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[F I F T H S E R I E S .]

ART. XXXVI.—*John Day Felidæ in the Marsh Collection*; by GEORGE F. EATON.

[Contributions from the Othniel Charles Marsh Publication Fund, Peabody Museum, Yale University, New Haven, Conn.]

To the surviving personal friends of O. C. Marsh, and also to the younger generation of vertebrate paleontologists, Marsh's eagerness to secure fossils from newly reported localities in the western United States, and the success of the collectors he employed, no longer present any novelty. It need therefore occasion no surprise that the Marsh Collection of Vertebrate Fossils in the Peabody Museum of Yale University should contain a considerable amount of material, from the John Day Valley of Oregon, that was collected principally between the years 1870 and 1877. The present short article is based on that portion of this material from the John Day Valley which includes the Felidæ.

While it would be ungracious to criticise the methods of collecting in vogue in the seventies of the last century, it appears that the superior value of a good skull over the other skeletal parts, which were then somewhat disparagingly termed "joints," was a little over-emphasized in Marsh's instructions to his collectors. A result of this is possibly to be seen in the predominance of cranial material, unaccompanied by other skeletal parts that might otherwise have been saved, and that would now greatly enhance the value of the collection. Then, too, the stratigraphy of the region was neither so well understood nor regarded as of the same importance in connection with the search for fossils as it has been of recent years, and accordingly it would be unwise to accept as authoritative, in some instances, the recorded statements of the collectors regarding the horizons from which specimens were obtained. For this reason the present article

must be limited, in the main, to a discussion of the osteology and affinities of the material examined, and less attention can be paid to stratigraphic considerations than would otherwise be desirable. Yet notwithstanding real or suspected shortcomings in field work during pioneer days, the fact remains that this material, collected half a century ago, is worthy of careful study, and contains forms specifically distinct from those previously described. It is a pleasant duty therefore to express the admiration that is felt for the generous enthusiasm that led Professor Marsh to be one of the first paleontologists to visit the John Day Valley and to encourage the search for fossils in that region.

Tables.—For convenience in comparing the new species, here described, with the earlier types, cranial measurements have been arranged in parallel columns in Table A (page 442). While most of the measurements, selected for this purpose, conform with those used by previous authors, three new measurements have been introduced, and an external palatal length has been substituted for the old mid-line measurement. This table as originally constituted included practically all the measurements of cranium and mandible used by Merriam and by Thorpe; but while extremely useful in the study of material in the laboratory, it was thought too large for convenience of publication at the present time. The table has therefore been cut down to about one third of its original size by the omission of all mandibular and nearly all dental measurements, as well as of several cranial measurements that, on trial, did not yield satisfactory differential indices. Although the number of measurements and indices has been reduced, it has seemed desirable that the series of specific types, and other crania, tabulated under the several genera, should be as complete as possible, in order that the range of the indices characterizing these genera might be reliably determined. For this purpose four of the best preserved crania of the genus *Nimravus* in the Marsh Collection have been measured and the resulting indices recorded. Examination of several of Cope's types, now in the American Museum of Natural History in New York, has been possible through the courtesy of Dr. W. D. Matthew of that institution; and Professor John C.

Merriam, lately of the University of California, has very kindly supplied certain measurements of his types of *Pogonodon davisii* and *Nimravus (Archælorus) debilis major* in addition to those given in his original description of these two types. The illustrations accompanying this article are by Mr. R. Weber, and have a value of their own quite apart from the text.

Where the number of species to be compared is large, interpretation of the absolute measurements is facilitated by a further table expressing *relative* cranial proportions. The system of indices, so extensively used by anthropologists, eliminates the factor of mere size and is admirably adapted to this requirement. Accordingly the basal length, measured from basion to prosthion, which is probably the most rational single element of size, has been chosen as a convenient basis for the comparison of the major cranial proportions. From several of the cranial measurements in Table A, indices have been derived by the simple process of dividing these measurements, as taken on each skull, by the basal length of that skull, and multiplying the quotient by 100. In the case of minor cranial proportions and dental proportions, other dimensions than the basal length are more suitable as the bases of comparison; but as in every case the definitions of the indices, arranged in Table B, refer to the serial numbers of the absolute measurements, recorded in Table A, no confusion regarding the identity of the indices in Table B need arise.

The measurements recorded in Table A call for little explanation. The axial length from the prosthion to the posterior surfaces of the occipital condyles has been retained principally because of its long use by previous authors as a convenient over-all dimension; but the basal length from basion to prosthion, which can be readily taken in some skulls where Cope's axial length is impracticable, has been preferred as a basis for the comparison of size and proportion. There has been little uniformity in the past regarding the measurement of palatal length. The margin of the palatine bones bounding the posterior nares is seldom perfectly preserved, and even when complete it seems to be subject to some individual variation of form due to the development of a posteriorly directed mid-line process homologous with the posterior nasal

spine of the human skull. It has seemed desirable therefore to discard the mid-line palatine length, and to substitute for it a palatal length measured from the prosthion to a line tangent to the posterior surfaces of the maxillary parapets. This is precisely the same as the external palatal length of human craniometry. Since the index of palatal length, computed from this dimension and the basal length, is remarkably constant in all the species of *Nimravus*, *Dinictis*, and *Pogonodon* examined during the preparation of these tables, the palatal length furnishes an excellent basis for computing indices of palatal breadth.

Pogonodon Cope.

This genus was founded by Cope¹ on the characters of a skull that he had originally described as *Hoplophoneus platycopis*.² In a later article³ he stated that "This genus [*Pogonodon*] represents a station on the line connecting *Dinictis* with the higher sabre-tooths, being intermediate between the former genus and *Hoplophoneus*," and provisionally referred to the same genus incomplete material which he had made the type (partim) of *Machærodus brachyops*.⁴ *Pogonodon platycopis* and *P. brachyops* were transferred by Adams⁵ to *Dinictis*, the reason for this change being that "The genus *Pogonodon* as proposed by Cope does not differ from *Dinictis* as regards tooth structure, and the absence of the second inferior molar, which in *Dinictis* is much reduced, is not sufficient grounds for retaining it as a distinct genus, since in several specimens of *Dinictis* it is variable in size and in one is absent from one side." Matthew⁶ referred *Pogonodon platycopis* to Cope's genus *Nimravus*, regarding *Pogonodon* as a distinct sub-genus; and to the same genus he referred *P. brachyops* also, stating his opinion that the latter species was "like *N[imravus]* *gomphodus* and doubtfully separable from it except by absence of the infracarnassial exostosis." In the same

¹ E. D. Cope, Am. Nat., 14, 143, 1880.

² E. D. Cope, Am. Nat., 13, 798a, 1879.

³ E. D. Cope, Am. Nat., 14, 847, 1880.

⁴ E. D. Cope, Proc. Am. Phil. Soc., 18, 72, 1878.

⁵ G. I. Adams, This Journal (4), 1, 433, 1896.

⁶ W. D. Matthew, Bull. Am. Mus. Nat. Hist., vol. 28, 310, 1910.

article, in his discussion of *Hoplophoneus*, Matthew notes that Merriam's *Pogonodon davisi*, which Matthew had not then had an opportunity to examine, "appears from Merriam's figures to be referable to this genus [*Hoplophoneus*] and distinct from any of the *Dinictis* phylum." On the other hand, Merriam⁷ in his announcement of *Pogonodon davisi* has stated at considerable length the reasons for which it seemed to him "advisable to use the arrangement proposed by Cope, and to separate *platycopis*, *brachyops*, and *davisi* [from the deinictid group in the John Day beds] as the *Pogonodon* group, of at least subgeneric rank." In this status *Pogonodon* has rested for several years. My colleague M. R. Thorpe⁸ has recently found it expedient to recognize the validity of Cope's *Pogonodon* in order satisfactorily to record the affinity of a feline mandible from the White River beds of South Dakota. Similarly in the case of the skull about to be described, the practical convenience of retaining *Pogonodon* as a distinct genus, or subgenus, is not to be denied.

Pogonodon serrulidens, sp. nov.

(Figs. 1-3.)

Holotype, Cat. No. 10520, Y. P. M. Upper Oligocene (John Day), Turtle Cove, John Day Valley, Oregon. Collected by L. S. Davis in 1875.

The type material consists of a cranium, not particularly well preserved, together with two fragments of the right mandibular ramus, the proximal portion of the right ulna, and the proximal portion of the left metatarsal III. From the indications of age afforded by the sutures alone, this skull would appear to be that of an animal nearly or quite adult, but the dentition proves that the animal was immature. The permanent premolar and molar series is, or was, complete, while the deciduous canine of the left side is still present, being but partly overlapped, on its inner side, by its permanent successor. On the right the deciduous canine has been lost with part of the maxilla, so exposing considerably more of the permanent canine than the portion that had actually protruded beyond the parapet. The premaxillary alveolar border has been damaged, and none of the

⁷ J. C. Merriam, Univ. of Calif., Bull. Dept. Geol., vol. 5, 57, 1906.

⁸ M. R. Thorpe, This Journal (4), 50, 223, 1920.

incisors are preserved. While the immature development of the skull admittedly detracts somewhat from its value as a specific type, this deficiency is nearly compensated by the fact that the teeth of the permanent set exhibit practically no signs of wear, and therefore present, so much the more clearly, their characteristic form.

The material is provisionally attributed to the upper John Day because of the gray color of the ashy matrix, which, although slightly tinged with green, can not be described as bluish-green; but as this stratigraphic reference is unsupported by field records or other data, it should not be regarded as established beyond question.

FIG. 1.

FIG. 1.—*Pogonodon serrulidens*, sp. nov. Holotype. $\times \frac{1}{2}$.

Dentition.— I^3 , C^1 , P^3 , M^1 . The upper canines are compressed. The anterior margin of the right upper canine, which is exposed to view for nearly half its length, is sharper than in *Nimravus*, the serrated anterior ridge following the actual anterior margin of the tooth for a greater distance from the point than is the case in *Nimravus*. P^2 is very small, practically vestigial, and single-rooted. P^3 is much smaller in proportion to P^4 than in *Dinictis* and *Nimravus*, in this respect nearly resembling *Pogonodon davisii*. P^4 is without a positive inner cusp (protocone), the inner root being small and closely adpressed to the anterior root. It has a small but definite anterior accessory cusp (parastyle) distinctly separated from the sharp anterior margin of the para-

cone by a narrow oblique cleft. This is a character which the present species shares with *Pogonodon davisii*, but not with *P. platycopis*, for according to Cope⁹ the upper sectorial of the latter species has no parastyle. The paracone and metacone of P^1 are separated by a deep notch much as in *Dinictis* and *Nimravus*, and judging from the illustrations of *Pogonodon davisii*, as in that species also. M^1 is small with much reduced inner lobe. P_4 which is fortunately preserved in one of the mandibular fragments, has a relatively greater transverse breadth than I have observed in specimens of *Nimravus*. In this greater breadth and in the extent and form of the notch separating the posterior basal tubercle from the principal cusp, this tooth closely resembles the P_4 of Thorpe's *Pogonodon cismontanus*, Cat. No. 10053, Y. P. M.

The cutting edges of all the teeth, including even the vestigial P^2 , are finely serrated. This condition would facilitate the sectorial action of the teeth of a young and comparatively weak animal. It would be of progressively less advantage as the jaws and their muscles acquired greater strength. By the time the animal was fully adult, the serrations would probably be nearly or quite worn away from all the cheek-teeth, while on the canines, which because of their special function are less subject to detrition, the serrations might be expected to persist much longer. Sand and gritty substances taken into the mouth with food are a constant cause of dental detrition among the Carnivora, not excepting even the cleanly *Procyon lotor*, and in view of the habit of some recent large felines of crunching bones,¹⁰ it is probable that similar habits, acquired as the large extinct felines approached maturity, would hasten the destruction of the serrated sectorial edges. The resemblance of these serrated teeth to small saws has suggested the specific name, but it is not assumed that the cheek-teeth were serrated only in this species, or indeed in this genus alone.

One of the mandibular fragments supports a lower permanent canine lacking the upper half of the crown.

⁹ E. D. Cope, Report of the U. S. Geol. Survey of the Territories, vol. 3, 981, 1884.

¹⁰ Dr. W. Reid Blair, D. V. S., of the New York Zoological Park, informs me that the lion, tiger, leopard and puma all use the large cheek-teeth for this purpose.

The tooth is not quite fully protruded. The order of dental replacement, exhibited in this skull, should be noted. Disregarding the incisors, none of which have been preserved, there are actually in place and functional, in the lower jaw, a permanent canine and a permanent P_4 , and in the upper jaw, on one side, all the permanent premolars and molars. On the left side the alveolar margin where P^2 should be has been destroyed. From

FIG. 2.

FIG. 2.—*Pogonodon serrulidens*, sp. nov. Holotype. $\times \frac{1}{2}$.

the foregoing it appears that the deciduous upper canines remained in place until all the permanent upper cheek teeth were fully erupted. The presence of P_4 in the mandible renders it probable that the replacement of the lower cheek-teeth also was nearly if not quite completed, for in recent carnivores the lower carnassial is the first permanent cheek-tooth to appear. The best example at hand of a recent wild feline, showing the dental replacement, is a skull of the bay lynx (*Lynx rufus*), No. 0926, Y. P. M. Comparison of this lynx skull with that of *Pogonodon serrulidens* shows that, the replacement of the canines being at approximately the same stage in the two skulls, the replacement of the cheek-

teeth has been relatively earlier in the fossil skull, for here the permanent cheek dentition is nearly or quite complete, while in the recent skull the upper deciduous carnassials and all the lower deciduous cheek-teeth are still in place and functional, although, on each side, the principal cusp of P^3 has just appeared, and the crowns of P^4 and M^1 have protruded to about half their height. If preferred, the cheek-teeth may be taken as the basis of comparison, in which case it would appear that the replacement of the canines was relatively tardier in the fossil skull than in the recent lynx.

Cranium.—The basal length of the skull, measured between the basion and the probable position of the prosthion, is 167 mm. This shows the skull to be considerably shorter than that of *Pogonodon davisii* where the similar measurement is about 198 mm. Viewed from the side, the general proportions of the skull of *P. serrulidens* resemble those of *P. davisii* more closely than they do those of *Nimravus*. This is especially noticeable in the low and straight nasal region, and in the frontal profile which rises higher from the base-line in the neighborhood of the bregma than in the region between the postorbital processes. The sagittal crest does not however, rise as high posteriorly in the present species as in *P. davisii*.

The maxilla and the jugal, on each side of the skull, contribute to the formation of what may conveniently be termed the anterior zygomatic pedicle. It is believed that the widely varying proportions of this part of the skull will be found of considerable taxonomic value in the extinct Felidæ. In certain genera the anterior zygomatic pedicle affords two excellent measurements, namely, a *height*, taken as the minimum distance between the inferior margin of the orbit and the alveolar margin of the maxilla, and a *length*, taken as the minimum distance between the external margin of the infra-orbital foramen and the posterior margin of the zygomatic process of the maxilla. By dividing the measured height by the length, and multiplying the quotient by 100, an index is obtained, admirably suited to the comparison of cranial form, since it is entirely independent of actual size. The anterior zygomatic pedicle of *Pogonodon serrulidens* is considerably higher than long, as it is in

P. davisii and *P. platycopis*, the indices of this part of the skull, in these three species, being 120, 148, and 162 respectively, and so differing greatly from *Nimravus* where the length of the pedicle is equal to, or slightly greater than, the height, the corresponding index of *N. gomphodus* being 100, of *N. debilis* 88, and of *N. debilis major* 92, while in *Dinictis cyclops* it is 106, and in *D. squalidens* (No. 8777, A. M. N. H.) it is 107.

FIG. 3.

FIG. 3.—*Pogonodon serrulidens*, sp. nov. Holotype. $\times \frac{1}{2}$.

Another remarkable characteristic of *Pogonodon serrulidens* is the large size of the infra-orbital foramen. The vertical and transverse diameters, taken within the foramen, not at its outlet, are respectively 13 mm. and 10 mm. This is a variant toward the typical *Hoplophonic* form that at once distinguishes the present species from *Nimravus*. The true significance of very large infra-orbital foramina in certain groups of extinct Felidæ is not clear. As the foramina are traversed by important branches of the external carotid artery and trigeminal nerve supplying the lower eyelid, side of the muzzle, and the upper lip, it may ultimately appear that the size of these foramina was directly correlated with the size and mobility of the upper lip in those extinct species that

had long upper canines. It is not known to what extent the long knife-like upper canines of the true saber-tooth cats were curtailed by pendulous upper lips when the mouth was closed in a state of rest; yet obviously such lips would have to be raised to avoid injuring them in the act of biting. Whatever the explanation, the fact remains that in the typical saber-tooth *Smilodon* the infra-orbital foramina are very large and in the false saber-tooth *Nimravus* comparatively small.

The fragment carrying P_4 shows that the mandible at this section is much shallower and broader than the mandible of *Nimravus*. The vertical and transverse measurements of the mandible of *Pogonodon serrulidens*, taken immediately behind P_4 , are 23 mm. and 14 mm. respectively, and in *P. cismontanus* 32 mm. and 14.5 mm. respectively. I can not quote exact corresponding measurements in the types of the several species of *Nimravus*, but in other material, referred to that genus, the height is uniformly about three times as great as the transverse diameter. Cope evidently thought this character to be of taxonomic value, for he stated of *Nimravus gomphodus*¹¹: "The ramus of the mandible is longer, deeper, and more compressed than in the recent species of *Uncia* and the *Pogonodon platycopis*"; and of *Pogonodon platycopis*¹² he wrote "The mandibular rami are robust, and not so high and compressed as in *Nimravus* and its allies." Regarding the form of the anterior portion of the mandible in *Pogonodon serrulidens*, little can be ascertained from the fragment carrying the lower canine; but the broad and flat anterior surface and the thickness of the bone external to the root of the canine are distinctly favorable to the supposition that there was a flange for the protection of the upper canine.

The foramina of the basicranial region, so far as it has been possible to locate them, occur as in *Dinictis* and *Nimravus*. The mastoid process, in point of size, resembles *Nimravus* rather than *Dinictis*, but it is directed a little more forward than in *Nimravus*, in this respect being more like *Dinictis*. The glenoid surfaces

¹¹ E. D. Cope, Report of the U. S. Geol. Survey of the Territories, vol. 3, 965, 1884.

¹² E. D. Cope, Report of the U. S. Geol. Survey of the Territories, vol. 3, 984, 1884.

are not projected downward as in *Hoplophoneus*, but, on the contrary, they rise considerably above the level of a line adjoining the basion and prosthion.

The two fragments of limb-bones, already mentioned, have been compared with the corresponding parts of a puma, *Felis concolor*, No. 015, Y. P. M., whose skull is of almost exactly the same basal length as that of *Pogonodon serrulidens*. The lengths of the ulnæ of the two animals can not be accurately compared, owing to the imperfection of the fossil bone, but a well-marked difference is presented in certain other proportions. While the shaft of the ulna of the fossil species is the more slender of the two, the diameter of its greater sigmoid cavity, measured in the axial direction of the limb, is considerably greater than in the recent species. This indicates also a greater diameter of the trochlea of the humerus. An analogous condition is presented by the fragmentary metatarsal III, the proximal articular surface of the bone being of almost exactly the same extent as in the example of *Felis concolor*, while the shaft of the fossil bone is slenderer.

The present species is differentiated from *Nimravus* and *Hoplophoneus* by the aggregate of the cranial and dental characters, mentioned above, although, as might be expected, not by each of these characters severally. From *Dinictis* its differentiation is not so clearly denoted; yet in consideration of the low nasal region and the relatively high parietal region, the reduction in size of upper premolars 2 and 3, the reduction of the inner root of P⁴ with loss of protocone and addition of a well-marked parastyle, I cannot consistently assign to it a place with *Dinictis felina*, *D. cyclops*, *D. squalidens*, and *D. paucidens*. *Pogonodon* alone of known genera seems open to its reception, and the species to which, on the whole, it shows the closest affinity is Merriam's *Pogonodon davisii*. From this it is specifically distinguished by its smaller size, relatively lower sagittal crest, more compressed form of superior canines,¹³ relatively greater diameter of the postorbital constriction, relatively lower and longer anterior zygomatic pedicle, and judging from Merriam's illustration of the teeth, by the lesser prom-

¹³ The canine alveoli of *P. davisii*, although they do not furnish an exact basis for comparison, indicate a considerably greater transverse diameter.

inence of the inner root of the P^4 . Yet so close to *Pogonodon davisi* is the present species, that the two must share the same fate, should *Pogonodon* in the final analysis fail of recognition as a distinct genus or sub-genus.

Dinælurus crassus, gen. et sp. nov.

(Figs. 4-6.)

Holotype, Cat. No. 10518, Y. P. M. Upper Oligocene (upper John Day), Turtle Cove, John Day Valley, Oregon. Collected by Wm. Davis in 1875.

The type is a cranium without the mandible. It is well preserved, except that the posterior part of the sagittal crest and the contiguous parts of the lambdoid ridges have been destroyed and the postorbital process of the right frontal has suffered some abrasion.

FIG. 4.

FIG. 4.—*Dinælurus crassus*, gen. et sp. nov. Holotype. $\times \frac{1}{2}$.

Dentition.— I^3 , C^1 , P^2 , M^1 . The teeth are worn to a degree that indicates middle age, but not to such extent as to involve any modification of the alveolar parapet. The incisors, in their present condition, closely resemble those of *Nimravus*. Of the right canine only the base of the crown remains protruding from the alveolus. The left canine too has been broken, and a little of the base of the crown is lacking, but its characteristic form is shown sufficiently well to differentiate it from *Nimravus*, *Dinictis*, *Pogonodon*, and *Hoplophoneus*. Briefly charac-

terized, it is more truly feline than the canines of these genera, being more nearly elliptical in section throughout its length and less flattened on the inner surface. The maximum (antero-posterior) diameter of the canine at the alveolar margin is 15.5 mm. and the transverse diameter 11 mm. Dividing the transverse diameter by the maximum diameter, and multiplying the quotient by 100, an index of 71 is obtained. The corresponding indices of the superior canines of several well-known species of extinct Felidæ are as follows: *Nimravus gomphodus* 47, derived from Cope's measurements; *N. debilis* 57; *N. debilis major* 56; *Pogonodon platycopis* 54; *P. davisi* 52, derived from alveolar diameters; *Dinictis cyclops* 64; *D. felina* 47. The diameters of the superior canine of *Pseudaelurus quadridentatus*, at the level of the neck, given by Filhol,¹⁴ transverse 8 mm. and antero-posterior 12.7 mm., yield an index of 71. In examples of three recent feline species I find the corresponding indices to be: *Felis tigris* 73; *Felis concolor* 81; *Cynaelurus jubatus* 79. The vertical length of the canine in the present species cannot be exactly determined because of its imperfection. Its length, however, appears to have been about the same, relative to the length of the skull, as in *Nimravus debilis*, and relatively less than in *N. gomphodus*. Except in young adult animals the length of the canines is of course an unsatisfactory quantity. The anterior ridge of the tooth lies further back from the actual anterior margin than in *Nimravus*, and in this respect also the present species is further advanced and more cat-like. The posterior ridge is not continued along the neck of the tooth to the alveolar margin. This has much to do with the broad, elliptical section of the neck of the tooth. There is no trace, on either side, of P² or its alveolus. For this reason two premolars only are postulated in the dental formula stated above. If in early adult life there was a P², it can hardly have been other than exceedingly small and vestigial, as the shortness of the postcanine diastema, 9.5 mm. on one side and 10 mm. on the other, renders the presence of a P² of any considerable size highly improbable. The shortening of the postcanine diastema with reduction of P² to vestigial size would have practically the same significance as the shortening of the diastema

¹⁴ H. Filhol, Annales des Sciences Géologiques, 21, 76, 1891.

with total loss of P^2 ; either condition would denote a variation from the more complete dentition of *Nimravus*.

P^3 is a large tooth, its principal cusp being sub-equal in size to the paracone of P^4 , as in *Nimravus debilis*. From the last named species it differs in having a slightly greater transverse diameter of the crown relative to the antero-posterior diameter, and the inner division of the

FIG. 5.

FIG. 5.—*Dinaelurus crassus*, gen. et sp. nov. Holotype. $\times \frac{1}{2}$.

posterior root is much stouter, a condition that suggests further advance toward *Pseudaelurus* and *Felis*. P^4 exhibits less development of the inner root than I have observed in any specimens of *Nimravus*, and the inner root does not support a positive protocone. There is less trace of a parastyle than in *Nimravus*, and the external outline of the crown is slightly convex instead of being slightly concave as is usually the case in *Nimravus*. This convexity of crown gives the tooth an appearance of greater breadth, if the buttress formed

by the inner root be disregarded, than in *Nimravus*. M^1 is a very small tooth, and the reduction of its inner lobe has proceeded so far that the transverse diameter of the tooth-crown is not greater than the antero-posterior diameter. Since the external margins of the premaxillæ, between the canines and the lateral incisors, are widely and deeply concave, when viewed from above or below, it may be inferred that the lower canines, which were given clearance by these concave diastemata when the jaws are closed, were also of larger transverse diameter than those of *Nimravus*; and this inference is supported by fragments of a lower canine that were found embedded in the matrix. So deeply concave are these precanine diastemata that they extend further to the rear than the anterior margins of the maxillary parapets enclosing the canine alveoli.

Cranium.—The skull in its general proportions shows a greater resemblance to *Nimravus* and *Dinictis* than to *Hoplophoneus*. From *Pogonodon*, which is in some respects intermediate between *Dinictis* and *Hoplophoneus*, it is not so distinctly separated by cranial proportions as by dentition. The foramina of the basi-cranial region, the height of the glenoid articulations relative to the base-line of the skull, and the form and position of the mastoid processes are essentially the same in the present species as in *Nimravus*; but in the wide spread of its zygomatic arches and in the breadth and massiveness of the entire fore part of the skull—characters that have suggested the specific name—the present species departs widely from the proportions of the species of *Nimravus* and *Dinictis*.

With a basal length of 174 mm., measured from basion to prosthion, the bizygomatic diameter is 164 mm. The relation of these measurements is expressed by the bizygomatic index of 94, which is well outside the range of the corresponding indices of *Nimravus*, *Dinictis*, and *Pogonodon*. The bizygomatic indices of the best known species of the three above-named genera are as follows: *Nimravus gomphodus* 72; *N. debilis* 76; *N. debilis major* 71; *Pogonodon davisii* 74 (approx.); *P. platycopis* 78 (approx.); *P. serrulidens* 77 (approx.); *Dinictis cyclops* 85; *D. squalidens*, No. 8777, A. M. N. H., 82; *D. felina* 76; *D. paucidens* 79; *D. fortis* 82 (from illustration).

Similarly the interorbital breadth of the present species exceeds the corresponding measurements in *Nimravus*, *Dinictis*, and *Pogonodon*, as may be seen from the comparison of the interorbital indices, computed from the interorbital diameter and the basal length. The interorbital breadth index of *Dinclurus crassus* is 35 while that of the other well-known species is as follows: *Nimravus gomphodus* 25 (approx.); *N. debilis* 26; *N. debilis*

FIG. 6.

FIG. 6.—*Dinclurus crassus*, gen. et sp. nov. Holotype. $\times \frac{1}{2}$.

major 24; *Pogonodon davisi* 28 (approx.); *P. platycopis* 27 (approx.); *P. serrulidens* 28 (approx.); *Dinictis cyclops* 33; *D. squalidens*, No. 8777, A. M. N. H., 28; *D. fortis* 33 (from illustration).

The diameter of the postorbital processes of the frontal, which here gives an index of 46 when contrasted with the basal length, is relatively much greater than in *Nimravus* where the range is from 34 to 36. In *Pogonodon* this index has a wider range, as the following values show:

TABLE A.
Measurements of Crania in mm.

Serial nos. of measurements.	<i>Nimravus gomphodus</i> Cope.	<i>Nimravus debilis</i> (Cope).	<i>Nimravus debilis major</i> (Merr.).	<i>Nimravus debilis</i> (Cope).	<i>Nimravus sp.</i>	<i>Umtitis cyclops</i> Cope.	<i>Umtitis squallidens</i> (Cope).	<i>Umtitis felina</i> Leidy.	<i>Pogonodon platycops</i> (Cope).	<i>Pogonodon davisi</i> Merr.	<i>Pogonodon serrulidens</i> sp. nov.	<i>Dimaclurus crassus</i> , gen. et sp. nov.
1 Basal length	198a	176	211.4	199	167a	132	142a	149a	226a	198a	167a	174
2 Axial length	206	180	225	207	175a	142	152	159	240a	208a	178a	185
3 Bizygomatic diameter	142a	133	150	150a	142	112	117	113a	176a	157	128a	164
4 Breadth of ant. nares	30a	29		36	34	22			42			36
5 Interorbital breadth	50a	46	50.7	51	54	44	38		60a	55.5	46	61
6 Diam. of postorbital processes	70a	63.5	71.3	73	77	64	50a	51	69a	84.5	60	81
7 Postorbital constriction	38	37	40.5a	41	41	39	32	33	39	41	42	44
8 Palatal length		84	95.5	93	91	81	65		108a	97a	87a	81
9 Ant. palatal breadth		30		27.5	34	28	23.5		38	30		31
10 Post. palatal breadth		48.5	56	52	51	48a	35		55	50	43.5	58
11 Height of ant. zyg. pedicle	37	29	36	34	34	29	25	15.5a	42	39.5	30	46
12 Length of ant. zyg. pedicle	37	33	39	36.5	38	36	23.5	26a	26	26.6	25	30.5
13 Sup. canine, max. diam.	17	14	16.5	17	18.5	14	12.5	15	26	21.5a		15.5
14 Sup. canine, trans. diam.	8a	8a	9.2	10	10	8	8	7	14	11a		11

a = approximate.

* Measurements 2, 3, 13, 14 are fide Riggs; 6 fide Leidy; 7 fide Adams; while 1, 11, 12 are taken from Leidy's figure of the skull.

Pogonodon davisii 43 (approx.); *P. platycopis* 31 (approx.); *P. serrulidens* 36 (approx.). From the following values of this index for *Dinictis*, it will be seen that only one species of this genus is known to have a relatively greater postorbital breadth than *Dinacelurus crassus*: *Dinictis cyclops* 51; *D. squalidens*, No. 8777, A. M. N. H., 35; *D. felina* 34; *D. fortis* 37 (from illustration).

The breadth of the anterior nares, relative to the basal length, when reduced to an index of 21, is also greater than in the other species with which it has been compared in Table B. *Pogonodon platycopis* with an anterior narial index of 19 approaches the present species most closely in this character, but this index has been computed for only a few type skulls. The breadth of the postorbital constriction, which may in like manner be expressed by the index 25, separates the present species from *Nimravus*, but not from all the species of *Dinictis* and *Pogonodon*, *Dinictis cyclops* having a corresponding index of 27 and *Pogonodon serrulidens* of 25 (approx.), while the highest value in *Nimravus* is an index of 21 for *N. debilis*. The bimastoid diameter is relatively greater than in *Nimravus gomphodus*, *N. debilis*, *Pogonodon platycopis*, *P. serrulidens*, and *Dinictis squalidens* (No. 8777, A. M. N. H.), but slightly less than in *Dinictis cyclops* and *D. felina*. With regard to the bicondylar diameter, the series of type skulls, on which this measurement has been taken, is too limited to admit of any definite statement about the generic value of the bicondylar index.

In conformity with the remarkable breadth of the fore part of the skull, the palate also is broader than in the allied genera with which comparison has been made. This is especially noticeable in the posterior palatal breadth as expressed by the transverse measurement between the inner roots of the upper carnassials. In the present species the index derived from this measurement and the palatal length is 72, which greatly exceeds the corresponding indices computed for *Nimravus debilis*, *N. debilis major*, *Pogonodon davisii*, *P. platycopis*, *P. serrulidens*, and *Dinictis cyclops*. The species that approaches nearest in this respect is *Nimravus debilis major* with an index of 59. The three species of *Pogonodon* and *Dinictis cyclops* fall short of this last value.

For the other species of *Dinictis* this index has not been computed, but, judging from published illustrations none of them appear materially to exceed *D. cyclops* in the relative posterior palatal breadth. The entire posterior portions of the maxillæ, including the zygomatic processes, are exceedingly massive, and the palatine processes of the maxillæ, instead of forming thin, sharp-edged orbital floors, as in the examples of *Nimravus*, *Pogonodon*, and *Dinictis* that I have examined, are thick and rounded posteriorly. The palatal vault is much deeper than in *Nimravus*. This is caused, not by a more pronounced arching of the palatines and the palatine processes of the maxillæ, but entirely by the greater vertical depth of the alveolar processes which form the sides of the vault. A direct result of this modification is seen in the almost complete elimination of the circular pits, in the palatine processes of the maxillæ, that in *Dinictis*, *Nimravus*, *Pogonodon*, *Pseudalurus*, and *Hoplophoneus* receive the principal cusps (protoconids) of the lower carnassials when the jaws are closed. Slight irregularities in the contours of the maxillæ, at the lowest points of origin of the masseter muscles, are by no means uncommon in the Felidæ, recent and extinct, and osteological peculiarities of this description would probably be most noticeable in middle-aged individuals of large size and robust form. Accordingly caution must be exercised lest too much importance be given to differences that may be due solely or largely to individual variation. It would, however, be a serious omission to fail to note the form of the maxillæ immediately external to the superior molars in the present species. On each side of the skull, the powerful development of the masseter muscles has apparently caused changes in the maxillary contours amounting almost to the production of bony masseteric processes. The lack of symmetry, displayed on the two sides, must of course be attributed to individual variation, yet so pronounced is the smaller outgrowth on the left side, that, in view of the unusually massive character of the entire fore part of the skull, it may properly be regarded as of at least specific value. In this connection, the following quotation from Wortman's¹⁵ description of *Dromocyon vorax* is of interest: "On the under surface

¹⁵ J. L. Wortman, This Journal (4), 12, 293, 1901.

of the arch, at the point of junction of the molar with the maxillary, there is a prominent process for the tendinous origin of the most anterior fibres of the masseter. This process is apparently wanting in the carnassident skull, but is large and prominent in that of the Opossum, Dasyure, and to a less extent in *Sarcophilus*."

One of the most distinctive characters of this skull is the form of the portion of the maxilla that, for want of a better name, I have termed the anterior zygomatic pedicle. The minimum height from the alveolar margin to the inferior margin of the orbit is 46 mm. and the minimum length, measured on the outer face of the maxilla, from the infra-orbital foramen to the posterior margin of the zygomatic process, is 30.5 mm. Dividing the first of these measurements by the second, and multiplying the quotient by 100, an index of 151 is obtained. Inspection of Table B for allied genera and species will show that by the proportions of this part of the skull, the present species is easily distinguished from *Nimravus* and from *Dinictis cyclops*, *D. squalidens*, and *D. felina*. Judging from Riggs' figure of the skull of *Dinictis paucidens*¹⁶ and Adams' figure of *D. fortis*,¹⁷ the anterior zygomatic pedicle in these species also is low and long, as in *D. felina*.

The glenoid fossæ are projected no further below the basicranial plane than in *Nimravus*. The mastoid and paroccipital processes are similar in size and direction to those of *Nimravus*. The basicranial foramina occur as in *Dinictis* and *Nimravus*, with this important exception that in *Dinacurus crassus* the posterior opening of the carotid canal is a veritable foramen, completely enclosed by the thin lateral expansion of the basi-occipital, and not merely an open notch in this lateral expansion, as is the case in various examples of *Nimravus*, and as represented in Cope's figure of the type of *Nimravus debilis*.¹⁸ Scott's illustration of the skull of *Dinictis felina*¹⁹ might be supposed to indicate that the carotid

¹⁶ Elmer S. Riggs, Kan. Univ. Quar., 4, No. 4, 239, 1896.

¹⁷ Geo. I. Adams, Am. Nat., 29, pl. XXVI, 1895.

¹⁸ E. D. Cope, Report of the U. S. Geol. Survey of the Territories, vol. 3, 952, 1884.

¹⁹ W. B. Scott, Proc. Acad. Nat. Sci., Philadelphia, 41, 213, 1889.

canal passes through the basioccipital, but I am inclined to believe that such is not the regular occurrence in *Dinictis*, for in Matthew's detailed figure of the basiocranial region of *Dinictis*,²⁰ presumably drawn from the excellent specimen of *Dinictis squalidens*, No. 8777, A. M. N. H., the entrance to the carotid canal is apparently through an open notch in the lateral expansion of the basioccipital, and precisely the same condition has been observed in a skull in the Marsh Collection, Yale University, Cat. No. 10048, identified as *Dinictis squalidens*. The otic bullæ, although incomplete, are much more fully developed than in *Nimravus*, a considerable portion of the thin wall of the bulla, on each side, being preserved in extension of the thickened tympanic ring, and traces of the median walls of the bullæ being visible, closely pressed against the lateral expansions of the basi-occipital. In this respect the present species shows a decided advance beyond the stage reached by *Nimravus*; and a like further development toward the recent Felidæ may be observed in the shortened length of the alisphenoid canal and in the slenderer proportions of the bridge of the alisphenoid bone, protecting the external carotid artery at this point. The brain-chamber appears to have been a little larger, in proportion to the basal length of the skull, than in *Nimravus*, but this superiority may be more apparent than real, since external measurements only are available, and it is possible that the cranial walls of the present species, in keeping with the robust development of the skull generally, may be slightly thicker than in the species with which comparison has been made.

The fossil skull and the hard ashy matrix are very light gray in color, and so appear to satisfy the requirements of the upper John Day beds, as they occur in the Cove on the John Day River, where the record states the specimen to have been found. This reference of the type to the upper John Day is further supported by the advance, shown in certain cranial and dental characters, beyond the stage of evolution denoted by *Nimravus debilis* and *Nimravus debilis major*, both of which species are understood to be from the middle John Day.

²⁰ W. D. Matthew, Bull. Am. Mus. Nat. Hist., vol. 28, 299, 1910.

Genus *Nimravus*.

Four of the crania in the Marsh Collection, whose measurements and indices have been included in the tables, require but brief mention. Those listed under the numbers 10044, 10045, and 10517 have been referred to *Nimravus debilis* because on the whole, although they differ mutually in minor characters, they resemble *N. debilis* and *N. debilis major* rather than *N. gomphodus*. It is true that these three crania have almost exactly the

FIG. 7.

FIG. 7.—*Nimravus debilis* (Cope). Cat. No. 10517, Y. P. M. $\times \frac{1}{2}$.

same basal length as the type of the latter species, viz., 198 mm.; but the argument, founded on size alone, fails, since within the species *N. debilis*, the basal length has a range variation from 176 mm. to 211.4 mm., as shown in Table A.

Three views of the cranium designated as No. 10517 are given in figures 7, 8, and 9, and two views of the cranium No. 10045 appear in figures 10 and 11. The mandible of the latter is the better preserved of the two, and is believed to show the form of masseteric fossa regarded by Merriam as characteristic of *N. debilis* and *N. debilis major*. The following is quoted from Merriam's painstaking discussion of Cope's *Nimravus gomphodus* and *N. (Archæolurus) debilis*: "Practically the only character which seems distinctive is found in

the form and size of the masseteric fossa. In *N. gomphodus* its inferior margin is separated from the lower border of the horizontal ramus by a wide bar. In *A. debilis* the fossa extends farther forward and reaches down to the inferior margin of the jaw, which it may follow for some distance.²¹ Cranium No. 10045 is in

FIG. 8.

FIG. 8.—*Nimravus debilis* (Cope). Cat. No. 10517, Y. P. M. $\times \frac{1}{2}$.

many respects better preserved than No. 10517, although the condyles have been lost, and it shows admirably the positions of the basicranial and palatal foramina, and also the delicate tympanic ring of the right side.

As regards the size of the infracarnassial exostoses, it may be said that in the mandibles of the three individuals, Nos. 10044, 10045, and 10517, these outgrowths are strongly developed. No. 10045 originally possessed four superior premolars on each side, P¹ on the right side being double-rooted. In the mandible of this specimen the first and second premolars have been lost, the only

²¹ J. C. Merriam, op. cit., p. 43.

FIG. 9.

FIG. 9.—*Nimravus debilis* (Cope). Cat. No. 10517, Y. P. M. $\times \frac{1}{2}$.

FIG. 10.

FIG. 10.—*Nimravus debilis* (Cope). Cat. No. 10045, Y. P. M. $\times \frac{1}{2}$.

trace of any of these teeth being the nearly closed alveolus of P_2 on the right side. Just how much reliance can be placed on the diameters of the superior canines, as specific characters, is uncertain; still, attention should be called here to the fact that, in the diametral indices of the superior canines, the three specimens, Nos. 10044, 10045, and 10517, agree much more closely with the types

FIG. 11.

FIG. 11.—*Nimravus debilis* (Cope). Cat. No. 10045, Y. P. M. $\times \frac{1}{2}$.

of *N. debilis* and *N. debilis major* than with *N. gomphodus*; and the same may be said with reference to the height index of the anterior zygomatic pedicle.

The fourth skull, No. 10046, Y. P. M. (fig. 12), whose measurements and indices are given under the genus *Nimravus*, is much smaller than the three last enumerated, being in fact even smaller than the type of *N. debilis*. The superior canines are relatively longer than in that type, yet their measured diameters are almost exactly equal to those of *N. debilis*. The postcanine diastemata are short; and in the reduction of the premolar teeth, as well as in the slight development of the infracarassial exostoses, this specimen differs from the type of

N. debilis. Viewed in profile, the anterior surface of the mandible appears to rise more nearly at a right angle with the horizontal ramus than in the types of *N. debilis* and *N. gomphodus*; and this squarely truncated appearance of the mandible is increased by the development of a prominent mental rugosity. Labels accompanying this skull show that, at one time, it was provisionally identified as *N. gomphodus*, at another time as *N. debilis*. On the whole its indices point to a closer affinity with *N. debilis* than with *N. gomphodus*. The skull of Cope's

FIG. 12.

FIG. 12.—*Nimravus* sp. Cat. No. 10046, Y. P. M. $\times \frac{1}{2}$.

N. confertus is but little smaller than No. 10046; but as *N. confertus* is represented only by a very imperfect mandible, a satisfactory comparison of the specimens is impossible. There is, however, a remarkable similarity in the form of their mandibular symphyses. In each the symphysis is very short horizontally and extends but little to the rear of the posterior margins of the lower canine teeth. No. 10046 is supposed to have been found in the middle John Day.