

Article XX.—OXYÆNA AND PATRIOFELIS RESTUDIED AS TERRESTRIAL CREODONTS.

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PLATES XVIII AND XIX.

Comparatively little was known of the skeletal structure of these animals until the American Museum Expeditions of 1891 and 1893 secured complete skeletons of each, which Dr. J. L. Wortman carefully described and figured. After a searching comparison with modern land and water Carnivora he concluded that *Patriofelis* was probably *aquatic in habit and possibly ancestral to the modern Pinnipedia* and that the much older type *Oxyæna* and the more recent type *Oxyanodon*, bore similar testimony to affinities with the Seals. In

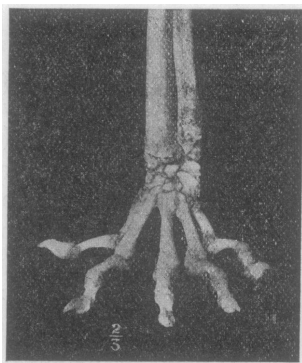


Fig. 1. *Didelphys virginiana*, left fore foot.

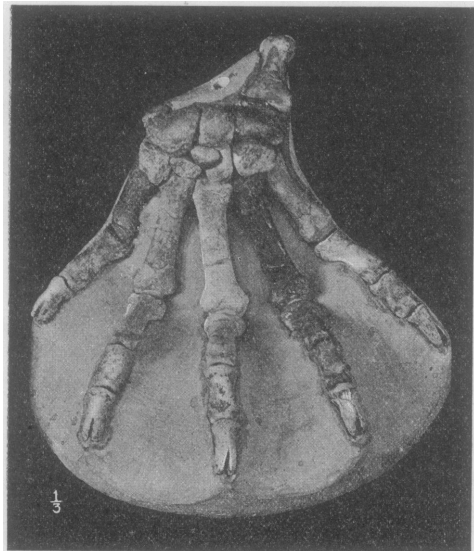


Fig. 2. *Patriofelis ferox*, left fore foot, from mounted skeleton.

describing *Patriofelis* he remarked: "The broad, flat, plantigrade feet with their spreading toes suggest at the first glance their use for swimming" ('94, p. 161).

Recently, under the direction of the present writer, the *Oxyæna lupina* skeleton has been mounted and the *Patriofelis ferox* skeleton taken apart and remounted by Mr. Hermann, head preparator. At the same time several

alterations were made in the restored parts of the skull of *Patriofelis*, the teeth were restored, one dorsal vertebra added, and, for reasons stated below, the feet reset in an angulate subdigitigrade instead of a plane plantigrade fashion. A more thorough study of the dentition of this animal was also made from all the materials in the Museum.

In this connection a careful restudy of all the evidence led the writer to the opposite conclusion, that these were powerful *terrestrial, or partly arboreal, animals, analogous to the Cats in habits of feeding*, with analogous (not homologous) sectorials, clumsy in limb structure, without prehensile claws, and presenting no evidence of successors among the modern Carnivora. The reasoning upon which this conclusion is based is, in brief, that the alleged points of resemblance to the Pinnipedia are in part persistent primitive characters due to the descent of the Oxyænidæ and Pinnipedia from a common Insectivore-Creodont ancestor, in part homoplastic adaptive characters due to similar habits or uses of certain parts of the body, while the main trend of adaptation is divergent from the Pinnipedia as seen both in the teeth and feet, and from all other modern Carnivora, especially as seen in the teeth.

In this paper the principal osteological and dental characters will be briefly restated with a number of corrections and additions, referring the reader back to Wortman's fuller papers for details.

I. EVIDENCE FOR TERRESTRIAL HABITS.

1. *The Feet.*

It was claimed (Wortman, '94, p. 161) that the plantigrade feet with spreading toes indicated a webbed ('94, p. 146) or swimming foot. It will be observed by comparison of the photographs (Figs. 1, 2) that the feet of *Patriofelis* are no more widely spread than those of the terrestrial and arboreal *Didelphys*. Moreover, the planes of the articular facets of the metapodials and phalanges in *Patriofelis* entirely forbid the supposition that this animal was plantigrade.

The writer has pointed out ('00, p. 91) that the angulation of the limbs in Ungulates is expressed in the angles which the prox-

imal and distal facets make with the long axes of the shafts; considering the shafts as perpendicular, facets in horizontal planes indicate straight limbs; facets in oblique planes indicate angulate limbs. Exactly similar principles apply to the hand and foot of Ungulates, as shown in Fig. 3. In the passage from *Otaria*

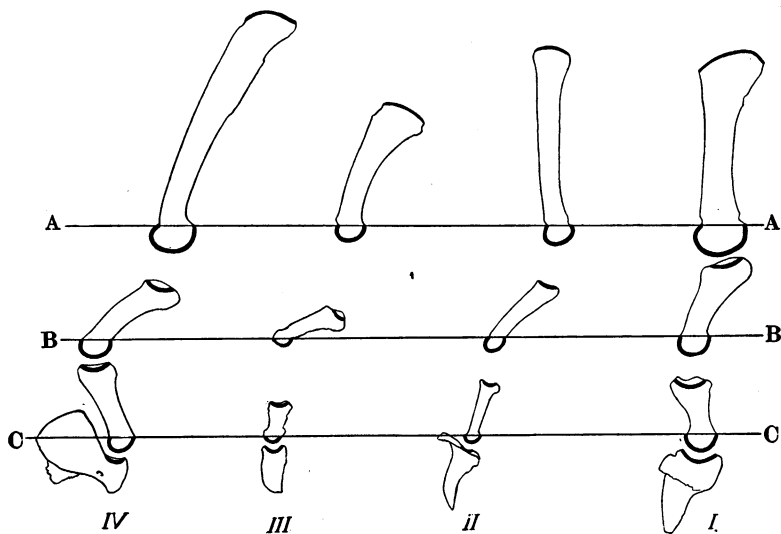


Fig. 3. Angulation of facets in feet of (I) *Ursus*, (II) *Procyon*, (III) *Patriofelis*, (IV) *Felis*, showing increased obliquity in relation to increased angulation. A, distal facets of metacarpals; B, distal facets of 1st phalanx; C, distal facets of 2d phalanx.

(secondarily plantigrade), *Ursus* (primarily plantigrade), *Procyon* (subdigitigrade), and *Felis* (digitigrade), we see that the planes of the distal facets give certain indication of the modes of progression.

1. As regards angulation, *Patriofelis* is shown to occupy a position intermediate between *Procyon* and *Felis*, with a decidedly *angulate* foot, the angles between phalanges 1 and 2 being especially acute. This proves that the metapodials, as well as phalanges 1 and 2, were raised off the ground by palmar and plantar pads as in *Felis*. Taking a conservative view, the feet of *Patriofelis* may be described as subdigitigrade in position. The straight terminal claws indicate that they entirely lacked the grasping and tearing power developed in *Felis*.

2. As observed by the writer and Wortman in *Oxyæna* ('99, p. 144) : "There is reason to believe that the habitual position of the



Fig. 4. *Patriofelis ferox*, typical lumbar vertebra, posterior view.

foot was digitigrade, but there is no evidence of any retractility of the claws." Beginning therefore with a subdigitigrade foot, the progression from *Oxyæna* to *Patriofelis* does not indicate an advance toward secondary plantigradism, as would be the case if these animals were becoming more and more aquatic in habit. On the contrary, the analogy of the feet of the known *Oxyænidæ* with those of *Procyon* and *Didelphys* would indicate that they were used mainly in slow terrestrial or arboreal locomotion, and

exceptionally if at all in swimming.

2. *The Dentition.*

The lack of prehensile power in the feet of *Patriofelis* is compensated for in an extraordinary manner by the increased prehensile power in the progressive evolution of the teeth; this again is analogous to that of the *Felidæ* in its *extreme heterodontism* or specialization, whereas the key-note of dental evolution among the *Pinnipedia* is a *secondary homodontism* or reduction of the premolars and molars to a common triconodont pattern. The dental parallelism of the *Oxyænidæ* with the *Felidæ* is well stated by Wortman ('99, p. 140).

The progression of both skull and teeth in the *Oxyænidæ* is towards a raptorial type with increasing temporal and masseter muscles, deep zygomatic arch and large temporal fossa, heavy jaw, deep and broad symphysis, with the biting power concentrated at three points, namely, the canines, the fourth lower premolar, and the enormous carnassial teeth; the carnassials

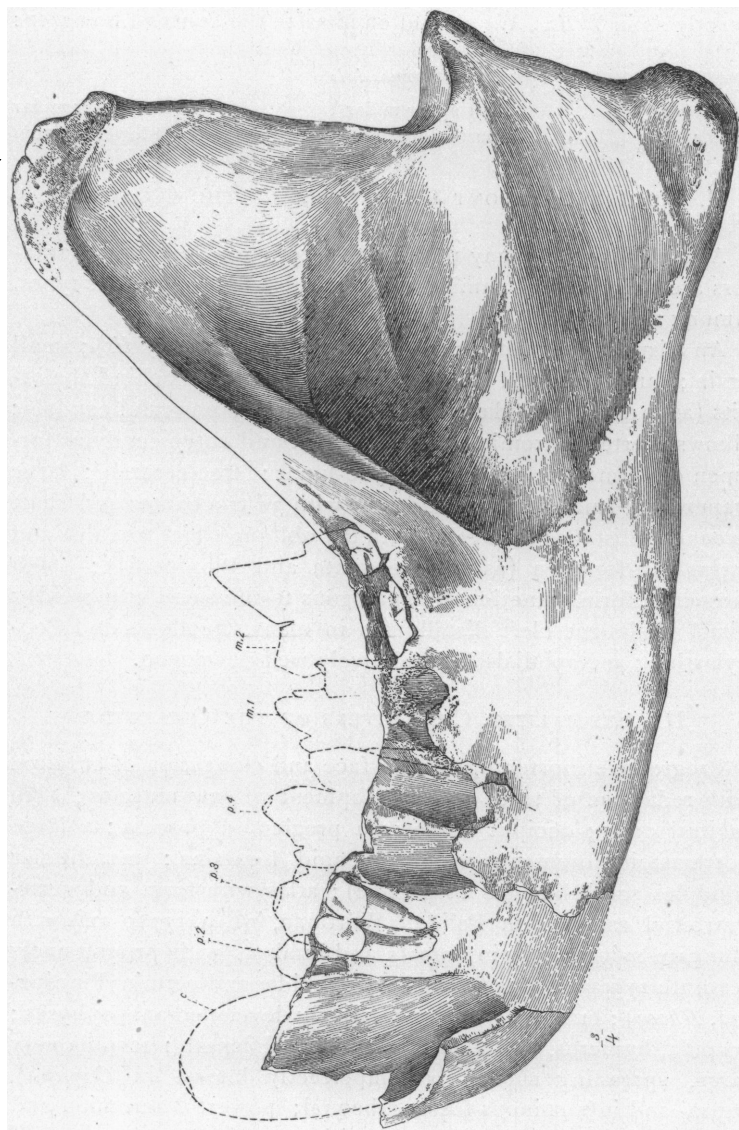


Fig. 5. *Patriofelis ferox*. Left lower jaw, external view (No. 1597 coll. A. M. N. H.).
Specimen included in mounted restoration.

are adapted to flesh and bone cutting by the loss of the talonid exactly as in *Felis*. We should emphasize the contrast however :

| | <i>Carnassials</i> | |
|-----------------|-----------------------|--------------------|
| <i>Oxyænida</i> | First upper molar | Second lower molar |
| <i>Felida</i> | Fourth upper premolar | First lower molar |

II. COMMON CREODONT CHARACTERS OF THE OXYÆNIDÆ.

As stated above, many primitive Insectivore-Creodont characters are found in this family which are also found in other types. Among these are :

An alisphenoid canal ; exposure of mastoid (*Patriofelis*) ; small brain ; large temporal fossa ; cranium constricted behind the orbits (as in *Mesonychidæ* and *Arctocytonidæ*) ; powerful caudals ; elbows everted ; prominent deltoid crest and entepicondylar foramen of humerus ; separate scapho-lunar ; free centrale ; large trapezium ; small trapezoid ; femur with 3d trochanter and shaft expanded distally ; astragalus with flat oblique tibial trochlea and astragalar foramen (as in *Creodonta* and *Pinnipedia*) ; small mesocuneiform (functionally analogous to the small trapezoid) ; distal phalanges cleft distally (as in many *Creodonts* and *Condylarthrs*) ; metapodials I-V relatively well developed.

III. SPECIALIZED CHARACTERS OF THE OXYÆNIDÆ.

Progressive shortening of the face and elongation of cranium with reduction of teeth and development of jaw muscles ; high sagittal crest ; occiput narrow ; a preglenoid process ; a large postmastoid foramen ; no postglenoid foramina ; mandibular condyles scroll-like (as in *Felidæ*) ; atlas with form and vertebrarterial canal as in *Felidæ* (Wortman, '94, p. 137) ; axis with elongate spine ; certain dorsals and lumbar with progressively revolute zygapophyses (as in *Mesonychidæ* and certain *Pinnipedia*, *Phoca*) ; lumbar with progressively developed anapophyses ; scapula, humerus, and ulna of about equal length ; scapula very large, spreading superiorly (imperfectly known in *Oxyæna*), supra- and infraspinous fossæ subequal ; powerful acromion and metacromion processes ; humerus with exceptionally elongate and prominent deltoid crest, powerful supinator ridge, large entepicon-

dyle and entepicondylar foramen ; olecranon process of ulna elongate, ulna grooved anteriorly ; limited rotation of forearm owing to proximal expansion of radius ; feet spreading ; trapezium extended transversely (as in Pinnipedia, Wortman) ; dorsal portion of distal metapodial facets hemispherical, ventral portion keeled (as in Fissipedia, Wortman) ; digits angulate, the second

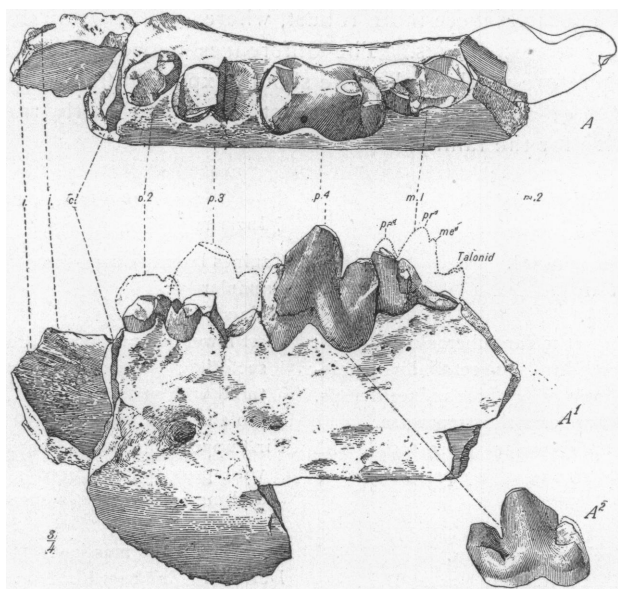


Fig. 6. *Patriofelis ferox*. Lower jaw, left side ; A, crown view ; A¹, external view ; A² internal view of 4th premolar (No. 1508 coll. A. M. N. H.).

phalanges strongly flexed upon first phalanges ; subungual (retractile) processes of distal phalanges well developed (as in Pinnipedia ; in Fissipedia subungual processes small, foramen vestigial, Wortman) ; ilium expanded on superior (post-iliac) border into a broad lamina ; pubic symphysis not ankylosed ; patella large ; fibula unreduced, articulating with side of astragalus but not articulating with calcaneum (progressive) ; tibia with twisted shaft and cnemial spine ; tibio-astragalar facet flat, obliquely placed ; calcaneo-cuboidal facet very oblique ; large astragalo-cuboidal facets ; external calcaneal tubercle large (as in many Creodonts and Amblypods).

IV. PROGRESSIVE AND SPECIFIC CHARACTERS.

The above and the following characters show probably the *main trend of evolution in the Oxyænidæ*; they are derived from a comparison of *Oxyæna lupina* (Wasatch, Sparnacien) and *Patriofelis ferox* (Bridger, Bartonien); it is important to note that *O. lupina* is an exceptionally slender species, some of its Wasatch contemporaries were more robust, whereas *P. ferox* is an exceptionally robust species. The differences between these species are therefore partly such as we should expect to find in the comparison of any slender and robust types, and partly truly progressive for the family.

| <i>Oxyæna lupina.</i> | <i>Patriofelis ferox.</i> |
|---|---|
| Incisors $\frac{3}{8}$ | ? Incisors $\frac{7}{2}$ |
| Canines sub-oval. | Canines laterally compressed. |
| Premolars $\frac{1}{4}$. | Premolars $\frac{3}{8}$. |
| Molars $\frac{3}{8}$. | Molars $\frac{1}{2}$. |
| First lower molar tuberculo-sectorial; second ditto sub-sectorial with talonid preserving three reduced cusps. | First lower molar reduced, tuberculo-sectorial; second ditto truly sectorial with vestigial talonid. |
| Second upper molar transverse. | Ditto absent. |
| First upper molar sub-sectorial, with protocone relatively prominent. | First upper molar blade-like, sectorial, with protocone reduced and para- and metacones greatly elevated and connate. |
| Skull relatively slender. | Skull broad and massive. |
| Dorsals 13, lumbars 7 = 20 D.L. | Dorsals 14, lumbars 6 = 20 D.L. |
| | Sacrals 3; 2 sacrals uniting with ilium. |
| Caudals numerous. | Caudals 28, large chevrons. |
| Limbs, chest, and back slender. | Ditto robust. |
| Lumbars typical with simple zygapophyses; small anapophyses on L 1-2. | Lumbars, massive, heavy, with extremely revolute zygapophyses; anapophyses on L 1-4. |
| Tibia with short cnemial spine. | Tibia with elongate cnemial spine. |
| | Six sternebrae. |
| | Ribs heavy. |

V. SYSTEMATIC REVISION.

Family *Oxyænidæ*. Terrestrial or arboreal Creodonts; strictly carnivorous in habit; enlarged canines; second upper molars when present transverse; powerful sectorials formed of first upper and second lower molars; incisors,

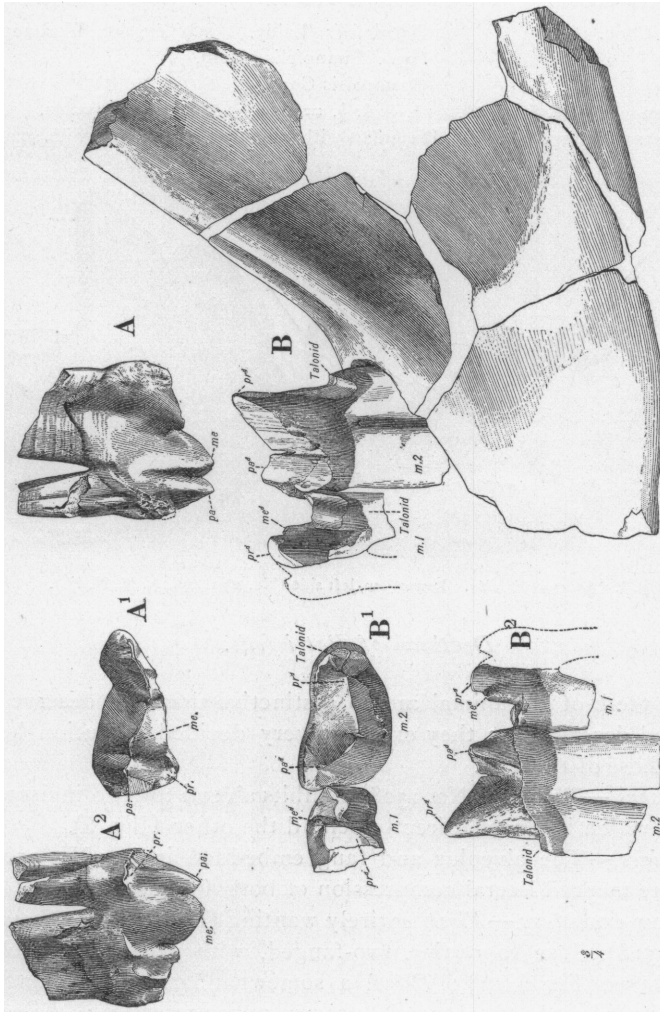


Fig. 7. *Patriofelis ferox*. A, external view; A¹, crown view; A², internal view of isolated 1st superior premolar (No. 2903 coll. A. M. N. H.). B, type of *Protoparacitellus* (No. 4805 coll. A. M. N. H.); external view of jaw; B¹, crown view of 1st and 2d molars; B², internal view of 1st and 2d molars.

premolars, and molars progressively reduced and specialized; subdigitigrade, metapodials 5-5 spreading, not interlocking.

| Lower Eocene. | Middle Eocene. | Upper Eocene. |
|--|--|--|
| <i>Oxyæna</i> Cope. | <i>Patriofelis</i> Leidy. Syn: <i>Limnofelis</i> Marsh. <i>Protopalsis</i> Cope. | <i>Oxyænodon</i> Wortman. |
| Dentition $\frac{2}{1} \cdot \frac{1}{1} \cdot \frac{4}{2} \cdot \frac{2}{2} = 40$. | $\frac{2}{1} \cdot \frac{1}{1} \cdot \frac{2}{2} \cdot \frac{1}{1} = ? 32$. | $\frac{2}{1} \cdot \frac{1}{1} \cdot \frac{4}{2} \cdot \frac{2}{2} = 40$. |
| Premolars with large talonids. | Premolars with talonids. | Premolars with small talonids. |

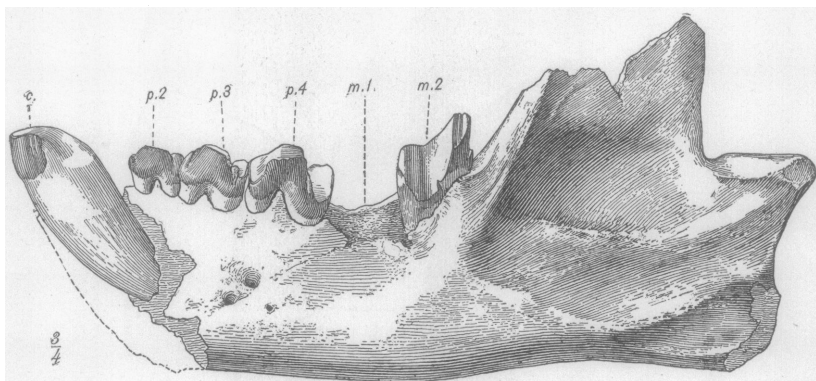


Fig. 8. *Patriofelis ulta*. Lower jaw, left side (No. 2691, coll. A. M. N. H.).

Dentition of Patriofelis.

The teeth of the animal are so distinctive that they deserve a detailed description; they exhibit a very decided evolution beyond those of *Oxyæna*.

Incisors.—The jaw (No. 1508) exhibits alveoli for two incisors, one of which is placed directly behind the other (Fig. 6).

Canines.—The alveolus and fang embedded in jaw No. 1508 indicate marked lateral compression of both fang and crown.

Lower premolars.—*First*, entirely wanting (Figs. 5, 6); *Second* (No. 1508), close to canine, two-fanged, with crown obliquely placed (see Fig. 6, A); *Third*, a somewhat larger tooth longitudinally placed, two-fanged, crown not preserved; *Fourth* (No. 1508, Fig. 6, A, A'), a triconodont type of tooth; enlarged, antero-posterior diameter of fangs = 210 mm.; a large central protoconid, an anterior cusp (broken away in No. 1508),

and a posterior cusp, or talonid, with a small basal postero-internal cusp.

Lower molars.—*First*, a relatively small tooth; antero-posterior diameter of fangs = 170; in No. 4805 the posterior half of the crown only is preserved; it exhibits the protoconid, a small elevated metaconid; the talonid is narrow and feebly tri-cuspidate; in No. 1508 the paraconid is partly preserved; *Second*, a powerful shear (No. 4508, Fig. 7, B) formed of an outwardly placed paraconid and a sharp elevated protoconid; the metaconid vestigial or represented by a very low ridge; the talonid reduced to a cingulum.

First upper molar.—(No. 2303, Fig. 7, A, and No. 1508, A, both teeth of the left side.) This is a powerful carnassial; the elongated shear (No. 2303) consists of the greatly modified trigon and metastyle; the protocone is depressed and reduced to a basal spur; the paracone and metacone consist of a pair of elevated connate subequal cusps; the metastyle is an elongate less elevated shear. In the greatly worn condition seen in No. 1508, A, as well as in No. 2691, *P. ulta*, the crown of the tooth retains its sharpness, proving that these teeth were employed as in *Felis*.

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