Concerning the proposed species, *C. procuspidatus*, the authors say: "the most important difference between this species and *C. dakotensis* is seen in the degree of separation of the internal cusps of the premolars from each other and the more decided approach toward the structure of the molars." As the figures of the two type-specimens show, these supposed differences are very largely due to different stages of abrasion. The teeth of the *C. procuspidatus* type are entirely unworn, while those of *C. dakotensis* show considerable wear. Small differences of size are not often a satisfactory ground for specific distinction, but there is a constant difference between the Chadron and the Brulé specimens of this genus, the former being uniformly smaller.

The most complete example of *C. dakotensis* yet obtained is a palate in the Princeton Museum (No. 12,700), which on one side, or the other, contains all the upper teeth except the first molar; a second specimen is a fragment of the mandible with all the cheek-teeth in place and a third comprises several pieces of the lower jaw, both rami, with the incisors and all the cheek-teeth except the last molar ($m\overline{3}$), and the ungual phalanx, which was figured by Hatcher.

The measurements of *C. dakotensis* and *C. occidentalis*, as given by Osborn and Wortman, are repeated in the subjoined table; *C. procuspidatus* "agrees very closely in size with *C. dakotensis*."

Measurements

| | *C. dakotensis* | *C. occidentalis* |
|---|---|---|
| Length of last two lower molars | 45 mm. | 34 mm. |
| Length of last lower molar | 25 | 19 |
| Length of last two lower premolars | 27 | 21 |
| Width of crown of last lower molar | 10 | 13 |
| Total length of upper molar series | 91 | — |
| Length of premolars above | 41 | — |

The dimensions of a Princeton specimen of *C. dakotensis* are as follows:

Measurements

| | *No. 12,700* |
|---|---|
| Upper dentition, length $i\underline{1}$ to $m\underline{3}$ incl. | 130 mm. |
| Upper incisor series, length | 23 |
| $I\underline{1}$, ant.-post. diameter | 8 |
| $I\underline{1}$, transverse diameter | 9 |
| $I\underline{2}$, ant.-post. diameter | 9 |
| $I\underline{2}$, transverse diameter | 9 |
| $I\underline{3}$, ant.-post. diameter | 8 |
| $I\underline{3}$, transverse diameter | 8 |
| Upper cheek-teeth series, length | 87 |
| Upper premolar series, length | 41 |
| Upper molar series, length | 46 mm. |
| $P\underline{1}$, ant.-post. diameter | 8 |
| $P\underline{1}$, transverse diameter | 9 |
| $P\underline{2}$, ant.-post. diameter | 10 |
| $P\underline{2}$, transverse diameter | 14 |
| $P\underline{3}$, ant.-post. diameter | 11 |
| $P\underline{3}$, transverse diameter | 16 |
| $P\underline{4}$, ant.-post. diameter | 11 |
| $P\underline{4}$, transverse diameter | 17 |

The dimensions of the pes are taken from the American Museum specimen, No. 10,751.

Measurements

| | *No. 12,700* |
|---|---|
| Astragalus, distal width | 21.5 mm. |
| Calcaneum, dist. thick. (dors.-plant.) | 18 |
| Navicular, prox.-dist. length | 12 |
| Navicular, width | 18 |
| Ectocuneiform, prox.-dist. length | 11 mm. |
| Ectocuneiform, width | 18 |
| Cuboid, prox.-dist. length | 22 |
| Cuboid, prox. width | 14.5 |



Measurements (*Continued*)

| | *No. 12,700* |
|---|---|
| Cuboid, dist. width | 11 mm. |
| Metatarsal II, length | 126 |
| Metatarsal II, prox. width | 11 |
| Metatarsal II, dist. width | 14 |
| Metatarsal III, length | 135 |
| Metatarsal III, prox. width | 17 |
| Metatarsal III, dist. width | 22 |
| Metatarsal IV, length | 127 mm. |
| Metatarsal IV, prox. width | 14 |
| Metatarsal IV, dist. width | 12 |
| Digit III, phalanx 1, length | 29 |
| Digit III, phalanx 1, prox. width | 18 |
| Digit III, phalanx 1, dist. width | 15 |

*Horizon:* Lower Brulé.
*Locality:* Big Bad Lands, So. Dak.

## Family 3. Rhinocerotidae Owen

The true rhinoceroses, which constitute this family, are a group of great antiquity and diversity, the origin and principal development of which took place in the Old World, where it still survives; in North America it became extinct in the older Pliocene. The family is of pre-eminently northern distribution, Africa being the only southern continent which they have invaded. The earliest known occurence of the true rhinoceroses in North America is in the upper Eocene, but it was in the White River that the whole superfamily reached its culmination in diversity and relative importance. Miocene and Pliocene rhinoceroses were more advanced and modernized than those of the Oligocene, but they were in no such variety, or relative importance. Nearly all the White River rhinoceroses were hornless, incipient horns first appearing at the end of the stage.

The particular characteristic of the family is seen in the canines and incisors; aside from certain late genera, in which all the anterior teeth have been lost, the first upper and second lower incisors are peculiarly modified; $i\underline{1}$ is a short trenchant blade, not unlike the sectorial of a carnivore, the sharp edge of which shears inside of the large, pointed, procumbent $i\overline{2}$, which is tusk-like in shape and points directly forward; the median lower incisors, $i\overline{1}$, are vestigial. These teeth are unique and occur in no other mammals and characterize all the genera of the family save such as have lost all the front teeth. Other incisors and canines are present in numbers which differ in various genera, but the formula may be written, $i\frac{1-3}{2}$, $c\frac{0-1}{0}$. In existing Asiatic species the number is $i\frac{1}{2}$, $c\frac{0}{0}$, and the same formula is found in most of the American members of the family, with certain interesting exceptions. The European *Epiaceratherium* is a member of this family which parallels the Amynodontidae in having the lower tusk either $i\overline{3}$ or a canine.

Professor H. E. Wood, who has made a particular study of American rhinoceroses, has very kindly given me the results of his examination of the White River genera, results which I can accept, though certain questions must remain doubtful, until more complete material is accessible. Wood recognizes five genera of this stage, which were only partially contemporaneous, a stratigraphic sequence being recognizable. The list of genera is as follows.

1. *Trigonias* Lucas, 1900. Chadron only. Manus with four complete digits. Nasals elongate and premaxillae appressed and maybe suturally connected. Dental formula: $i\frac{3}{3}$, $c\frac{1}{0}$, $p\frac{4}{4}$, $m\frac{3}{3}$; upper premolars extremely variable; $p\underline{1}$ relatively large; $p\underline{2}$ most advanced

of the series and often molariform; $\mathrm{p}\underline{3}$ sometimes molariform, which $\mathrm{p}\underline{4}$ never is and has valley opening posteriorly; the two internal cusps are connate.

2. *Amphicaenopus* Wood, 1927. Large animals with dental formula: $\mathrm{i}\frac{2-1}{3-2}$, $\mathrm{c}\frac{0}{0}$, $\mathrm{p}\frac{4-3}{4-3}$, $\mathrm{m}\frac{3}{3}$; $\mathrm{p}\underline{2}$ most nearly molariform and may have parallel, transverse crests; $\mathrm{p}\underline{3}$ not molariform, postero-internal cusp an isolated cone.

3. *Caenopus* Cope, 1879; small true rhinoceros: $\mathrm{i}\frac{2}{2-1}$, $\mathrm{c}\frac{1-0}{0}$, $\mathrm{p}\frac{4}{3}$, $\mathrm{m}\frac{3}{3}$; upper premolars more advanced than in *Subhyracodon*, or *Amphicaenopus;* cingulum of cheek-teeth much weaker than in former; order of change in upper premolars to molar pattern, $\mathrm{p}\underline{4}$, $\mathrm{p}\underline{2}$, $\mathrm{p}\underline{3}$. $\mathrm{I}\underline{1}$ and $\overline{2}$ not markedly enlarged: manus tridactyl.

4. *Subhyracodon* Brandt, 1878; medium size, manus tridactyl; dental formula $\mathrm{i}\frac{2}{2}$, $\mathrm{c}\frac{0}{0}$, $\mathrm{p}\frac{4}{4-3}$, $\mathrm{m}\frac{3}{3}$; first upper and second lower incisor enlarged tusks; $\mathrm{p}\underline{2}$ most advanced of of upper premolars, order of change $\mathrm{p}\underline{2}$ to $\mathrm{p}\underline{3}$ to $\mathrm{p}\underline{4}$; cingula of cheek-teeth heavy; antero-internal cusp of upper molars set off from transverse crest; lower Brulé.

5. *Diceratherium* Marsh, 1875; like *Subhyracodon*, but larger and with incipient paired horns on nasals, which are much thickened to support them; upper Brulé.

All of the Oligocene species of this family are of moderate size, few of them exceeding the American tapir in height and the skeleton has the proportions of its various parts, neck, trunk, limbs and feet, much more as in the tapirs than as in the modern rhinoceroses. Except *Trigonias*, which has the fifth digit in the manus, all the Oligocene and subsequent genera of the family have tridactyl feet both before and behind.

Each of the three substanges of the White River had its characteristic genera of rhinoceroses: *Trigonias* is exclusively Chadron, *Subhyracodon* is almost confined to the lower Brulé and *Diceratherium*, which is especially characteristic of the John Day, makes its first appearance in the apper Brulé, *Caenopus*, which is very rare, seems to occur in the Chadron and upper Brulé, but has not been found in the lower. *Amphicaenopus* is typically from the upper Brulé, but has also been reported from the Chadron.

### **Trigonias** Lucas

### Pls. LXXXI, LXXXII

*Trigonias* Lucas: Proc. U. S. Nat. Museum, Vol. XXIII, p. 221. 1900.

Fossils referable to this genus are comparatively rare in the Big Bad Lands of South Dakota, but are abundant and finely preserved in the Chadron of Weld County, Col., whence have been taken the remarkable series of skulls and skeletons in the Colorado Museum of Natural History at Denver. The genus includes much the most primitive of White River rhinoceroses, which retain several significant features of their Eocene ancestors.

#### Dentition

The formula, which is $\mathrm{i}\frac{3}{3}$, $\mathrm{c}\frac{1}{0}$, $\mathrm{p}\frac{4}{4}$, $\mathrm{m}\frac{3}{3}$, is very important as fixing the homologies of the of the anterior teeth in the more advanced genera, which have been variously interpreted.



*Upper Teeth.* The first incisor $\mathrm{i}\underline{1}$ already has the shape characteristic of the family, being low verticially, much extended antero-posteriorly and with a trenchant edge that occludes inside of the large lower tusk, $\mathrm{i}\overline{2}$. The second incisor, $\mathrm{i}\underline{2}$, is very much smaller than the first and of entirely different shape, the crown being a low, asymmetrical cone, with blunt apex. The third incisor, $\mathrm{i}\underline{3}$, is much smaller than the second, but has nearly the same shape. The *canine* is still smaller than $\mathrm{i}\underline{3}$, but resembles it in form; these three small teeth would seem to have been useless to their possessor and are to be regarded as vestigial.

The *premolars* are of an extraordinary degree of variability, as has been shown in great detail by Messrs. Gregory and Cook,[1] but a general account may be given in which the variations are little considered. The premolars increase in size posteriorly, $\mathrm{p}\underline{1}$ being much the smallest of the series and $\mathrm{p}\underline{4}$ slightly larger than $\mathrm{p}\underline{3}$; they all have the external wall somewhat different from that of the molars and are, in varying degrees, like the molars. $\mathrm{P}\underline{1}$ is least molariform; it has a hinder cross-crest, which is so recurved, as to enclose a posterior valley, but the anterior crest is longitudinal, not transverse, and is parallel to the outer wall; the main valley is, thus, open in front. $\mathrm{P}\underline{2}$ is much larger than $\mathrm{p}\underline{1}$ and is the most nearly molariform of all the premolars; the two transverse crests, which are not so oblique in direction as are those of the molars, are complete, parallel and well separated. $\mathrm{P}\underline{3}$ is less completely like a molar, though it is larger than $\mathrm{p}\underline{2}$; the anterior cross-crest is complete, but the posterior one is separated from the postero-internal cusp, or tetartocone, which is an independent conical cusp. $\mathrm{P}\underline{4}$ is still less like a molar; the posterior crest is hardly half as long as the anterior one and the tetartocone is a mere tubercle. All of the premolars have a strong tuberculated cingulum around three sides of the crown, front, back and inner side.

The *molars* are typically those of the family and superfamily in form and in the pattern of the masticating surface, without any of the accessory spurs save a faintly marked antecrochet on $\mathrm{m}\underline{1}$ and $\mathrm{m}\underline{2}$. $\mathrm{M}\underline{3}$ has the posterior crest and external wall indistinguishably fused, producing the trihedral crown so characteristic of the whole group. A conspicuous difference from the premolars is in the development of the cingulum, which is restricted to the anterior side of the crown except in $\mathrm{m}\underline{3}$, in which the cingulum is on the front and rear faces. None of the cheek-teeth has any external cingulum, except for occasional patches, and this lack is in decided contrast to *Hyracodon* and *Subhyracodon*, but not to *Metamynodon.*

*Lower Teeth.* These depart less from the conditions seen in such Recent genera as have incisors than do the upper teeth. As in *Subhyracodon* and subsequent American rhinoceroses, the first incisor is very small and procumbent and can have been of no service to the animal; the second, $\mathrm{i}\overline{2}$, is a large, pointed, procumbent tusk, which occludes outside of the large, shearing first upper incisor. Of the third incisor and the *canine* no vestige remains; the difference between upper and lower jaws in the degree of reduction of the anterior teeth is surprising.

The *premolars* increase in size from before backward; $\mathrm{p}\overline{1}$ is much the smallest of the four and least like a molar; it is implanted by two roots and has a narrow, compressed-conical crown, with three cusps arranged in the same fore-and-aft line and obscure valleys on the lingual face. $\mathrm{P}\overline{2}$ is very like $\mathrm{p}\overline{1}$, but is much larger and with all the elements more distinctly shown and, in addition, has a division on the buccal side into anterior and posterior

[1] Gregory, W. K., and Cook, H. J. Proc. Colorado Museum of Nat. History, Denver, Vol. VIII.

lobes, which p$\overline{1}$ does not display; in particular, the postero-internal valley is much larger and deeper than in p$\overline{1}$. P$\overline{3}$ is still more molariform and p$\overline{4}$ differs from a molar only in unimportant details.

The *molars* are those common to all the family and, as Hatcher says of them, "they exhibit no distinctive characters."

### Skull

The skull differs in several respects from that of *Subhyracodon,* to say nothing of the later genera from the Miocene to the Recent. The upper profile is almost horizontal from the tips of the nasals to the mid-parietal point, whence the contour rises steeply to the occiput. In *Subhyracodon* the whole upper contour of the skull is straight and nearly horizontal and another difference is that, in the latter, there is hardly any sagittal crest, but rather a narrow, flattened sagittal area, whereas, in *Trigonias,* the crest is high and thin. The occiput is high and narrow and the supraoccipital is deeply emarginated in the median line and extended into the paired, wing-like processes which recur in all of the White River rhinoceroses with the exception of *Metamynodon,* in which the occiput is much lower and wider than in the other contemporary genera. The paroccipital process is short and blunt, but the long post-tympanic and post-glenoid processes of the squamosal are in contact, closing the auditory meatus below. In *Subhyracodon* the two processes are separate, one of the few features in which the older genus, *Trigonias,* is the more advanced.

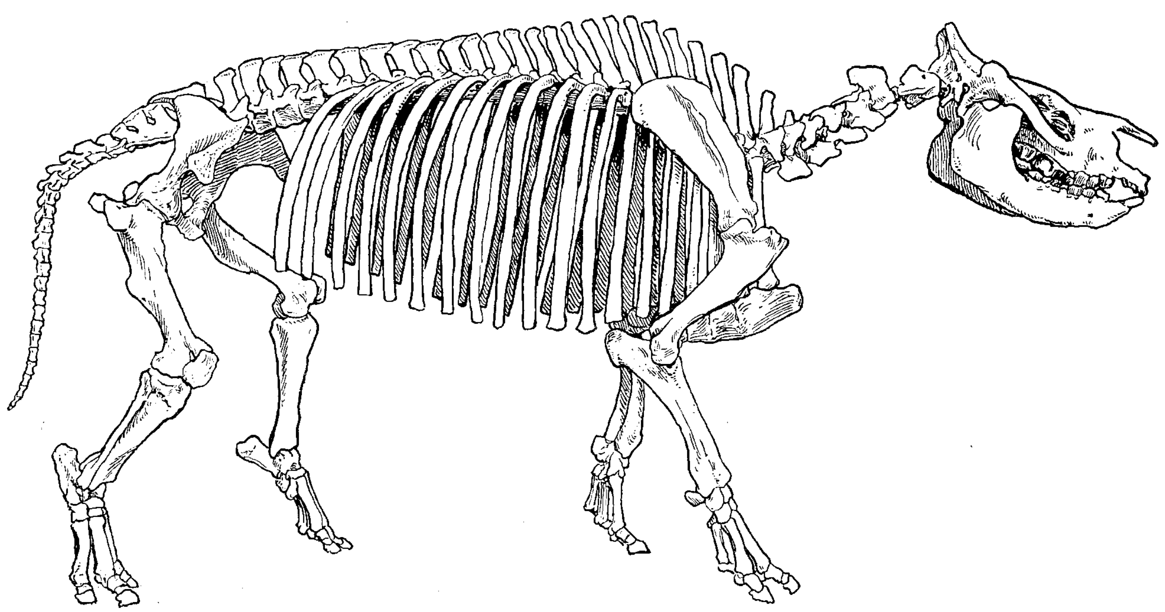

Fig. 137. *Trigonias osborni:* Skeleton, right side: Colorado Mus. Nat. Hist.

The zygomatic process of the squamosal is broad vertically, thin and plate-like transversely, its dorsal border rising high above the horizontal portion much more than in *Subhyracodon,* making a deep valley between the arch and the side of the cranium and the border descends much more steeply forward than in the latter. The postglenoid process is large, heavy and curved, with concave anterior face, on which is an extensive articular



surface for the posterior side of the mandibular condyle; distal to this, the postglenoid process descends inside of the post-cotyloid process of the mandible. The jugal is long and extends back to the glenoid cavity; the orbit varies much in size and in the prominence of the post-orbital process of the jugal.

The *maxillary* forms a large pre-orbital area of the face, which is relatively low. The very deep nasal incision emarginates the anterior border of the maxillary, which, as in the members of this family generally, sends forward a narrow bar, upon which the premaxilla rests. The palatine processes are thin and arise all along the maxillaries back to the posterior nares and forward to the incisive foramina, along the bars upon which the premaxillae lie. The *premaxillaries,* in correlation with the full number of incisors which they support, are different from those of any other known member of the family. Each premaxilla is straight and its dorsal border is horizontal, as there is no distinction of horizontal and ascending ramus. The alveolar portion is heavy, but laterally compressed, making the dorso-ventral diameter the principal one; the two premaxillae are in contact with each other in a considerable symphysis. The suture with the maxillary ends behind above the middle of p$\underline{2}$, but there is no contact with the nasal. The *nasals* are very long and have a long, freely projecting portion, which is thin and weak and terminates in a sharp point. This projection is decidedly longer than in *Subhyracodon.*

The *mandible* has certain characteristic peculiarities; the horizontal ramus is long, slender and shallow, with gently convex ventral border; the ascending ramus is rather narrow and its angle projects backward less abruptly than in *Subhyracodon* and has a thickened border, which is much more conspicuous than in *Hyracodon* and is, definitely, an early stage of the great thickness displayed in all Recent rhinoceroses. The masseteric fossa is small and is placed high up on the side of the jaw, but is deep and is bounded by prominent ridges; the sigmoid notch is deeper and better defined than in *Subhyracodon.* A very distinct post-cotyloid process is present and this, together with the thickened angle makes plain the relationship of *Trigonias* with the recent genera of the family.

### Vertebrae, Ribs and Sternum

In the skeleton from Colorado, mounted in the American Museum, which all belongs to one animal, the vertebral formula is: C7, D18, L5, S5, Cd 23. The neck is of moderate length, about equal to that of the head; the trunk is long, with the number of vertebrae usual among perissodactyls, and the tail is long, somewhat exceeding that of *Subhyracodon.*

The *atlas* agrees with the of the other White River rhinoceroses in the moderate expansion of the transverse processes and in having diapophysial notches, not foramina. The external sides of the cotyles for the occipital condyles are limited by grooves, which descend from the foramina for the first pair of spinal nerves. Neural and inferior arches are strongly convex and the neural spine is a rugose prominence, much as in *Subhyracodon;* a small hypapophysial tubercle projects from the hinder border of the inferior arch.

The *axis,* which is keeled, is broad anteriorly and has broad facets for the atlas, with short, slender and rod-like transverse processes. The neural spine is large and blade-like and of somewhat irregular shape; its anterior prolongation is very small and does not extend over the atlas; the dorsal border of the spine rises, first steeply and then gently, to the hinder end, which is the highest point; the posterior border is somewhat concave. The postzygapophyses are prominent, though rather small, and face obliquely outward.

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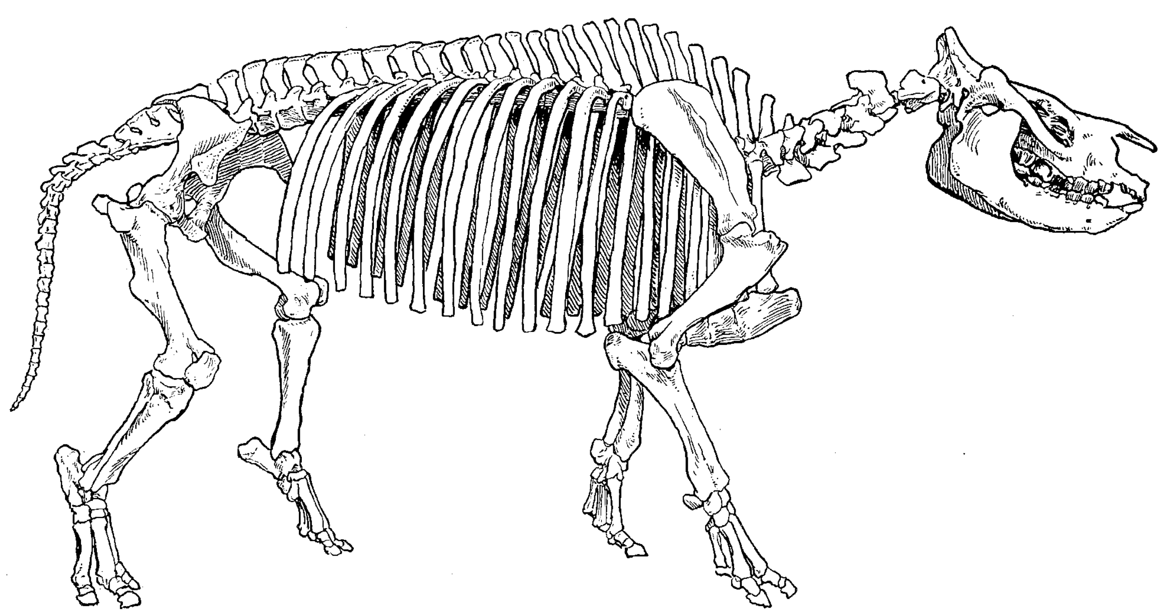

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The *third*, *fourth* and *fifth cervicals* are much alike in size and structure; they have keeled and moderately opisthocoelous centra, low and broad neural arches, hardly emarginated between the large and prominent zygapophyses, which are almost horizontal and face upward and downward; the pedicles of the neural arches are relatively narrow and make the lateral openings between the successive vertebrae very large. The spines are low, hardly more than vestigial, but that on the third vertebra is the highest. The transverse processes are short and have very large inferior lamellae, each extending outside of the one succeeding it; diapophyses are obscurely marked on the 3rd and 4th vertebrae and much more distinct on the 5th. The *sixth cervical* is shorter than those which precede it in the series and is distinguished by several characters; the neural spine is high and conspicuous, ¾ as high as the anterior dorsal spine; the pedicles of the neural arch are narrower and the diapophyses much longer and more prominent; the inferior lamella is less extended antero-posteriorly and has a more regularly curved and thickened ventral border. The *seventh cervical* differs, as usual, from all those that precede it in being shorter and in having an elongate, heavy and club-like diapophysis, which is imperforate and has no inferior lamella. The neural spine is considerably higher than that of the sixth vertebra, but of similar shape, broad at the base and narrowing much to the tip.

The *dorsal vertebrae*, behind the first, which is transitional from the cervical form, have short, sub-cylindrical centra, with high, conspicuously slender neural spines, which diminish in length behind the 4th; they form no hump at the withers, but so compensate for the upward curvature of the spinal column, that the summit line of the back must have been nearly horizontal as far as the loins. The spines incline posteriorly as far as the 14th dorsal, which is the anticlinal; behind that point they have a very slight forward slope. Metapophyses are conspicuous on all of the dorsal vertebrae, from the fourth backward.

The *lumbar vertebrae* have relatively large and heavy centra and rather high, narrow and thin neural spines, which increase in length posteriorly; they have a slight forward inclination and are antero-posteriorly expanded at the ends, with thickened and rugose tips. This terminal expansion makes the anterior border of the spine concave and the posterior somewhat less so. On the last lumbar the spine has a different shape; it is narrower antero-posteriorly and has straight, parallel fore and hind margins, thickened and slightly expanded tip. The transverse processes of the lumbars are strikingly short and weak, except in the last vertebra, the transverse processes of which are twice as long as those on the 4th. As is usual in perissodactyls, each process bears on its hinder border an articular facet for the sacrum. On the lumbar vertebrae, the metapophyses are prominent, diminishing in height posteriorly and hardly recognizable on the fourth and fifth lumbars.

The *sacrum* consists of five vertebrae, of which the anterior three are in contact with the pelvis; the neural spines are long, diminishing in height posteriorly, and thin transversely; they are broad and plate-like antero-posteriorly, rugose, thick and expanded at the free ends, which, in the 2nd, 3rd and 4th, are in contact and may co-ossify in old animals. The spine of the last sacral inclines backward more steeply and is separated by a wide gap from that of the 4th. The transverse processes of each side are fused into a long, narrow plate, with nearly parallel borders; zygapophyses are present on the first vertebra only.

The *caudal* vertebrae, which number 23, more or less, are indicative of a long tail, which hung down to the level of the calcaneum. The first 10 vertebrae have distinct neural canals, arches, spines and transverse processes, all of which and the centra also, grow



smaller posteriorly; the 11th and 12th retain very small neural canals and low spines, but are without transverse processes; zygapophyses cease after the third caudal; from the 12th backward, the vertebrae diminish in length and diameter, but are of essentially similar shape; they are subcylindrical, slightly contracted in the middle and expanded at the ends, and the various processes are mere vestiges.

The *Ribs* differ from those of modern rhinoceroses in their much greater slenderness and lack of flattening. The successive genera of the Miocene and Pliocene show this to have been a progressive change and even in *Subhyracodon occidentalis*, of the lower Brulé, the ribs are stouter. In *Trigonias*, the first rib is short and straight, broad and plate-like; the second is much broader and longer and the anterior five are relatively broad and compressed; from the 6th onward they grow more and more rod-like. They are all relatively long and strongly curved, making the thorax broad and capacious.

The *sternum* has a keel-like manubrium of perissodactyl type, which is not boat-shaped but has parallel dorsal and ventral borders and is abruptly cut off in front. Several, at least, of the mesosternal segments are narrow and dorso-ventrally thick.

### Pectoral Girdle and Limb

In all of the White River Rhinocerotidae, the proportions of head, neck, trunk, limbs and feet are tapiroid, though the details of the teeth and skeleton and their fundamental form are unmistakably rhinocerotic, not tapir-like.

The *scapula* is narrow in comparison with that of the other White River genera of the family; the neck is broad and the coracoid small and inconspicuous. The coraco-scapular notch is broad and shallow and the coracoid border very gently concave. The suprascapular border is curved and does not form a distinct angle with either of the other borders. The glenoid border is concave, which is due to the broadening of the upper part of the blade, where the post-spinous fossa is considerably wider than the prespinous. The spine is of the shape and position usual in the family and rises gently to the large, rugose and recurved metacromion, whence it descends still more gently and dies away on the neck without an acromion.

The *humerus* is relatively short; the head projects upward, rising well above the level of the tuberosities. The external tuberosity is not very prominent, but massive and prolonged across the whole anterior breadth of the humerus and divided by a broad notch into inner and outer portions; the internal tuberosity is even less prominent and the bicipital groove is narrow and unusually deep. The deltoid crest is greatly developed, making the whole proximal part of the bone extremely thick antero-posteriorly; the deltoid hook is present, but not conspicuous. Below the deltoid crest, the shaft is subcylindrical and then broadens much distally. The anconeal fossa is very deep and prolonged far proximally and the supratrochlear fossa is also deep, but there is no perforation connecting them. The external epicondyle is a low rugosity and the internal one is hardly distinguishable. The supinator ridge is inconspicuous, little more than a *linea aspera*, in fact. The trochlea is low and of the simple, hour-glass shape common to the family and there is no such intercondylar ridge as occurs in *Hyracodon*.

The fore arm bones are rather long and not very stout. The *radius* extends across the whole breadth of the humeral trochlea; the shaft, which gradually contracts below the head, is decidedly heavier than that of the ulna; it is rather broad and antero-posteriorly compressed and of transversely oval cross-section. The distal end is both broad and thick. The *ulna* has a large and very prominent olecranon, with thickened and rugose free end; the shaft, which tapers rapidly below the humeral articulation, is comparatively reduced and slender and has the ordinary trihedral shape, expanding somewhat at the distal end, where the facets for the pyramidal and pisiform form a saddle-shaped surface. As compared with the middle Eocene perissodactyls, almost all of which have a functionally tetradactyl manus, the ulna in *Trigonias* has undergone a reduction, a course of development which was reversed in the Miocene and Pliocene genera, such as *Aphelops* and *Teleoceras*, in which bulk and body-weight were so greatly increased, that more massive limb-bones were requisite.

### Manus

In *Trigonias* the fore foot is structurally tetradactyl, but the fifth digit, though complete in all its parts, is so reduced as to be little more than a vestige without function. Nevertheless, much of the tetradactyl arrangement persists. The first description of the forefoot in *Trigonias* was that given by Hatcher,[1] which may be paraphrased as follows.

The *Carpus* forms a transitional stage between the three-toed and the four-toed relations of its elements. The scaphoid is much the largest bone of the proximal row; its articulation with the radius is by means of a concave surface of irregularly pentagonal outline; distally, the scaphoid covers the trapezium and the trapezoid, but only about half of the breadth of the magnum on the dorsal side, while in the tridactyl genera, *Subhyracodon*, *Caenopus*, *Diceratherium*, etc., the scaphoid covers the whole breadth of the magnum on the dorsal side. The facet for the trapezium is slightly concave and is narrowly elliptical in outline; that for the trapezoid is saddle-shaped, concave transversely and convex palmodorsally; two rather sharp ridges separate this facet from that for the trapezium on the radial side and that for the magnum, on the ulnar. The surface for the magnum is triangular in outline and gently convex transversely.

The proximal surface on the *lunar* for articulation with the radius is strongly convex palmo-dorsally, distally it covers the magnum, by an elongated, deeply concave facet, which is broad on the palmar side, but somewhat constricted dorsally. With the unciform, the lunar also has an extensive contact by a surface which is ovate in outline and concave palmo-dorsally. In *Subhyracodon* and the other tridactyl genera, the carpal elements have shifted, so that, seen from the dorsal side, the lunar appears to rest entirely upon the unciform, while the scaphoid covers the magnum. This displacement is evidently occasioned by the suppression of the fifth digit.

The *pyramidal* displays the usual proximal facets for the ulna and pisiform and, distally, it articulates only with the unciform, covering somewhat less than half of the proximal width of that bone. The *pisiform* articulates about equally with pyramidal and ulna; its neck is much constricted, while the distal portion is greatly expanded and terminates in an elevated process.

The *trapezium* is the smallest of the carpals; it articulates proximally with the scaphoid and, on the ulnar side, with the trapezoid and terminates distally in a small, pointed process without articular surface. The *trapezoid* is also small and has saddle-shaped facets on the proximal and distal ends for the scaphoid and second metacarpal respectively. The *magnum* is comparatively large and bears, on its proximal end, three articular facets; one radial and

[1] Hatcher, J. B., Ann. Carnegie Mus., Vol. I, pp. 140–142.



dorsal for the scaphoid, a second, narrow dorsally, but expanding toward the palmar side, side, which is situated about midway between the ulnar and radial borders and articulates with the lunar; the third is dorsal and ulnar and articulates with the unciform. Distally the magnum bears only upon mc. III, but there is also a radio-distal facet, against which abuts a process from mc. II. The hook-like process from the palmar face is narrow and is directed obliquely distally. The *unciform* is much expanded distally and articulates by a continuous surface with mc. V and IV and a process from the ulnar side of mc. III. In addition, the unciform extends over upon the magnum and covers about a third of its proximo-dorsal border. This extensive and continuous articular surface is exceptionally regular in outline and its dorsal border describes an almost perfect semicircle.

The *metacarpus* consists of four members, one of which, mc. V is greatly reduced. As Hatcher remarks, this manus, though tetradactyl in structure, shows a decided tendency toward tridactylism. The third metacarpal is the longest and much the stoutest bone of the series, while mc. II and IV are subequal. Mc. III is decidedly asymmetrical and the axis of the manus passes on the ulnar side of its median line, while the proximo-dorsal side of the magnum is not so completely covered by the scaphoid as it is in the later, tridactyl forms. "The inevitable suppression to which digit V is destined is already distinctly indicated by the inferiority of its metacarpal and by that of the succeeding phalanges. Nevertheless, there is still a very considerable modification necessary before the manus of *Trigonias* assumes the typically tridactyl structure of the later Rhinoceroses and Aceratheres." (Hatcher, *loc. cit.*)

*Phalanges.* "As in all the Rhinocerotidae, the phalanges are short and rather flat, with rugose upper surfaces. The unguals, especially those of the digits II, III, and IV, are broad and very short." (Hatcher, *loc. cit.*)

### Pelvic Girdle and Limb

The *pelvis* is less specialized and more tapiroid than in the subsequent genera of the family. The *ilium* has a relatively short, trihedral peduncle, expanding into a very large anterior plate, which is strongly everted and shows the beginning of the great, forward-facing basin which, in the very large ungulates, supports the mass of viscera. The iliac plate is in two portions, which are much less plainly demarcated than in *Subhyracodon;* the sacral portion is upturned and rises as high as the summit of the sacral spines. From the base of the sacral process, the anterior border of the iliac plate is a regular and gentle curve, terminating externally in a large, triangular rugosity, from which the acetabular border describes a concave curve to the acetabulum. The iliac surface is broad, but has no iliopectineal process.

The *ischium* is long, slender and compressed, with an obscurely marked tuberosity, but conspicuous spine and sciatic notch; the descending branch is of the ordinary, plate-like form, but is narrowed by the great antero-posterior extension of the obturator foramen, which deeply emarginates the ischium. Apparently the ischium takes no part in the formation of the symphysis, the two descending branches being separated by a deep notch. The *pubis* is short and stout and forms an unusually short symphysis with its fellow, the notch between the two ischia invading the pubic region also. A very exceptional feature is the presence of a ventral keel on the anterior part of the pubic symphysis, which projects well in front of the pelvic opening.

The *femur* is considerably longer than the humerus and is tapir-like. The head is not sessile as in so many genera of the family, but is set upon a long neck, which projects obliquely inward and upward, raising the large, hemispherical head high above the level of the great trochanter. There is no sigmoid notch, a broad bridge of bone descending steeply from head to trochanter. The great trochanter is low, but very large in other dimensions, and on the external and posterior sides of the proximal end it forms a massive, rugose, and prominent projection, which on the postero-internal side ends in a blunt hook. The digital fossa, which is roofed by the blunt hook just mentioned, is deep but very small. The greatest difference in the structure of the femur between *Trigonias* and *Subhyracodon* lies in this proximal end. The second trochanter is a long, low, and inconspicuous ridge, and no intertrochanteric ridge is visible. The third trochanter is a little more proximal in position than it is in *Subhyracodon*, but of similar shape, being a massive introverted hook, with rugose margin; gently sloping crests continue the process proximally and distally and, including these crests, the third trochanter occupies half of the length of the shaft.

The shaft of the femur is of moderate thickness and nearly cylindrical shape, though the flattening of the posterior side prevents its being entirely so; the distal part of the shaft, as distinguished from the epiphysis, is not much expanded and has a small, rather shallow, supra-patellar fossa, with elevated interior border. The distal portion of the femur, which is included in the epiphysis, is exceptionally large and massive, distinctly more so than in *Subhyracodon*. The rotular trochlea is extremely prominent, especially on the inner side, thus making the antero-posterior diameter of the distal end proportionately very great, as it is in the rhinoceroses generally, *Hyracodon* excepted. The trochlea is much extended proximo-distally, describing a curve of some 120° and separated from each condyle by a notch; the trochlea is made very asymmetrical by the great prominence of the internal border. The condyles are large and unequal, the external one being larger and projecting farther behind the plane of the shaft; the epicondyles are low rugosities.

The *patella* is like that of the true rhinoceroses generally in being very heavy and rugose and in having internal and external grooves, with a ridge between them, the articular surface of which is uninterrupted.

The *tibia* is somewhat shorter than the radius and has little about it that is characteristic, for it closely resembles the tibia of *Subhyracodon occidentalis*. The cnemical crest is rough and prominent, but is not extended far distally. The shaft is of the usual trihedral form, becoming broad and planto-dorsally compressed near the distal end; the grooves for the astragalus are deep, and the intercondylar tongue is far over toward the fibular side.

The *fibula* is much reduced; the proximal end is expanded, chiefly in the antero-posterior dimension, and its contact with the tibia is lateral, for the tibia does not project over it; this relation is usual in the family and, in some of the later genera, the two bones are co-ossified. The shaft of the fibula is slender, laterally compressed, and nearly straight; the distal end is much larger than the proximal, and forms a heavy external malleolus, which is grooved on the outer side by the sulcus for the peroneal tendon.

### Pes

Among the White River genera of the true rhinoceroses, there is little difference in the structure of the hind foot, since in all of them it is tridactyl. Even in the hyracodonts, the pes is not unlike that of *Trigonias*, but was obviously tending toward monodactylism, while in the amynodonts it is widely different. In *Trigonias*, the separate elements of the pes are very much like those of *Subhyracodon*, such slight differences as may be observed being merely of size and proportion. The *astragalus* has the typical rhinocerotic character; the trochlea is broad and wide open between the condyles; the neck is very short, and the distal end is almost completely covered by the navicular, while the facet for the cuboid is narrow, especially on the dorsal border, broadening somewhat toward the plantar side. This limited articulation between astragalus and cuboid, and the correlated proportions of the calcaneo-cuboid connection, form one of the most conspicuous differences in foot-structure between the Rhinocerotidae of the Oligocene and those of the upper Miocene and later times. In the latter, the contact of the astragalus with the cuboid is greatly enlarged, while the cubo-calcaneal articulation is correspondingly reduced. Presumably this change was brought about in adjustment to the greatly increased bulk and weight which are so striking in these later genera.



The *calcaneum* of *Trigonias* is closely similar to that of *Subhyracodon;* the tuber has the same shape, with parallel dorsal and plantar borders, and thickened, club-like proximal end; the distal end is completely covered by the surface for the cuboid, a notable difference from the upper Miocene genus *Aphelops*, which may be taken as typical of the later Tertiary and Recent true rhinoceroses. In *Aphelops* the cuboid facet covers hardly more than half of the distal end of the calcaneum, the remainder being a rough, tuberculated mass.

The *navicular* is relatively broader than in *Aphelops*, but with greater proximo-distal diameter; as in *Subhyracodon*, it articulates extensively with the cuboid, but is excluded from the calcaneum by the astragalo-cuboid junction. The *entocuneiform* is a very large, oval, and scale-like bone, which depends from the planto-distal border of the navicular, and is also applied to an oblique surface of the tibio-plantar angle of mt. II. The *mesocuneiform* is the functional support of mt. II, and its dorsal face is subquadrate, but the bone narrows to the plantar side. The *ectocuneiform* is much the largest of the three; it is both broad, in correspondence with the size of the median metatarsal, and elongate proximo-distally, as in *Subhyracodon*, much more so than in *Aphelops*. The *cuboid* also resembles that of *Subhyracodon* in its relatively great proximo-distal elongation, its narrow surface for the astragalus and much broader one for the calcaneum. In all of these respects the cuboid of *Aphelops* is very different; it is shorter proximo-distally, has a much broader surface for the astragalus, and a correspondingly narrower one for the calcaneum.

The *metatarsals* and *phalanges* differ very little from those of *Subhyracodon*, except that the former are somewhat heavier and shorter, while in *Aphelops*, as well as in the modern genera, the metatarsals and phalanges are very much shorter and stouter than in any of the White River genera.

*Species*. In nearly all the White River genera described in this monograph the problem of species has proved to be exceedingly difficult; in *Trigonias* the difficulty is exaggerated, so great is the variability displayed in the remarkable series of skulls and skeletons from Weld County, Colorado, in the Denver Museum.

Three different methods of treating this problem have been suggested; at one extreme is the solution offered by the late Professor W. D. Matthew,[1] who writes: "Ancestral to the

[1] Matthew, W. D., Univ. California Publ. in Geolog. Sci., Vol. XX, p. 5, 1931.

*Caenopus* [i.e., *Subhyracodon*] group stands the genus *Trigonias*, admirably represented now by the fine series of skulls and partly associated skeletons obtained by the Denver Museum from a single fossil quarry in the Chadron beds of Weld County, Colorado. There is every reason to believe on ecologic and other grounds that this series represents one genus and one species thereof, the wide range of variation in structure of the cheek-teeth illustrating how little value should be attached to the complex detailed phylogenies with numerous species and many so-called genera, that have been built up on the comparison of numerous fragmentary specimens from various localities."

Dr. Matthew [1] had formulated more general principles, in a preceding paper, that bear directly on this case. "The range of modern species should be our guide in determining the range of fossil species, based always on much less adequate material. We should expect to find in a single fossil quarry that the material of each genus represents a single ecologic niche, or, if more than one, that they are quite distinct. We should not, in other words, expect to find two or more closely related species living together at the same time, within the same area and with the same habitat, causing their remains to be preserved together in the same quarry."

Director Figgins, of the Colorado Museum, wrote in agreement with Matthew (Proc. Col. Mus. Nat. Hist., Vol. XIII, No. 3, p. 11).

At the opposite extreme is the opinion and practice of Professor W. K. Gregory and Mr. Harold Cook,[2] who made a remarkable study of the dentition of this genus and came to a very different conclusion. These authors are greatly impressed by the extreme variability of the many skulls collected in the Colorado Museum, especially of the upper premolars. They say: "Very wide differences, not only in the form of the skull, length of the premaxillary rostrum, character of the incisors and canines, but especially in the patterns of the upper premolars, are found in the series of skulls already prepared. Indeed, if the series were less complete, were the specimens from different localities or horizons, and had we chanced to find only the extremes of variation, we should have felt no hesitation, according to widely accepted standards in palaeontology, in describing at least seven 'new species' representing possibly three different genera; but these extreme differences are bridged over by numerous intergrading conditions and combinations of characters, so that one soon gets the impression, on the one hand, that the Weld County series reveals a highly plastic condition of the rhinoceros population; . . . on the other hand, that extensive hybridism between formerly distinct races was actively going on."

Messrs. Gregory and Cook admit two genera, and seven species, and three subspecies of true rhinoceroses in the Chadron formation of Weld County, Colorado, but they do not use these terms in the ordinary sense, qualifying them as follows: "While we thus incline to the hypothesis of extensive hybridism between originally distinct races, for the sake of convenience in describing and cataloguing the material, we nevertheless designate the various groups or individuals as variants or "species" realizing full well that these terms in this instance, and perhaps in many others, merely signify a definable set of characters in certain individuals." (*Loc. cit.*)

Professor H. E. Wood,[3] who has done so much extremely valuable work on this family,

[1] Bull. Geol. Soc. America, Vol. 41, pp. 271–4, 1930.
[2] Proc. Colorado Mus. Nat. Hist., Vol. VIII, p. 4.
[3] Wood, H. E., Journal of Mammalogy, Vol. 12, pp. 414–28.



occupies a position on the problem of the *Trigonias* species intermediate between Gregory and Cook, on the one hand, and Matthew on the other. He writes: "This *Trigonias* material brings up the old question of what is a species . . . However, from the viewpoint of convenience, it is certain that some of these specimens are sufficiently different from the rest to require individual mention, and may, therefore, deserve individual designations. . . . Convenience is the only real criterion, especially in palaeontology, for deciding whether or not to give taxonomic recognition to morphologically distinct variants. It is, at least, a tenable point of view that it is legitimate to name any variant sufficiently distinct to require individual discussion." (*Op. cit.*, p. 416.)

"The question as to just what taxonomic recognition should be given to the different strains has been answered in diametrically opposed fashion by Gregory and Cook and by Matthew, without any serious difference of opinion as to the actual facts involved. I have taken a somewhat intermediate position, solely on the basis of convenience, and without any mystical views as to what constitutes a 'real' species in paleontology." (*Op. cit.*, p. 427.)

In this paper Wood recognizes the following species and varieties, omitting the species from South Dakota:

1. *Trigonias osborni* Lucas.
   a. *T. osborni osborni* Wood
   b. *T. osborni secundus* G. & C.
   c. *T. osborni figginsi* G. & C.
   d. *T. osborni precopei G. & C.* (species G. & C.)
2. *T. taylori* G. & C.
3. *T. hypostylus* G. & C.
4. *T. cooki* Wood sp. nov.

In 1937 Dr. Wood very kindly prepared the subjoined table for my use; it represents his latest views on this subject.

"Key to 'Species' of Trigonias

"1. *Trigonias osborni osborni* Lucas, 1900—P$\underline{2}$ usually nearly molariform; median valleys of p$\underline{3}$–$\underline{4}$ open posteriorly; synonyms: *nanolophus* Troxell, 1921; *figginsi* Gregory and Cook, 1928; *secundus* G. & C., 1928.

"2. *T. osborni precopei* G. & C., 1928, not more than a variety, if that. Synonym: *preoccidentalis* G. & C., 1928.

"3. *T. taylori* G. & C., achondroplasia, whether individual or racial.

"4. *T. hypostylus* G. & C., 1928: hypostyles on otherwise primitive p$\underline{3}$–$\underline{4}$; ancestral to *T. wellsi?*

"5. *T. cooki* Wood, 1931. P$\underline{3}$–$\underline{4}$ molariform, with median valleys opening internally: P$\underline{4}$ still primitive, but with well defined hypocone; near line of ancestry of *T. gregoryi*.

"6. *T. wellsi* Wood, 1931. Large size: P$\underline{2}$–$\underline{4}$ premolariform, with median valleys opening to rear, and with large hypostyles usually present.

"*T. paucidens* Wood, 1927. Upper canine lost; i$\underline{3}$, c$\underline{0}$, p$\underline{4}$, m$\underline{3}$; otherwise close to *T. osborni;* appears ancestral to *Amphicaenopus*.

"*T. gregoryi* Wood, 1927. Large size for *Trigonias:* p$\underline{2}$ molariform, p$\underline{3}$–$\underline{4}$ incompletely so; no hypostyles."

In this arrangement several of the "species" named by Gregory and Cook are reduced to synonyms and four new species are described, i.e., new since the appearance of Gregory and Cook's paper.

In this monograph, the difficulty, often the impossibility, of distinguishing between contemporary fluctuating variants and successive mutants, has been emphasized. All the Weld County skulls and skeletons of *Trigonias* have been taken from so thin a deposit of sediment, that they must have been substantially contemporaneous and, therefore, they should, in my opinion, be treated like Recent material. There is no gain in making a lot of "species" which, everyone agrees, are not species. So far as it is necessary, or desirable, to distinguish and describe these variants, it can be accomplished by giving them numbers, rather than names. The South Dakota specimens, which Wood has named *T. wellsi* and *T. gregoryi*, are in a somewhat different category, and one or other of them may ultimately prove to be distinct.

I find myself, therefore, in almost complete agreement with Dr. Matthew, differing from him only in recognizing *T. taylori* as a separate species. The fact that this rare stray occurs in the same bed with the typical *T. osborni* does not necessarily prove that it had the same habitat; it may have been an upland, or a forest-dweller, and its carcass may have been carried a long distance by a flooded stream. Its exceptional character, differing from *all* the other skulls, and the absence of intergradations, make this difference of habitat probable. This reasoning, obviously, does not apply to the *T. osborni* cycle.

### Trigonias osborni Lucas

*Trigonias osborni* Lucas: Proc. U. S. Nat. Mus., Vol. XXIII, No. 1207, p. 221, 1900.
*Trigonias hypostylus* Gregory and Cook: Proc. Colorado Mus. Nat. Hist., Vol. VIII, p. 15, 1928.
*Trigonias precopei* G. & C.: Ibid.
*Trigonias preoccidentalis* G. & C.: Ibid., p. 16.
*Trigonias cooki* H. E. Wood: Journ. Mammalogy, Vol. XII, p. 425, 1931.
*Trigonias paucidens* Wood: Bull. Amer. Palaeont., Vol. 13, No. 50, p. 51, 1927.
*Trigonias tetradactylum* Osborn: Nat. Hist., Vol. XXIII, No. 3, p. 214, 1923.
*Caenopus platycephalus nanolophus* Troxell (*fide* Wood): Amer. Journ. Sci., Ser. 5, Vol. II, p. 46, 1921.

This is the common and relatively abundant species in the Chadron of both Colorado and South Dakota; the extreme variability of the upper premolars has been sufficiently dwelt upon, but, as Gregory and Cook point out, there is also great variation in the form of the skull. However, all the skulls referable to this species show certain constant and marked differences from the unique specimen which Gregory and Cook named *T. taylori*. All the skulls referred to other species agree essentially in being long and narrow, though meso- rather than dolichocephalic, except for the very prominent zygomatic arches. A conspicuous difference from *Subhyracodon* is to be seen in the dorsal contour of the cranium which is nearly straight in the latter, while in *Trigonias* it is made deeply concave by the great elevation of the occiput, which is higher and projects farther backward in *T. osborni* than in *T. taylori*. The zygomatic arch is comparatively long and slender and its dorsal border rises gently from the orbit backward to the postero-superior angle, which is little, or not at all, elevated above the sagittal crest, and the ventral border is a somewhat sinuous line, without "elbow," which is elongate and has a very gentle slope downward from the glenoid cavity to the maxillo-jugal suture. The jugal is narrow and elongate and has an angulation which indicates the postorbital process.



The forehead is broad and nearly flat, but made convex above the orbits by the frontal sinuses, which have smooth surfaces, in strong contrast to the "heavy rugose knobs" of *T. taylori*. The nasals are very long, decurved and pointed, and the anterior nasal incision is deep and its lateral boundary slopes gently upward to the naso-maxillary suture. The coronoid process of the mandible is comparatively short and erect and the sigmoid notch is broad and shallow.

A comparatively constant feature of this species is bodily size, which, on the average, is approximately the same as in *Subhyracodon occidentalis*. The very large skulls which Wood named *T. wellsi* and *T. gregoryi* are here treated as a variety of *T. osborni*.

### Trigonias osborni wellsi Wood

*Trigonias wellsi* Wood: Bull. American Palaeont., Vol. 13, No. 50, p. 46, 1927.
?*Trigonias gregoryi* Wood: *Ibid.*, p. 48.
?*Trigonias cooki* Wood: Journ. of Mammalogy, Vol. 12, p. 425, 1931.

The original description is: "The holotype is A.M.N.H. No. 13226 (1). This animal is a third larger than *Trigonias osborni:* $I\frac{3}{2}\ C\frac{1}{?}\ P\frac{4}{?}\ M\frac{3}{?}$. The canine is larger than the third incisor. None of the upper premolars are anywhere near molariform. The metaloph is incomplete on $P\underline{2}$. The hypocone on $P\underline{2}$–$\underline{4}$ is merely a bud on the protocone, the two cusps being fully confluent, with an internal notch. The median valley opens widely posteriorly. A well developed hypostyle is present on $P\underline{2}$ and $P\underline{3}$ of both sides, but is absent on right $P\underline{4}$. The presence of a hypostyle as a free cusp (not an upgrowth of the cingulum), which is otherwise unrecorded among rhinoceroses, living or fossil, bars this species from ancestry to any other known form. . . . A weak internal cingulum is present on all the molars. The ectoloph and metaloph of $M\underline{3}$ form a straight line. The posterior cingulum of $M\underline{3}$ is reduced. The post-glenoid and post-tympanic processes are well separated below the external auditory meatus."

"The first and third left incisors, both canines, what is apparently the left deciduous canine abnormally retained to old age, and all the cheek-teeth are present. There is also associated a loose first right upper incisor, which may have dropped out of this specimen. If so, it must have done so after death, but before fossilization, since the alveolus is filled with completely consolidated matrix."

Wood's description of *T. gregoryi* is as follows: "The holotype is A.M.N.H. No. 13226*a*. This form is almost as large as *Trigonias wellsi*. . . . The upper canine is larger than the third incisor. The pattern of the P 1/s is similar to that of the paratype of '*Caenopus*' *platycephalus*, figured by Osborn (1898, Pl. XIII, Fig. 9). Upper premolars 2–4 are very progressive for *Trigonias*, bearing more resemblance to '*Caenopus*' *platycephalus* than to either of the other species of *Trigonias* (i.e., *T. osborni* and *T. wellsi*), or to any other hitherto known form. There is no hypostyle on the upper premolars. $P\underline{2}$ is virtually molariform, with a complete metaloph which is separate from the protoloph down to the level of the cingulum. $P\underline{3}$ and $P\underline{4}$ are also progressive although less advanced than $P\underline{2}$. The hypocone of $P\underline{3}$ is nearly independent of the protocone, but is not completely joined to the metaconule. It is more advanced in both respects, however, than *Trigonias wellsi* or *Trigonias osborni*. The metaloph is almost complete on the right $P\underline{4}$, but much "less so on the left P4, where the hypocone is rudimentary. There is what appears to be an antecrochet on the right P4. This is an unprecedently early appearance for this structure. The molars have no internal cingulum. The ectoloph and metaloph of M3 form a straight line. The posterior cingulum of M3 is well developed. The posterior margin of the nasal incision is vertically above the anterior border of P2."

"*Trigonias gregoryi*, especially in the progressiveness of P2, tends to break down the clear distinction between *Trigonias* and the later forms, usually referred to *Caenopus*, as this term was used by Troxell (1921*a*)."

If the differences in premolar complication between the typical skulls of *T. osborni* and *T. gregoryi* should prove to be constant, there will then be no question as to the specific distinctness of the latter. In the South Dakota area, however, there is no such abundance of *Trigonias* remains as there is in Colorado, and transitional forms are far less common. It is quite possible, therefore, that *T. gregoryi* will prove to be merely one of the fluctuating variants of the type-species, *T. osborni*.

*Trigonias cooki* Wood is very like *T. gregoryi*, but much smaller.

The difference, still unexplained, between the Colorado and the Dakota localities in the abundance of *Trigonias* remains is very striking.

Measurements

| | *A.M.N.H. No. 13,226 T. wellsi type* | *A.M.N.H. No. 13,226a T. gregoryi type* |
|---|---|---|
| I1, ant.-post. diameter | 26 mm. | 22 mm. |
| I1, transverse diameter | 13 | 12.5 |
| I3, ant.-post. diameter | 13 | 12.5 |
| I3, transverse diameter | 9.5 | 7.5 |
| Upper canine, ant.-post. diameter | 11.5 | 12.5 |
| Upper canine, transverse diameter | 7 | 7.5 |
| Diastema C–p1, length | 46 | 37 |
| Cheek-tooth series, length | 256 | 252 |
| P2–m3, length | 230 | 226 |
| Upper premolar series, length | 120 | 114 |
| Upper molar series, length | 141.5 | 139.5 |
| P1, length | 25.5 | 26 |
| P1, width | 23 | 23 |
| P2, length | 28 | 27.5 |
| P2, width | 37.5 | 35 |
| P3, length | 27.5 | 29 |
| P3, width | 47 | 45 |
| P4, length | 32.5 | 32 |
| P4, width | 52 | 50 |
| M1, length | 43 | 43.5 |
| M1, width | 55 | 55.5 |
| M2, length | 49.5 | 48 |
| M2, width | 61 | 63 |
| M3, length | 50 | 49.5 |
| M3, width | 59 | 60 |

*Horizon:* Chadron.

*Locality:* Corral Draw, Big Bad Lands, So. Dakota, Weld Co., Col.



**Trigonias taylori** Gregory and Cook

*Trigonias taylori* Gregory & Cook: Proc. Colorado Mus. Nat. Hist., Vol. VIII, p. 17, 1928.

*Trigonias osborni* Figgins (*nec* Lucas): Proc. Colorado Mus. Nat. Hist., Vol. XIII, No. 3, p. 11, 1934.

"In some ways, this is the most remarkable skull so far found in the Weld County series. Unlike all other known *Trigonias* skulls, it is short, wide, and deep, brachycephalic in type, with a number of marked peculiarities when compared with the other described forms, or with any skulls so far found. . . . The general conformation of the skull is strongly suggestive of a type that could have led up readily to such a later development as we find in *Peraceras* in the late Miocene and lower Pliocene. The back of the skull is very much elevated but the occiput ends anterior to the condyles, whereas in the other described species it extends backward, in most types to a very marked degree. The whole basi-cranial region is crowded and the external auditory meatus is nearly closed below: the wide and slender occipital condyles are, on the outside, slightly overlapped by the paroccipital processes of the exoccipital; these in turn, by the postglenoid processes, which are peculiarly wide, angular, and backward sloping. The zygomatic arches have the same type of sharp elbow-angulation that is so marked in *Peraceras*. One of the most striking features is the development of a remarkable pair of heavy rugose knobs in the frontal over the orbits, quite unlike the rudimentary horn development in other known Oligocene Rhinocerotidae, either in position or in size. The nasals curve rather sharply downward, extending over a pair of rugged premaxillae, thick and short, with the three incisors and canines crowded together; all functional teeth, more comparable to conditions found in horses than in rhinoceroses! This crowding is so marked that I 2 and I 3 are both forced transversely in the jaw. The posterior edge of the second incisor turns outward, while the anterior edge of the third turns out. Unfortunately, the first upper incisor is absent on both sides, but from the alveoli it is obvious that they were relatively smaller than is usual in *Trigonias*. This, together with the presence of functional teeth behind it, points to a primitive condition, all of these teeth showing marked and heavy wear.

"The zygomatic arches rise considerably above the top of the small braincase at their posterior tips. Premolar two nears complete molarization, with the deuterocone and tetartocone distinct; the metaloph still slightly more slender than the protoloph and just becoming connected with the tetartocone, a structural stage not shown in other types illustrated herewith. P 3 has the protoloph developed in a large, heavy curve, extending around the whole inner side of the tooth, broadly expanded at the deuterocone. There is no suggestion of the tetartocone, and the wearing crest ends confluently with the cingulum on the posterior side of the tooth, near the middle, transversely. The ectoloph is wide and heavy, and the metaloph very short, but relatively wide. P4 is almost identical in pattern to P3, but very pinched and crowded and correlated with the excessively short face, so that its transverse diameter greatly exceeds the antero-posterior measurement. M1 is relatively small and crowded. The molar patterns are closely comparable to those of the other species.

"The lower jaw is remarkably curved and heavy, and the coronoid process actually curved forward over the molars at an angle of 15 degrees, a character correlated with the extremely brachycephalic skull. The incisors, both upper and lower, and the canines in this skull are much heavier than in the other types described." (Op. cit., pp. 17, 19.)

This remarkable form, of which only a single skull is known, seems to me to be an unquestionably valid species; among the many skulls of *T. osborni* which are contained in the museums of Denver, Pittsburgh, and New York, there is not one which approximates *T. taylori*. The only writers who have rejected the species are Figgins[1] and Matthew. (Loc. cit.)

The following measurements are selected from those given by Gregory and Cook, p. 21.

MEASUREMENTS

| | | | |
|---|---|---|---|
| Skull, length premx. to occ. cond. | 474 mm. | Upper cheek-tooth series, length | 185 mm. |
| Skull, breadth over zygomata | 262 | Upper premolar series, length | 80 |
| Skull, length fr. tip of nasals to occ. crest | 479 | Upper molar series, length | 107 |
| Premaxilla length | 45 | | |

*Horizon:* Chadron.
*Locality:* Weld Co., Colorado.

### **Amphicaenopus** Wood

*Aceratherium* O. & W. (*nec* Kaup): Bull. Amer. Mus. Nat. Hist., Vol. VI, p. 206, 1894.
*Caenopus* Osborn & Matthew (*nec* Cope): Ann. N. Y. Acad. Sci., Vol. XIX, p. 41, 1909.
*Amphicaenopus* H. E. Wood: Bull. Amer. Palaeont., Vol. XIII, No. 50, p. 72, 1927.

This is a name of doubtful validity but its exact status will remain uncertain until a larger suite of better and more comprehensive specimens shall have been collected. According to Professor Wood, this somewhat questionable genus is defined as follows: "Large form with p$\underline{2}$–$\underline{4}$ primitive, especially p$\underline{3}$; appears direct continuation of *Trigonias:* $i\frac{2-1}{3-2}$, $c\frac{0}{0}$, $p\frac{4-3}{4-3}$, $m\frac{3}{3}$. P$\underline{2}$ protoloph and metaloph may be separate and parallel, most advanced upper premolar; p$\underline{3}$ not molariform, hypocone an isolated hill." (Wood, Ms.)

The single known species, *A. platycephalus* (O. & W.) was thus defined by Osborn (1898) making the necessary corrections for the homology of the lower incisors: (*a*) Lateral upper incisors reduced, median lower incisors greatly reduced, second lower incisors greatly enlarged and procumbent. (*b*) Permanent canines absent. (*c*) The upper premolars are very primitive; p$\underline{2}$ has anterior and posterior cross-crests which are complete, but are separate from the outer wall; the valley opens internally; in p$\underline{3}$ and $\underline{4}$ the posterior crest is very short and, in little worn teeth, is not connected with the internal cusp, which is conical and free. (*d*) Upper molars 1 and 2 have antecrochets. (*e*) Skull broad, sagittal crest nearly obsolete; post-glenoid and post-tympanic processes in limited contact.

### **Amphicaenopus platycephalus** (O. and W.)

*Aceratherium platycephalum* O. & W.; Bull. Am. Mus. Nat. Hist., Vol. VI, p. 206, 1894.
*Caenopus platycephalus* O. & M. Ann. N. Y. Acad. Sci., Vol. XIX, p. 41, 1909.
*Amphicaenopus platycephalus* Wood: Bull. Amer. Pal., Vol. XIII, No. 50, p. 75, 1927.

The type was obtained in the upper Brulé (*Protoceras* Beds) and the species was subsequently reported from the Chadron, but unless the identification is a mistake, it implies that the genus must have persisted through lower Brulé time, though it may possibly have

[1] Figgins, J. D., Proc. Color. Mus. Nat. Hist., Vol. XIII, No. 1, p. 11.



withdrawn from the Great Plains area for some unknown reason. It is much more likely, however, that its seeming absence from the lower Brulé beds is one of the accidents of fossilization and collecting of which so many have been reported. The following table is taken from Osborn's memoir.[1]

MEASUREMENTS IN MM.

| | *Type No. 540* | *Cotype No. 542* | *Jaw No. 545* | *Jaw No. 1444* | *Chadron No. 1478* |
|---|---|---|---|---|---|
| Upper m–p series | 238 | 236 | | | 227 |
| Upper molar series | 133 | 139 | | | 128 |
| Lower m–p series | | | 228 | 222 | 213 |
| Lower molar series | | | 135 | 142 | 133 |
| Skull, prmx. to occ. cond. | | | | | 590 |
| Skull, width of zygomata | | ?360 | | | 294 |
| Jaws, angle to point of symphysis | | 530 | | | 501 |

The type skull (A.M.N.H. No. 340) has been much distorted by vertical crushing and a second skull, with mandible, in the Princeton Museum, has suffered from lateral compression, and although it shows well the relatively large size of these animals it is very different from the type in appearance; it is probable that the difference in the direction of crushing has caused the unlikeness in the two skulls.

*Horizon:* Upper Brulé and ?Chadron.
*Locality:* Big Bad Lands, So. Dak.; Hat Creek, Nebraska.

### **Caenopus** Cope
(Pl. LXXXVIII)

*Aceratherium* Cope (*nec* Kaup): Ann. Rep't. U. S. Geolog. and Geogr. Surv. Terr's for 1873, p. 493.
*Aceratherium* (*Subhyracodon*) Brandt (in part): Mém. Acad. Sci. de St. Pétersb., III$^{me}$, Sér., T. XXVI, p. 30, 1878.
*Caenopus* Cope, Amer. Natural., Vol. XIV, p. 611, 1880.
*Hyracodon* Scott & Osborn (in part. *nec* Leidy): Bull. Mus. Comp. Zool., Vol. XIII, p. 170, 1887.
*Caenopus* Wood: Bull. Amer. Palaeont. Vol. XIII., No. 50, p. 55, 1927.
?*Procaenopus* Figgins: Proc. Col. Mus. Nat. Hist., Vol. XIII, No. 3, p. 11, 1934.

As restricted by Wood, this genus is probably distinct, though it is still very imperfectly known, being represented by fragmentary specimens. Fossils referable to the genus are rare.

Consistently small size characterizes the species of this genus throughout their history; but size alone is, of course, insufficient as a generic character. Of more significance, yet not altogether certain, is one found in the incisor teeth: the first upper and second lower seem to be relatively much less enlarged than in other White River members of the family; and in the lower jaw the symphysis is so narrow that the median incisors must have been

[1] Osborn, H. F., Mem. Amer. Mus. Nat. Hist., Vol. I, p. 141.

very small, and in *C. dakotensis* their presence is doubtful. The premolars are more nearly molariform than in other White River genera, and in particular p$\underline{4}$ is more advanced toward the molar plan than in the other White River genera.

*Caenopus* has been found in the Chadron and the upper Brulé, but not in the intervening lower Brulé, and the two sets of fossils admit of little direct comparison between them. Statements that are true of the earlier species (*C. mitis*) may not apply to the later (*C. dakotensis*), and *vice versa.*

A fore limb of a small rhinoceros from the Chadron (Princeton Univ. Mus. No. 11,418) unfortunately not associated with teeth, very probably belongs to this genus because of its size, for it seems too small to be referable to *Trigonias* or *Subhyracodon.* The only noteworthy feature of this specimen is the tridactyl manus, which, of course, removes it from *Trigonias.* The scapula and limb-bones, humerus, ulna, and radius, are so like the corresponding parts of *Subhyracodon* as to require no description or figuring, and the manus, which has certain peculiarities, is most appropriately described under the species, *C. mitis.*

### Caenopus mitis Cope

*Aceratherium mite* Cope: Ann. Rept. U. S. Geol. and Geogr. Surv. Terr's., 1873, p. 493.
*Aceratherium (Subhyracodon) mite* Brandt: Mém. Acad. Sci. de St. Pétersb. III$^{me}$ Sér. T. XXVI, p. 30, 1878.
*Caenopus mitis* Cope: Amer. Natur. Vol. XIV, p. 611, 1880.
?*Hyracodon planiceps* Scott & Osborn: Bull. Mus. Comp. Zoöl., Vol. XIII, p. 170, 1887.
*Caenopus pumilis* Cope: Geol. Surv. Canada, Cont. to Canad. Paleon. III., p. 17, 1891.

The only known species from the Chadron, *C. mitis,* is uncommon and is represented by fragmentary remains. The type specimen (A.M.N.H. No. 6325) consists of much of the skeleton in a more or less fragmentary state, parts of the palate, basis cranii, and mandible. No lower teeth are preserved, but p$\underline{1}$–m$\underline{2}$ in fairly complete condition remain. Several vertebrae, including a nearly perfect axis, distal end of scapula, both ends of humerus, radius, magnum, femur, tibia, distal end of fibula, and the astragalus are in condition and permit comparison of the Princeton fore leg and foot with the type. All these bones are like those of *Subhyracodon* on a smaller scale. The type specimen was a young adult, for some of the vertebrae have lost their epiphyses, but the referred fore leg (P.M. No. 11,418) was of a fully adult animal.

The *manus* (No. 11,418) is in very complete preservation except for the loss of certain phalanges; the absence of the fifth digit and the tridactyl structure immediately remove it from *Trigonias.* While close to that of *Subhyracodon,* there are characteristic differences which support Wood's contention that *Caenopus* should be recognized as a separate genus, especially the relative shortness and sturdiness of the metacarpals; the proportions are more as in *Trigonias* (Cf. Pl. LXXXIII, Fig. 7, with Pl. LXXXVIII, Fig. 3). In *Subhyracodon* the metapodials are decidedly more slender and elongate (Pl. LXXVII, Fig. 1), proportions which are further emphasized in *Diceratherium* of the upper Brulé and the John Day, and show that those genera cannot have been ancestral to any of the modern rhinoceroses, their development leading away from the latter.

The *carpus* of *Caenopus,* like the whole manus, is proportionally shorter, broader, and palmo-dorsally thicker than in *Subhyracodon,* and each of the carpal bones shows similar relative differences; it also differs considerably from that of a Recent rhinoceros and, despite its tridactylism, the carpus has more resemblance to that of a tapir. The scaphoid is short and heavy, broader and thicker than in *Subhyracodon,* but otherwise very much as in the latter, and differing from that of *Rhinoceros* in very similar fashion. Distally, the scaphoid rests upon the trapezium, trapezoid, and magnum, for each of which it has a facet.



The *lunar* is likewise broader than in *Subhyracodon,* and more widely removed from any dorsal contact with the magnum; the distal end is less contracted and has a wider facet for the unciform, the dorsal border of which is straight. This is a marked difference from *Rhinoceros,* in which the distal end is a beak, made by the oblique facets for magnum and unciform, which meet at an acute angle. The pyramidal is lower and wider than in *Subhyracodon,* otherwise closely similar in shape and connections. The pisiform is short and broad, with much expanded and club-like free end, compressed and contracted neck and broad proximal end; the facets for the ulna and the pyramidal are large, of nearly equal size, and join in an acute angle.

The carpal elements of the distal row differ rather more in form and proportions from those of *Subhyracodon* than do the bones of the proximal row. The *trapezium* is a small, irregular nodule, which articulates only with the scaphoid and trapezoid and, unlike the genus last named, is visible when the foot is seen from the dorsal side. The *trapezoid* is shorter proximo-distally and wider than in *Subhyracodon,* but is yet actually narrow and elongate; it articulates, as usual, with trapezium, magnum, and scaphoid and, distally, with the second metacarpal, for which it bears a saddle-shaped facet. The *magnum* differs decidedly from that of *Subhyracodon* in being larger and, especially, broader and having a more extensive contact with the lunar, while, dorsally, it appears not to touch the scaphoid at all; the disto-radial facet for the process from the head of mc. II is larger and less oblique than in the other genus, while the surface for mc. III is broader and more convex transversely. The *unciform* is distinctly wider than in *Subhyracodon,* especially the beak-like extension beneath the lunar, the facet for which and that for the magnum meeting at almost a right angle. The surfaces for the magnum and the third and fourth metacarpals form one continuous curve, but that for the vestigial fifth on the ulno-distal side is an angulation.

The *metacarpus* consists of three functional members, mc. II, III, IV, and a nodular vestige of mc. V, and yet, despite the complete reduction of the fifth digit, the appearance and proportions of the functional metacarpals are more as in *Trigonias* than in *Subhyracodon,* which has such long and narrow feet, which become increasingly elongate in its descendant *Diceratherium.* In those two genera the metacarpals have a slightly divergent arrangement, whereas in *Caenopus* they are closely applied for nearly their whole length.

In general, the shape and relative proportions of the metacarpals are very much as in *Subhyracodon,* except for the distinctly greater breadth and thickness of the shafts, and for slight differences in the articulations with the carpals. The second metacarpal, mc. II, has a more concave surface for the trapezoid and a larger, more vertical and lateral facet for the magnum; the shaft is stouter and less curved, and the distal trochlea is more nearly hemispherical. The third metacarpal, mc. III, is more distinctly different from the corresponding bone of *Subhyracodon* than any other of the metapodials, and the most obvious difference is its greater relative stoutness; the facet for the magnum is larger and transversely more concave, and that for the unciform is more oblique; the shaft is broader throughout. The fourth metacarpal is very much like that of *Subhyracodon,* except for the greater stoutness of the shaft. Metacarpal V is a small nodule, which is clearly vestigial and useless. The complete reduction of digit V and the changes in the carpus which followed loss of the fifth digit are the principal differences from the manus of *Trigonias*.

Of the phalanges, three are preserved, a different one for each digit; in digit II it is the ungual, in digit III, the proximal one, and in digit IV, the second; they differ hardly at all from those of *Subhyracodon*.

Measurements

| | *P.U.M. No. 11,418* | *A.M.N.H. No. 6325* |
|---|---|---|
| Upper premolar series, length | | 53 mm. |
| P$\underline{1}$, ant.-post. diameter | | 13 |
| P$\underline{1}$, transv. diameter | | |
| P$\underline{2}$, ant.-post. diameter | | 18 |
| P$\underline{2}$, transv. diameter | | 19 |
| P$\underline{3}$, ant.-post. diameter | | 23 |
| P$\underline{3}$, transv. diameter | | 28 |
| p$\underline{4}$, ant.-post. diameter | | 24 |
| p$\underline{4}$, transv. diameter | | 33 |
| m$\underline{1}$, ant.-post. diameter | | 29 |
| m$\underline{1}$, transv. diameter | | 32 |
| m$\underline{2}$, ant.-post. diameter | | 36 |
| m$\underline{2}$, transv. diameter | | 37 |
| Axis, length excl. odont. | | 57 |
| Axis, length incl. odont. | | 73 |
| Axis, ant. width | | 73 |
| Axis, post. width | | 35 |
| Scapula, vert. length | 271 mm. | |
| Scapula, ant.-post. diam. glen. cav. | 43 | 43 |
| Scapula, transv. diam. glen. cav. | 35 | 36 |
| Humerus, length fr. head | 251 | |
| Humerus, prox. thickness | 49 | 61 |
| Humerus, dist. width over epicond. | 58 | 58 |
| Humerus, dist. width over troch. | 44 | 43 |
| Radius, length | 234 | 201 |
| Radius, prox. width | 48 | 44 |
| Radius, dist. width | 41 | 40 |
| Ulna, length | 295 | |
| Carpus, max. length | 51 | |
| Carpus, width | 59 | |
| Magnum, prox.-dist. length dorsal face | 19 | 19 |
| Magnum, transv. width dorsal face | 22 | 18 |
| Mc. II, length | 103 | |
| Mc. II, prox. width | 17 | |
| Mc. II, dist. width | 17 | |
| Mc. III, max. length | 120 | |
| Mc. III, length in median line | 109 | |
| Mc. III, prox. width | 30 | |
| Mc. III, dist. width | 24 | |
| Mc. IV, length | 92 | |
| Mc. IV, prox. width | 19 | |
| Mc. IV, dist. width | 20 | |
| Mc. V, length | 19 | |

*Horizon:* Chadron.
*Localities:* Cedar Creek, Col.; Big Bad Lands, So. Dak.



### **Caenopus dakotensis** Peterson

*Aceratherium mite* Osborn (*nec* Cope): Mem. A.M.N.H., Vol. I, p. 136, 1898.
?*Caenopus dakotensis* Peterson: Mem. Carn. Mus. Pittsb., Vol. VII, p. 402, 1920.

This species was founded upon a nearly perfect mandible, with the anterior end of the symphysis somewhat broken. In addition, Wood identified as belonging to this species a fossil in the Berlin Museum comprising the base of a skull with both series of cheek-teeth in place, lacking p$\underline{1}$ on the right side, p$\underline{1}$ and p$\underline{2}$ on the left. In addition there is a large fragment of each horizontal ramus of the mandible with the molar series in place. Professor Wood has kindly supplied me with a cast of the Berlin specimen, from which the following description and measurements have been taken. So far as they are comparable, the two individuals are of almost exactly the same size save in thickness of ramus, and there is every reason to assume that they belong to the same species, though the provenience of the Berlin specimen is not definitely stated.

In the type (A.M.N.H. No. 1110) the number of lower incisors is indeterminate because of the fractured condition of the symphysis, but, to all appearances, the median pair(i$\overline{1}$) was lacking. The laterals (i$\overline{2}$), of which the root remains on the right side, are semiprocumbent tusks, relatively smaller than in the other White River genera of the family. The six cheek-teeth, which are much worn, display no characteristic features other than their small size. The angle is somewhat thickened in rhinocerotic fashion, but very much less so than in Recent genera and relatively less than in *Subhyracodon*. The post-cotyloid process is a prominent and rugose, but thin ridge, which is much less massive than in *Subhyracodon*. The masseteric fossa is placed very high upon the side of the jaw and is shallow and ill-defined. The condyle is narrow and obliquely placed, sloping steeply inward and, near the internal end, the articular surface is reflected as a narrow band upon the hinder side of the condyle for the corresponding surface on the postglenoid process. One of the few respects in which the Berlin mandible differs decidedly from that of the type is in having the ascending ramus considerably thickened, the breadth of the anterior border, just behind m$\overline{3}$, being in the proportion of 5 : 4.

The upper grinding teeth, all of which except p$\underline{1}$ are preserved in the Berlin skull, are somewhat more complex than in *C. mitis*. The transformation of the upper premolars has proceeded farther than in any of the genera or species described in the foregoing pages. This individual was much younger than the type of *C. mitis;* the premolars are but moderately abraded and the third molar is hardly at all worn. As in other White River rhinoceroses, the external side of the premolar crowns remains different from the molar form, having two equal cusps, each marked by a rib. But, except for the buccal surface, p$\underline{2}$–$\underline{4}$ are very like molars; each has two parallel, transverse crests, which are rather less oblique and more directly transverse than in the molars. In p$\underline{2}$, which is the smallest of the three, the anterior crest is very short and thin and only touches the antero-internal cusp, which retains its conical shape; in p$\underline{3}$ and $\underline{4}$ both crests are fully developed and the valley between them is wide open internally; in each tooth there is a small, but very distinct crochet which arises from the posterior crest and gives to these teeth a characteristically different appearance from the same in *C. mitis*, though a minute crochet may be seen on p$\underline{4}$ of the type of that species. In the first and second molars a *crista* is given off from the inner face of the external wall, though in m$\underline{1}$ abrasion has removed almost all trace of it. In m$\underline{1}$, at least of *C. mitis*, there is a well defined ante-crochet, which does not appear in *C. dakotensis*.

Osborn (1898, p. 140) gives the following measurements of Peterson's type: mandible, length angle to symph. 255 mm: cheek-tooth series, length, 124 mm, lower molar series, length, 77 mm; horiz. ramus, depth below $m\overline{3}$, 54 mm.

*Horizon:* Upper Brulé.

*Locality:* Big Bad Lands, So. Dak.

### **Subhyracodon** J. F. Brandt

(Pls. LXXXIV–LXXXVII)

*Rhinoceros* Leidy (*nec.* Linn.) in part: Proc. Acad. Nat. Sci. Philad., Vol. V, p. 276, 1850.

*Aceratherium* Leidy (*nec.* Kaup): *Ibid.*, p. 331, 1851.

*Subhyracodon* Brandt (Subgenus of *Aceratherium*): Mém. Acad. Sci. St. Pétersbourg, VII Ser., Tom. XXVI, p. 30, 1878.

*Anchisodon* Cope: Amer. Naturalist, Vol. XIII, p. 270, 1879.

*Caenopus* Cope, in part: *Ibid.*, Vol. XIV, p. 48; 1880.

*Leptaceratherium* Osborn: Mem. Amer. Mus. Nat. Hist., Vol. I, p. 182, 1898.

*Subhyracodon* H. E. Wood: Bull. Amer Palaeontology, Vol. XIII, No. 50, p. 59, 1927. Raised to generic rank.

As shown by Professor H. E. Wood, Brandt's most unfortunate and ill-chosen term must be employed for this genus, which, for half a century, has been familiarly known by Cope's name *Caenopus*. The latter term, as has been seen, need not be discarded, but may be employed in a restricted sense. *Subhyracodon* apparently came into existence before the end of the Chadron substage, but is especially characteristic of the lower Brulé, where it took the place of the Chadron *Trigonias* and may have been one of the direct descendants of that genus. There are two structural features in which *Subhyracodon* is distinctly more advanced and modernized than is *Trigonias:* (1) the manus has lost the fifth digit and is tridactyl; it was to this that Cope's term *Caenopus* referred; (2) the incisors are present in reduced number and the upper canine has been lost.

#### DENTITION

The dental formula is: $i\frac{2}{2}$, $c\frac{0}{0}$, $p\frac{4}{4}$, $m\frac{3}{3}$; in very young animals there may be a small upper canine, which is early shed and not replaced, and it is not clear whether this tooth belongs to the first or second set.

*Upper Teeth.* The first incisor, $i\underline{1}$, has the form characteristic of all the Oligocene Rhinocerotidae, with the probable exception of *Caenopus*, in which this tooth appears to have been but little enlarged: in the present genus the first incisor is more or less like the sectorial of a carnivore, shears inside of the lower tusk and differs from that of such modern genera as retain the incisors merely in being smaller. The second incisor, $i\underline{2}$, which no existing rhinoceros has, is much smaller than the first and of a different shape, being simply conical, and, as in *Trigonias*, must have been a useless vestige; no third incisor has been found in any of the skulls.

The *canine,* as before noted, is of somewhat uncertain status, for it is seldom preserved and was shed early, and may be of either the milk or the permanent series; at all events, it is merely vestigial.



The *premolars,* four in number, follow the second incisor after a long diastema and are partially molariform; but the transformation was taking place in an irregular manner and not, as it did in the horses, gradually from behind forward. Even in the existing rhinoceroses the molarization of the upper premolars is not altogether complete, the external wall still remaining somewhat different, though, otherwise the premolars of the Recent genera may fairly be called molariform. Though there is considerable individual variation in the form of the upper premolar teeth, the variability is not comparable to that displayed by those of *Trigonias.*

The first premolar, $p\underline{1}$, is much the smallest of the series and is usually like a very little molar, with two short transverse crests, separated by a valley. The second premolar, $p\underline{2}$, is more generally molariform than any of the others; its two transverse crests are well separated, and the principal and posterior valleys are both present, but the crests are less inclined backward than in a molar and the external cusps are much more nearly equal. The third premolar, $p\underline{3}$, is more variable; it may be as nearly molariform as $p\underline{2}$, or the inner ends of the cross-crests may be connate, closing the valley internally. The same is true of $p\underline{4}$, except that in that tooth the confluence of the inner cusps appears to be the rule. The premolars have much more prominent internal cingula than do the molars; externally these are inconspicuous.

The *molars* are those of the true rhinoceroses in their simplest expression; none of the accessory cusps or spurs are present, except the antecrochet which is conspicuous in $m\underline{1}$, faintly marked in $m\underline{2}$, and absent from $m\underline{3}$. The latter has the form characteristic of all known members of the family, with triangular outline, the external wall and posterior crest being connate, the wall not extending behind the crest as it does in *Hyracodon* and *Metamynodon.* The internal cingulum is far better developed in the premolars than in the molars, in which the external cingulum is more prominent.

*Lower Teeth.* The *first incisor* is a small vestige, which must have been without function; it is, therefore, of interest to note that in those Recent rhinoceroses which have retained incisors, those useless teeth are no farther reduced than they were in the Oligocene. The *second incisor,* as in the family generally, is a procumbent tusk, of which the size and the degree of procumbency vary much in different individuals; in some, the tooth is almost horizontal, while in others it may form an angle of 45° with the symphysis. In shape, the crown is nearly constant; it is an elongate, laterally compressed cone, bluntly pointed, and with its lingual surface worn by the abrasion of the large upper incisor, $i\underline{1}$.

The *premolars* are, for the most part, incompletely molariform; the first one, $p\overline{1}$, is very much the smallest and simplest of the series; it is inserted by a single root, and the crown is compressed and conical in form, with minute inner and outer folds and complete cingulum; that this tooth was of some use is shown by the worn apex. The *second* premolar, $p\overline{2}$, is more than twice as large as the first and the elements are more distinctly shown; there are two internal valleys, of which the posterior is much the larger; externally, the anterior lobe is much the larger; the postero-internal cusp is very small. $P\overline{3}$ is an enlarged copy of $p\overline{2}$ and is not altogether molariform, though $p\overline{4}$ is completely so; as in the molars, the postero-external lobe is the largest.

The *molars* are very uniform in all of the American genera of the family, though in the upper Miocene and lower Pliocene species the teeth are higher-crowned than in those of the Oligocene, which are low-crowned. *Metamynodon* has higher crowns, but in the White River members of the other two families all the teeth are brachyodont.

Milk Dentition. A young skull in the American Museum (No. 584) has all of the temporary teeth in place and gives the formula, di$\frac{2}{2}$, dc$\frac{0}{0}$, dp$\frac{4}{4}$; the lack of any trace of a canine in this very complete specimen may be interpreted, either as showing that the vestigial canine is a variable structure, present in some individuals and absent in others, or else that it belongs to the second dentition.

*Upper Teeth.* The deciduous *incisors* are very much smaller than the permanent ones, but resemble them in shape; the first one, di$\underline{1}$, is relatively prolonged in the antero-posterior direction, thin, and compressed transversely; the enamel-covered crown is very low and has a bluntly trenchant edge. The next succeeding milk-incisor, di$\underline{2}$, is separated by a long interspace from the first and, judging from this position alone, one would be inclined to call it the third rather than the second of the series. The crown is a minute cone, so small that it can have been of no possible use.

The deciduous *premolars* are molariform only in part. The first one (dp$\underline{1}$) was apparently not replaced, but persisted in the permanent series; at least, I have seen no individual in which such a change is indicated. In the present specimen, the tooth is entirely unworn; the outer wall seems to consist of a single lobe, with faintly marked median rib, ending below in a point; the single lobe is a compressed cone, with trenchant border, and there is a small, pointed, anterior basal cusp; the external cingulum is incomplete and is faintly marked, except in the hinder half. There are two internal cusps, conical in shape and connate, but with separate apices; even after a considerable amount of wear, the distinction is plain. There is an anterior, but no posterior, transverse crest; the ridge divides the valley into two parts, the anterior one of which is a deep pocket, enclosed between the transverse crest and the outer wall. The main valley is closed inwardly by the connate inner cusps, but opens freely behind.

The *second* milk-premolar, dp$\underline{2}$, is much larger and more nearly molariform than the first, yet differs notably from a molar in the constitution of the external wall, which seems to be made up of two equal lobes, demarcated by a median rib. Between these lobes, there is a slight difference, the anterior one being a little more convex; there is no antero-external style, or basal cusp. There are two cross-crests of equal height, between which is the valley which opens freely inward, except for a small enamel ridge, or tubercle that depends from the cingulum; the crests have a less oblique course than in the true molars.

The *third* milk-premolar is much larger than the second, and differs decidedly from that tooth in the appearance of the external side; the two outer cusps, of equal size, have each a definite median rib, which produces a point in the cutting edge below, and there is an obscure anterior style. Cross-crests and valleys are much the same as in dp$\underline{2}$, but there is no minute enamel ridge at the inner end of the valley.

A curious reminiscence of its Eocene ancestry is retained in dp$\underline{3}$ of *Subhyracodon* in the difference of its two external lobes, the anterior one being convex, and the posterior concave, less markedly so than in *Hyrachyus*, or even *Colodon*, but yet unmistakably so.

The *fourth* milk-premolar is the largest and most nearly molar-like of the series; the antero-external cusp is narrow, the postero-external one broad and nearly plane; and the anterior style, which is absent from dp$\underline{2}$ and obscure on dp$\underline{3}$, is very distinct; the transverse crests have a more oblique course, and the posterior one is shortened. Even so, however, the outer side of this tooth is not exactly like that of a molar.



*Lower Teeth.* The *incisors*, like those of the upper jaw, are very much smaller than their permanent successors. The *first* one, di$\overline{1}$, is exceedingly small, antero-posteriorly compressed, and entirely unworn. As these teeth were not opposed by any others, they cannot have had any functional importance.

The second incisor, di$\overline{2}$, is a minute tooth, with pointed, conical crown, which is implanted in the erect position, thus differing notably from its procumbent and very much larger successor. In view of the considerable amount of wear of the cheek-teeth in this specimen, the completely unworn condition of the incisors is worthy of notice, as showing that in the young animal the front teeth were little or not at all used.

The temporary *premolars* number four, the permanent ones three, for the *first milk-premolar*, when shed, was not replaced. This tooth differs completely from the other cheek-teeth of the first dentition; it is much smaller and more simple, having a compressed conical crown, with trenchant border and acute anterior basal cusp. On the posterior side of the principal cusp are two parallel enamel ridges, which enclose a small fossette.

The *second milk-premolar*, dp$\overline{2}$, is nearly twice as long antero-posteriorly as the first, and has a bilobate crown; the anterior lobe is like the whole of dp$\overline{1}$ on a larger scale, and with the anterior basal cusp much enlarged. The posterior lobe is lower vertically and of crescentic shape, with shallow internal valley.

The *third milk-premolar*, dp$\overline{3}$, is bicrescentic, and its anterior basal cusp is nearly obsolete.

The *fourth milk-premolar* is altogether like a molar.

### Skull

The skull of *Subhyracodon* is very closely similar to that of *Trigonias*, but differs in a number of details; for example, the nasals are much shorter, broader and less acutely pointed, and the cranium rises much less steeply from the forehead. *Trigonias* is peculiar

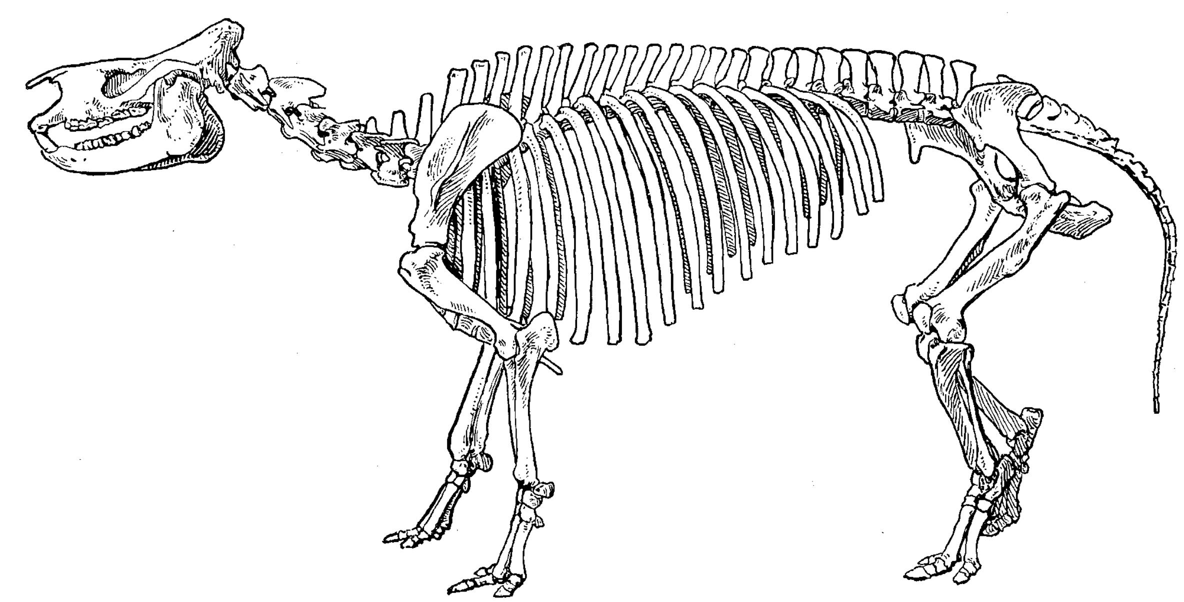


Fig. 138. *Subhyracodon occidentalis:* Skeleton, left side: A.M.N.H.

in this respect, resembling the later rhinoceroses which have developed horns. The general aspect of the skull may be described first before the details are taken up.

*Lateral View.* While completely rhinocerotic in character, this skull differs in a great many respects from the modern members of the family. In the first place, the skull is very flat and the upper profile is nearly straight, rising very gently from the supra-orbital region to the occiput. The face is relatively elongate, and the post-orbital cranium is short in comparison with that of the later species, which are horn-bearing. The face is also low vertically, in correspondence with the extremely brachyodont teeth. The nasal incision is long. The premaxillary region is also elongated in comparison with modern species. The orbit is widely open behind, as it is in the Recent rhinoceroses; but the postorbital process which some modern forms show on the jugal is nothing more than an angulation. The occiput is prolonged very far posteriorly, and extends much farther beyond the line of the lower jaw than in existing rhinoceroses. The mandible is long and shallow, the ventral border rising gently to the symphysis, which is nearly procumbent. Among modern species, the Indian *Rhinoceros unicornis* is most like *Subhyracodon* in the shape of this symphysial region.

The horizontal ramus is shallow and slender; and the angle, while distinctly thickened, is very much less so than in the species from the upper Miocene to the present, in which the broad, massive angle is characteristic of all forms. The masseteric fossa is notably smaller than in Recent species, and the coronoid process higher.

*Superior View.* The sagittal crest is distinctly present, giving this aspect of the skull a very different appearance from that of any modern species. Though present, the crest is very short, and speedily broadens into a sagittal area. The widest portion of the skull is across the zygomatic arches at the glenoid cavities. From that point forward, it narrows gradually and gently to the premaxillae. The occipital wings are not prominent. The zygomatic processes are thin and plate-like; the forehead broad and slightly convex; and the nasals, which are very long, are decidedly convex, with a depression along the suture between them.

The likeness of this skull to that of Eocene genera, such as *Hyrachyus*, is very marked; but in *Hyrachyus* the brain-case is relatively much less capacious, and the sagittal crest very much longer.

*Forms and Connection of the Skull Bones.* The *basioccipital* is very broad behind, the condyles being much extended transversely, and narrows forward rapidly to the suture with the basisphenoid; the exoccipitals are low and broad, and the paroccipital process is very long and laterally compressed. The supraoccipital is large, extending high above the foramen magnum, and ending above in a transverse crest, which is very little notched in the adult, quite deeply so in the young skull. It extends well over upon the roof of the cranium. The *parietals* are very long and form nearly all of the roof of the cerebral fossa, owing to the low vertical height of the squamosals and the shortness of the frontals. The *frontals*, as noted, are decidedly short. They broaden regularly from the parietals to the roof of the orbits, where they reach their maximum width at the postorbital process. Anteriorly, each frontal is deeply incised by the nasal, with the short median nasal process between. The frontals have no lateral nasal processes, the suture being curved but only transversely. Frontal sinuses are no doubt present, but they do not cause protuberances of the forehead. The orbit is small, and is demarcated by a rather prominent postorbital process of the



frontal. The *nasals* are very long, extending forward from the anterior rim of the orbit, although they form no part of these openings, being excluded by the junction of frontal and lachrymal. Posteriorly, they are very broad and short, the hinder ends diverging so as to admit the median process of the frontal. The nasals are very convex and show broadly in lateral view, where they have a long suture with the frontal. The free portion of the nasals, which extends over the anterior nares, is long, extending almost as far forward as the premaxillaries, though not quite; and this portion is much broader than in *Trigonias*.

The *premaxillae* are quite unlike those of modern genera, although it is easy to see that the latter condition must have been derived from that seen in the White River genera. There is a distinction between the horizontal and ascending rami, though the angle between them is very low. The horizontal portion is small but stout, with alveoli for the two incisors. The ascending portion rises gently to the limited contact with the nasals. The maxillary suture is a long gentle slope, descending from the nasal suture. The incisive foramina are rather small but deeply incising the palatine processes of the maxillaries. The palatine plates of the premaxillaries are narrow. The *maxillary* is a very large bone, and forms almost the whole of the face. Its pre-orbital portion, although relatively high, is lower than in the modern genera. There is a long suture with the nasal, and a lachrymal or glandular pit in front of the orbit. The infraorbital foramen is placed high up and over the hinder part of the second premolar. The palatine processes form a broad palate which narrows forward and is mostly flat. There is an edentulous part of the palate between the second incisor and the premolars. The *palatines* form but a small part of the hard palate, extending to the anterior part of $m\underline{1}$. The posterior nares are large, extending to the anterior portion of $m\underline{2}$; the opening is lanceolate, broadening to the line of the third molar. The posterior palatine foramina are on each side of the posterior nares opposite $m\underline{1}$. None of the skulls show the pterygoids or the orbito- or alisphenoids.

The *jugal* is compressed and narrow, but deep dorso-ventrally; posteriorly, it extends beneath the zygomatic process of the squamosal to the glenoid cavity.

The *squamosal* is very low in its cranial portion, forming none of the roof and but little of the side wall of the cerebral fossa. The post-tympanic and postglenoid processes are well separated. The glenoid cavity is very like that in modern rhinoceroses. There is a convex anterior ridge with a concave fossa behind it. The postglenoid process is partly tapiroid and partly rhinocerotic. It is much broader than in the modern rhinoceroses, but still it has a facet for the postcotyloid process of the mandible which is such a characteristic feature of the family from its earliest known members. The zygomatic process of the squamosal is long and broad dorso-ventrally, but rather thin and plate-like transversely. Its border is elevated so as to make a concave valley with the side of the skull.

The *lachrymal* is rather small, but forms the dorsal half of the anterior orbital boundary. It articulates with frontal, maxillary, and jugal, and has a very limited suture with the posterior part of the nasal. The spine is prominent, and the foramen is within the orbit. The *jugal* is a massive bone, but plate-like and compressed. It articulates with the lachrymal above, the maxillary in front and below, and the squamosal behind.

The general aspect of the mandible seen from the side has already been described. It is primitive, having a decided resemblance to that of *Hyrachyus*, and yet at the same time characteristically rhinocerotic. The symphysis is very low and procumbent, the lower incisors pointing almost directly forward. The edentulous part of the ramus behind the second incisor is very slender, but the jaw deepens posteriorly from that point regularly to the angle. The thickening of the angle, as already mentioned, is present, but very much less than in one of the modern genera. The masseteric fossa is limited to the portion of the jaw above the level of the teeth, a marked difference from the later genera. The condyle is less sessile, and the sigmoid notch is decidedly deeper, while the coronoid is higher and more recurved than in the later genera.

### Vertebrae and Ribs

Like *Trigonias* and the other White River genera of the family, this animal is much like a tapir in proportions. The exceptionally complete skeleton of *S. occidentalis* in the American Museum of Natural History is somewhat larger than the South American *T. terrestris*, and considerably larger than *Trigonias osborni*, which it closely resembles in structure and proportions, though differing in a great many details in nearly every part of the skeleton. The *atlas* is very like that of *Trigonias* except that the hypapophysial tubercle is larger and much more conspicuous. In the *axis*, the principal difference from *Trigonias* is in the shape of the neural spine, which is much more extended antero-posteriorly, the anterior portion projecting much farther forward and extending over the atlas. The "broad-axe" shape of the spine is more like that of a carnivore than that of an ordinary perissodactyl, the dorsal border curving regularly upward to the posterior projection, which overhangs the third vertebra. *Cervicals* 3–7 are like those of *Trigonias* in a general way, though with several minor differences: thus nos. 4 and 5 have short neural spines, and those of 6 and 7 are not quite so long. The inferior lamellae are more prolonged antero-posteriorly, and the diapophyses are less prominent on 3, 4, and 5. As a whole, the neck is longer and heavier.

The *dorsal* vertebrae have even more slender spines than in *Trigonias* and are more widely spaced apart; they differ somewhat in shape, being more regular in outline. They are highest at the shoulder and incline backward to the 16th, which is the anticlinal. The height of the spines so compensates the curve of the vertebral column as to make the summit line of the back nearly level, with a gentle descent from the shoulder to the rump. The *lumbar* spines are higher and narrower than in *Trigonias*, and the transverse processes are much better developed, both in length and width. The *sacrum* is remarkably long and narrow, and is made up of six vertebrae, of which the anterior two are in contact with the ilia; the spines are shorter and have a more decided backward inclination than in *Trigonias;* no two spines are in contact at the tips.

*Caudal* vertebrae are 21 in the mounted skeleton, and they indicate that the tail was rather shorter and thinner at the root than in *Trigonias*. In the anterior part of the tail the various processes are much less complete than in the latter; only the first five caudals have distinguishable neural arches and transverse processes, and on the 5th these are hardly more than vestigial. The anterior vertebrae are much narrower than those of *Trigonias* and indicate that in the latter the root of the tail was much broader and, presumably, was more flattened dorso-ventrally. Behind the 5th caudal the vertebrae are of the usual sub-cylindrical shape with contracted middle and expanded ends; these are stouter than the 11–23 in *T.*; in length the two tails are much alike. The *ribs* are substantially as in *Trigonias*.



### Pectoral Limb and Girdle

In describing the *scapula* it will not be necessary to do more than point out the features in which it differs from that of *Trigonias,* for the two scapulae are essentially alike and differ only in minor details. In *Subhyracodon* the scapula is broader, especially the post-spinous fossa. The coracoid is much larger and more prominent, making the coraco-scapular notch much better defined. The spine rises nearer to the supra-scapular border and ascends more gradually to the metacromion, but the ventral part does not descend so far upon the neck and ends more abruptly.

The *humerus* is more slender than in *T.*, but otherwise very much like it. The external tuberosity is very large, but low, extending across the whole anterior face of the proximal end and forming a very deep and narrow bicipital groove. This tuberosity is less distinctly divided into two lobes, internal and external, than it is in *T.*, for the narrow notch in the latter is, in *Subhyracodon*, a gradual depression of the border. The deltoid crest descends for nearly half the length of the shaft, but ends more gradually below and is less rugose; a low thickening distinctly foreshadows the deltoid hook, which is so characteristic of the modern rhinoceroses and which is distinct in the genera of the upper Brulé substage. The supinator ridge, on the other hand, is more prominent and rugose.

The bones of the fore arm are longer and somewhat stouter than in *T.* The shaft of the *radius* is more curved, and the anconeal process of the *ulna* is rather larger and more thickened at the end. In the *manus*, which is tridactyl, there are a number of differences in the carpals and metacarpals. The lunar, which rests in *T.* almost equally upon the magnum and unciform, has in *Subhyracodon* shifted toward the ulnar side and, dorsally at least, lies upon the unciform only; the latter is no narrower than in *T.*, for the vestigial mc. V occupies as much distal space as does the complete bone in *T.* The functional metacarpals are longer and decidedly stouter, especially mc. III, and are arranged in a more spreading manner. Phalanges are substantially alike. The *carpus* is thoroughly adjusted to the tridactyl condition, while in *Trigonias* the effect of the greatly reduced, though complete, fifth digit is visible in the carpus. The *scaphoid* is the largest of the carpal elements, and has a greater number of articulations with other carpals; in shape, it is irregularly cubical, with its three dimensions not far from equal. The facet for the radius has the shape of a broad saddle, convex transversely and slightly concave palmo-dorsally; the pommel of the saddle is very low and placed at the dorso-ulnar angle of the bone, with the articular surface reflected over upon the dorsal side. In the existing genera of the family this pommel is far more conspicuous and rises high above the proximal end of the lunar, deeply emarginating the distal end of the radius. On the ulnar side the scaphoid sends out a projection into the deeply concave radial side of the lunar; when these two carpals are viewed from above, the line between them appears as a nearly sigmoid curve, the bones being closely interlocked; the palmar face of the scaphoid is much wider than the dorsal. On the distal side are three facets, for the trapezium, trapezoid, and magnum respectively; that for the trapezium is small, and the curvature of the radial side of the scaphoid carries this facet so far to the palmar side that it is not visible from the front. The surface for the trapezoid is broader than that for the trapezium; and the magnum facet is still wider, almost as wide as the other two taken together. The scaphoid covers the whole dorsal part of the proximal end of the magnum; in the view from the front there seems to be no contact between lunar and magnum, but there is one on the palmar projections of the two bones. The facet for the magnum on the distal end of the scaphoid is very concave; that for the trapezoid is of very similar shape, but the articular surface is carried up farther on the dorsal side. The facet for the vestigial trapezium is very small and is crowded back to the palmar side. On the ulnar side are the usual two facets for the lunar, one proximal the other distal, separated by a broad concavity.

The *lunar* is proportionally high and narrow and is in two quite distinct parts, the broader dorsal portion and the narrow palmar projection; the proximal end for the radius is the segment of a cylinder, which is slightly oblique, rising somewhat toward the inner side; the bone narrows distally; connection with the scaphoid is close, while that with the pyramidal is loose, but there is always a distal facet on the ulnar side. Dorsally, the lunar has shifted over entirely upon the unciform and does not touch the magnum, but on the palmar extension is a cavity, lateral rather than distal, into which fits the head of the magnum. The dorsal border of the unciform facet is abrupt and nearly straight.

The shape and connections of the lunar form one of the greatest differences between *Trigonias* and *Subhyracodon;* in the former the distal end of the lunar is wedge-like and rests almost equally upon magnum and unciform. In *Subhyracodon*, the displacement of the lunar toward the ulnar side is even greater than in existing genera of the family. In *Ceratorhinus*, for example, the lunar retains a small dorsal connection with the magnum.

The *pyramidal* is high and narrow, but palmo-dorsally thick; the proximal end bears an obscurely saddle-shaped facet for the ulna, which is feebly concave palmo-dorsally. On the dorsal side the pyramidal is proximo-distally elongate, but on the palmar side it is much shorter in this dimension, the bone being cut away, as it were, to form a facet for the pisiform. On the radial side near the distal end, is a broad, crescentic facet for the lunar; the distal end is broad, much more so than that of the lunar, and is occupied by the large concave surface for the unciform.

The *pisiform* is large, broad vertically, with upper and lower borders that are slightly concave, but not much, for the bone is of nearly uniform width and is thin and plate-like, except at the ends, which are thickened, especially the distal one; facets for ulna and pyramidal are relatively narrow.

The *trapezium* is a small nodule, seemingly vestigial, which is attached by small surfaces to the scaphoid, trapezoid and mc. II.

The *trapezoid* is much larger and has an irregularly quadrilateral dorsal face; its articulations with the scaphoid, trapezium, magnum, and mc. II are of the usual kind. As compared with the carpus of *Trigonias*, the trapezium is proportionally smaller and the trapezoid larger, but the connections of the latter are similar in the two genera.

The *magnum* is not very much larger than the trapezoid; as noted above, it does not articulate dorsally with the lunar, but only with the scaphoid; the "head" is low, not rising above the level of the dorsal portion, but bears an oblique, convex surface for the lunar. The magnum is narrowest at the proximal end, broadening distally, where it forms a wide surface for mc. III, which is convex transversely, concave palmo-dorsally; on the radial side, near the distal end, is a small surface, against which abuts a process from the head of mc. II. On the ulnar side is an oblique surface which the unciform covers.

The *unciform* is a relatively large bone, especially in the proximo-distal axis, and differs greatly in its proportions from that of *Trigonias*, in which this bone is relatively low and broad, because of the fifth digit which is attached to it. The greatest proximo-distal diameter falls between mc. III and IV. The proximal end is unequally divided between the convex surfaces for the lunar and pyramidal, the latter the larger, the former more oblique. The distal and radial sides form a continuous curve made up of the facets for the magnum, mc. III and IV; the meeting of the oblique facets for the lunar and magnum makes a sharp edge, so that the radial and ulnar borders of the unciform are in strong contrast.



The *metacarpus* consists of three members, mc. II–IV, and a vestigial nodule of mc. V. Mc. II is longer and more slender than in *Trigonias* and somewhat more curved; the proximal end articulates with the trapezoid and, on the ulnar side, sends out a short process which overlaps mc. III and abuts against the magnum. The shaft is of trihedral shape and of almost uniform diameter throughout its length. The distal end of the shaft is somewhat broader than the trochlea, but bears inconspicuous processes for the lateral ligaments.

Mc. III is much the broadest of the series, more so, relatively, than in *Trigonias;* the proximal end is made broad by the large process which reaches the unciform and overlaps, though not extensively, the head of mc. IV. Distal to this process the shaft is narrowest, broadening thence distally to the lower end where it unites with the epiphysis and is considerably broader than the trochlea, the ligamentous processes increasing the breadth. The trochlea is low and has an inconspicuous carina.

Mc. IV is almost the counterpart of mc. II except for the shape of the proximal end, which bears a simple concave facet for the unciform.

The *phalanges*, other than the unguals, are much the same as in *Trigonias*, except that they are longer in proportion to their breadth; the unguals, on the other hand, are of quite different shape and proportions. That of digit III is much shorter proximo-distally, and very much broader and more deeply emarginated in the middle, altogether more like that of a modern rhinoceros. The unguals of the lateral digits are somewhat shorter, with regularly curved distal border and an altogether more tapir-like shape, though they lack the pointed process from the border seen in tapirs.

### Pelvic Girdle and Limb—Pes

The *pelvis* differs considerably from that of *Trigonias* and, strange to say, in being more tapiroid, less rhinocerotic, than in that genus; the ilium is relatively longer, as a whole, and has a much longer peduncle, which makes the anterior expansion more abrupt and of a different shape. In *Rhinoceros* the anterior expansion of the ilium is not distinctly divided into dorsal and ventral processes, but the supra-iliac border is a continued convex curve. In *Tapirus*, on the contrary, the dorsal and ventral processes are very conspicuous, and between them the supra-iliac border is concave. In *Subhyracodon*, as in the latter genus, the supra-iliac border or crest is plainly in three parts; on the ventral process the border is thickened, rugose, and slightly convex; the dorsal process is strongly upcurved, so as to rise well above the sacrum, and its border is thick and rough, but straight and hardly more than half as long as that of the ventral process; between the two processes the border is concave. The peduncle of the ilium is not only longer than in *Trigonias*, but also relatively narrower. The acetabulum is larger and more nearly circular, and is much less deeply invaded by the sulcus for the round ligament.

The ischium is decidedly shorter proportionally than in *Trigonias*, and rather more slender, but the posterior expansion is as broad and the tuberosity is more prominent; the spine of the ischium is small, but distinct, and the sciatic notch is deeper; the posterior expansions of the two ischia are widely separated by a deep notch, which, however, is shallower than in *Trigonias,* and the posterior ends of the ischia are everted. The pubis is slender and its antero-posterior process is comparatively short; the process on the median line at the anterior end of the pubic symphysis is very much less prominent than in *Trigonias,* and is little more than a vestige. The transverse branch of the pubis is stout, and the obturator foramen is comparatively small and regularly oval in outline.

The *femur* is, in general, similar to that of *Trigonias,* though differing in several minor respects, in which it is more tapiroid than rhinocerotic. The head is more sessile, the neck broader and less constricted, and the great trochanter is much larger and more rugose and is separated more deeply from the head; the hinder part of the process is less extended and hook-like, but there is a larger digital fossa. The second trochanter is much more prominent than in *Trigonias,* but of similar shape; in both genera it is a low ridge and is so placed as to be concealed, when the bone is seen from the front. The third trochanter is decidedly larger and more prominent and has a slightly inferior position. The shaft of the femur is somewhat stouter and more compressed antero-posteriorly; the distal end is not so massive, which is due to the smaller size of the less prominent condyles. The rotular groove is made similarly asymmetrical by the great prominence of the inner border, and the supra-patellar fossa is narrower and less extended proximo-distally.

The *patella* differs in being less massive and thinner, and in having a less rugose anterior face.

In both genera the *tibia* is of similar shape and proportions; the cnemial crest is massive and rugged and, on the anterior side, is divided into two parts by a groove which is much more distinct in *Trigonias.* The shaft is less straight in *Subhyracodon,* and more bowed toward the inner side. As in all of the rhinoceroses, the proximal facet for the fibula is placed on the external side of the tibial head, not on the distal face of the projecting outer condyle, as is the usual mammalian arrangement.

The *fibula,* which shows no tendency to co-ossify with the tibia, is considerably reduced; the shaft, though complete and uninterrupted, is rather more slender and reduced than in *Trigonias,* but thickens downward; the distal end is both broader and thicker than the proximal, and the sulcus for the tendon is shallow.

*Pes.* As in all known members of the Rhinoceratoidea, the hind foot is tridactyl, and there is little difference in its structure between *Subhyracodon* and *Trigonias,* but the proportions are somewhat different, the foot being longer and narrower in the former. In all of the Oligocene true rhinoceroses, the proportions of the feet, both fore and hind, are more tapir-like than rhinoceros-like. Nevertheless, the characteristic features of the various foot-bones are unmistakably rhinocerotic, not tapirine. The *astragalus* is especially rhinoceros-like and yet markedly different from the shape seen in the Pliocene and Recent genera of the family. The trochlea is broadly and not very deeply grooved, the ginglymus having the hourglass-like shape; the neck is very short and the distal end has a very large saddle-shaped facet for the navicular, and a much smaller one for the cuboid. This cuboid articulation is intermediate between the condition seen in the tapirs and that found in such Pliocene genera as *Aphelops,* in which the modern proportions are nearly attained.

The *calcaneum* is much like that of *Trigonias,* differing only in certain unimportant details; the tuber calcis is rather narrower and more compressed; the dorsal and plantar borders are nearly parallel, and the free end is thick, rugose and club-like; the sustentaculum is less prominently developed than in *Trigonias.* *Navicular* and *cuneiforms* are much the same as in *Trigonias;* in both genera the proximo-distal length greatly exceeds relatively this dimension in *Aphelops* and the Recent genera, which have such shortened feet.



The *cuboid* likewise is similar to that of *Trigonias* and differs strikingly from that of the Recent genera in its much greater proportional length and less width transversely, as does also the tarsus, as a whole. The plantar process is a broad and massive hook, which is separated from the distal half of the cuboid by a deep notch. The cuboid differs from that of *Aphelops* and its modern successors, not only in the much greater proximo-distal length and narrowness transversely, but also in the smaller size of the astragalar facet.

The three *metatarsals* are somewhat longer in proportion to the length of the limb-bones than they are in *Trigonias,* and very much longer than in the Pliocene and later genera of the family. It does not seem likely that any of the Oligocene genera of North American rhinoceroses can have given rise to any of the existing forms, all of which appear to be of exclusively Old World descent; the North American genera would seem to have been collaterally related to those of Eurasia, but, because of parallelism in development, they throw much light upon phylogenies in the Eastern Hemisphere. Among the White River rhinoceroses there are two types of feet; one, in which the metapodials are comparatively elongate and slender, exemplified by the *Subhyracodon–Diceratherium* series, and the other, displayed by *Caenopus,* in which the metapodials are relatively shorter and sturdier; *Trigonias* is, in a sense, intermediate between the two types and might have given rise to either or both of them. *Caenopus* (*q.v.*) is happily named, for it has a decidedly more modern-looking foot than any of the other White River rhinoceroses. Except for this comparatively small difference in proportions, the metatarsals are so like those of *Trigonias* as to need no separate description.

*Phalanges,* on the other hand, differ more decidedly; in *Subhyracodon* they are distinctly longer and narrower, most conspicuously so in the median digit; the second phalanx of that digit is especially long and narrow, as compared with that of *Trigonias.* The *unguals* also differ in similar fashion; in *Subhyracodon* they are more extended proximo-distally but much less so transversely. In this respect also *Trigonias* has a more modern look than its supposed descendant.

*Species.* Notwithstanding all the labour that has been expended upon this problem, especially by Professor H. E. Wood, it has not been possible to arrive at a satisfactory discrimination of the supposedly different species of *Subhyracodon,* so great is the range of individual variation and of differences probably due to age and sex. As a rule, species have been established upon single individuals and specimens which have subsequently been referred to the same species seldom agree entirely with the type in diagnostic characters. The narrowly limited number of species of a single genus which can co-exist at the same time and place has usually been overlooked; only Dr. Matthew and Mr. Figgins have given proper weight to this consideration in estimating the species of *Trigonias.* It applies almost equally to *Subhyracodon,* though in that case there is no such wealth of finely preserved skulls to display the endless variations.

In general, there is a stratigraphic succession of the various forms, whether one calls them species, subspecies, or varieties. With a certain amount of overlapping, each of the three subdivisions of the White River beds has its characteristic genera and species of rhinoceroses. The typical and most common species of *Subhyracodon* is *S. occidentalis* (Leidy).

### **Subhyracodon occidentalis** (Leidy)

*Rhinoceros occidentalis* Leidy: Proc. Acad. Nat. Sci.; Vol. V, p. 276, 1851.
*Aceratherium occidentale* Leidy: Journ. Acad. Nat. Sci., 2nd Ser., Vol. VII, p. 390, 1869.
*Aceratherium* (*Subhyracodon*) *occidentale* J. F. Brandt: Mém. Acad. Imp. Sci., St. Pétersbourg, VII Ser., T. XXVI, p. 30, 1878.
*Anchisodon quadriplicatus* Cope: Amer. Naturalist, Vol. XIII, p. 270, 1879.
*Caenopus occidentalis* Hay: Bull. U. S. Geol. Surv. No. 179, p. 643, 1901.
*Caenopus trigonodus allus* Troxell (*fide* Wood): Amer. Journ. Sci. 5th Ser. Vol. II, p. 41, 1921.
*Subhyracodon occidentalis* H. E. Wood: Bull. Amer. Palaeont., Vol. 13, No. 50, p. 63, 127.

This species is much the commonest of the White River rhinoceroses and is especially characteristic of the lower Brulé, to which it seems to be confined; it is of medium size, of nearly the same stature as *Trigonias osborni* and the American tapir, *Tapirus terrestris*. According to Osborn, the species "is readily distinguished from *Leptaceratherium trigonodum* [= *Subhyracodon trigonodus*] and *Aceratherium mite* [= *Caenopus mitis*] by the absence of canines in both the milk and adult series. The form of the skull approximates that of *A. tridactylum* [= *Diceratherium tridactylus*] to which this species is undoubtedly ancestral, but the relatively large size of the lateral upper incisors is in great contrast with the reduced condition of these teeth in *A. tridactylum*." [1]

Wood's definition, in abbreviated form, is as follows: Dental formulae: $i\frac{2}{2}$, $c\frac{0}{0}$, $p\frac{4}{3}$, $m\frac{3}{3}$, $di\frac{2}{2}$, $dc\frac{0}{0}$, $dp\frac{4}{4}$. Second upper incisor large; crests of p$\underline{2}$ separate and parallel, but in p$\underline{3}$ and p$\underline{4}$ they unite internally; i$\overline{2}$ semi-erect.

Antecrochets, in incipient form, are usually present on m$\underline{1}$ and m$\underline{2}$. The upper contour of the skull has some sinuosity and slopes upward from the vertex to the occipital crest very gradually and gently and, to a small amount, contrasting strongly with *Trigonias osborni* and *Diceratherium tridactylus*, in both of which species the occiput is much higher and the rise of the profile from the vertex to the crest much steeper. In other species of the genus, *S. trigonodus* and *S. copei*, the rise is similarly gradual and may be regarded as a generic character.

A very perfect skeleton of this species is mounted in the American Museum (No. 1132) and its dimensions are given in the subjoined table, with those of a remarkably complete and uncrushed skull in the Princeton Museum (No. 11,111) which was derived from a somewhat smaller individual. For convenience of comparison, the measurements of the American Museum skeleton of *Trigonias osborni* (No. 9847) are given in the same table.

Measurements

| | *Trigonias osborni* | *Subhyracodon occidentalis* | |
|---|---|---|---|
| | *A.M.N.H. No. 9847* | *A.M.N.H. No. 1132* | *P.U. No. 11,111* |
| Upper incisor series, length | 44 mm. | 45 mm. | 35 mm. |
| I$\underline{1}$ antero-posterior diameter | 21 | 22.5 | 19.5 |
| I$\underline{2}$ antero-posterior diameter | 10 | 12 | 11 |

[1] Mem. Am. Mus. Nat. Hist., Vol. I, p. 151.



Measurements (*Continued*)

| | *Trigonias osborni* | *Subhyracodon occidentalis* | |
|---|---|---|---|
| | *A.M.N.H. No. 9847* | *A.M.N.H. No. 1132* | *P.U. No. 11,111* |
| I$\underline{3}$ antero-posterior diameter | 9 mm. | | |
| Upper dentition, length i$\underline{1}$–m$\underline{3}$ | 270 | 281 mm. | 253 mm. |
| Upper cheek-tooth series, length | 195 | 189 | 180 |
| Upper premolar series, length | 87 | 94 | 88 |
| Upper molar series, length | 109 | 105 | 97 |
| P$\underline{1}$, ant.-post. diameter | 19 | 19 | 20 |
| P$\underline{2}$, ant.-post. diameter | 24 | 23 | 21 |
| P$\underline{3}$, ant.-post. diameter | 23 | 21 | 22 |
| P$\underline{4}$, ant.-post. diameter | 25 | 25 | 22.5 |
| M$\underline{1}$, ant.-post. diameter | 31 | 33 | 28 |
| M$\underline{2}$, ant.-post. diameter | 43 | 40 | 35 |
| M$\underline{3}$, ant.-post. diameter | 34 | 37 | 34 |
| Lower dentition, length i$\overline{1}$–m$\overline{3}$ | 263 | 270 | 242 |
| I$\overline{1}$, transverse diameter | 12 | 10 | 8 |
| I$\overline{2}$, transverse diameter | 19 | 27 | 23 |
| Lower cheek-tooth series, length | 185 | 185 | 168 |
| Lower premolar series, length | 85 | 83 | 74 |
| Lower molar series, length | 106 | 103 | 93 |
| P$\overline{1}$, ant.-post. diameter | 17 | | |
| P$\overline{2}$, ant.-post. diameter | 23 | 24 | 21 |
| P$\overline{3}$, ant.-post. diameter | 23 | 28 | 24 |
| P$\overline{4}$, ant.-post. diameter | 25 | 31 | 24 |
| M$\overline{1}$, ant.-post. diameter | 29 | 32 | 27 |
| M$\overline{2}$, ant.-post. diameter | 34 | 37 | 31.5 |
| M$\overline{3}$, ant.-post. diameter | 37 | 36 | 32.5 |
| Skull, median basal length | 425 | 460 | |
| Skull, extreme length, prmx.-occ. wing | 473 | 493 | 474 |
| Skull, max. width over zyg. arches | 226 | 237 | 193 |
| Skull, width at p$\underline{4}$ | 146 | 148 | 115 |
| Cranium, length to ant. bord. of orbit | 218 | 297 | 275 |
| Face, length orbit to prmx. | 217 | 203 | 201 |
| Occiput, width at base | 136 | 136 | 111 |
| Occiput, height fr. b. occip. | 145 | 133 | |
| Zygomatic arch, length | 205 | | |
| Mandible, extreme length | 388 | 409 | 375 |
| Mandible, depth at p$\overline{2}$ | | 50 | 40 |
| Mandible, depth at m$\overline{3}$ | | 65 | 57 |
| Mandible, width across angles | 170 | 205 | 123 |
| Mandible, length of symphysis | 71 | 103 | 80 |
| Mandible, height of coronoid | 202 | 212 | 195 |
| Mandible, height of condyle | 170 | 161 | 150 |
| Atlas, ant.-post. length | 104 | 105 | |
| Atlas, max. width | 199 | 199 | |
| Axis, length of centrum | 73 | 85 | |
| Axis, anterior width | 96 | 101 | |
| Axis, posterior width | 42 | 54 | |
| Third cervical, length of centrum | 56 | 64 | |

MEASUREMENTS (*Continued*)

| | *Trigonias osborni* A.M.N.H. No. 9847 | *Subhyracodon occidentalis* A.M.N.H. No. 1132 |
|---|---|---|
| Fifth cervical, length of centrum | 54 mm. | 71 mm. |
| Seventh cervical, length of centrum | 47 | 42 |
| First dorsal, length of centrum | 45 | |
| First dorsal, height of spine | 160 | 159 |
| Fifth dorsal, height of spine | 110 | 101 |
| Twelfth dorsal, length of centrum | 47 | 38 |
| Twelfth dorsal, height of spine | 110 | 101 |
| First lumbar, length of centrum | 50 | 45 |
| First lumbar, height of spine | 81 | 92 |
| Fifth lumbar, length of centrum | 42 | 39 |
| Fifth lumbar, breadth over trans. proc. | 154 | 165 |
| Sacrum, length | 204 | 274 |
| Last sacral, width of centrum | | 31 |
| First caudal, length | 35 | 39 |
| First caudal, width | 17 | 12 |
| Scapula, prox.-dist. height | 321 | 321 (est.) |
| Scapula, max. width | 188 | 204 |
| Scapula, width of neck | 69 | 70 |
| Scapula, ant.-post. diam. of glen. cav. | 56 | 68 |
| Humerus, length from head | 280 | 300 |
| Humerus, prox. width | 98 | 100 |
| Humerus, dist. width | 60 | 69 |
| Radius, length | 253 | 279 |
| Radius, prox. width | 61 | 61 |
| Radius, distal width | 63 | 56 |
| Ulna, length | 335 | 350 |
| Ulna, length of olecranon | 89 | 100 |
| Ulna, distal width | 30 | 27 |
| Carpus, prox.-dist. length in med. line | 60 | 59 |
| Carpus, width | 72 | 78 |
| Metacarpal II, length | 108 | 128 |
| Metacarpal II, prox. width | 27 | 28 |
| Metacarpal II, dist. width | 21 | 23 |
| Metacarpal III, length | 119 | 139 |
| Metacarpal III, prox. width | 32 | 37 |
| Metacarpal III, dist. width | 31 | 32 |
| Metacarpal IV, length | 100 | 119 |
| Metacarpal IV, prox. width | 25 | 26 |
| Metacarpal IV, dist. width | 29 | 23 |
| Metacarpal V, length | 80 | 26 |
| Metacarpal V, prox. width | 15 | 20 |
| Metacarpal V, dist. width | 15 | |
| Digit II, phalanx 1, length | 23 | 26 |
| Digit II, phalanx 1, prox. width | 24 | 30 |
| Digit II, phalanx 2, length | 15 | 18 |
| Digit II, phalanx 2, prox. width | 20 | 24 |
| Digit II, ungual, length | 24 | 28 |



MEASUREMENTS (*Continued*)

| | *Trigonias osborni* A.M.N.H. No. 9847 | *Subhyracodon occidentalis* A.M.N.H. No. 1132 |
|---|---|---|
| Digit II, ungual, prox. width | 21 mm. | 20 mm. |
| Digit III, phalanx 1, length | 27 | 29 |
| Digit III, phalanx 1, prox. width | 31 | 36 |
| Digit III, phalanx 2, length | 16 | 20 |
| Digit III, phalanx 2, prox. width | 31 | 32 |
| Digit III, ungual, length | 14 | 30 |
| Digit III, ungual, prox. width | 28 | 40 |
| Digit IV, phalanx 1, length | 22 | 27 |
| Digit IV, phalanx 1, prox. width | 22 | 27 |
| Digit IV, phalanx 2, length | 12 | 15 |
| Digit IV, phalanx 2, prox. width | 19 | 19 |
| Digit IV, ungual, length | 25 | 28 |
| Digit IV, ungual, prox. width | 22 | 25 |
| Digit V, phalanx 1, length | 13 | |
| Digit V, phalanx 1, prox. width | 15 | |
| Digit V, phalanx 2, length | 10 | |
| Digit V, phalanx 2, prox. width | 13 | |
| Digit V, ungual, length | 8 | |
| Digit V, ungual, prox. width | 12 | |
| Pelvis, length | 383 | 448 |
| Pelvis, anterior width | 492 | 460 |
| Pelvis, width over acetabula | 249 | 248 |
| Pelvis, width over ischia | 162 | 174 |
| Ilium, length | | 240 |
| Ilium, max. width | 267 | 246 |
| Obturator foramen, ant.-post. diam. | 73 | 78 |
| Pubic symphysis, length | 68 | 124 |
| Femur, length from head | 341 | 369 |
| Femur, length fr. gr't. trochanter | 335 | 378 |
| Femur, proximal width | 124 | 123 |
| Femur, distal width | 109 | 90 |
| Femur, distal thickness | 122 | 70 |
| Patella, prox.-dist. diameter | 65 | 65 |
| Patella, transverse diameter | 67 | 60 |
| Tibia, length | 254 | 275 |
| Tibia, prox. width | 87 | 83 |
| Tibia, dist. width | 59 | 63 |
| Fibula, length | 235 | 264 |
| Fibula, prox. width | 19 | 24 |
| Fibula, dist. width | 13 | 10 |
| Astragalus, length | 54 | 56 |
| Astragalus, max. width | 51 | 51 |
| Calcaneum, length | 105 | 104 |
| Calcaneum, width over sustentac. | 65 | 54 |
| Metatarsal II, length | 99 | 118 |
| Metatarsal II, prox. width | 24 | 22 |
| Metatarsal II, dist. width | 23 | 21 |

MEASUREMENTS (*Continued*)

| | *Trigonias osborni* A.M.N.H. No. 9847 | *Subhyracodon occidentalis* A.M.N.H. No. 1132 |
|---|---|---|
| Metatarsal III, length | 106.5 mm. | 133 mm. |
| Metatarsal III, prox. width | 36 | 36 |
| Metatarsal III, dist. width | 40 | 30 |
| Metatarsal IV, length | 98 | 110 |
| Metatarsal IV, prox. width | 31 | 22 |
| Metatarsal IV, dist. width | 32 | 17 |
| Digit II, phalanx 1, length | 27 | 25 |
| Digit II, phalanx 1, prox. width | 24 | 26 |
| Digit II, phalanx 2, length | 15 | 13 |
| Digit II, phalanx 2, prox. width | 18 | 22 |
| Digit II, ungual, length | 20 | 27 |
| Digit II, ungual, prox. width | 22 | 25 |
| Digit III, phalanx 1, length | 21 | 32 |
| Digit III, phalanx 1, prox. width | 35 | 32 |
| Digit III, phalanx 2, length | 12 | 19 |
| Digit III, phalanx 2, prox. width | 30 | 31 |
| Digit III, ungual, length | 27 | 37 |
| Digit III, ungual, prox. width | 36 | 40 |
| Digit IV, phalanx 1, length | 19 | 24 |
| Digit IV, phalanx 1, prox. width | 20 | 24 |
| Digit IV, phalanx 2, length | 13 | 15 |
| Digit IV, phalanx 2, prox. width | 18 | 21 |
| Digit IV, ungual, length | 23 | 26 |
| Digit IV, ungual, prox. width | 19 | 28 |

*Horizon:* Lower Brulé.
*Localities:* Big Bad Lands, So. Dak.; N. E. Neb. and Col.

### **Subhyracodon trigonodus** (O. & W.)

*Aceratherium trigonodum* Osborn & Wortman: Bull. Amer. Mus. Nat. Hist., Vol. VI, p. 201, 1894.
*Aceratherium* (*Caenopus*) *mite* Osborn & Wortman, in part (*nec* Cope): *Ibid.*, p. 203.
*Leptaceratherium trigonodum* Osborn: Mem. Amer. Mus. Nat. Hist., Vol. I, p. 182, 1898.
*Aceratherium copei* Osborn (in part): *Ibid.*, p. 146.
*Caenopus* (*Leptaceratherium*) *trigonodus* Troxell: Amer. Jour. Sci., 5th Ser. Vol. II, p. 43, 1921.
*Subhyracodon trigonodus* Wood: Bull. Amer. Paleontology, Vol. 13, No. 50, p. 60.

This and the following species, *S. copei*, are smaller, more primitive, and more ancient than *S. occidentalis*. The original description is: "(*a*) *Upper canine* apparently persistent and well developed. (*b*) *Upper premolars* subtriangular; third premolar with an incipient postero-internal cusp, well developed toward the base; fourth premolar with a feeble or incipient postero-internal spur and a somewhat prominent elevation of the postero-internal cingulum which presents the appearance of a 'cingule' when worn. (*c*) *Upper molars* with well developed cingulum upon protoloph; cingulum feeble or short on metaloph; incipient



antecrochet at base of metaloph [*sic*], becoming apparent on wear. Skull fairly elevated; sagittal crest low; nasals rather short, not notched; postglenoid and posttympanic processes widely separated."

To this description Wood adds: "Slightly larger than *Subhyracodon copei* or *Caenopus mitis*, slightly smaller than *Subhyracodon occidentales* [*sic*], $I\frac{2}{2}$, $C\frac{1\text{–}0}{0}$, $P\frac{4}{(4)\text{–}3}$, $M\frac{3}{3}$. $P\underline{2}$ is fully molariform, with the lophs united well above the cingulum. In both $P\underline{3}$ and $P\underline{4}$ the hypocone is very slightly developed as a distinct cusp." [1] In the subjoined table the dimensions are taken from three skulls in the American Museum.

MEASUREMENTS

| | *No. 528* (*Type*) | *No. 1131* | *No. 529* |
|---|---|---|---|
| Upper cheek-tooth series, length | 173 mm. | 183 mm. | 183 mm. |
| Upper molar series, length | 100 | 100 | 100 |
| Lower cheek-tooth series, length | | | 165 |
| Skull, length fr. occ. to tip of nasals | | | 435 |
| Skull, width over zygomatic arches | | 197 | 200 |
| Occiput, height | | 107 | 113 |
| Occiput, width at base | | 94 | 100 |

*Horizon:* Type from the Chadron; referred specimens from the lowest beds of the Lower Brulé.
*Localities:* Big Bad Lands, So. Dak.

### **Subhyracodon copei** (Osborn)

*Aceratherium* (*Caenopus*) *mite* Osborn and Wortman (*nec* Cope): Bull. Amer. Mus. Nat. Hist., Vol. VII, p. 203, 1894.
*Aceratherium copei* Osborn: Mem. Amer. Mus. Nat. Hist., Vol. I, p. 146, 1898.
*Subhyracodon copei* Wood: Bull. Amer. Paleont., Vol. 13, No. 50, p. 60.

This is another species defined by the degree of molarization of the upper premolars, and the propriety of separating it from *S. trigonodus* is very doubtful; indeed, much confusion has arisen in attempting to distinguish between these two "species" of *Subhyracodon*. Wood writes me that it is "essentially an earlier, smaller, slightly more primitive ancestor of *S. occidentalis*."

Osborn's original definition, in somewhat abbreviated form, is as follows: Upper canine present in immature skull, shed in adult; second upper premolar with both transverse crests, third and fourth with strong postero-internal spurs connected with *anterior* crest; in unworn or moderately worn condition, these premolars are very distinctive. "It is apparently a direct ancestor of *Aceratherium occidentale* and *A. tridactylum*." The skull differs from that of the former species in having an even more horizontal upper profile and lower occiput and in displaying a long low sagittal crest, which is composed of the two temporal ridges, which are not united, but separated by a narrow groove; postglenoid and posttympanic processes widely separated.

In the table below the dimensions are taken from the type-specimen, which is a fine skull, slightly flattened by dorso-ventral compression, in the possession of the American Museum of Natural History (No. 522).

MEASUREMENTS

| | |
|---|---|
| Upper dentition, length i1–m3 | 235 mm. |
| I1, ant.-post. diameter (alveolus) | 21 |
| I2, ant.-post. diameter (alveolus) | 14 |
| Upper canine, antero-posterior diameter | 6 |
| Upper cheek-tooth series, length | 156 |
| Upper premolar series, length | 75 |
| Upper molar series, length | 88 |
| P1, ant.-post. diameter | 17 |
| P1, transverse diameter | 16 |
| P2, ant.-post. diameter | 19 |
| P2, transverse diameter | 26 |
| P3, ant.-post. diameter | 22 |
| P3, transverse diameter | 27 |
| P4, ant.-post. diameter | 22 |
| P4, transverse diameter | 31 |
| M1, ant.-post. diameter | 31 |
| M1, transverse diameter | 34 |
| M2, ant.-post. diameter | 35 |
| M2, transverse diameter | 36 |
| M3, ant.-post. diameter | 26 |
| M3, transverse diameter | 34 |

N.B. The overlapping of the cheek-teeth is such that the sum of the antero-posterior diameters of the individual teeth exceeds the length of the series, as a whole.

| | |
|---|---|
| Skull, extreme length | 420 mm. |
| Skull, length prmx.-occ. cond., incl | 405 |
| Skull, max. width over zygomatic arches | 195 |

*Horizon:* Type from base of lower Brulé; referred specimens from uppermost Chadron.
*Locality:* Big Bad Lands, So. Dak.

### **Subhyracodon gidleyi** Wood.

*Subhyracodon gidleyi* H. E. Wood: Bull. Amer. Paleont., Vol. 13, No. 50, p. 65.

"The holotype, U. S. N. M. No. 11,337, was collected by Mr. J. B. Hatcher in 1886, from the 'White River Tertiary.' It is slightly smaller than the type of *Subhyracodon occidentale* [sic], from which the premolars are indistinguishable. The name is given for Dr. J. W. Gidley. M1 and M2 have part of the median valley completely cut off by the upgrowth of the antecrochet, to form medifossettes.

"The specimen consists of left P2–M2, with the roots of P1 and fragments of M3, and right P4–M2, with the roots of P1–P3 and the first half of M3, fragmentary lower teeth, and the astragalus. Associated with it are Mesohippus and Oreodon teeth." (H. E. Wood, *loc. cit.*)

If the exceptional character of the upper molars should prove to be constant, this will be a well defined species, but until then its status will be doubtful. "An aberrant individual or 'species' according to taste." (Wood, Ms.)

*Horizon:* The associated "*Oreodon*" teeth indicate the lower Brulé.
*Locality:* Not given.



### **Subhyracodon metalophus** (Troxell).

*Aceratherium occidentale* Osborn (*nec* Leidy): Mem. Amer. Mus. Nat. Hist., Vol. I, p. 154, Pl. XIII, Fig. 7, 1898.
*Caenopus tridactylus metalophus* Troxell: Amer. Journ. Sci., 5th Ser., Vol. II, p. 47, 1921.
*Subhyracodon metalophum* Wood: Bull. Amer. Paleont., Vol. 13, No. 50, p. 67, 1927.

Holotype, Peabody Museum, Yale University, No. 10,245, and, according to Troxell, "probably Middle Oligocene [=lower Brulé], Rushville, Nebraska." (Troxell, E. L., *loc. cit.*)

"Another specimen virtually identical with this, A.M.N.H. No. 1123, from the Upper Oreodon Beds, collected by American Museum Expedition of 1894, was described and figured by Osborn. This form was larger than *Subhyracodon occidentale*, smaller than *Subhyracodon tridactylum* [*sic* = *Diceratherium tridactylus*] and probably hornless in both sexes. $I\frac{2}{?}\,C\frac{0}{?}\,P\frac{4}{?}\,M\frac{3}{?}$. I2 is still large. The protoloph and metaloph of P4 are separate and parallel. The upper molars are smaller individually and collectively than in *Subhyracodon tridactylum* and have no secondary folds.

"Osborn regarded this form as an advanced evolutionary stage of *Subhyracodon occidentale*, whereas Troxell considered it a primitive subspecies of *Subhyracodon tridactylum* [*sic*]. It is probably simplest to raise it to specific rank, and this would seem to be justified by its difference in character and level. Both stratigraphically and morphologically, it succeeds the typical *Subhyracodon occidentale* and precedes the typical *Subhyracodon tridactylum.*" (Wood, *loc. cit.*)

*Horizon:* Upper part of lower Brulé.
*Localities:* Type found at Rushville, Nebraska; referred specimens from Big Bad Lands, So. Dak.

The situation with regard to the supposed species of *Subhyracodon* may be briefly summed up as follows: The dominant genus of the rhinoceroses in the Chadron is *Trigonias*, but, presumably, in the latter part of that substage, it was associated with two closely allied (perhaps identical) species of *Subhyracodon*, *S. trigonodus* and *S. copei*, which continued into the basal part of the lower Brulé and were succeeded by *S. occidentalis*, the abundant and characteristic species of that substage, and this, in turn, was followed by *S. metalophus*. Whether or not that form is regarded as a distinct species, it is obviously a link between *Subhyracodon* and *Diceratherium*. The latter genus makes its first appearance in the upper Brulé, where it is characteristic of the channel sandstones of the "Protoceras Beds." The recognized species of *Subhyracodon*, thus, form a genetic series and were, for the most part, successive rather than contemporaneous.

### **Diceratherium** Marsh.

*Diceratherium* Marsh: Amer. Journ. Sci., 3rd Ser., Vol. IX, p. 242, 1875.
*Aceratherium* Osborn (*nec* Kaup) Bull. U. S. Geol. Surv., No. 179, p. 64, 1902.
*Diceratherium* Hatcher: Amer. Geologist, Vol. XIII, p. 390, 1894.
*Subhyracodon* Wood (in part, *nec* Brandt): Bull. Amer. Paleont., Vol. 13, p. 69, 1927.

The generic term which should be applied to the large rhinoceroses of the "Protoceras

Sandstones" in the upper Brulé is largely a matter of taste. So gradual and complete is the transition from the species of *Subhyracodon*, which characterize the lower Brulé, to those of the fully developed *Diceratherium*, found in the John Day and the lower Miocene, that any drawing of lines of separation seems arbitrary. The essential feature which is diagnostic of *Diceratherium* is the presence of a transverse pair of nasal horns on the male skull and there can be no doubt that in the species of the upper Brulé, incipient nasal horns were present and functional. Wood writes me: "*Subhyracodon—Diceratherium* is a continuous series, so that the line of demarcation is essentially arbitrary. In 1927 I drew it just above *tridactylus*, following Osborn; the line below *tridactylus*, where you propose to draw it has some advantages. With the line in this position, a tendency toward mures on the upper premolars and secondary crenulations on and near the anterior face of the metaconule on the upper cheek teeth would be additional generic characters." (H. E. Wood, Ms.)

In the unquestioned species of this genus in the John Day and the lower Miocene, the bony horn-bases are conspicuous, almost hemispherical knobs, placed at the anterior end of the nasal bones, which are much thickened, to give the necessary support. In the upper Brulé species, on the contrary, the nasals retain the same shape that they have in *Subhyracodon*, long, narrowing forward and terminating in sharp points, and the bases of the horns are small rugose areas on the outer sides of the nasals well removed from the anterior ends. The rugosities themselves are hardly sufficient to prove the former presence of dermal horns on the skull, but the conspicuous thickness of the nasal bones, which is almost twice as great as in *Subhyracodon*, is strongly confirmatory of the inference as to horns.

As the White River species are so different from those of the John Day and the lower Miocene, it is not advisable to attempt any description of the genus *Diceratherium* here, rather confining attention to the typical White River species, *D. tridactylus* Osborn, of which material in an extraordinary state of preservation is available.

### **Diceratherium tridactylus** Osborn.

*Aceratherium tridactylum* Osborn: Bull. Amer. Mus. Nat. Hist., Vol. V, p. 85, 1893.
*Diceratherium proavitum* Hatcher: Amer. Geologist, Vol. XIII, p. 360, 1894.
*Caenopus tridactylus* Hay: Bull. U. S. Geol. Surv., No. 179, p. 643, 1902.
*Diceratherium tridactylum* Osborn: Nat. Hist., Vol. XXIII, p. 215 (Explanation of figure) 1923.
*Subhyracodon tridactylum* Wood: Bull. Amer. Paleont., Vol. 13, No. 50, p. 69, 1927.

The type specimen of this species is a wonderfully complete and perfectly preserved skeleton, found in the channel-sandstones of the upper Brulé in the Big Bad Lands of South Dakota. It was described by Osborn in several papers, culminating in his great monograph on *The Extinct Rhinoceroses*, of 1898.[1] A somewhat abbreviated version of this paper will be useful as furnishing an adequate account of a most remarkable and interesting skeleton.

"*Aceratherium tridactylum*" $i\frac{2}{2}$, $c\frac{0}{0}$, $p\frac{4}{3}$, $m\frac{3}{3}$; digits 3–3; vertebrae C7, D19, LV, S3, Cd. 21. The species was named at a time when it was believed that the lower Miocene rhinoceroses of America and Europe were very generally tetradactyl. On the contrary, all the post-Chadron species of White River genera of this family are three-toed. "The skeleton measures seven feet nine inches in length, and four feet in height to the top of the lumbar vertebral spines. . . . The pelvis is long and rather slender, and the limbs are of an intermediate type, heavier than in *A. occidentale* and much longer than in the Upper Miocene *A. fossiger*. . . . The total length of the skull is 51 centimeters, while in *A. occidentale* it measures 44. The occiput is high and rather narrow . . . the upper line of the skull thus curves upwards, and the sagittal crest is considerably shortened. Another progressive feature is that the molars show, besides the strong 'antecrochet,' a beginning of the crochet, which is wholly undeveloped in *A. occidentale*. The median upper incisors are much larger than the outer pair and the lower canines ($i\overline{2}$) are correspondingly enlarged. The first lower premolar ($pm_{\overline{1}}$) is rudimentary or wanting.

[1] Osborn, H. F., *The Extinct Rhinoceroses*, Memoirs Amer. Mus. Nat. Hist., Vol. I, pp. 75–164.



"Another distinctive feature of the skull is the union of the post-glenoid and post-tympanic processes to enclose the external auditory meatus inferiorly.

"Owing to the paired convexities and rugosites upon the nasals in the skull of this and other types, the animal was reported by letter from the field as a *Diceratherium*, and this conjecture as to its probable relationship has subsequently proved to be correct from evidence brought forward by Hatcher (1897) and the writer in the present memoir. . . .

"*Comparison with A. occidentale.*—The species is at once seen to be a progressive form of *Aceratherium occidentale* in the same line of descent. It agrees with this ancestor in many details, such as the subtriangular form and oblique position of the lower canines [i.e., the second incisors], the very frequent presence of both internal and external cingula upon the molars, and in minor superficial characters of the skull. . . . It differs from *A. occidentale* in the marked reduction of the lateral upper incisor, in the greater arching of the nasals, in the more elevated occiput, in the usual closure of the external auditory meatus inferiorly, in the crenulation of the upper premolar and molar enamel, in the incipient development of the 'crochet' and 'crista' upon the molars, in the less distinctly triangular section of the canines [$i\overline{2}$] in the widening out of the supratemporal ridges and consequent flattening of the cranium, and in the development of rudimentary paired rugosities on the nasals of old males." (Pp. 158–9.)

#### Dentition

Two upper incisors, $i\underline{1}$ and $i\underline{2}$, were present and functional, but the diameter of $i\underline{2}$ is hardly more than one-third that of $i\underline{1}$; $i\underline{2}$ is decidedly more reduced than in *Subhyracodon* and, in some skulls this tooth is greatly reduced while $i\underline{1}$ is correspondingly enlarged.

The upper *premolars*, as is true throughout the family, differ from the true molars, especially in the character of the external wall, or *ectoloph* in Osborn's nomenclature. In all of the Rhinocerotoidea the ectoloph of the upper molar is composed almost wholly of the very large and externally flat metacone, and the paracone is reduced to a narrow convexity, while in the premolars of such species as have acquired the molariform grinding surface, the outer wall is made up of two nearly equal lobes, the protocone and tritocone, which have slightly convex external faces with faintly marked median ribs. In this species, *D. tridactylus*, the first upper premolar, $p\underline{1}$, has two transverse crests; the anterior one, or protoloph, is short and the posterior one, or metaloph, is relatively long and recurved. $P\underline{2}$ and $\underline{3}$ are similar; each has two transverse crests, which are separated internally; $p\underline{4}$ is not fully molariform, for the crown is not completely quadrate and the metaloph early becomes connected internally with the protoloph by abrasion. The enamel on the anterior side of the metaloph is faintly crenulated, as is also the inner side of the external wall.

The upper *molars* have the enamel of the ectoloph and metaloph more decidedly crenulate than in the premolars; it varies much in degree, but is always present, according to Osborn, who regarded it as a specific character. The incipient "crista" is well developed and constant. The "inner crochet" or fold between hypocone and metaconule, is well shown on m$\underline{1}$ and m$\underline{2}$ and constant; in much worn teeth it is conspicuous. A variable character is the enamel pillar at the entrance to the internal valley of m$\underline{3}$, which is sometimes prominent, sometimes absent. "It is an inconstant character, but it is noteworthy because it occurs in the *Diceratherium* of the John Day." (Osborn, p. 160.)

The lower teeth differ in no significant respect from those of *Subhyracodon*.

### Skull

"The superior view is imperfect because crushed. . . . In lateral view (No. 538) the nasals are long, well arched from side to side and antero-posteriorly; they have a double longitudinal convexity which is increased by lateral crushing, and they exhibit slight lateral rugosities; in front they suddenly contract and extend forwards as paired tapering cylinders; they extend well down at the sides of the anterior nares quite close to the premaxillary suture. . . . The lachrymals have a very extended exposure, and the knob, which we observed as a rudiment upon the front border of *A. occidentale*, is now very prominent. Back of the orbits the upper border of the cranium rises very sharply and the supra-temporal crests are rugose and clearly defined. The parietals upon either side of the high and narrow cranium present a waving surface and two nutrient foramina. The zygomatic arches also rise sharply and swell suddenly outward above the glenoid fossae, a feature which is highly characteristic of this species, and most sharply marked in the males. Other progressive features are the strongly internal position of the post-glenoid process; the extended junction of the post-glenoid and post-tympanic processes below the auditory meatus; the long, slender paroccipital processes, and the marked shortening of the skull behind the auditory meatus. . . . In *superior* view the supratemporal ridges come together so far back that the sagittal crest is reduced to an extremely high and narrow ridge, constricted in the mid-region and spreading superiorly.

"The lower jaw exhibits a well-developed post-cotyloid process, a prominent angle and slender coronoid process." (Osborn, p. 161.)

The most characteristic feature of this skull is the form of its dorsal, or upper profile; anteriorly, there is the slight longitudinal convexity of the nasals and posteriorly the very steep rise to the high occiput. These characters are to be correlated with the appearance of horns, which necessitate the strengthening of the skull, as appears especially in the great thickening of the nasal bones, as compared with those of *Subhyracodon*. The steep rise of the upper contour from the forehead to the inion is shared with the hornless *Trigonias*, a puzzling circumstance.

### Skeleton

Osborn's brief note on the skeleton is repeated above in the generic diagnosis and it is not necessary to add much to that, for the skeleton is much like that of the other White River members of the family, with certain differences of proportions; *Diceratherium tridactylus* is decidedly larger than the common rhinoceroses of the lower Brulé, and of the Chadron, *Subhyracodon occidentalis*, or *Trigonias osborni* (which agree well in size), and is



differently proportioned. The legs are decidedly longer and give to the animal a somewhat stilted appearance in comparison with the more ancient species, and the feet, especially the metapodials, are longer and more slender. The spinal column agrees with that of the two genera named, in having 24 trunk-vertebrae, while all existing rhinoceroses and tapirs have 23; in the horses the number fluctuates between 23 and 24. The larger number is a primitive character in both artiodactyls and perissodactyls and in the course of evolutionary development the number of trunk-vertebrae has undergone a reduction in both orders. In all existing artiodactyls, for example, the number of trunk-vertebrae is 19, but in two of the White River families, the *Hypertragulidae* and the *Merycoidodontidae*, the number is 20. Entire skeletons of single individuals are rare in the Eocene, but in such instances as they are known of Eocene perissodactyls, like *Hyrachyus* and *Helaletes*, the number may be 25 or more.

The backbone of *Diceratherium tridactylus* differs considerably from that of *Subhyracodon*, or *Trigonias* in appearance, especially in the development of the neural spines, which are distinctly longer and heavier, especially in the lumbar region, than in the preceding genera. The centra are arranged in a gentle longitudinal curve, the line being highest at the end of the dorsal region, thence bending down to the neck; the changing length of the spines compensates this curve, making the upper line of the back nearly straight.

Measurements (from Osborn)

| *A.M.N.H.* | ♂ *538* | ♂ *541* | ♂ *1126* | *1111* | ♂ *1137* | *1137* ♀ *1127* | ♀ *1122* | ♀ *1121* | ♂ *1124* | ?♂ *1120* |
|---|---|---|---|---|---|---|---|---|---|---|
| Upper tooth series, length mm. | 212 | 207 | 205 | 212 | | | 205 | 183+ | 197 | 218 |
| Upper molar series, length mm. | 121 | 112+ | ?115 | 111 | 119 | 115 | 113 | 110+ | 101 | 122 |
| Skull, length occ. cond. to prmx. (incl.) | 510 | 475 | 485 | | | | 475+ | 425+ | | |
| Skull, height of occiput | 175 | 182 | 180 | | | | 140 | 150 | 133+ | |
| Skull, breadth of occiput | 100+ | 104 | ?80 | | | | 76 | 104 | 90+ | |
| Skull, breadth of zygom. arches | | 265 | ?246 | 246 | | | 237 | 255 | 282− | 308 |

The sign + or − indicates that measurements have probably been increased or diminished by crushing of the skull.

*Horizon:* Upper Brulé.
*Locality:* Big Bad Lands, South Dakota.

There remain two forms, obviously nearly related to *D. tridactylus*, which are differently treated by different writers; Troxell, who named them, described them as subspecies of *D. tridactylus*, while Wood prefers to raise them to the rank of apecies, though without attaching much importance to the distinction.

### **Diceratherium tridactylus metalophus** (Troxell)

*Aceratherium occidentale* Osborn (*nec* Leidy): Mem. A.M.N.H., Vol. I, p. 153, 1898.
*Caenopus tridactylus metalophus* Troxell; Amer. Journ. Sci., 5th Ser., Vol. II, p. 47, 1921.
*Subhyracodon metalophum* Wood: Bull. Amer. Paleont., Vol. 13, No. 50, p. 67, 1927.

Troxell's type (No. 10,245, Peabody Mus., Yale Univ.) is from Rushville, Neb. and a virtually identical skull (A.M.N.H., No. 1123) described and figured by Osborn, is from

South Dakota, in "the Upper Oreodon Beds." Wood writes of it: "This form was larger than *Subhyracodon occidentale*, smaller than *Subhyracodon tridactylum* and probably hornless in both sexes. . . . I2 is still large. The protoloph and metaloph of P4 are separate and parallel. The upper molars are smaller individually and collectively, than in *Subhyracodon tridactylum* and have no secondary folds.

"Osborn regarded this form as an advanced evolutionary stage of *Subhyracodon occidentale*, whereas Troxell considered it a primitive sub-species of *Subhyracodon tridactylum*. It is probably simplest to raise it to specific rank and this would seem to be justified by its difference in character and level. Both stratigraphically, and morphologically it succeeds the typical *Subhyracodon occidentale*, and precedes the typical *Subhyracodon tridactylum*. Morphologically, it is also possible to derive it from *Subhyracodon*. Stratigraphically, either form would answer equally well as an ancestor." (H. E. Wood, *op. cit.*, p. 67.)

The three authorities cited are in substantial agreement as to the character and significance of this form and differ only as to names.

*Horizon:* Upper levels of lower Brulé.
*Localities:* Rushville, Neb. (type); Big Bad Lands, So. Dak.

### **Diceratherium tridactylus avus** (Troxell)

*Caenopus tridactylus avus* Troxell: Amer. Journal Sci., 5th Ser., Vol. II, p. 49, 1921.
*Diceratherium avum* Wood: Bull. Amer. Paleont., Vol. 13, No. 50, p. 71, 1927.

Troxell's original description reads: "This is very probably a true form of this species, but as a subspecies shows a decided trend toward *Diceratherium armatum*. . . . The first three premolars (P4 is also uncut) are notable for the parallel, separate lophs, uniting only with wear. The metaloph is at first longer, but because of the extended base of the deuterocone, the protoloph soon surpasses it in length. P1 has two parallel, backward curving crests, but the metaloph does not encircle a lake (post-fossette) as does Osborn's paratype. . . . On the other premolars, small sharp folds appear on the ectoloph, and on P3 (left) one has an unusual position behind the metaloph. On P2 and P3 (right) there is a fold in the anterior angle between the two lophs.

"Cristas and crochets may be seen on the molars, and the latter, especially on M1, have encroached so far on the median valley as to isolate a small lake (medifossette). On the protoloph of M1, two vertical valleys, anterior and posterior, partly separate the protocone from its protoconule; the posterior valley emphasizes and sets off the moderate antecrochet. The inner cingula are broaken across the bases of protocone and hypocone and are peculiarly offset where the two ends join in the median groove." (Troxell, *loc. cit.*)

Wood adds to Troxell's account: "This form was described and figured by Troxell, who regarded it as an advanced subspecies of *Subhyracodon tridactylum*. It seems sufficiently advanced over that form to deserve specific rank. Its greater size and the increasing complexity of the cheek teeth made it seem preferable to include it tentatively in *Diceratherium*. The intergradation of the two genera is so close, that any line of separation is rather arbitrary." [1]

"I still regard *Caenopus tridactylus avus* Troxell, 1921, as intermediate between *tridactylus* and *armatum* (of the John Day.)"

[1] Wood, H. E., Bull. Amer. Paleont., Vol. 13, No. 50, p. 71.



"The series *Subhyracodon copei—S. occidentalis—S. metalophus—Diceratherium tridactylus—D. avus—D. armatum*, is the best established and longest close phylogenetic sequence so far discovered among the rhinoceroses." [1]

### Family 4. Hyracodontidae Cope

*Rhinocerotidae*, Leidy (*nec* Owen).

This family is not known to be represented outside of North America, yet, nevertheless, it was more probably of Old World than indigenous origin. In this continent it has not been found in beds more ancient than the Uinta, or Upper Eocene and the Middle Eocene ancestors which have been suggested (e.g. *Hyrachyus*, of the Bridger), do not seem to be suitable or satisfactory. To derive the White River *Hyracodon* from any known American genus would involve such a degree of convergence as cannot be accepted without very strong evidence, evidence that is not yet forthcoming.

The stratigraphic extension of this family would indicate a short life, geologically speaking; the first known appearance is in the Uinta stage of the Eocene; the preceding Bridger, or middle Eocene has genera, such as *Hyrachyus*, and *Triplopus* which, as noted above, cannot be regarded as probable ancestors. The upper limit of the family, so far as is at present known, is the lower Brulé, or "*Oreodon Beds.*" No smallest trace of them has been found in the *Protoceras* Channels, the *Leptauchenia* Beds or any part of the John Day, or the Sespé of California. But a single genus of the family, *Hyracodon* itself, has been found in the White River and this narrow limitation, taxonomic, geographical and geological, is a strong indication that *Hyracodon* is a straggler from some other region and that its occurrence in the Great Plains area is more or less an accident.

Compared with the other two families of the Oligocene rhinoceroses, the Hyracodontidae are very sharply demarcated. (1) The incisors and canines are all of nearly the same size and similar form, small, recurved and pointed; (2) the teeth are present in but slightly reduced number, 42; (3) grinding teeth have a typically rhinocerotic pattern, though in m3 the fusion of the posterior crest with the external wall is incomplete; (4) the skull has a long, high sagittal crest and no indication of horns; (5) the neck is relatively much longer than in the other rhinoceros families, almost as elongate as in the horses; (6) the limbs are much longer and lighter than in the other two families; (7) the feet are always tridactyl, long and slender, the median digit of each foot enlarged and the laterals reduced almost as much as in the contemporary horses, *Mesohippus;* (8) everything goes to show that the hyracodonts were swift-moving, cursorial rhinoceroses, dependent altogether upon speed for their safety, for they had no weapons of defense, neither tusks, horns, nor claws.

### **Hyracodon** Leidy

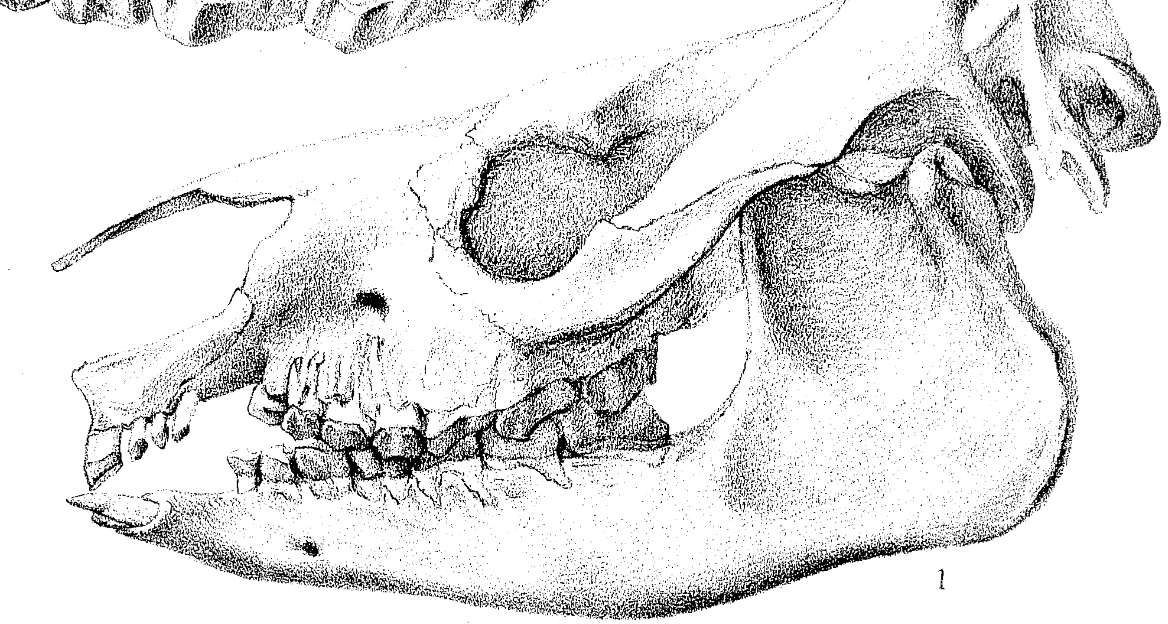
(Pl. LXXXIX and XC)

*Rhinoceros* Leidy (*nec* Linn.): Proc. Acad. Nat. Sci. Philad., Vol. V, p. 121, 1850.
*Hyracodon* Leidy: *Ibid.*, Vol. VIII, p. 91, 1856.

Though rather a common fossil in the lower Brulé substage of the White River, well-preserved specimens are rare. A remarkably perfect skull in the Field Museum, free from crushing and distortion and a skeleton in the museum of Princeton University have fur-

[1] Wood, H. E., Ms. 1938.

3



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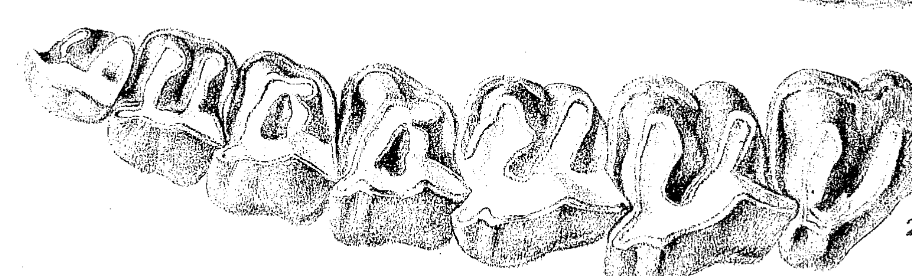
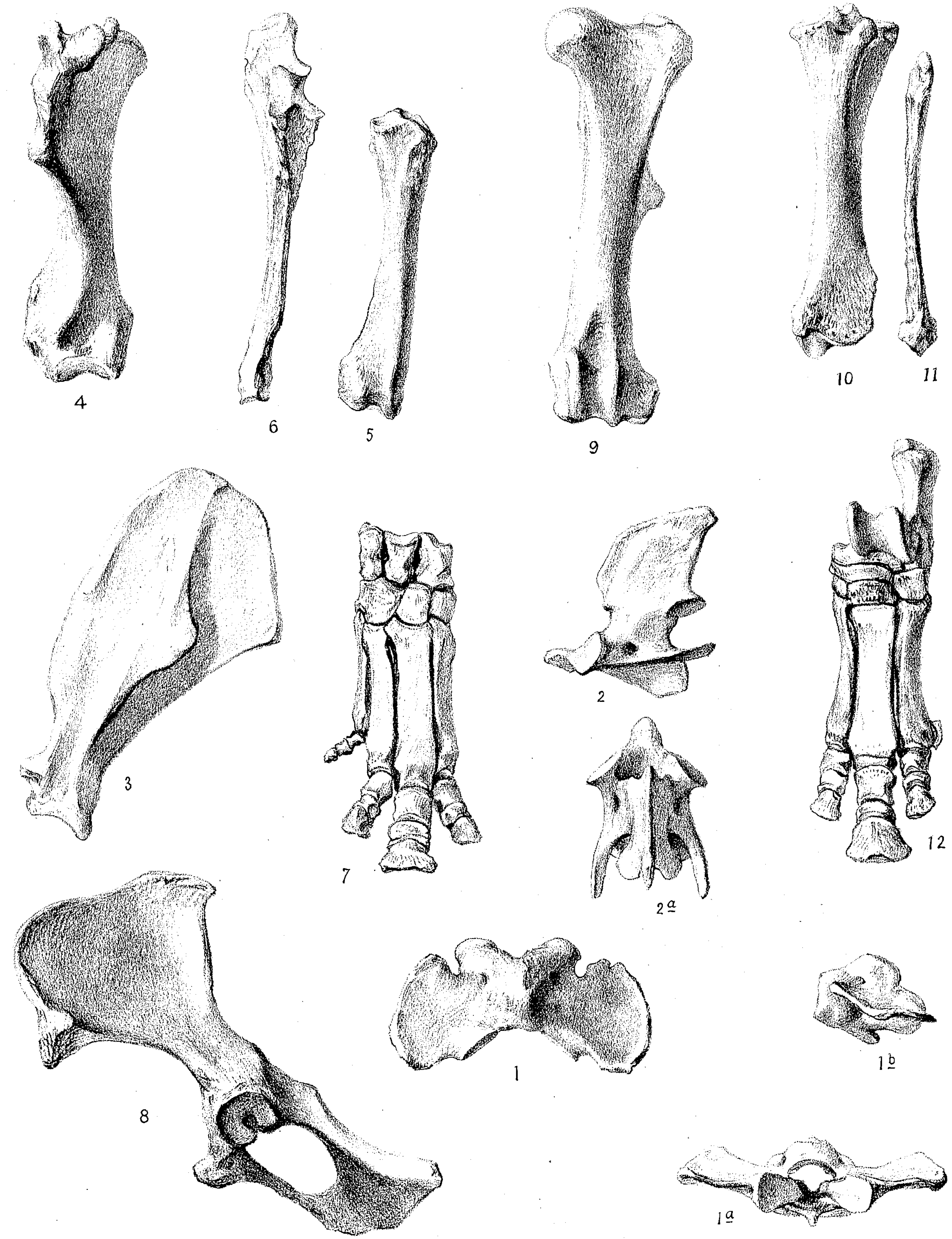
1[a]



2

TRIGONIAS—CAENOPUS—SUBHYRACODON

PLATE LXXXIII

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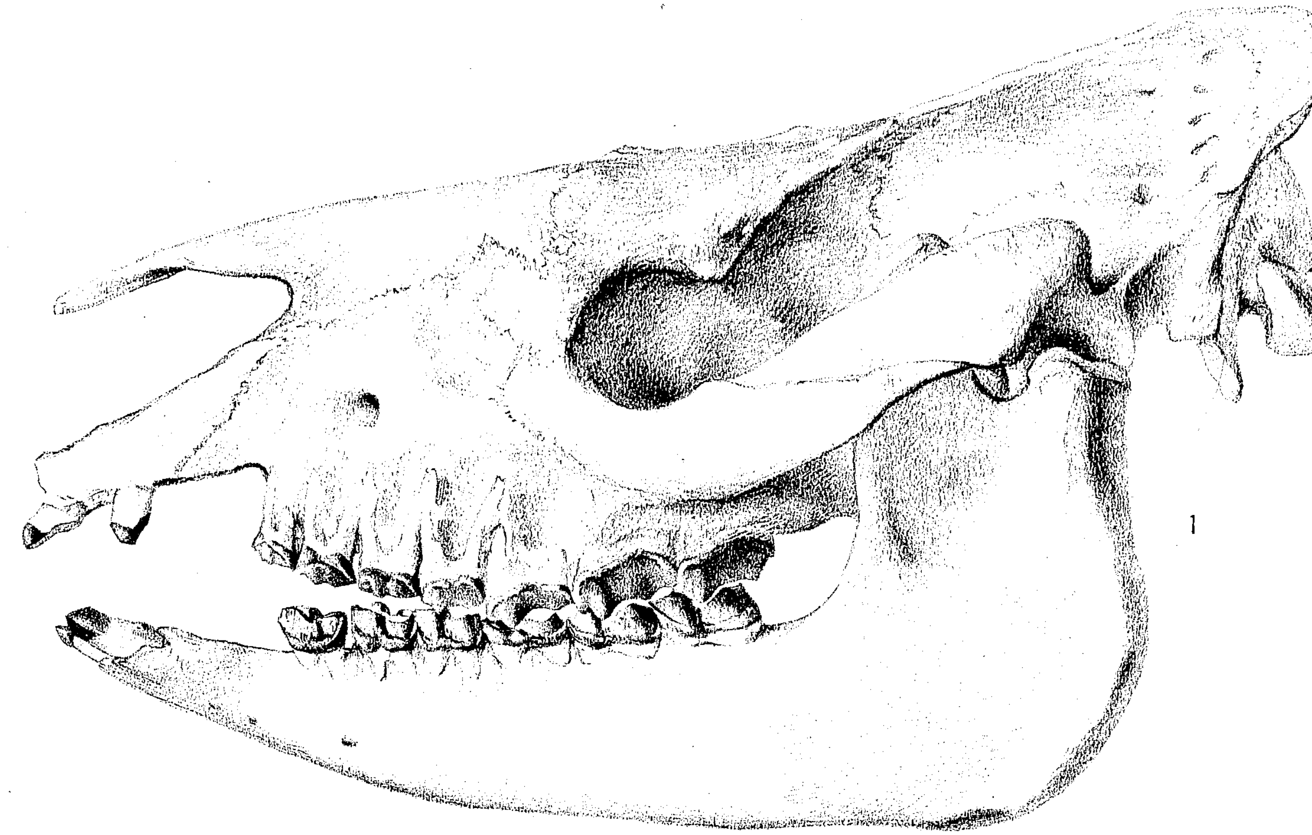

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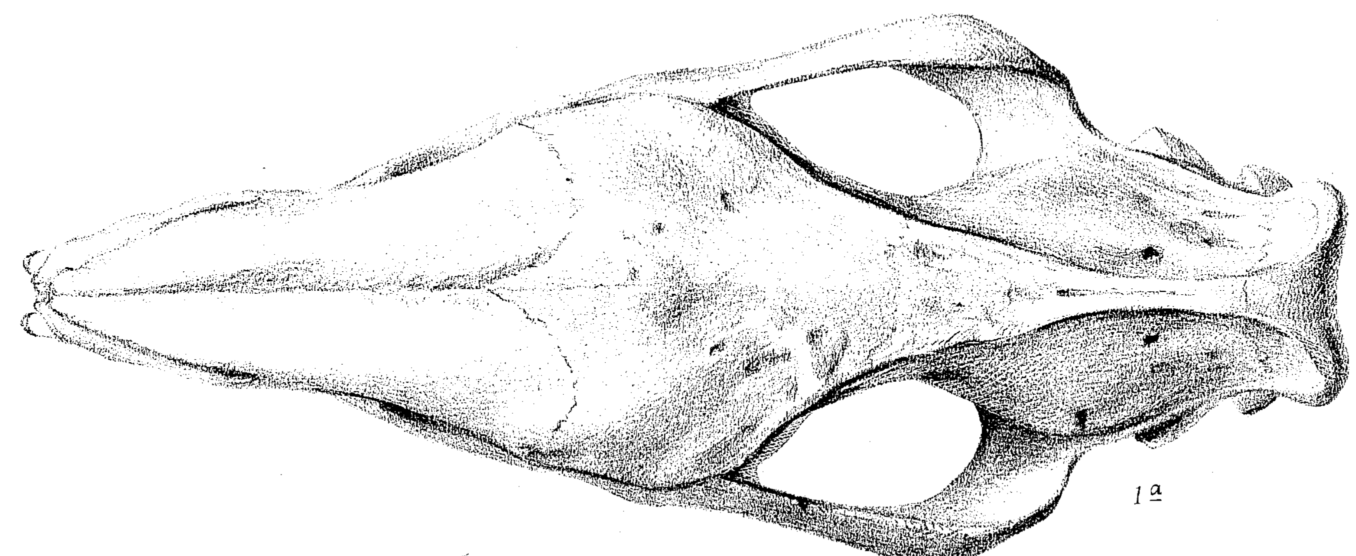

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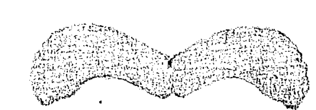
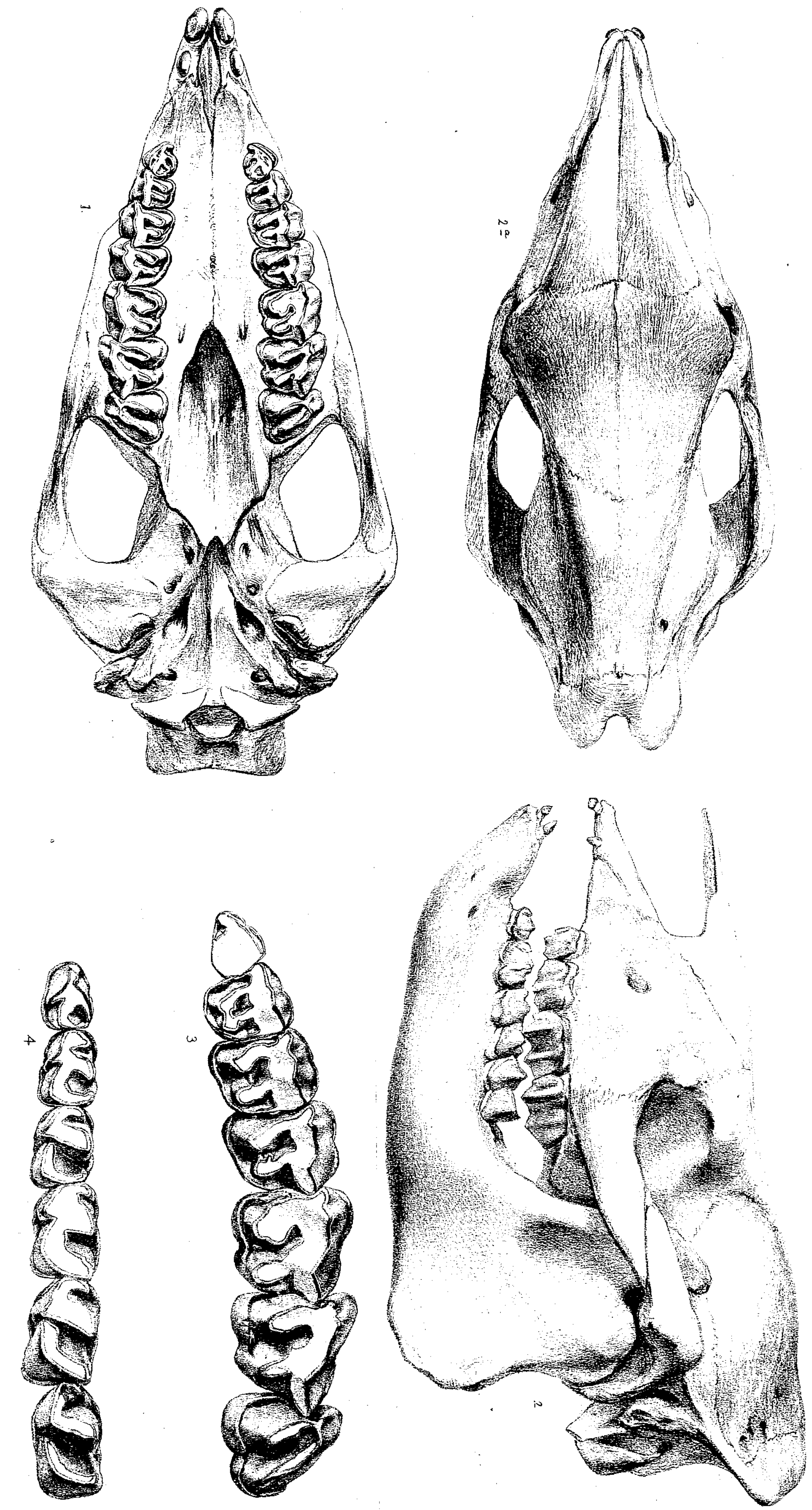


2 a

1 b

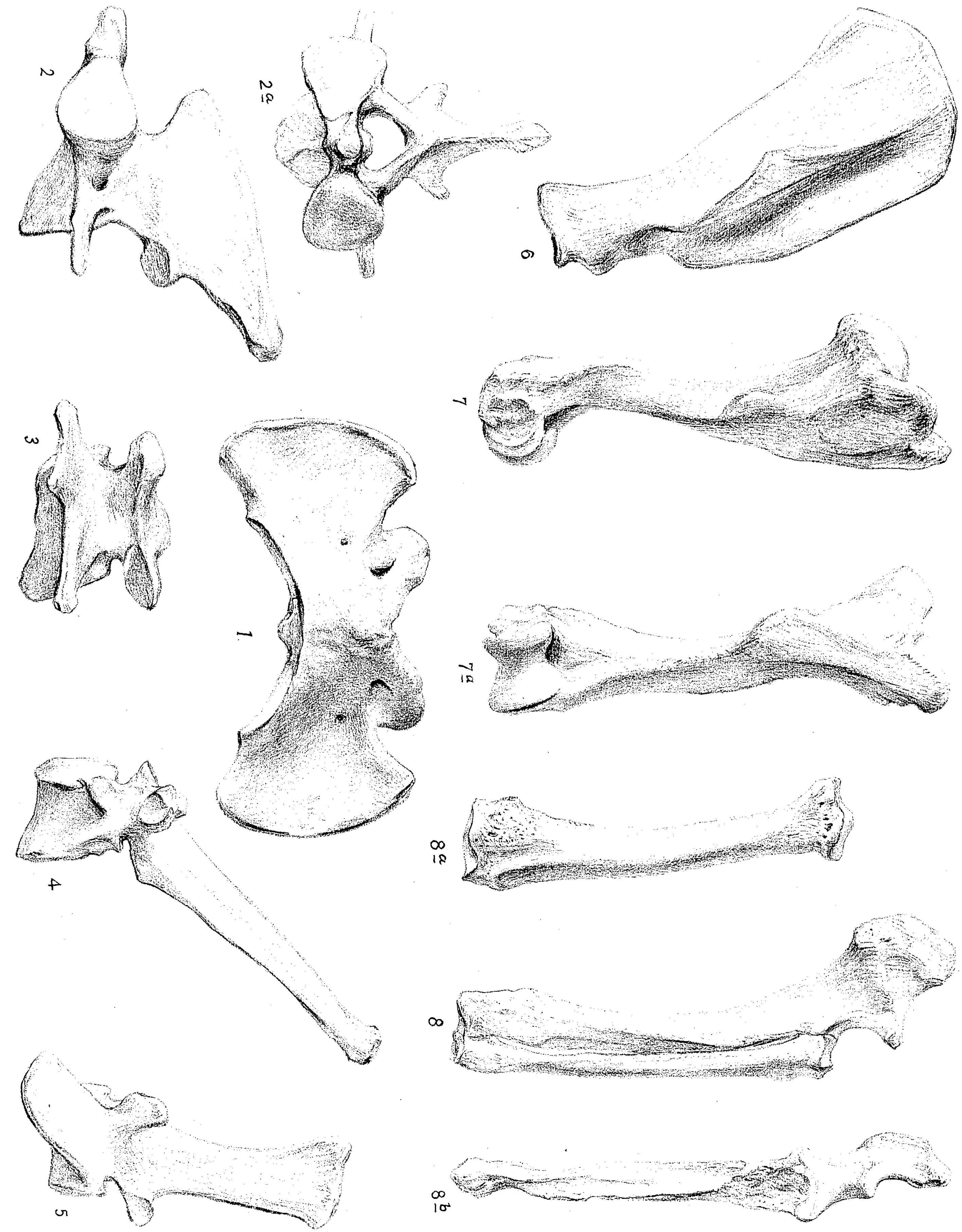
SUBHYRACODON — DICERATHERIUM

PLATE LXXXV



SUBHYRACODON

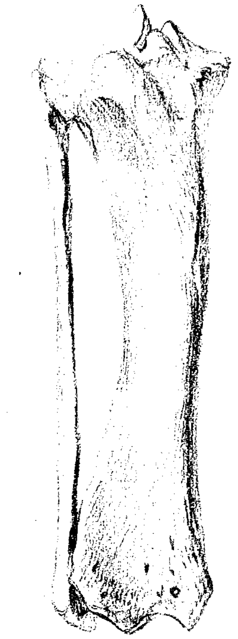
PLATE LXXXVI



SUBHYRACODON

Plate LXXXVII

2a



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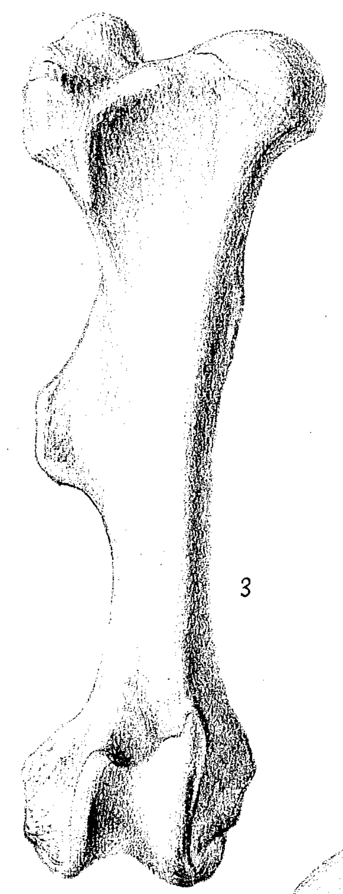


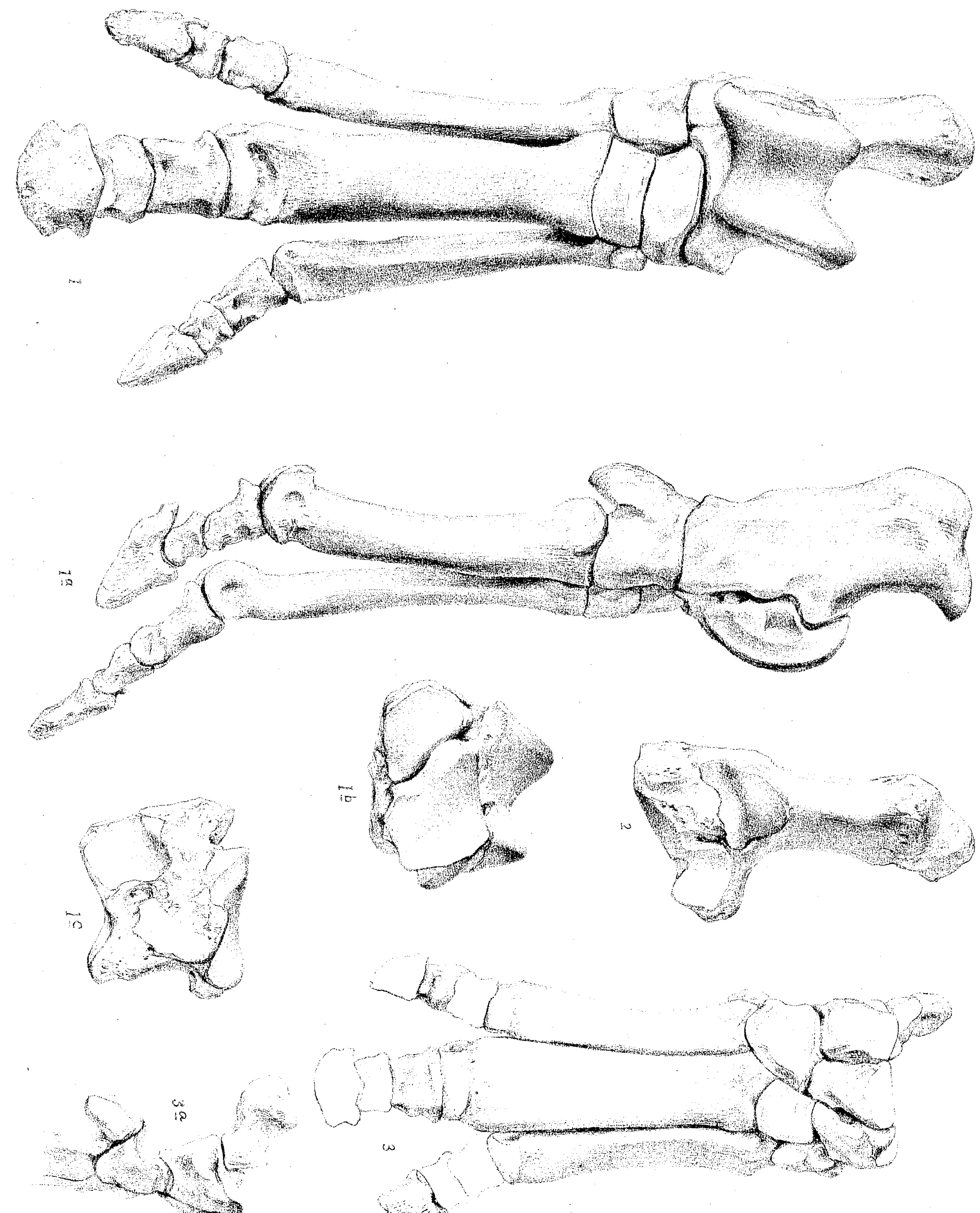
3

2

1

SUBHYRACODON

PLATE LXXXVIII




SUBHYRACODON—CAENOPUS