are used. Dots represent single specimens or holotypes, dots within circles means of more than one specimen. In lieu of specific names, names of local faunas from which the species come are indicated at the bottom in presumed chronological order from left to right. For names of species concerned, see check list of species, Table II.

however, from the P/4s of primitive species of *Osteoborus* such as *O. pugnator* and *O. diabloensis*.

The size and form of P/4 have given the group the sobriquet "hyaenoid dogs." The function of this large, conical, and pointed premolar has been the cause of some speculation. Ewer (1954) believed that similarly modified teeth in hyaenoid were crushing teeth. The best explanation seems to be that of Galiano and Frailey (1977:4), who consider such teeth "piercing" structures. I understand this to mean that the tooth was used for breaching the shafts of upper limb bones of large animals. It is well known in engineering mechanics that one of the most effective means of piercing a hard, strong material is by the application of heavy pressure to as limited an area as possible, which can only be done by employing a conic, somewhat acutely pointed tool. The theory of Galiano and Frailey also explains why there is no similar tooth in the upper jaw. Only one would be necessary. Why a premolar should be selected for this function is cause for further speculation. Possibly the carnassials and molars were already too specialized for other functions. A primitive canid premolar, being already a pointed tooth, could be more readily modified. The canines would be too far forward for the application of maximum force; the molars would be too far back to permit applying it to large objects. On the other hand, in the jaws of

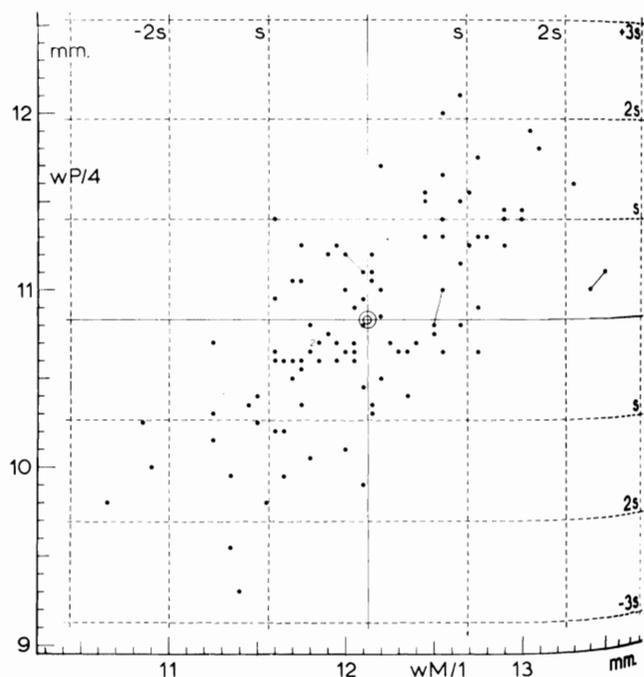


Figure 6. Scattergram showing variation in the P4 and M1 in 99 mandibular rami of *Osteoborus cyonoides* from the Coffee Ranch Quarry, Hemphill County, Texas. The means (shown by a double circle) and the standard deviations are calculated. Dots connected by a line represent right and left rami of same individual.

old individuals the P/4 is usually worn down to the point where it must have lost its piercing function altogether. Probably only young adult animals used the tooth for piercing bones. The specialization could nevertheless have benefitted the entire population, since many canids are social hunters and feeders with a well-established social system.

The P/4 in *Osteoborus cyonoides*, Coffee Ranch

Figure 6 was prepared to show the actual distribution of variations in two key structures of one species of *Osteoborus*. The width of M/1 was chosen as a second variate to be plotted together with wP/4 because of the difficulty frequently encountered in measuring the length of P/4 accurately. A grid composed of calculated multiples of the standard deviation is superimposed. A check was made for normalcy of the distribution of values for the width of P/4 by counting the dots which fall within $\pm 1s$, $\pm 2s$, and $\pm 3s$ of the mean, respectively. The numbers, converted to percentages, gave roughly 69, 96, and 100 percent respectively. This may be compared with the 68.26, 95.46, and 99.73 percent of the normal frequency distribution (Sokal and Rohlf, 1973). We may therefore say that the distribution of this variate in the Coffee Ranch population is quite close to normal. It is obvious from inspection of Figure 6 that the distribution of values for the width of the lower molar (wM/1) is also quite close to normal. The configuration of this scattergram should be kept in mind when examining other graphs involving either the P/4 or M/1. Generally, for the sake of clarity, only the $\pm 2s$ limits are shown on the other graphs.

The most notable feature of Figure 6 is the relatively sharp limits of the band of distribution on either side of the basically linear trend. In other words, there are no specimens with a very large P/4 and a very small M/1, or vice versa. Within limits, a certain proportion is maintained between the sizes of the two teeth. This seems to support my contention, made in a later section of this paper, that the relative size of P/4 is more important than its absolute size. For any given size of M/1, the width of P/4 varies within a range equivalent to about $2\frac{3}{4}s$. This is much less than the total range of variation of wP/4, which is about $5s$.

Comparing the P/4 and M/1 in Various Species

Figure 7 is a simple plot of the widths of P/4 and M/1. It is reproduced here for the benefit of readers who may be disturbed by ratios or logarithms. The graph represents essentially raw data, with the statistical parameters of the standard population added. A significant feature of Figure 7, evident by mere inspection, is that the total range of variation in all of the borophagines plotted is greater for the width of P/4 than for the width of M/1. The divergence of the very large *Aelurodon validus* and *A. ricardoensis* from the *Osteoborus-Borophagus* line is visible on this graph, but is not particularly striking.

Widths of P/4 and M/1 Expressed as a Ratio. Figure 8 is the most significant graph prepared for this study. The measurements used are the same as for Figure 7. On the ordinate scale, the values are the quotients obtained by dividing the width of P/4 by the width of M/1. Otherwise expressed, each value on the ordinate plotted for a dentition is a ratio in which the width of M/1 is taken as 1. No unpaired data were used for the statistics of the standard population. In a few cases, unpaired data were used for other occurrences where the number of specimens available was very small. It might be objected that a high position on the ordinate of Figure 8 reflects a large M/1 as much as it does a small P/4. This is only partly true. For we have seen in Figure 6 that a large M/1 is going to be associated with a relatively large P/4, thus restoring the proportion to a large extent. The position of a specimen on the ordinate of Figure 8 should express the relative width of P/4. It is expressed as a pure number, independent to a certain extent of the size of the specimen and the overall size of the species.

Figure 8 seems to express, better than any of the other charts, the relations of the species to each other, and the phylogeny in which they are involved. Most important, perhaps, is the profound dichotomy which now appears between the *Aelurodon validus* group of species and *Osteoborus*. Unfortunately, this chart does not provide any good clues as to the ancestry of *A. validus*. Probably its ancestor was some primitive member of the family which does not appear at present on the chart because it is classified as a species of *Aelurodon*. Probably some member of what McGrew (1944) has called "The *Aelurodon saevus* group" was the ancestor. It can be argued that the separation between the *A. validus* group and the other species on Figure 8 is artificial, produced by the arbitrary scale selected for the ratios: if a more condensed scale had been used, the separation would not have seemed so great. However, we may legitimately compare the separation of *A. validus* and *A. ricardoensis* from the various species of *Osteoborus* and *Borophagus* with the separation of these species from each other. In such a case, the *A. validus* group appears relatively isolated. It also shows a different trend, in the direction of large size without a corresponding increase in the relative size of P/4.

Width of P/4 Plotted Logarithmically

The differences between species and specimens may be compared and their standard deviations estimated without resorting to ratios. This is done by plotting the logarithms of the various values on ordinary graph paper (Fig. 9). The standard deviation scale is constructed by plotting $\log(\bar{x} + 1s)$, $\log(\bar{x} - 1s)$, $\log(\bar{x} + 2s)$, and so on. If the coefficient of variation is assumed to be the same for all species, then the scale thus obtained will be the same for any part of the chart. Only one variate at a time can be plotted on charts such as Figure 9. The variate chosen for Figure 9 is the width of P/4. Some differences will be noted between this chart and a

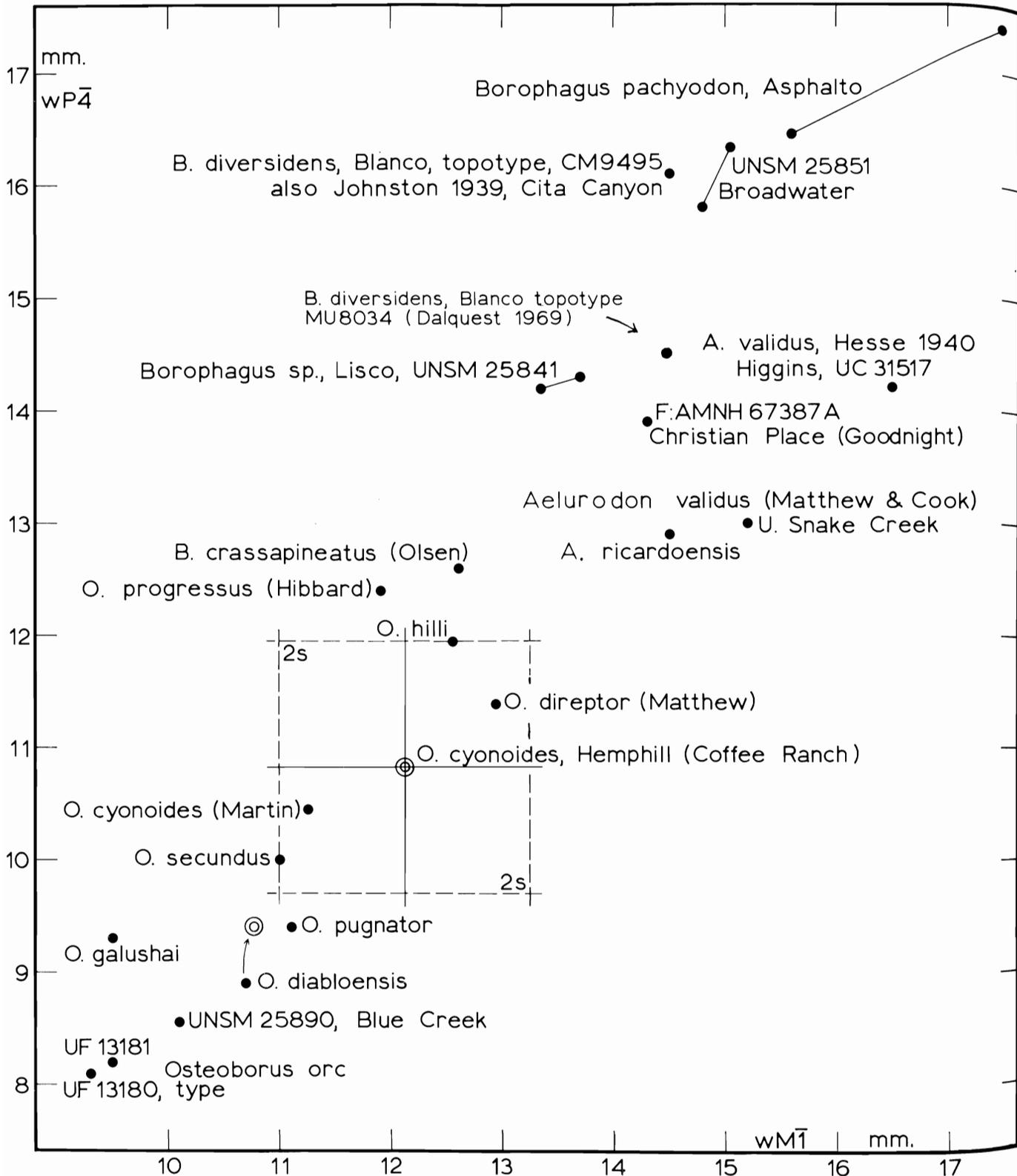


Figure 7. Comparison of the widths of the fourth lower premolar and the first lower molar (carnassial) in various species of *Osteoborus*, *Borophagus*, and *Aelurodon*. For explanation of conventions and symbols, see Figure 2 and list of abbreviations.

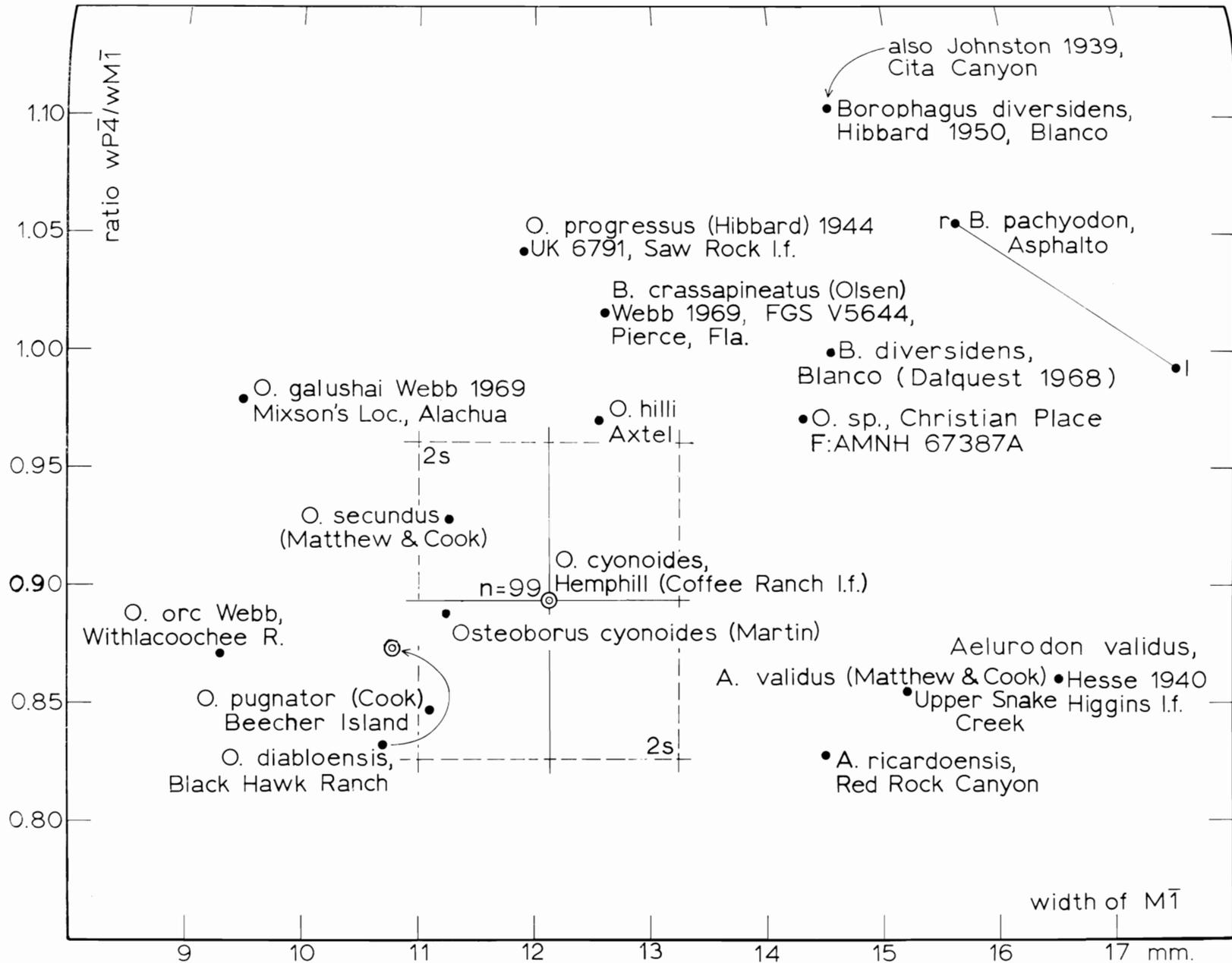


Figure 8. Relative width of the fourth lower premolar shown as a ratio (quotient) and plotted against the width of the first lower molar as a measure of absolute size, for various species of *Osteoborus*, *Borophagus*, and *Aelurodon*. Values shown on the ordinate are numbers, and the scale chosen is arbitrary; values on abscissa are millimetric. All data paired from same ramus of one individual. For explanation of other conventions and symbols, see Figure 2 and list of abbreviations.

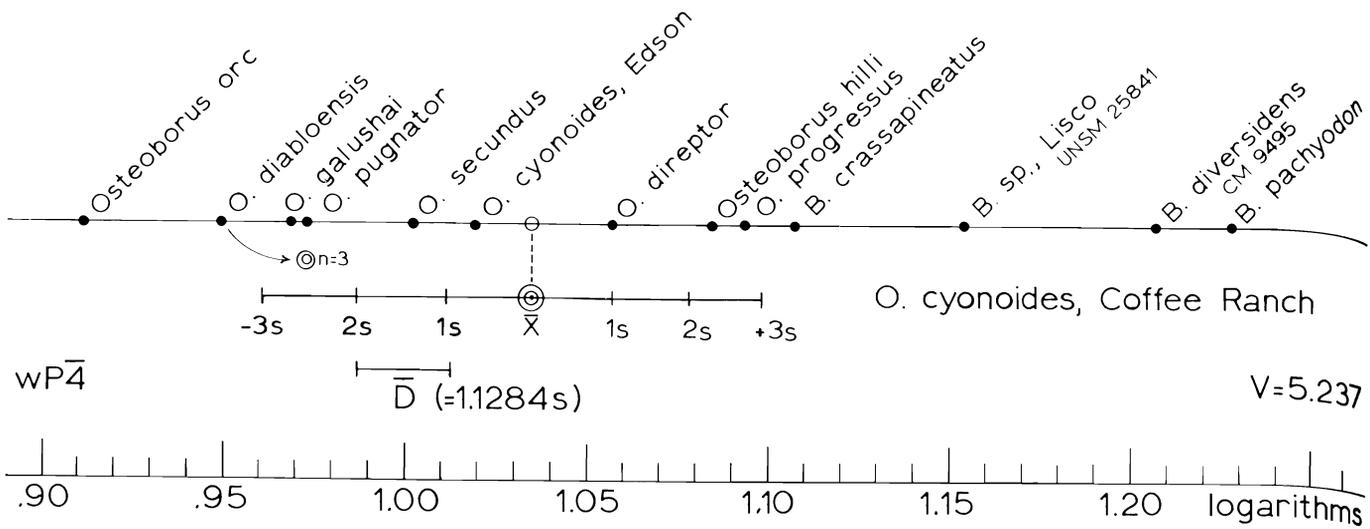


Figure 9. *Logarithmic* plot of width of the fourth lower premolar in holotypes of various species and in other specimens with statistical parameters of *Osteoborus cyonoides* from Coffee Ranch, added below for variation scale. Mean difference is also shown (see text for explanations). Plotted on ordinary graph paper. Dots represent holotypes or single specimens; double circles represent means.

comparable chart, such as Figure 7. This is because, on a numerical scale such as is used in Figure 7, standard deviations are not exactly the same on different parts of the chart.

The Mean Difference in P/4s of a Species

In evaluating two specimens on a logarithmic scale such as Figure 9, we might ask ourselves: Supposing that two specimens were from the same population, what would be the expected difference between them? In other words, what is the average difference between two specimens chosen at random from a population? In response to my inquiry, Robert F. Mumm called my attention to the proper statistic. It is the "mean difference," sometimes referred to as "Gini's mean difference." This statistic is discussed in Johnson (1970). It is symbolized here by \bar{d} . It is estimated by $\bar{d} = 2/\sqrt{\pi}s$. This is equivalent to writing $\bar{d} = 1.12838s$. Without inquiring into the proofs of the derivation of this formula, I made a test by drawing 20 pairs of measurements of wP/4 from the 99 used in computing the statistics of the Coffee Ranch *Osteoborus* material. The mean difference obtained was 0.685 mm, or approximately 1.21s. Such an expected difference may seem surprisingly small, in view of the rather large total range of variation of such a species. This statistic is also discussed by Steel and Torrie (1960).

The mean difference may be plotted on a chart of logarithms such as Figure 9, by a method adapted from Simpson, Roe, and Lewontin's (1960) method for plotting extreme possible ranges of variation. The logarithmic range, or limits, of \bar{d} for the standard population, *Osteoborus cyonoides*, Coffee Ranch, may be added to the chart simply by plotting two points, $\log(\bar{x} + 1/2\bar{d})$ and $\log(\bar{x} - 1/2\bar{d})$, and connecting them

with a line. If we assume that all populations have the same coefficient of variation, the distance \bar{d} will be the same on any part of the scale. The interval \bar{d} (Fig. 9) may be transferred by means of dividers or a scale to other parts of the chart. It is not necessary to use the statistics of a known population, as long as the coefficient of variation V is assumed to have a certain value. On Figure 9 I assumed a hypothetical mean and computed s by means of the well-known relation: $s = V\bar{x}/100$.

Unfortunately, this statistic, like so many others, cannot serve as a basis for hard-and-fast taxonomic conclusions. If two isolated specimens are more than \bar{d} distance apart in several important characters, it does not prove that they came from different populations or species; if they are less than \bar{d} distance apart, it does not prove that they came from the same population. The statistic is shown in Figure 9 to indicate to what extent a single specimen may be used as an estimator of the mean characteristics of a population, and to show the hazards involved in basing species upon such specimens.

THE UPPER PREMOLAR TEETH

The anterior upper premolar teeth (P/1-3) are in general similar to the corresponding lower teeth. They afford one of the best means of comparing isolated upper and lower dentitions from different sites. In the Coffee Ranch *Osteoborus* the anterior premolar teeth tend to be a little wider in the upper jaw than in the lower (Figs. 4 and 10). According to the statistics given by Dalquest (1969), the upper teeth are also considerably longer than the lower.

First and Second Upper Premolars—P/-2/

First Upper Premolar—P1/. In the Coffee Ranch *Osteoborus*, the first upper premolars were always erupted, so far as is known. I did note one specimen, F:AMNH 61676, in which the alveolus was partly closed, as if the tooth had been lost during life. As Dalquest (1969) gave no statistics on the P1/ of the Coffee Ranch material, they are supplied here (Table I). In *Borophagus* the situation is less clear. Hibbard and Riggs (1949) reported “no evidence of P1/” in a maxillary from Kansas. Dalquest (1968) reported the P1/ present on both sides of a skull of *Borophagus diversidens* Cope from the Blanco. A palate in the University of Nebraska collections, UNSM 2687, is somewhat crushed, and the tooth is missing on both sides. There is a good-sized space for it on one side and what seem to be the remains of the root; on the other side there is a very small space for it behind the canine, but it is not clear whether the tooth had been actually erupted. It seems that in *Borophagus*, if the P1/ may have sometimes failed to erupt, it was probably more often present than the P1/ of the lower jaw.

Second Upper Premolar—P2/. The P2/ is very much like P3/ in *Osteoborus* and *Borophagus*, except for being smaller. As there is nothing notable about P2/, I have not burdened this article with a graph of its proportions. Dalquest (1969) has supplied the necessary statistics.

Third and Fourth Upper Premolars—P3/-4/

P3/ and P4/ are plotted together in Figure 10. Although the function of the two teeth is quite different, this expedient was adopted to save space and also to provide a standard of size with which to compare the variable P3/. The P4/, being a carnassial, should be more conservative than P3/, which undergoes reduction in the evolution of the group. It will be noted that a number of species and specimens appear on Figure 10 which were not seen on previous graphs. These are species or occurrences known only from the upper dentition. The actual plot of the dot representing the *Aelurodon validus* skull from Sebits Ranch, Texas (Johnston, 1939), is omitted, because it unduly increases the size of the chart. There is, however, an indication of its approximate position and dimensions.

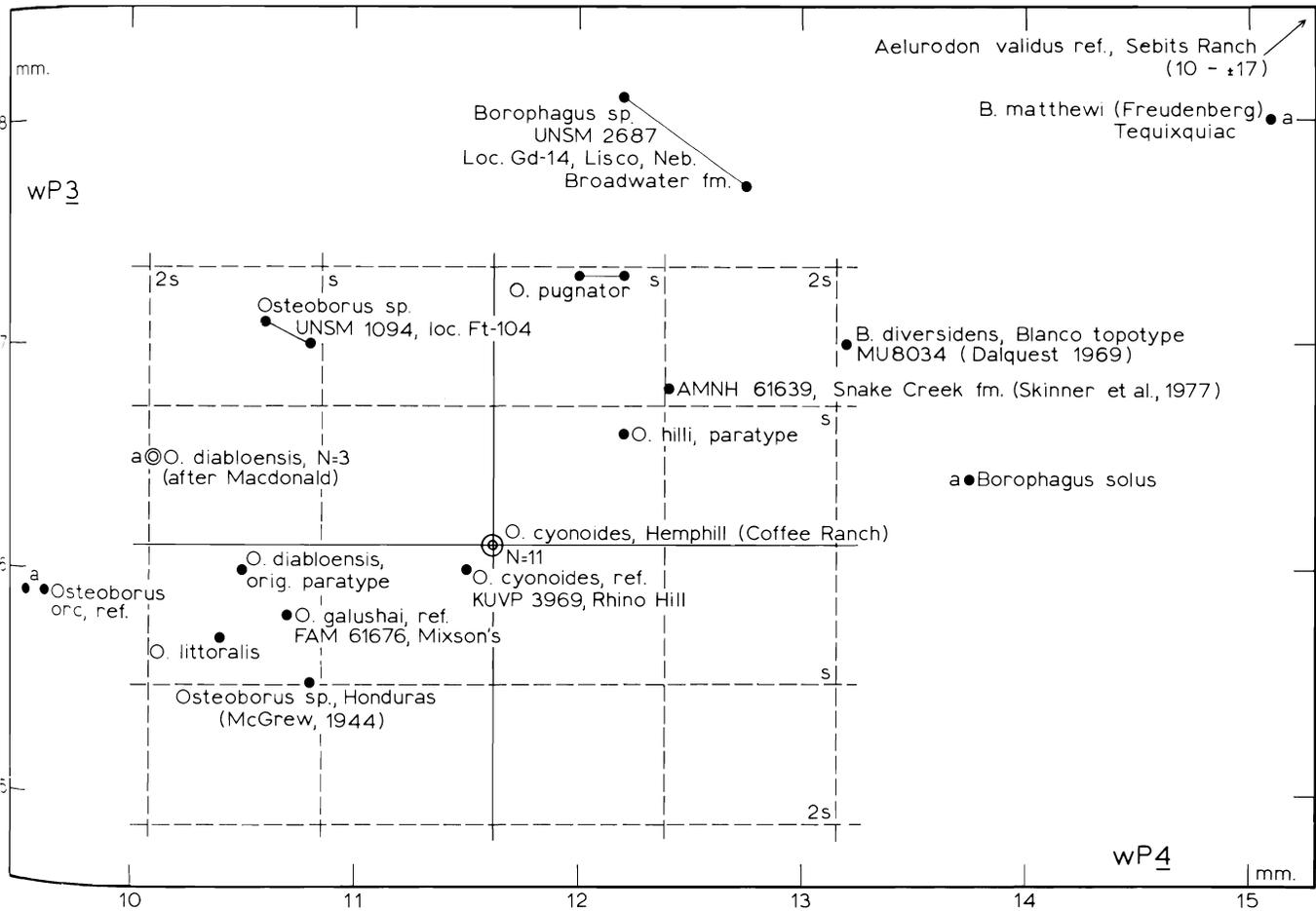


Figure 10. Comparison of the widths of the third and fourth upper premolars in various species of *Osteoborus*, *Borophagus*, and *Aelurodon*. For explanation of conventions and symbols, see Figure 2 and list of abbreviations.

Figure 10 is perhaps the most ambiguous of the graphs. It will be noted that a great many named species occur within the 2s range limits of the standard population, *Osteoborus cyonoides* from Coffee Ranch. Even the ranges of three occurrences of *Borophagus* probably overlap that of the Coffee Ranch species. The known primitive species of *Osteoborus* occur either to the left (same sized P3/), or upper left or upper center (larger P3/), with respect to the Coffee Ranch species. The probable evolution of the main lineage on this chart would evidently form a loop: beginning in upper left-center, then to lower left, then through the center of the chart to upper right center. I submit this chart in the hope that it may be of some use in determining the evolutionary advancement of newly found occurrences consisting only of the upper dentition. In any case, the position of a new specimen on this chart would probably be less important than the form of the teeth.

VARIATION IN *OSTEOBORUS* AND *BOROPHAGUS*

Variation in Osteoborus cyonoides, Coffee Ranch. The only borophagine species whose variation is known at all well is *O. cyonoides* from Coffee Ranch. The variation is shown by a scatter (Fig. 6), and by standard deviations and coefficients of variation calculated for the various teeth (Table I). According to Simpson, et al. (1960), most functional mammalian structures such as teeth have a coefficient of variation (V) of 3 to 7. It will be noted in Table I that the Vs of most teeth of *O. cyonoides* from Coffee Ranch fall within the expected limits of variability, and that the Vs of wP/4 and wM/1 are relatively low. The highest Vs are observed in the unspecialized and degenerate premolar teeth such as P/2, P1/, and P3/. The Vs seem to be higher in the upper premolars than the lower. This suggests that the degenerate teeth tend to be more variable than unreduced or functional ones.

Variation in Other Species. Very little is known directly about the variation in the other species. In some of the charts I have pooled the specimens from a formation or area, which may or may not result in better knowledge, depending upon the reliability of the stratigraphic units. These species and the number of specimens available depending upon the teeth concerned are: *O. diabloensis*, Black Hawk Ranch (2-3), *B. diversidens*, Blanco (2-3), *Borophagus* sp., Cita Canyon (2-6), *B. sp.*, Lisco (2), *Osteoborus orc*, Withlacoochee R. (2). Because of the small samples available, the variation of these forms in large part, and that of the species based on single types entirely, must be assumed by analogy with the standard species. The basic assumption is that all have approximately the same coefficients of variation as the standard population. The grid composed of multiples of the standard deviation (s, 2s, 3s) of the standard population gives only a rough idea of the range of variation in other species. It should be kept in mind that standard deviations and the various segments of the range of variation would be expected to be somewhat greater for large species and somewhat smaller for small

species. This mental adjustment is unnecessary in Figure 1 because of the logarithmic values used.

I would like to call the reader's attention to one aspect of the variation which is not readily apparent from the standard deviation grids alone on Figures 2-4, 7-8, and 10. This is that the variants do not fill the entire square or rectangular space of the grid, but occupy a band, more or less wide, from the lower left-hand corner of the grid to near the upper right-hand corner. This is plainly evident from the scatter in Figure 6. It is due to the fact that any dimension of a tooth is due in part to the overall size or development of the individual from which it came, and only in part to genetic factors affecting variation.

VALIDITY OF SPECIES

As no systematic revision is attempted in this report existing species' names are accepted as a matter of reference without any attempt to pass upon their validity or non-validity. However, the statistical approach taken suggests some ideas and principles which should be of interest where questions of systematics might arise. The first of these ideas is that the course of evolution of *Osteoborus* into *Borophagus* appears to have been gradual and continuous. I can see little evidence of "punctuated equilibria" in the case of this lineage (see Eldredge and Gould, 1972). The existing species' names presumably represent distinct stages in this evolution which have been determined by fortuitous episodes in the preservation, discovery, and description of the fossil materials. Since we have to deal unavoidably with the factor of individual variation in any case, it seems desirable to delimit the species in space and time as much as possible. Hence, we should tend to be "splitters" rather than "lumpers" in the matter of species.

Holotypes Within the Range of *O. cyonoides*, Coffee Ranch

Those typologic species which fall within the range of the standard population from Coffee Ranch (*O. direptor*, *O. secundus*, and the typical *O. cyonoides* itself, Figs. 7-9) are not necessarily conspecific with it, because we cannot prove that they lived at the same time. Individuals this similar to the mean of the Coffee Ranch population could hardly have lived as distinct populations in the same region at the same time as the Coffee Ranch population. But they could have lived at different times. There is no rule which says that the difference between the means of two species living at different times needs be great. This leads to the rather surprising conclusion that, as species are presently constituted, there may be more difference between two specimens of the same species than between the means of two different but closely related species. An example is the case of the wP/4 of *Osteoborus direptor* (Figs. 7 and 9). Its mean probably lies within the range of the holotype. In whichever direction it lies, it would

not be more than 4s from the mean of *O. cyonoides*, Coffee Ranch. Yet a few pairs of specimens from Coffee Ranch are 5s apart (Fig. 6).

Typologic Species, Single Specimens. Regarding those species based on single specimens (Figs. 7-9), the only statement that can be made with 95 percent probability is that the mean of each lies within $\pm 2s$ of the specimen and that the extreme possible limits of range lie within about $\pm 4s$. On the other hand, there is about 68 percent probability that the mean of each lies within $\pm 1s$ of the specimen. The probability that the mean lies in the direction of another species (i.e., a mean or a holotype), whether larger or smaller, is only 50 percent. Finally, the probability that the mean lies within $1s$ and in the direction of another specimen is only about 34 percent. The uncertainties are compounded in the case of two adjacent species (Fig. 9) both based upon single specimens. I conclude from this that it is impossible to prove or disprove the validity of such species. The names of most of these species are not likely to be abandoned, however, because of their value as references to the fossil materials.

In general, the variation in the teeth of these dogs seems to be much greater than previous investigators, working usually with single specimens or types, suspected. Nevertheless, I feel that most of the species which have been erected are valid, simply because these species are scattered by the hazards of discovery through about eight million years of time. A majority of the holotypes are within $1s$ of the means of the "species," and nearly all are within $\pm 2s$. The extreme deviations are great, but the average or mean deviation is moderate. The mean deviation of the $wP/4$ of the Coffee Ranch population is only 0.453 mm, which is approximately $.8s$. In a few cases, no doubt (perhaps in one or two of the species existing) the mean of the population may be quite far from the specimen described. There is no way of knowing, pending the discovery of topotypes, which these species are. In all cases, therefore, of typologic species based on a unique specimen, we have to live with a large amount of uncertainty. The lesson is not to avoid drawing any conclusions from such types, but to draw only properly qualified conclusions, and always to be ready to change them.

Traditionalists, on studying Figure 9, will probably conclude that there are already too many species of Borophaginae. In his 1962 thesis, Williams lumped all of the North American forms into seven species of *Aelurodon* and three species of *Borophagus*, doing without *Osteoborus* altogether. Nevertheless, the species names currently in use will probably continue to be recognized for some time because of their usefulness as references to both the literature and to the fossil materials. In this respect it might even be well to have a few more names. A species name for the Coffee Ranch population for example, would be very convenient, even though it can not be proved that the holotype of *Osteoborus cyonoides* (Martin) did not belong to that population. (The opposite cannot be proved, either.) A species name for the Christian Place form (Figs.

7-8) would also be useful. Experience has also shown that there is a certain value in having a distinct species name for the representative specimens of a genus from each recognized formation, member, or faunal zone. Unfortunately it is the scholarly and experienced systematist who will most likely hesitate about applying a new name, while it will be the eager, naive, and inexperienced student who will rush into the breach, believing sincerely that he has a new species, when all that he can prove is that he has a unique specimen.

EVOLUTION OF *OSTEOBORUS* AND *BOROPHAGUS*

Although the origin of *Borophagus* from *Osteoborus* is clear, the detailed evolution of these genera still presents many problems. These problems are due in part to the comparative scarcity of the fossils, and in part to problems of geologic dating. Geologic ages of various occurrences of borophagines mentioned in this paper are shown in Figure 11. This table attempts to show the best consensus as to age relationships available at the present time.

The Last Surviving Borophagine? *Borophagus pachyodon* (Merriam) is apparently the largest species of *Borophagus* and might therefore be considered the end-form of the evolution of the subfamily. The left M/1 is much larger than the right, although both are apparently wider than the M/1 of any other known specimen of *Borophagus* (Fig. 7). In the relative width of P/4, the right P/4 is about as advanced as the average of two Blancan specimens of *B. diversidens*; while the left (because of the very large M/1) has a ratio less than 1, which would make it no more advanced than a very advanced *Osteoborus* (Fig. 8). It seems, therefore, that the only respects in which *B. pachyodon* is particularly advanced are the large size and the complete absence of a metaconid. It seems barely necessary to point out that the holotype of *B. pachyodon* is not so large but what it could be conspecific with *B. diversidens*.

In the matter of stratigraphy, Merriam (1903) did not know the exact site or geologic age of *B. pachyodon*. He suggested the age might be Quaternary because of the association with a large "*Smilodon*." Matthew and Stirton (1930) reported additional collecting in the type area. They stated that the site of the type locality was "in an asphalt vein at a depth of nearly 200 feet." They identified the cat as *Ischyrosmilus* and considered it Pliocene. Nevertheless, in a table they showed *B. pachyodon* as from the Lower Pleistocene. Stock (1932) discussed several species of *Borophagus* (*Hyaenognathus*) based upon the upper dentitions. The largest of these is apparently *B. matthewi* (Fig. 10). Here again there is some indication of possible Pleistocene age, but the evidence is contradictory.

There is also a semantic problem. Some recent writers on geochronology, such as Savage and Curtis (1970), place the Blancan in the Lower Pleistocene, while others (Boellstorff, 1976) place it in the Pliocene. The problem apparently must be restated, as follows: Did *Borophagus* persist into a post-

		CALIFORNIA	COLO. - NEBR. - KANS.	OKLA. - TEXAS	FLORIDA	
P L I O C E N E	PLEIST.	Asphalto				
	BLANCAN	Pittsburg Coso Mts.		Blanco - Cita Canyon		
	HEMPHILLIAN	U		Edson U. Snake Creek Beecher Island (Wray)	Axtel Coffee Ranch	Bone Valley Withlacoochee R.
		L			Higgins	Mixson's Bone Bed
	CLARENDONIAN	U	Red Rock Canyon (U. Ricardo) Black Hawk Ranch Crocker Springs	Snake Creek		
		L				

Figure 11. Geologic age allocations of the various local faunas in which the species of *Osteoborus*, *Borophagus*, and *Aelurodon* mentioned in this report occur. Age determinations in accord with best consensus presently available, but subject to change.

Blancan age? No positive answer can presently be given to this question.

Aberrant Species of Borophagus. Most of the known occurrences of *Borophagus* fall within the expected range of variation of a single species, *B. diversidens* (Fig. 9). One species, however, does not seem to fit very well into the lineage. *Borophagus crassapineatus* (Olsen) seems very borophagine with its very short premolar space and heavy carnassial. However, the extremely large canine would seem to indicate, as Webb (1969) suggested, that this is either an aberrant individual or a species which was off the main line of borophagine evolution. Webb renamed this form *Osteoborus dudleyi* (White) and dated it in the lower part of the upper half of Hemphillian time. I place this species in *Borophagus* because of the $wP/4 \div wM/1$ ratio greater than 1 and the extremely short face.

Links Between Osteoborus and Borophagus. C. Stuart Johnston (1939a) correctly supposed that his *Osteoborus hilli* was probably ancestral to *Borophagus*. Although the holotype of this species falls barely within the observed range of *O. cyonoides*, the Coffee Ranch sample in certain characters (including the width of P/4; Figs. 3-4 and 6-7), it lies so far

on the periphery of the $wP/4$ range that the chance of such a specimen being found among the Coffee Ranch population is quite small. The $wP/4 \div wM/1$ ratio of .968 is higher than that of any observed specimen from Coffee Ranch. I therefore feel that this is a valid intermediate form, although one closer to advanced species of *Osteoborus* than to any named species of *Borophagus*.

Another specimen has come to my attention which probably supplies an additional "missing link" in the ancestry of *Borophagus*. This is an as yet undescribed specimen in the Frick collection, F:AMNH 67387A, from the Christian Place (Ranch ?), near Goodnight, Armstrong County, Texas. (This is presumably in at least the same area as the "Christian Ranch Locality" discussed by Johnston and Savage, 1955.) This well-preserved lower jaw is larger overall than the type of *O. hilli* (Fig. 7) but scarcely any more advanced in widening of P/4 (Fig. 8). Although the $wP/4 \div wM/1$ ratio is less than 1, it could conceivably have been a member of either the *O. hilli* or the *Borophagus diversidens* populations. Johnston and Savage considered the associated fauna to be a correlative of the Axtel. There may seem to be a gap in the distribution of forms between *O. hilli* and the Christian Place specimen (especially in Fig. 7). This might suggest that *Borophagus*

evolved quite rapidly from *Osteoborus* and then remained little changed until its extinction. I would rather attribute the gap to the fortuitous distribution of rather few specimens.

Aberrant Species of Osteoborus. *Osteoborus progressus* Hibbard is a species which does not seem to fit very well into any evolutionary lineage (Figs. 7-9). If the measurements given by Hibbard are correct, the $wP/4 \div wM/1$ ratio is considerably greater than 1, which might lead one to put it in *Borophagus*. But it is very small to be placed in that group. The M/1 of the right ramus of the holotype seems abnormally small and narrow. This may be the factor responsible for its $wP/4 \div wM/1$ ratio greater than 1. Hibbard (1944) states that this dog is "nearly as large as *Osteoborus validus*. . . ." Yet his measurements show it to be scarcely any larger overall than the Coffee Ranch *Osteoborus*. I have left this dog in *Osteoborus* pending an opportunity to reexamine the holotype.

Osteoborus galushai might seem to be an aberrant species. It is rather small overall (Fig. 7). The presence of P/1 is an indication of a species more primitive than the Coffee Ranch form. The lower premolars of *O. galushai* are simpler in form than those of *O. diabloensis*, therefore less primitive than that species. But if Webb's (1969) measurements are correct, this species is even more advanced than *O. cyonoides* in the relative width of P/4 (Fig. 8). I suspect that there is something wrong with the data on this species. Webb gives dimensions only of the M/1 of the right ramus, which seems to be mostly missing, judging from the figure. He gives no dimensions of the left M/1, which appears to be present.

The Origin of Osteoborus. In describing *Osteoborus diabloensis*, I stated that it was the most primitive species known at the time (Richey, 1938). Macdonald (1948), describing five additional rami, showed that it was less primitive than I had supposed. Meanwhile, several species with one or more primitive characters have been described from Florida (Webb, 1969). If size alone was the criterion, the tiny *Osteoborus orc* would be the most obvious ancestor (Fig. 7). A specimen from Blue Creek, Garden County, Nebraska, is nearly as small. Yet Webb (judging apparently from the degree of crowding and simplification of the premolar teeth) considered *O. orc* relatively advanced. In enlargement of P/4 it is about on a par with *O. diabloensis* (Fig. 8). But the P/3 of the holotype right jaw is clearly more reduced than that of *O. diabloensis*. It therefore seems most likely that *O. orc* is a slightly advanced species on a lineage diverging from the main course of borophagine evolution along the line of small size. Of three specimens discussed by Webb, only one was missing the P/1. On the laws of chance, this indicates a much higher incidence of P/1 than in the Coffee Ranch population. This character, then, is in keeping with the lower degree of development of P/4.

Osteoborus pugnator (Cook, 1922) is another somewhat primitive borophagine which might be near the origin of

Osteoborus. P/3 is apparently not stepped in this species, but the jaw is more elongate than is normal in *Osteoborus*. This might eventually turn out to be a small *Aelurodon*.

CONCLUSIONS

In summary, the early development of *Osteoborus* presents many unanswered questions. Presumably, these questions cannot be resolved without an investigation in depth into the origin of *Aelurodon* and its relation to *Osteoborus*. This inquiry would probably have to be extended to the question of some possible common ancestor to be found in the genus *Tomarctus*.

The hope of identifying a species and determining its exact stage of evolution from a single lower jaw by means of the charts presented in this paper has proved vain. A single specimen leaves too much uncertainty as to the positions of means, which to a very large extent define the species. Tentative conclusions, however, can be drawn within certain broad limits of probability. Where a larger sample is unobtainable, any probability greater than 50 percent is worth considering. In so doing, it should constantly be borne in mind that it is not only possible to go wrong, but to go quite far wrong in case one should chance to have a specimen with dimensions lying near the extreme limits of range of variation in one or more critical characters.

Otherwise, the charts developed in the course of this study should prove useful as a mechanical aid in comparing individual specimens or means of species. The stage of development of the individual, at least, can be exactly seen on these charts. Plotting the ratio of the width of P/4 to the width of M/1 seems to be a valid and especially useful technique of comparison with this particular group of carnivores. This kind of chart definitely proves the distinctiveness of the *Aelurodon validus* group of species from *Osteoborus*.

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Abbreviations in Text and Figures. a, approximate; c, composite (two or more individuals); l, length; l.f., local fauna; r, right; sp., undetermined or unnamed species; w, width.

Depositories of Fossil Materials. AMNH, American Museum of Natural History; CM, Carnegie Museum; F:AM and F:AMNH, Frick Collection, American Museum of Natural History; MU, Midwestern University; PPHM, Panhandle Plains Historical Museum; UF, University of Florida; UNSM, University of Nebraska State Museum; UC, University of California Museum of Paleontology.

Statistical Symbols. \bar{D} or \bar{d} , mean difference; N or n, number of specimens in the sample; s, standard deviation; $s\bar{X}$, standard error of the mean; \bar{X} , arithmetic mean; V, coefficient of variation.