Article XVIII. — CHARACTERS OF PROTOCERAS (MARSH), THE NEW ARTIODACTYL FROM THE LOWER MIOCENE.

By Henry Fairfield Osborn and J. L. Wortman.

Among the many interesting discoveries made by the American Museum Expedition of 1892 were the feet and portions of six skulls of a species of Artiodactyl which appeared to present entirely new characters. The finest specimen has proved to be a perfect skull with complete dentition; associated with another skull are the complete fore and hind feet. In writing from the field-camp Dr. Wortman described the skull as four-horned, but in the Museum, while the specimen was being worked out of its sandy matrix, we found six, eight and finally no less than ten bony protuberances upon different portions of the cranium! The chief pairs are on the parietals and maxillaries; prominent laterally projecting plates are also developed upon the supraorbital ridges of the frontals, and the frontals develop a second conical pair close to the nasal suture above the lachrymals. Besides the great vertical plates, the maxillaries present two lateral protuberances just above the third premolar on either side. The shape of these processes dismisses at once the idea that they were horn cores and indicates that they bore simply a dermal covering. Other features of the skull while less striking and novel are no less unique; among these are the deep cleft between the maxillary plates, the abbreviated nasals, the small vacuity between the nasals and frontals, the prominent ridge extending forward from the anterior margin of the orbit, and the prominent rugose sagittal crest. The grotesque appearance is heightened by the large canines which lend to the lateral aspect of the skull a decided suggestion of resemblance to that of *Uintatherium*.

The edentulous premaxillaries and short-crowned selenodont molars have the true ruminant appearance, but the structure of the feet at first sight suggests the Tragulines. We find two large and two small toes in the fore foot, all of them entirely

separate, while the hind foot is supported upon two elongated and closely conjoined digits which form an incipient cannon bone.

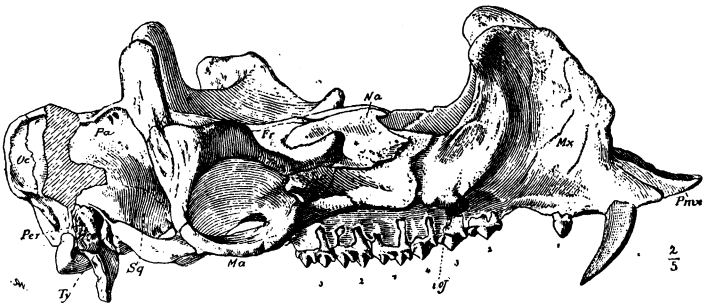


Fig. 1. Lateral view of the male skull slightly oblique in position, $\frac{2}{5}$ natural size.

Before looking for relatives of this remarkable animal, a second skull was uncovered, and it at first appeared to represent an entirely distinct species. The parietals were unfortunately lost in this specimen, but the frontals are complete and display no traces of either of the protuberances. Further examination, however, indicated the bases of the maxillary plates and of feebly developed canines, which suggested the idea that this skull might represent the female type while the former skull represented the male type of the same species. At this point Marsh's description of *Protoceras celer* was carefully studied and finally the supposed female skull was taken to the Yale College Museum, and upon being placed side by side with the type of *Protoceras* it was at once evident that they belong to the same species.

This enables us to fully characterize the male and female skulls of *Protoceras celer* Marsh, and to define the family *Protoceratidæ*, which Marsh was unable to do from lack of sufficient material.

We may now (1) define the family, (2) give a new definition of the genus based upon the discovery of the sexual characters and differences between the male and female, and upon the characters of the feet, (3) define the species. (4) We will then expand Marsh's description of the female skull; (5) in comparison with the male skull; (6) the structure of the fore and hind feet together with the cranial characters throws some light upon (7) the affinities of *Protoceras*.

Order ARTIODACTYLA.

Family PROTOCERATIDÆ *Marsh.*[1]

Molars brachy-selenodont. Upper and lower canines in both sexes. No upper incisors. Lower canines and incisors forming a single series. Male skull with bony protuberances upon parietals and frontals and vertical plates upon frontals and maxillaries. No true horns. Females with small parietal protuberances (maxillary plates unknown). Orbits posterior in position, prominent, widely separated. Optic foramina not confluent. Lachrymal duct with single orifice within rim of orbit. No lachrymal vacuity. Lachrymals articulating with nasals. Nasals extremely abbreviated. Maxillaries with large, free, superior border, produced (in the males) into a broad thickened plate rising above vertex of skull.

Fore feet with trapezium, trapezoid and magnum developed and distinct. Four complete, separate and functional metapodials, carpo-metacarpal articulation 'inadaptive.' Lunar resting equally upon unciform and magnum. Hind feet with two functional metapodials, lateral toes (II and V) incomplete. All elements of the pes separate in the young; tendency to form a cannon bone (III and IV) in adult stage. Ectocuneiform and navicular tending to combine (not with each other) with cuboid.

Fibula reduced to a malleolar bone tending to coösify with tibia. Ulna well developed, tending to coösify distally with radius.

This family is at present only known to include the genus *Protoceras* from the upper part of the White River Beds (Lower Miocene) of North America.

Genus **Protoceras** *Marsh.*[2]

Dentition: I $\frac{0}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$. First upper and lower premolars simple, bifanged, in diastema midway between canine and second premolar. Third and second upper premolars with strong internal cingula. Fourth upper premolar with single external and internal crescents. Lower incisors and canines with narrow spatulate crowns. Posterior nares open between second molars. Tympanic bulla not inflated. A strong lateral maxillary ridge.

Species **Protoceras celer** *Marsh.*[3]

Male: parietal protuberances large, laterally compressed, close together.
Female: parietal protuberances small, conic, widely separated.
Type: a female skull in the Yale College Museum.

[1] "A Horned Artiodactyle (*Protoceras celer*) from the Miocene," American Journal of Science, January, 1891, pp. 81, 82.

[2] Loc. cit.

[3] Loc. cit.

The Skull.

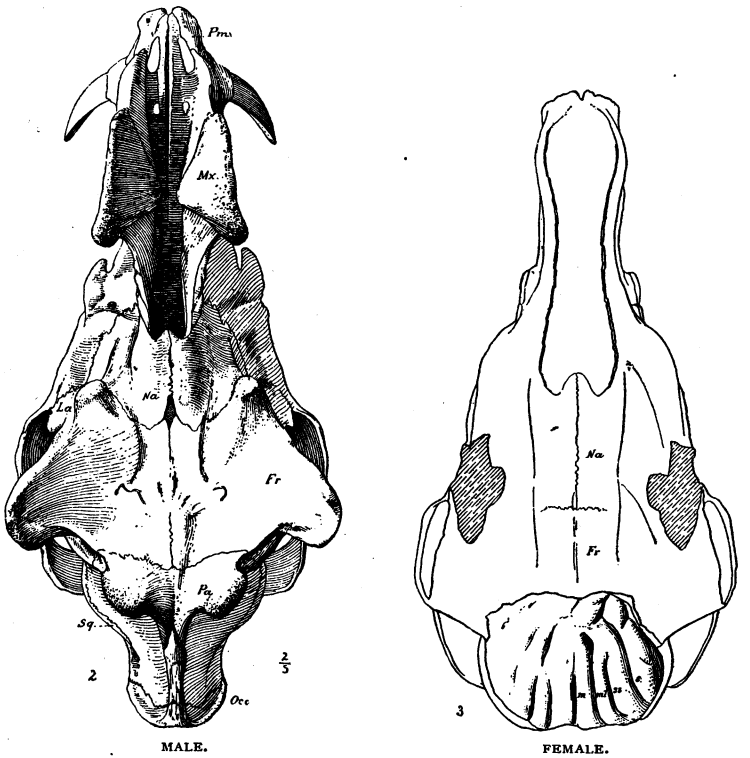
The Female Skull of Protoceras. History.—Marsh's type specimen is a skull with the posterior portion in fair preservation and the anterior portion broken off in a line just behind the anterior extremity of the nasals passing down just in front of the second premolar. In the following abstract of the author's description we omit some of the details, such as the absence of the first premolar, which are found to be incorrect:

"In general form and proportions this skull is of the ruminant type. Its most striking feature is a pair of small horn-cores situated, not on the frontals, but on the parietals immediately behind the frontal suture....The horn-cores are well separated from each other, and point upward, outward and backward, overhanging somewhat the temporal fossæ. They are conical in form with obtuse summits....The occiput is very narrow, indicating a small cerebellum, and the occipital crest is very weak. The occipital surface slopes backwards....The facial region of the skull is narrow and elongate. On the outer surface of the maxillary just above the antorbital foramen, there is a deep depression which probably contained a gland. The usual ruminant fossa in front of the orbit appears to be wanting. The orbit is large, and completely closed behind by a strong bar of bone....The paroccipital processes were well developed, but there were apparently no auditory bullæ....As the animal represented by this skull is very distinct from any hitherto described, the genus may be named *Protoceras* in allusion to the early appearance of horns in this group. The species may be named *Protoceras celer.* The characters now known suggest affinities with the giraffes, but indicate a distinct family which may be called the *Protoceratidæ.*"

Measurements of Type.—Distance between orbits across frontals, 75 mm., about 3 inches. Distance between summits of horn-cores, 32 mm., about 1¼ inches. Width of palate between true molars, 32 mm., about 1¼ inches. Length of skull, estimated at 200 mm., about 8 inches.

The female skull in the American Museum collection is in fair preservation; it has the cerebral hemispheres exposed, and entirely lacks the parietals and the occipital ring; the nasals are complete to the tip; the maxillaries have lost the superior border; the premaxillaries are complete. It is thus impossible to determine whether the maxillaries bore the large vertical plates which constitute so striking a feature of the male skull. Three features indicate that these plates were absent; first, the upper broken

border of the maxillaries is very thin; second, there are no protuberances or plates upon the frontals; third, the lateral ridge upon the maxillaries in front of the orbits is comparatively feeble and lacks the anterior projection. The wide contrast between the male and female skull is exhibited in the accompanying figures of the dorsal surface, and may be briefly summarized. The male skull is ornamented or armed with ten protuberances; the female skull bears but two small, low protuberances upon the parietals, not larger than the anterior pair upon the frontals of the male.



MALE. FEMALE.

Figs. 2 and 3. Top views of the male and female skulls, $\frac{2}{5}$ natural size.

The *brain* is deeply convoluted. We observe upon each hemisphere four longitudinal gyri, these according to Owen's nomenclature would be the median (*m.*), medilateral (m^1.), supersylvian (*ss.*), and sylvian (*s.*). This skull measured when complete about

225 mm. Below are the principal measurements of the male skull, which belonged to a younger individual, and is slightly inferior in size, measuring 215 mm.

Measurements of Male Skull.

	MM.
From occipital condyles to tips of premaxillaries	215
Greatest width, outside supraorbital plates	111
Length of face, from anterior margin of orbit forwards	130
Length of cranium from anterior margin of orbit to occipital crest	100
Greatest depth of maxillary plates	115
Outside measurement, upper molars	57
Length pm^2–m^3 inclusive	65

The Male Skull, Figs. 1, 2, 3.—The complete skull belongs to an animal about the size of a sheep, and is in an almost perfect state of preservation; all the sutures can be made out with certainty as outlined in the figures. The collection also contains portions of two other male skulls, one complete except in the posterior part and somewhat crushed; another, consisting of the complete posterior region and molar teeth; a third consisting of the anterior portion of the skull with the lower jaw as far back as the first premolar; with this individual the fore and hind feet were found associated. There are also two other fragmentary skulls not yet removed from the matrix.

Aside from the protuberances, the skull is long and low. Compared with the cervine type it is remarkable in the relative non-expansion of the olfactory chamber; there is in fact no space for great extension of the turbinals. Upon the upper junction of the frontals and nasals is an apparent foramen (this is less open in the more mature female skull).

A second distinctive feature is the exceptional development, correlated with the protuberances, of prominent ridges of bone which form a strong outer framework, thus the temporal fossa is bounded by rugose lambdoidal and sagittal crests, and by a strong buttress extending from the parietal horns to the postorbital bar and supraorbital plate. In front of the orbits the lachrymals are depressed between two ridges, the upper ridge extending into the frontal protuberance, the lower ridge consisting first of the malar (*ma.*) and then passing into the maxillaries, and terminating in a

stout incurved hook above the infraorbital foramen. From this hook extends forward and upward a stout flange to brace the high maxillary plates. Immediately above this hook is the pit mentioned by Marsh; it probably did not contain a gland. Again, the vertical maxillary plates have a strong inward convexity, but are not quite in contact.

The protuberances are of two kinds; there are, *first*, the subconical projections, such as the elevated parietal processes crowning the superciliary ridges, which diverge, <-like, from the sagittal crest to the orbits; these parietal processes are flattened oval, and obliquely placed. Of somewhat the same character are the small semiprocumbent processes at the anterior margins of the frontals just above the lachrymals. The smallest of these processes are the hooks upon the lateral maxillary ridges, which none the less illustrate the extraordinary tendency of this little skull to rival the Dinocerata in developing a protuberance at every available point.

There are, *second*, the bony plates, which are flattened, with rugose margins. The supraorbital plates are developed upon the frontals and completely overhang the orbits, as shown in Fig. 2. Somewhat similar plates are seen in other Ungulates. The whole conformation of the maxillaries is, so far as we know, unique among the mammalia; the superior borders curve sharply upward into two powerful plates of bone, concave on the outer side and convex on the inner, and rising to the level of the parietal processes, with a concave posterior and convex anterior border.

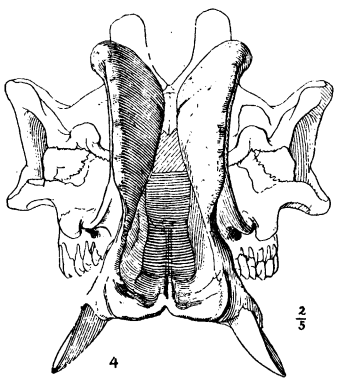


Fig. 4. Anterior view of the male skull, $\frac{2}{5}$ nat. size.

Cranial and Facial Bones.—The limits of the various elements of the skull can be clearly made out. The occiput is narrow and overhanging, the occipitals extend into the temporal fossæ; the paroccipitals are overlapped by the rugose periotics, beneath which the slender paroccipital processes emerge. The external

auditory meatus is narrow and incompletely surrounded by the small tympanic elements. The squamosals have a small ascending plate ; as observed by Marsh, the postglenoid processes are small ; the zygoma is rather slender. The malars are large, forming a horizontal infraorbital plate and extending forwards upon the face. The lachrymals are depressed but extend into a narrow surface of contact with the nasals ; the foramina are internal. The parietals embrace the bases of the two posterior protuberances. The frontals bear the supraorbital plates and median protuberances ; their upper surface has a strong median convexity bounded laterally by grooves for the supraorbital arteries and frontal nerves. This convexity continues into the nasals and terminates at their tips ; in the female it forms the vertex of the skull, but in the male it lies in the centre of a hollow basin. The nasals are somewhat overlapped anteriorly by the maxillaries. The base of the skull displays a long narrow palate, narrowing opposite the diastema and broadening out into the smooth, perforated premaxillaries. The posterior nares open between the second molars.

The Foramina.—The infraorbital foramen is placed directly above the third premolar. The lachrymal foramen is within the orbit. There is a postglenoid foramen. The foramina lac-medius and lac-posterius are small. The foramen ovale is distinct.

The Dentition.—In the male the superior canines are trihedral and project outwards and backwards ; the outer and inner faces are very slightly convex ; the posterior face is flat and slightly worn. At a short interval are the first premolars, simple, laterally compressed crowns supported upon two fangs. The second premolars are behind a slightly greater interval. The outer surface is divided into a central cusp and two basal cusps, flanked by anterior and posterior styles ; there is a sharply defined internal cingulum. The second premolar repeats the same characters, being more sharply defined. The fourth premolar has a shorter external crest, and the internal cresent is strongly developed, replacing the internal cingulum of the second and third premolars.

The true molars present a strong internal basal cingulum which envelops the inner surface of the crown; the outer surface of the crown is marked by prominent basal cusps, viz.: the parastyle, mesostyle and metastyle; the main external cusps are sub-crescentic, and present a strong median external ridge, their outer surface therefore is convex rather than flattened; the internal cusps, protocone and hypocone, are sharply crescentic. The molar dentition is therefore of an early type and decidedly brachyodont.

The inferior incisors present delicate spatulate crowns; the median second incisors are slightly larger than the lateral incisor, which is very delicate. The canine has precisely the same delicate structure as the lateral incisor. In the female the canines are apparently very much smaller, not exceeding half the diameter exhibited in the male.

In the fragment of the lower jaw the first lower premolar is seen to be separated widely from the canine.

The Fore and Hind Feet.

The materials upon which this description is based consists of an almost complete manus, including the distal ends of ulna and radius, together with both hind feet, to which the distal ends of the tibia and fibula are attached. Associated with these feet was found the anterior portion of the cranium bearing the lower jaw, so that their reference to *Protoceras* is undoubted. These are all that remained of what was once a complete skeleton deposited in position, but which had been almost completely destroyed by weathering away of the matrix. They pertain to a comparatively young animal in which the epiphyses had not yet fully united.

A second specimen is represented in the collection, consisting of the greater portions of both hind feet. This also pertains to a moderately young animal, but the epiphysis appear to be well joined to the rest of the bone and it can perhaps with safety be said to be fully adult.

In a general survey of the proportions of the limbs the same striking disparity in length and size is to be observed as is found in the Tragulidæ. The pes is much longer and stronger than the manus and, as in the Tragulines, had become much more

highly specialized in the matter of reduction of the lateral digits. The pelvis, scapula and long bones are unknown.

The Fore-arm.—The ulna and radius, as indicated by their distal ends, display nearly the same proportions as are to be found in the existing Tragulines. The ulna is perhaps a trifle larger and stronger in proportion to the radius, with a greater expansion of its distal end. It is much better developed than in any of the existing Cervidæ. These two bones, although pertaining to a young animal in which the epiphyses are clearly indicated, are closely applied to one another, and display what may be regarded as a tendency to coössification. In old individuals it is highly probable that they will be found to be more or less completely joined by bony union.

The shaft of the radius, or what remains of its distal portion, is slightly crushed laterally so that its section cannot be made out, but there can be little doubt that it had the usual pattern displayed by the Tragulines and modern Deer. Upon the front of the bone, just above the articular extremity, there is a wide tendinal sulcus somewhat more marked than in either *Tragulus*, *Leptomeryx* or *Cariacus*. (In these latter genera there is an additional tendinal groove situated well over towards the ulnar side of the bone, which is apparently absent in *Protoceras*. Its absence in this specimen, however, may be due to age.) The distal extremity of the bone is marked by two facets for articulation with the scaphoid and lunar. That for the scaphoid is strongly convex from before backwards and is terminated in front by a shallow pit or depression which receives the anterior convex head of the scaphoid.

The process of bone which bears this facet is not produced backwards as it is in *Tragulus*, nor has it the marked obliquity seen in *Leptomeryx* and *Cariacus*, and to a less degree in *Tragulus*. The scaphoid facet is not sharply defined by a prominent ridge from that of the lunar as it is in *Cariacus*, *Leptomeryx* and *Tragulus*, the two articular surfaces being quite continuous in front.

The lunar facet is somewhat wider than that for the scaphoid, and like the latter is strongly convex from before backwards. It has little or no obliquity. It differs markedly from that of *Lep-*

tomeryx, in which it consists of a shallow cup-like depression with little posterior convexity associated with great obliquity. In *Protoceras*, as in *Tragulus*, the scaphoid surface occupies a lower level than that for the lunar, while in *Leptomeryx* the two facets are almost upon the same level.

In the complete absence of any articular facet for the cuneiform, the distal end of the radius differs from all modern Pecora and from the existing Tragulines, and agrees with *Leptomeryx*, an older Traguline.

The ulna is much compressed and applied closely to the radius at its lower fourth. Its distal extremity is occupied by an antero-posteriorly convex facet which articulates with the cuneiform. Except in its slightly increased size, in proportion to the radius, it does not differ from the corresponding bone in *Tragulus*.

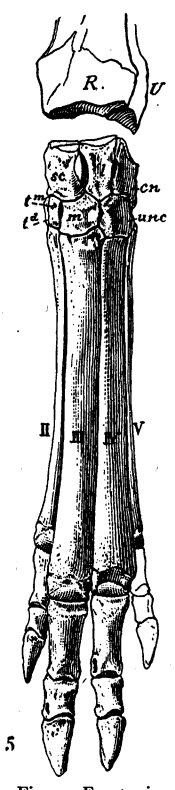


Fig. 5. Front view of manus, ⅔ nat. size.

The Carpus.—The carpus, while it resembles that of the Tragulines in a general way, nevertheless presents many features in details of structure which are different enough. One character in particular in which it appears to differ from both the Tragulines and the modern Cervidæ is the degree of elevation observable in the distal row of carpal bones. In *Cariacus* the vertical flattening of these bones is very marked, and it is also to be observed in the Tragulines, including *Leptomeryx*, although to a less degree. In *Protoceras* the elevation is considerably greater, so that the height of the two rows of bones is more nearly equal. In this respect it approaches *Oreodon* and the more generalized members of the Artiodactyla.

The scaphoid is one of the largest and strongest bones of the carpus. Proximally it presents a saddle-shaped articular facet where it joins the radius, in conformity with the usual pattern in the Artiodactyla. The anterior portion of this articular surface is occupied by a well-rounded transverse ridge extending entirely

across the superior face and giving a width almost equal to that of the lunar. This ridge is received into the transverse depression upon the distal end of the radius. In *Tragulus* the proximal articular surface of this bone is much narrower than that of the lunar, and the anterior portion is thrown up into a prominent bony tubercle which is received into a corresponding pit or depression upon the articular face of the radius. Although the scaphoid is unknown in *Leptomeryx*, one would conclude from the depression in the radius at its point of articulation, that its structure is similar to that of *Tragulus*. In *Cariacus* the bone is similar to that of *Tragulus*, although the lateral narrowing is not relatively so great. Distally the scaphoid of *Protoceras* rests upon the magnum and trapezoid, being at the same time in contact with the rudimental trapezium.

The lunar is relatively high and narrow, being slightly wedge-shaped. Proximally it presents the usual pattern of the Pecora and Tragulines, but distally its articular surface is divided almost equally between the unciform and magnum. In this respect it differs radically from *Leptomeryx* and all other Tragulines, in which it rests almost entirely upon the unciform, offering to the magnum only a lateral contact. This character is considered by Cope[1] and adopted by Scott[2] as especially characteristic of the Traguline group.

The cuneiform is proportionally stronger than in the *Cervidæ*, and the saddle-shaped proximal facet is not extended down upon the external surface to the same extent as in either the Tragulines or the modern Pecora. It does not articulate with the radius.

The unciform is the largest bone of the carpus and articulates proximally with the lunar and cuneiform. Posteriorly it develops a strong hook-like process of bone, which is absent or nearly so in *Cariacus* but present in *Tragulus*. Distally it articulates with with metacarpals III, IV and V.

The magnum of *Protoceras* differs from that of both the Tragulines and the Pecora in that it is entirely free, and exhibits no tendency to coössification with the trapezoid. It articulates

[1] On the Structure of the Feet of the Extinct Artiodactyla of North America. Proc. Amer. Assoc. for Advancement of Science, 1884.

[2] On the Osteology of Mesohippus and Leptomeryx. Jour. Morphology, 1891, Vol. V, No. 3.

proximally with scaphoid and lunar, distally with metacarpals II and III.

The trapezoid is comparatively large and well developed. It assists in the support of the scaphoid and in turn rests solely upon metacarpal II. Internal to this bone is a small bone which represents the reduced trapezium. It has a small articular facet where it touches the scaphoid, but distally there is apparently no facet for the support of metacarpal I. If this first digit or any representative of it were present it was reduced to the merest rudiment. In the presence of this small trapezium the carpus of *Protoceras* is of a more generalized type, differing from both the Tragulines and the Pecora. This bone is, however, occasionally seen in the modern Cervidæ.[1]

The Metacarpus.—The metacarpus consists of four digits, all of which are distinct and show no tendency to unite. As regards the existence of the first digit, as remarked above, if present, it consisted of a rudiment. The lateral digits II and V are remarkable for their unusual size as compared with the median ones III and IV. They are relatively as large as those of *Oreodon*, although much more elongated and slender, to conform to the general pattern of the foot. They are but little inferior to the median digits in length, in this respect resembling *Leptomeryx*. Metacarpal II is slightly larger and slightly exceeds metacarpal V in length. Its principal articulation is with the trapezoid, but it offers a small oblique facet to the magnum, and is overlapped behind by the rudimental trapezium.

As metacarpal II articulates with two principal elements of the carpus, so does metacarpal III. The head of the bone is largely occupied by an articular facet for the magnum, but on its ulnar side it sends out a considerable process which joins the unciform and at the same time overlaps the head of metacarpal IV. Metacarpals IV and V articulate proximally with the unciform only.

The distal ends of all the metacarpals are provided with keels, which are confined to the palmar surfaces. These keels are flanked upon either side by a well-developed sesamoid, well preserved in the specimen described.

[1] See Baur: 'Der Carpus der Paarhufer,' Morphol. Jahrb., IX, 509, 602.

Summary.—A summary of the principal characters of the forelimb, or, at least, what we know of it, may be made as follows: (1) Distal ends of ulna and radius tend to coössify. (2) There is no radial facet for the cuneiform. (3) There is little or no obliquity of the scaphoid and lunar facets on the radius. (4) The lunar rests equally upon unciform and magnum. (5) Trapezoid and magnum are not coössified. (6) A trapezium is present though small. (7) The unciform has a well-developed hook posteriorly. (8) The lateral digits are large, almost equaling the median ones in size. (9) Metacarpal III does not articulate with trapezoid, and the manus is therefore of the 'inadaptive' type. (10) The distal keels of the metacarpals are confined to the palmar surface.

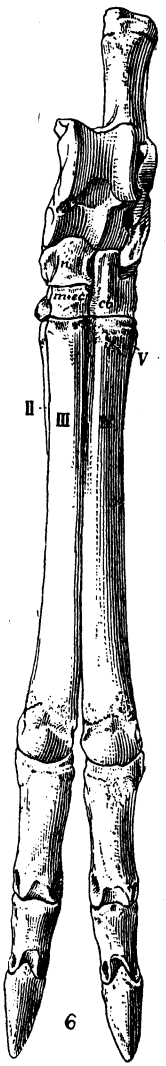


Fig. 6. Front view of pes, $\frac{2}{3}$ nat. size.

The Hind Limb.—All that remains of the tibia and fibula are the extreme distal ends. Of the tibia we note the deep grooves for articulation with the astragulus, very much as in the recent genus *Cariacus*. The fibula is as completely reduced as in the modern Deer, the distal end consisting of a nodule of bone wedged in between the tibia and calcaneum. While this nodule, or malleolar bone, is free in the single specimen in which it is preserved, it nevertheless exhibits some tendency to coössify with the tibia, and it would not be at all surprising to find it completely joined to the tibia in older specimens.

Of the tarsus, the calcaneum has a relatively shorter *tuber* than is found in the modern Deer, and the facet for the malleolar bone is much more flattened. The astragulus presents no points of especial interest; it resembles very closely the corresponding bone in *Cariacus*.

The cuboid is relatively high and narrow, in this respect, resembling the Tragulines rather than the Deer.

Although closely applied to the navicular and the ecto-cuneiform it is not coössified with them as is the case in the Tragulines and Pecora. In a young specimen of *Leptomeryx* in our collection the cuboid and navicular are fully united and all traces of the suture are obliterated, notwithstanding the fact that the epiphyses had not yet united with the shafts of the long bones. Now in our young specimen of *Protoceras* the cuboid and navicular are perfectly free, but in the adult specimen there is some bony union. The line of junction, however, is clearly indicated by a more or less open suture. What is here said of the cuboid and navicular also applies to the cuboid and ecto-cuneiform, so far at least as the union of the latter with the cuboid is concerned. There appears to be no tendency to bony union of the ecto-cuneiform with the navicular.

The comparatively large bone which furnishes the principal support for the navicular, is, upon good and sufficient authority, stated to be a compound of the ecto- and meso-cuneiform in all the Pecora and some of the Tragulina. A very similar bone is found in *Protoceras*, but there is apparently no trace of any suture separating the two elements. It is safe to assume therefore that this bone represents the coössified ecto- and meso-cuneiform. Almost immediately behind this is to be found the ento-cuneiform. It differs in no important particulars from that of the Tragulines, *Leptomeryx*, and the Pecora.

The metatarsus consists of four elements of which the two median bones, metatarsals III and IV, are well developed and functional. The two median ones, viz.: Metatarsals II and V, are rudimental, incomplete and splint-like. In the young specimen metatarsal II greatly exceeds metatarsal V in size, extending somewhere between a third and a half of the way down the shaft of the large metatarsal III, while metatarsal V is but a short splint. In the adult specimen metatarsal II is very much shorter and is reduced quite as much as metatarsal V is in the young specimen. This is perhaps to be explained upon the basis of individual variation.

Metatarsal II articulates proximally with both the ento- and the meso-cuneiform, being applied closely to the shaft of metatarsal III. Its distal portion is not preserved, if it were ever

present, so that no statement can be made concerning it. This is likewise true of metatarsal V.

Metatarsals III and IV are large and strong. In the young specimen they are entirely free, but in the adult there is some tendency to bony union exhibited, just as is observed in the cuboid, navicular and ecto-cuneiform of the tarsus. The fact of the matter is, the pes of *Protoceras* furnishes us with the transition stage between the condition wherein the elements are free, upon the one hand, and that wherein they become fused on the other. It is highly probable, as our specimens tend to prove, that previous to, and up to the time that the animal was fully adult, the elements of the pes were entirely free, but as age advanced there was a tendency for certain of the bones to become coössified. We are of the opinion, however, that bony union had, at no time during the life of the individual, gone so far as to obliterate all traces of the connections between the originally separate elements. In this sense no cannon bone can be said to exist in *Protoceras*. The bony union at most was but incipient.

In metatarsals III and IV the distal keels are confined to the plantar surface and are therefore not complete as in the modern Ruminants. The phalanges do not offer any important points of difference from those of allied forms.

Systematic Position of Protoceras.

It now remains to discuss briefly the systematic position of this unique genus. Scott, following Rütimeyer,[1] gives the principal characters of the traguline skull, including the American Miocene genus *Leptomeryx*, which, as he has shown, probably belongs here, as follows: "(1) Size very small. (2) Cranio-facial axis straight. (3) The orbits very large, median in position, and separated by a thin septum, but not projecting much beyond the sides of skull; optic foramina confluent. (4) The cranium long, narrow and low, and the parietal zone correspondingly long. (5) Occipital surface unusually high, narrow and convex (flattened or concave in *Leptomeryx*), and supraoccipital extended upon the side walls of cranium. (6) The alæ orbitales

[1] On the Osteology of Mesohippus and Leptomeryx, pp. 358, 359.

extraordinarily extended, reaching roof of the skull. (7) A short sagittal crest formed. (8) Frontal zone limited to roof of the orbits and nasal cavity. (9) Auditory bullæ large and filled with cancellous tissue (small and not filled with cancellous tissue in *Leptomeryx*)." To these we may add: (10) no horns or bony protuberances upon the cranium, and (11) "the lachrymal orifice single and placed outside the orbit (McAllister)," "inside the orbit in *Leptomeryx* (Scott)."

If now we contrast the characters of the skull of *Protoceras* with those of the Tragulina just given, it will be seen that the differences are very great. (1) Omitting Scott's first character as of comparatively little value, since it is a matter of specific variation in other forms, they may be tabulated as follows: (2) In *Protoceras* the face is considerably bent down upon the cranio-facial axis as in the Pecora. (3) The orbits are large, lateral in position, widely separated and project well beyond the side wall of the skull. The optic foramina are not confluent. (4) The cranium is long, flattened and of great breadth between the orbits; the parietal zone is relatively short. (5) The occipital surface is high and narrow and the occipitals overlap the lambdoidal crests so as to appear upon the side walls of the skull. (6) This character cannot be fully determined in our specimen. (7) A very prominent, although moderately short crest is formed in the male, less prominent in the female. (8) Frontal zone limited behind by parietal protuberances. (9) The auditory bullæ not inflated. (10) Strong bony protuberances on parietals, in males well developed, in females rudimental; in males there are in addition bony protuberances over the orbit and in front of the orbit on the frontals, besides the large maxillary plates in front. (11) The orifice of the lachrymal duct is single and situated inside the orbit.

From this it will be seen that in the general pattern of the skull *Protoceras* differs widely from that displayed by any member of the Tragulina. The more striking and important of these differences are to be seen in the position and wide separation of the orbits, the possession of parietal protuberances and the general conformation of the muzzle. It is true that in the character of the occiput it resembles the Tragulines, but it is not certain but

that some of the more primitive members of the Pecora were possessed of a similar structure. In the matter of the tympanic bullæ and the position of the lachrymal orifice it agrees with *Leptomeryx*, but differs from the rest of the Tragulines. These latter characters are probably but parallelisms and have little bearing upon the general question of genetic affinity.

In the structure of the limbs we meet with more decided resemblances to the Tragulines, but in the absence of more complete knowledge of the limb structure of the earliest representatives of the Pecora we are not prepared to say whether these resemblances are not equally great to this latter group. The manus furnishes two striking characters in which *Protoceras* differs from all the Tragulina, viz.: the support for the lunar being furnished by the unciform and magnum equally and the manus being of the 'inadaptive type,' whereas in the Tragulina the principal support for the lunar is furnished by the unciform, and the manus is of the 'adaptive type.' The character of the lunar articulation is considered by Cope to be especially distinctive of the Tragulines, and it is undoubtedly true that it is very constant and serves to distinguish them sharply from the Pecora. The adaptive or inadaptive character of the manus is perhaps of less value in indicating relationship, since it appears, in some measure at least, to be influenced by the reduction of the digits. Such a condition is met with in the Oreodontidæ.

Other characters of the carpus, such as the separate condition of magnum and trapezoid, the presence of separate trapezium, and the very large size of the lateral metacarpals are features common to the more generalized types of the Artiodactyla, and serve to distinguish *Protoceras* sharply from both the Pecora and the Tragulina. The lack of obliquity of the facets at the distal end of the radius is also a character which belongs to the primitive members of the order and serves to distinguish it from both the Tragulines and the Pecora, while the absence of a cuneiform facet on the radius, as well as the presence of the distal keels of the metapodials on the palmar surface only are shared with certain members of the Tragulina, notably *Leptomeryx*.

If we associate *Leptomeryx* with the Tragulines, then the differences in the structure between the pes of the Pecora and the

Tragulina is comparatively slight. The pes of *Leptomeryx*, as was shown by Scott, is remarkably like that of the modern Ruminants in the reduction of the lateral digits and the coössification of the cuboid and navicular, and at the same time in having ecto-meso-cuneiform free. In *Protoceras* the condition is more primitive, in that the cuboid and navicular are not fully united, nor can the cannon bone be said to be fully formed. In these particulars it departs from both the Tragulina and Pecora and again approached the lower types.

If now we compare *Protoceras* with any family of the Pecora, there are so many striking differences at once apparent that we are compelled to conclude that there are no marked affinities in the direction of any of these families. In the possession of bony protuberances on the parietals, which are probably processes of this bone and not developed separately as in the Giraffe, in the general architecture of the skull, together with so many primitive characters of the feet, this genus apparently occupies a distinct position and cannot be consistently referred to either the Tragulina or the Pecora as at present constituted and defined. The possession of multiple horns suggests the possible relationship of this family to the Sivatheriidæ, but the likeness does not extend to other features of the skull.

That it represents a distinct family there can be little doubt. Of its successors we know nothing whatever, and our ignorance is equally great in the matter of its ancestry.

The following table exhibits, in condensed form, the principal characters of this family in contrast with those of the families of the Tragulina and the Pecora:

TRAGULINA. *Tragulidæ.*	PROTOCERATIDÆ.	PECORA. *Giraffidæ, Cervidæ, Bovidæ.*
(1) No horns, antlers or bony protuberances upon cranium.	(1) Paired bony protuberances on parietals, frontals and maxillaries in males.	(1) Horns, antlers or bony protuberances present.
(2) Orbits median in position, not projecting laterally; optic foramina confluent.	(2) Orbits lateral in position, projection well beyond side wall of skull; optic foramina not confluent.	(2) Orbits as in Protoceratidæ.
(3) Nasals normal and articulating with superior border of maxillaries in front. No flanges on maxillaries.	(3) Nasals much reduced and not articulating with superior border of maxillaries in front. Maxillaries in males produced into a pair of large bony plates rising above the vertex of the skull.	(3) Nasals normal (somewhat reduced in *Alces*) and articulating with superior border of maxillaries in front. No maxillary plates.
(4) Occiput high and narrow; occipitals overlapping lambdoidal crest; a sagittal crest formed.	(4) Occiput high and narrow; occipitals overlapping lambdoidal crest; a sagittal crest.	(4) Occiput low and broad; occipitals not overlapping lambdoidal crest. No sagittal crest.
(5) Distal end of radius with or without facet for articulation with cuneiform. Facets for scaphoid and lunar oblique.	(5) Distal end of radius without facet for articulation with cuneiform. Facets for scaphoid and lunar with little or no obliquity.	(5) Distal end of radius with facet for articulation with cuneiform. Facets for scaphoid and lunar very oblique.
(6) Carpus of the adaptive pattern.	(6) Carpus of the inadaptive pattern.	(6) Carpus of the adaptive pattern.
(7) Lunar resting almost exclusively upon the unciform, and having only a lateral contact with magnum.	(7) Lunar resting equally on magnum and unciform.	(7) Lunar resting equally upon magnum and unciform.

(8) Trapezoid and magnum coössified.	(8) Trapezoid and magnum separate.	(8) Trapezoid and magnum coössified.
(9) Trapezium absent or coössified with trapezo-magnum.	(9) Trapezium present and separate.	(9) Trapezium absent, rudimental or coössified with trapezo-magnum.
(10) Lateral digits of manus complete; cannon bone present or absent.	(10) Lateral digits of manus complete, large and well-developed; no cannon bone.	(10) Lateral digits incomplete and splint-like; a cannon bone always present.
(11) Distal keels of metacarpals incomplete and confined to palmar surface.	(11) Distal keels of metacarpals incomplete and confined to palmar surface.	(11) Distal keels of metacarpals complete (except in Giraffe).
(12) Cuboid, navicular and cuneiforms coössified (excepting in *Leptomeryx*, where ecto-meso-cuneiform is free) with obliteration of suture in adult.	(12) Cuboid tending to coössify separately with navicular and cuneiforms, persistent suture in adult.	(12) Cuboid and navicular coössified, with obliteration of suture in adult.
(13) Lateral digits of pes complete (except in *Leptomeryx*); cannon bone present or absent.	(13) Lateral digits incomplete, splint-like; median metatarsals, if coössified into a cannon bone, a persistent suture present.	(13) Lateral digits incomplete, splint-like; and median metatarsals always coössified into a cannon bone, with suture obliterated in adult.
(14) Distal keels of metapodials confined to plantar surface.	(14) Distal keels of metapodials confined to plantar surface.	(14) Distal keels of metapodials complete (except in Giraffe).
(15) Posterior limbs greatly exceeding anterior limbs in size and length.	(15) Posterior limbs greatly exceeding anterior limbs in size and length.	(15) No marked disparity in length between fore and hind limbs.

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