24. Some Cranial and Dental Characters of the existing species of Asiatic Rhinoceroses.

By R. I. Pocock, F.R.S. (Zool. Depart. British Museum of Natural History).

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(Text-figures 1–5.)

CONTENTS.

INTRODUCTION.

In his classical paper (Proc. Zool. Soc. Lond. 1876, pp. 443–457), on the skulls and teeth of existing Rhinoceroses, based upon specimens in the Museum of the Royal College of Surgeons* and in the British Museum, Flower summarised the differences between the three Asiatic species pointed out by earlier authors, notably by Owen, Blyth, Gray and Buxton, and added some new and important characters not previously detected. But an examination of the skulls he saw in the British Museum and of additional material acquired since that date has revealed a few features not formerly taken into account and has shown that several of his statements need qualification or correction. Some of the results of this examination are embodied in the following pages; and the need for their publication is emphasised by the issue two years ago of a paper by Colbert (Amer. Mus. Novit. 1207, p. 2, 1942) in which he tabulates eleven alleged cranial and some additional differences between *Rh. unicornis* and *Rh. sondaicus*. Most of these are copied from Flower's paper, sometimes *verbatim*, and always without question. The author appears to have had only one skull of each of the species in his hands and to have assumed the specific stability of the differences they presented.

Some cranial differences between the two-horned genus Didermocerus *and the one-horned genus* Rhinoceros

To the well-known characters distinguishing the Asiatic two-horned genus *Didermocerus*, better known by the later names *Dicerorhinus* and *Ceratorhinus*, from the one-horned genus *Rhinoceros*, I can only add one that appears to have been neglected. In *Didermocerus* the facial portion is longer than the area behind it, whereas in *Rhinoceros* it is shorter. In eight skulls of the former the average length from the anterior edge of the orbit to the tip of the nasal, the orbitonasal length, is about 11 inches and the length from the anterior edge of the orbit to just behind the auditory orifice, the orbitoaural length, is about

* Practically the whole of the osteological collection in this Museum, including the skulls in question, was destroyed during an air-raid in the winter of 1940–41.

9·5 inches. In the same number of skulls of *Rh. sondaicus* the average length of those areas is respectively about 9·8 and 11·5 inches and of *Rh. unicornis* slightly over 11 and 12 inches.

In connection with the principal cranial difference between these two genera, namely, the open or closed channel beneath the auditory orifice, the subaural channel, it is perhaps worth recording that this may narrow with age in *Didermocerus*. In a youngish adult ♂ skull from Mogok, Upper Burma (31. 5. 28. 1), with the last molar just erupting in front of it only a little worn, the channel at its lower end is about 15 mm. wide, whereas in an old ♂ from Mount Ophir, Malay Peninsula (79.7.14.2), with all the teeth greatly worn, it is only 2 mm. wide. Possibly in some old skulls the post-tympanic and post-glenoid processes may meet and close the channel for a short distance. This would necessitate a slight modification of the definitions of the genera in this respect, but it would not appreciably affect the main difference, namely the extensive contact between those two processes even in very young skulls of *Rhinoceros*.

Another well-known skull difference between the two genera is the subvertical plane of the occipital surface in *Didermocerus* and its forward inclination from below in *Rhinoceros*. A clear indication of this is supplied by comparing the condylonasal length with the occipitonasal length in the two genera. In *Didermocerus* the two dimensions are very nearly equal, their averages in eight skulls being respectively 21·8 and 21·3 inches. In *Rhinoceros*, on the contrary, the condylonasal length is several inches longer than the occipitonasal. In eleven skulls of *Rh. sondaicus* the average condylonasal length is about 24·5 inches and the average occipitonasal length just over 20 inches. In the same number of skulls of *Rh. unicornis* the averages are a trifle over 26·5 and 23 inches respectively. These figures also show the average differences in total length between the skulls of the three species, although the old ♀ skull of the type of *D. sumatrensis lasiotis* from Chittagong has the condylonasal length about the same as in an old ♂ skull of *Rh. sondaicus* from the Sanderbans.

Some differences in dentition between the two genera are described below (p. 448).

Some cranial differences between Rhinoceros unicornis *and* Rh. sondaicus.

The mesopterygoid fossa.—Flower's statement that this fossa is always actually narrower in *Rh. unicornis* than in *Rh. sondaicus* is only borne out in part. Its average width between m^3 is as nearly as may be the same in the two species, namely 2·5 inches, which makes it merely relatively narrower in *unicornis* at that point; but it is actually narrower in the latter between the upper ends of the pterygoids, where it is manifestly constricted, the average outside width just in front of the posterior apertures of the alisphenoid canals being about 1·7 inches, whereas in *Rh. sondaicus* it is about 2·2 inches.

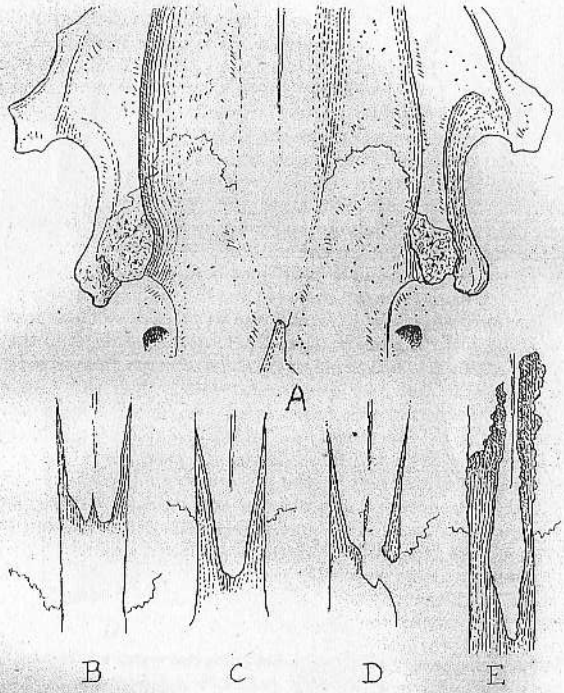
Flower also claimed that the anterior or palatal edge of the fossa is more uniformly concave in *Rh. unicornis*, the median projection being larger in *Rh. sondaicus*. This is merely an average difference, the two species completely intergrading in that particular.

There are two differences in the fossa to which he made no reference. In conformity with the greater height of the skull, the fossa is posteriorly about 1 inch deeper in *unicornis* than in *sondaicus*; and in the former the nasal chambers are longer and encroach more extensively on the floor of the fossa in front, so that a larger area of them is visible below the posterior edge of the palate when the skull is viewed from below. This obvious and apparently constant difference is well shown in figs. 3 and 4, pp. 446–447 of Flower's paper.

The basioccipital.—My series of skulls confirms Flower's statement that the base of the skull at the swollen junction of the occipital and sphenoid bones is narrower in *unicornis* than in *sondaicus*, its average width just in front of the clefts (*foramina lacera media*) in the two species being about 1·7 and 2·2 inches respectively, practically the same as the width at the posterior apertures of the alisphenoid canals.

The Vomer.—Flower regarded as absolutely diagnostic of the two species a character connected with the vomer which he detected in the skulls he examined. In *Rh. unicornis*, he stated, the posterior portion of the vomer is firmly united laterally to the base of the pterygoid bones and ends in a thickening between them, no part of it being free. In *Rh. sondaicus*, on the contrary, the posterior

Text-figure 1.



A. Posterior portion of the mesopterygoid fossa of an old ♂ skull of *Rhinoceros sondaicus* from Cochin China with the vomer fused throughout its length by a nearly obliterated suture. Showing also the bilobate angle of the fossa, the inner thickening on each side being the free end of the pterygoid.

B. The free end of the vomer of a youngish ♀ skull of the same species from S. Tenasserim, the vomer with its bifid tip not reaching the pterygoid sutures.

C. The free end of the vomer of an adult ♂ skull of the same species from the Sunderbans, the tip of the vomer reaching beyond the pterygoid sutures.

D. The end of the vomer of a very old ♀ skull from Perak with its tip united on one side to the adjoining wall of the fossa just behind the pterygoid suture.

E. The free end of the vomer of a skull from Java. The anterior part of the bone is broken at the sides, but the median part persists and is continued posteriorly into a long, lanceolate process surpassing the pterygoid sutures.

end of the bone is thin, lamelliform, pointed and free, *i.e.*, not fused laterally to the pterygoids.

In all the skulls of *Rh. unicornis* in the British Museum the posterior end of the vomer, as in the two-horned Asiatic species (*Didermocerus sumatrensis*), is united to the floor of the mesopterygoid fossa, the suture, which is visible in

young skulls, being obliterated as age advances. But in none of them is the bone thickened at the end, which, when traceable, is thin and usually apically emarginate, and its sides, at least in the specimen figured (text-fig. 2, A), are united to the sphenoid, not to the pterygoids. The thickening, described and figured by Flower, must have been an individual peculiarity in a skull in the College of Surgeons.

In *Rh. sondaicus* the posterior part of the vomer is variable in its attachment. When preserved* it is usually free for about 30 mm. from the walls of the mesopterygoid fossa and from the base of the skull, so that a knife-blade can be passed beneath it. This is the condition Flower described and figured; and it is presented by a youngish skull from Java (No. 2.12.18.1) in which the terminal part, broken in front laterally, is an exceptionally long, delicate process ending between the pterygoids, but not in contact with them (text-fig. 1, E). In a young ♀ skull from Lower Tenasserim (No. 21.5.15.1) its free part is shorter, does not reach the pterygoid suture and ends in a blunt deeply bifid tip (text-fig. 1, B). In an adult ♂ from the Sanderbans (No. 76.3.30.1) the tip is also blunt, but simple, and lies between the pterygoids (text-fig. 1, C). In a very old ♀ from Perak (32.10.21.1) it is blunt, mesially grooved, between the pterygoids and free on the right side, but on the left side its extreme tip is attached by a bony lamina to the adjoining pterygoid just behind the suture (text-fig. 1, D). Finally, in an old ♂ from Cochin China (61.6.30.9) no part of the vomer is free, its terminal portion being fused throughout to the floor of the fossa, the junctional suture being just discernible (text-fig. 1, A). In this skull the vomer does not differ from that of *Rh. unicornis* or of *Didermocerus sumatrensis*.

The mesopterygoid angle.—Flower's statement that the free ends of the pterygoids in *Rh. unicornis* are compressed and deeply grooved, whereas in *Rh. sondaicus* they are "flattened and laterally expanded," does not express the facts of the case. By "the free ends of the pterygoids" he seems to have meant the entire posterior angle of the mesopterygoid fossa; but the free end of the pterygoid is not grooved and it constitutes only the inner portion of this angle and in youngish skulls is separated from the outer portion by a distinct suture which becomes gradually obliterated with advancing age, the divisional line between the two being typically represented by a superficial narrower or wider, deeper or shallower groove sometimes ending in a notch behind.

The angle of the mesopterygoid fossa, indeed, being a point of muscular attachment, is very variable in individuals of the same species, sometimes differing on the two sides, seldom alike in any two skulls, and in some cases so similar in the two species as to make it almost impossible to distinguish one from the other.

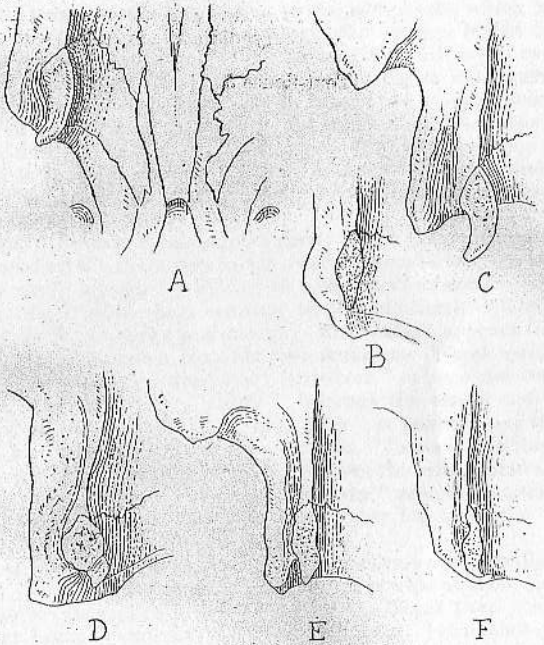
In a young skull of *Rh. unicornis*, the type of *stenocephalus* Gray (46.3.23.4, 722 *e*), the upper† end of the pterygoid is thickened and posteriorly produced, so that superficially it looks like a distinct process curving slightly outwards and backwards (text-fig. 2, A). In a young skull from Dacca (84.1.22.3) the summit is thicker but less produced. In another subadult skull, from the Nepal Terai, there is no such hook-like thickening, the summit of the pterygoid being a little thickened and lanceolate and everywhere closely applied to the outer portion of the angle (text-fig. 2, B). In two old unlocalised skulls (722 *a* and 722 *f*), with m^3 in use and worn, the upper end, with its thickened and hook-like appearance, is similar to that of the type of *stenocephalus*, except that it is roughened and separated by a more pronounced emargination from the posteriorly produced outer portion of the angle (text-fig. 2, C). In three adult or old skulls from Gauripore (72.12.30.1), from Assam (84.1.22.1) and from the Zoological Society (51.11.10.2) ? locality, the upper end is variously thickened and rugose but not produced so as to resemble a hook-like process superficially (text-fig. 2, D, E, F).

* As Flower pointed out, it is not infrequently broken off in cleaned skulls; but in that case the line of fracture is always manifest.

† The following descriptions are taken from the inverted skull which makes its morphologically lower surface uppermost.

In *Rh. sondaicus* equal individual variation in the mesopterygoid angle is exhibited. In one of Gray's specimens of *nasalis*, a youngish skull (55.4.4.4; 273 *b*), the thickened upper end of the pterygoid is tolerably similar in its superficial hook-like curvature to that of the type of *stenocephalus* which, as explained above, is a young *unicornis*, but its suture is much longer (text-

Text-figure 2.



A. Posterior part of the mesopterygoid fossa of a young, unlocalised skull of *Rh. unicornis* (the type of *stenocephalus*, 46.3.23.4), with the sutures clearly defined, showing the usual apical emargination of the vomer, which is fused with the sphenoid, not with the pterygoids, and one angle of the fossa, with the thickened free end of the pterygoid suggesting a hook-like process.

B. The same angle of the fossa in a young-adult, unnumbered skull from the Nepal Terai showing the simple thickening of the free end of the pterygoid.

C. The same of an oldish, unlocalised skull (722 *a*) with the free end of the pterygoid thickened and superficially hook-like as in A.

D. The same of an adult skull from Gauripore, Assam (72.12.30.1).

E. The same from an old skull from Assam (84.1.22.1.)

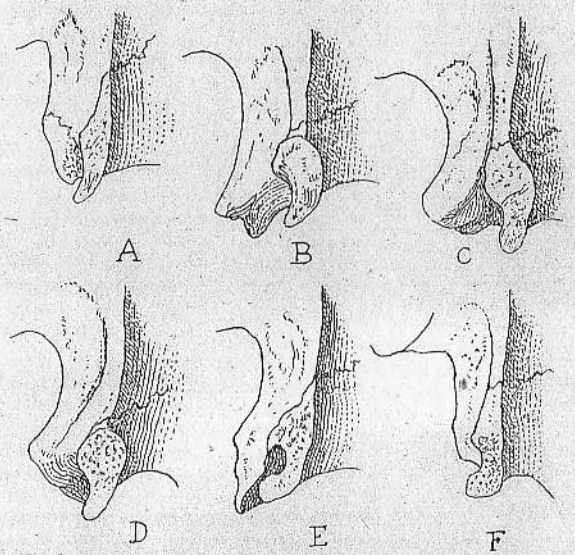
F. The same of an old, unlocalised skull (Zool. Soc. 51, 11.10.2.).

The last three skulls show additional variations in the shape of the mesopterygoid angle with its pterygoid thickening.

fig. 3, A). Also, as in the latter, the external edge in front of the angle, running towards the socket of m^3, is nearly straight and the external portion of the angle bulges very much as in the youngish skull of *unicornis* from the Nepal Terai. An old unlocalised skull (723 *a*) has the hook-like thickening shorter and more curved and the outer portion of the angle considerably more produced, so that the external edge above described is decidedly concave (text-fig. 3, B). Additional variations of the outer and inner portions of the meso-

pterygoid angle are shown in the adult male skull from Cochin China (text-fig. 1, A); in an old ♂ skull (79.11.21.178) from the Malay Peninsula, in which m^3 is considerably worn (text-fig. 3, C); in an adult ♂ skull (76.3.30.1) from the Sanderbans (text-fig. 3, D) and in two from Java (723 *d* and 2.12.18.1) (text-fig. 3, E, F). The differences between the last two from the same country are striking. In both the pterygoid thickening is abruptly bent outwards posteriorly, but in the first it is much wider in front, the outer portion of the angle is also much wider and the edge in front of it is strongly concave, whereas in the second the outer portion, unbroken, is narrow and the edge is comparatively straight. In this specimen the mesopterygoid angle is on the whole more like

Text-figure 3.



A. Angle of the mesopterygoid fossa in a young-adult skull of *Rh. sondaicus* (one of Gray's specimens of *nasalis*, 55.4.4.4., 723 *b*) showing its general resemblance to that of the young *Rh. unicornis* (text-fig. 2, A).
B. The same of an adult unlocalised skull of *Rh. sondaicus* (723 *a*).
C. The same of an adult ♂ skull fron the Malay Peninsula (71.11.21.178).
D. The same of an adult ♂ from the Sanderbans (76.3.30.1).
E. The same of an adult ♂ from Java (723 *d*).
F. The same of an adult ♂ from Java (2.12.18.1).

that of the skull of *unicornis* from Assam (see text-fig. 2, E) than it is like that of the other Javan skull.

The skulls of the two species in the British Museum at most suggest that the only difference between them in the conformation of the mesopterygoid angle may possibly be the average greater expansion of its outer portion and the resulting more deeply concave edge in front of it, in *sondaicus* than in *unicornis*.

Some average dimensional differences.—A few details of actual measurements may be added in confirmation of the general statements made by Blyth, Flower, and other authors concerning the differences in size between the skulls of *Rh. unicornis* and *Rh. sondaicus*, the former being admittedly the larger of the two.

The average condylonasal and occipitonasal lengths in a considerable number of skulls of these two species, nearly a dozen of each, were given above

under the section dealing with *Didermocerus sumatrensis*. To these may be added the following:—In *Rh. unicornis* the average condylobasal length is about 26·5 inches, the average zygomatic width 15·5 inches and the average height at the interorbital area, including the mandible, 14 inches. In *Rh. sondaicus* the averages of the same dimensions are respectively 24 inches, 13·5 inches and 11 inches. This last difference in the height is very noticeable.

It has often been pointed out also that the postdental portion of the mandible is higher in *Rh. unicornis*. It is not only actually, but relatively higher, the average height at the condyle being about 11·8 inches, exceeding half the average total length from the condyle to the symphysis, which is about 21·7 inches. In *Rh. sondaicus*, on the contrary, the average height is just under 9 inches and less than half the average total length, which is just over 19 inches.

The occipital surface has been described as higher and narrower in *Rh. unicornis* than in *Rh. sondaicus*. To be precise its average height from the lower edge of the *foramen magnum* to the summit in *Rh. unicornis* is about 9·5 inches and in *Rh. sondaicus* about 8 inches, whereas the average width about 1 inch below the summit is nearly the same in the two species, namely, just under 7 inches. This makes the surface relatively wider in *Rh. sondaicus* in which the skull is smaller in other respects.

The alleged differences tabulated by Colbert.—Since Colbert in his paper quoted above repeated all the characters in the mesopterygoid fossa, the vomer and the base of the skull, alleged by Flower to distinguish *unicornis* from *sondaicus*, it is needless to refer to them again or to the additional differential features pointed out by Blyth, Gray and others. But Colbert appears to have added one or two derived, it seems, from the two skulls, one of each species, which he figured. In *unicornis*, he states, the "horn-boss" is large and rounded and in profile view there is a deep "saddle" between the nasals and the occipital vertex, whereas in *sondaicus* the "horn-boss" is pointed and the "saddle" shallow. This is only true of some specimens. In *unicornis* the horn-boss is quite frequently low, hardly if at all higher than the area behind it, so that the "saddle" is quite shallow; and in *sondaicus* the "saddle" is often deeper than in some skulls of *unicornis* owing to the greater height of the "horn-boss," and this may be low and rounded even in males.

The "horn-boss," however, is wider both relatively and actually in *unicornis*. In two old ♂♂ the nasals are close upon 6 inches wide at their broadest point, 5·9 inches to be precise, and in one old ♀ from the Nepal Tarai (Oldfield) and an adult ♀ from Assam (Vanderbyl) they are 4·8 inches. In an adult ♂ of *sondaicus* from the Sanderbans their width is 4·8 inches. But this seems to be exceptionally wide for the species, seing that in an old ♂ from Cochin China and another from Java they are only 3·6 and 3·5 inches respectively. In a very old ♀ from Perak (Vernay) they are 3·6 inches.

Also Colbert's claim that the two species differ in the shape of the zygomatic arches which are rounded posteriorly in *unicornis* and angled in *sondaicus*, cannot be maintained, although it is obviously true of his figures of the two skulls, the curvature in his *sondaicus* being almost rectangular. But this is an individually variable character. A glance at Gray's figures of the skulls of the types of *floweri* and *nasalis*, representing respectively an old and a youngish *sondaicus*, shows that the zygomatic angle is obtusely rounded. In this respect the two species intergrade.

Some characters of the Cheek-teeth.

A noticeable variation in the cheek-teeth is the position of the anterior edge of the mesopterygoid fossa as regards the posterior molar teeth. A few instances will serve to illustrate this. In an old skull of *sondaicus* from Java (723 *a*) the edge of the fossa is 15 mm. behind the anterior edge of m^2; in another from the Malay Peninsula (79.11.21.178) it is 20 mm. behind it, whereas in a third of the same species (722 *h*) it is 15 mm. in front of it. The variation is probably due, I think, to the forward shifting of the entire tooth row.

In *Rh. unicornis* the teeth, as Colbert stated, show an approach to the hypsodont condition which is not manifest in *Rh. sondaicus*. They are also actually larger in the former. Excluding pm^1, which is frequently shed and m^3, which is late coming into use, the average length of the remaining five teeth in ten skulls of *unicornis* is about 8·5 inches, whereas in twelve skulls of *sondaicus* the average is just under 7·9 inches. Thus the teeth, although actually smaller, are relatively about as large in *sondaicus*.

Apart from the character above referred to, Colbert mentioned three additional differences in the cheek dentition of the two species. In *Rh. unicornis*, he stated, the ectoloph is rather flat, whereas in *Rh. sondaicus* it is sinuous. Presumably by "rather flat" he meant nearly straight. At all events in his figure of m^2 in *unicornis* the external enamel ridge of the ectoloph is decidedly straighter than it is in his figure of the same tooth in *sondaicus*, in which it is noticeably sinuous. He also said that the parastyle is suppressed in *unicornis* whereas in *sondaicus* the parastyle-buttress is prominent*, and that in *unicornis* the "crochet" and "crista" are well developed and joined in worn teeth to form a fossa, but that in *sondaicus* although the "crochet" is present, the "crista" is generally absent.

A glance at my figures of the teeth of the two species shows that his statement regarding the ectoloph cannot be upheld, its outer enamel-edge being often as sinuous in some skulls of *unicornis* as in some skulls of *sondaicus*. It is true, however, that the antero-external angle of the teeth is different in the two, that of *sondaicus* being typically noticeably bilobate, whereas in *unicornis* it is not so. But I am not convinced with the truth of his affirmation that this difference is due to the loss of the parastyle in *unicornis* and its development in *sondaicus*. The parastyle, I understand, is a product of the cingulum; but the cingulum, forming a manifest shelf on the anterior surface of the teeth, becomes gradually attenuated externally and disappears before reaching the antero-external angle in both species. It appears to me that the external angular prominence is homologous in the two, whether it be the parastyle or not, and that the bilobate condition in *sondaicus* is due to the somewhat variable development of a secondary lobe or bulge just behind it and of this there may be indications in *unicornis*.

I am also sceptical about the invariable formation of the "accessory" fossa from the junction of the "crochet" and "crista," although admitting it results from that union in some cases. The "crochet" is an integral part of the metaloph and is usually well developed in existing species of Rhinoceroses; but the "crista" appears to be one of those spurious processes which may be developed as projections into the median fossa from the wall of either the ectoloph or metaloph. At all events the skulls of *unicornis* that I have seen do not supply evidence that it is a constant feature in the cheek-teeth of that species.

Some interesting individual variations in structural details of the teeth and the changes they undergo with wear are illustrated by the skulls in the British Museum.

It is known that the general change with wear is the gradual expansion of the main crests, the ectoloph, protoloph, metaloph and "crochet," with the exposure of more and more of the dentine and the obliteration of the fossæ or pits, which are first of all closed externally and finally represented merely by dark scars on the nearly flat plate of dentine, when the crown is worn down almost to the roots.

In a subadult skull of *Rh. unicornis* from Kuch Behar (3.2.13.1), with pm^1 retained and m^1 just showing in the bone, pm^4 is fully erupted and almost unworn (text-fig. 4, A). The three fossæ, the anterior, median and posterior, are widely open to the exterior and in communication with each other in the central area of the tooth, the metaloph being separated by a narrow space from the hypocone. They might be described as a single fossa subdivided by the metaloph and

* Carter and Hill (Amer. Mus. Novit. 1206, pp. 1–3, 1942) previously claimed that the antero-lateral buttress on the molars is diagnostic of *sondaicus*.

crochet. The antero-external angle is prominent and the ectoloph is represented superficially by a narrow, strongly sinuous ridge with two slightly worn expansions representing respectively the tips of the paracone in front and the metacone behind. Similar slightly worn areas indicate the tips of the protocone and hypocone. The protoloph does not form a complete ridge superficially, the paracone and protocone being separated by the anterior fossa, which is widely open in front. The sharp-edged metaloph, on the contrary, jutting inwards from the metacone, is complete but too deep to be worn. It is shaped like a hammer-head, with a short handle, the anterior part of the head, constituting the "crochet," curving forwards and outwards towards the paracone, but not quite reaching it superficially, so that no accessory fossa is cut off, and the posterior, thicker part of the head curving backwards towards the hypocone but not quite reaching it superficially. A small deep set vertical crest projects inwards from near the middle of the hammer-head to touch the inner face of the protocone.

In this skull pm^3, although more worn than pm^4, is similar to it in all essentials; so also is pm^2, but being still more worn, the accessory fossa is complete. It is also complete in m^1, which is considerably worn, has the anterior fossa closed in front but the posterior fossa is still open behind; from the "crochet" two short ridges jut into the median fossa; the antero-lateral angle is very little produced forwards and the outer enamel-edge of the ectoloph has a sinuous curvature (text-fig. 4, A).

In a much older skull from Assam (Vanderbyl, 1.3.10.1), with m^3 fully erupted and worn, pm^4 (text-fig. 4, B) differs greatly from that of the last; it is so worn that the anterior fossa is obliterated, the posterior fossa is reduced and cut off from the exterior to form an isolated pit and the median fossa is also reduced, although still in communication with the exterior. Its inner portion is cut off as an accessory fossa by the fusion of the "crochet" with the widely worn ectoloph. The antero-lateral angle of the tooth is not so prominent as in the skull from Kuch Behar and the external enamel-edge of the ectoloph is more sinuous in its anterior half but less so in its posterior half. This tooth is remarkable for the development of small supernumerary crests of which one projects from the ectoloph into the accessory fossa and four, one very small, from the "crochet" into the median fossa, three of them just reaching the inner wall of the protoloph.

In this skull pm^4 slightly overlaps m^1 (text-fig. 4, B), which is more worn than m^1 of the Kuch Behar skull; the median fossa having a very narrow outlet to the exterior owing to the wide expansion of the worn areas of the protocone and hypocone and the posterior fossa is almost cut off from the exterior. A single ridge juts into the median fossa from the "crochet." The antero-lateral angle is less prominent than in the Kuch Behar skull and the external enamel-edge of the ectoloph is not so sinuous in its posterior half.

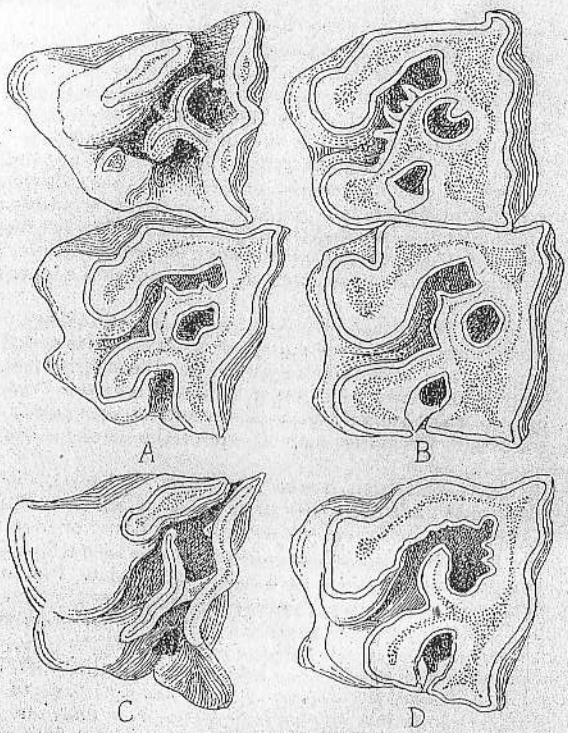
A skull from the Nepal Tarai (The Prince of Wales) resembles the skull from Kuch Behar in retaining pm^1, in having m^3 just appearing in the bone, in the anterior fossa opening in front on pm^2 and pm^3, obliterated in m^1 but still just open in m^2 (text-fig. 4, C), in the completeness of the "accessory" pit in pm^2 and m^1 and its incompleteness in pm^3 and m^2; but, being a little younger, it differs in retaining pm^4 of the milk set, which is worn down to the cingulum so that the anterior fossa is obliterated, the median fossa is shut off from the exterior by contact, but not fusion, of the protoloph with the metaloph, by the closure behind of the posterior fossa and the completion of the accessory fossa.

A greatly worn m^2 of an unlocalised skull of *Rh. unicornis* (722 *d*) with the "crista" short and duplicated, no accessory fossa and the posterior fossa closed behind is shown in text-fig 4, D.

The openness of the anterior fossa in front in the teeth above referred to in the two skulls of *Rh. unicornis* from Kuch Behar and the Nepal Tarai is of interest in comparison with its closure in almost all the skulls of *Rh. sondaicus*.

A youngish skull of *Rh. sondaicus*, the type of *nasalis* (723 *c*), said to be from

Text-figure 4.



A. Newly erupted slightly worn pm^4 and considerably worn m^1 of *Rh. unicornis* from Kuch Behar showing in pm^4 the three fossæ in communication and widely open to the exterior, the enamel- edge of the ectoloph and the summits of the protocone and hypocone slightly worn, but the hammer-shaped metaloph and "crochet" with the enamel- edge unworn; also in m^1 the anterior fossa closed in front and the "accessory" fossa cut off by the junction of the "crochet" with the ectoloph.

B. The same much worn teeth in an older skull from Assam generally resembling m^1 of A, but pm^4 has several supplementary crests jutting into the median fossa and one into the "accessory" fossa and the posterior fossa is isolated.

C. Slightly worn m^2 of a skull from the Nepal Tarai, a little more worn than pm^4 in A, showing the anterior fossa nearly closed in front and the median cut off from the posterior fossa behind, also the very differently shaped metaloph and "crochet" with the enamel-edge unworn. In both the summit of the "crista" is a tubercle-like, deep set process projecting into the anterior fossa from the anterior half of the ectoloph.

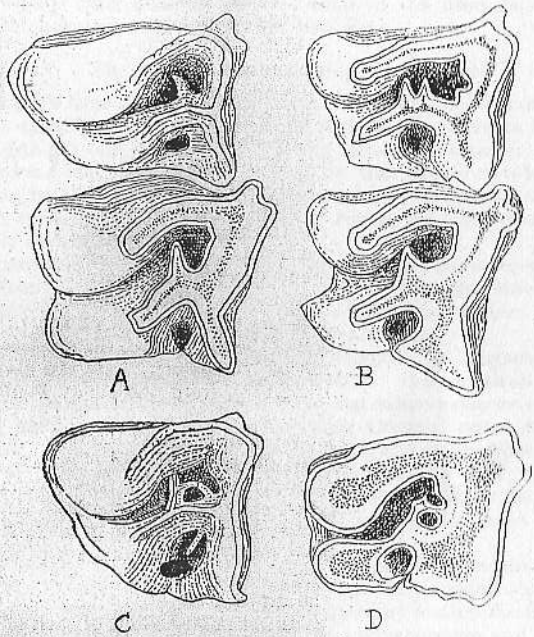
D. Greatly worn m^2 of unlocalised skull (722 *d*), with short duplicated "crista," no "accessory" fossa and posterior fossa closed behind.

In these figures, which are $\frac{2}{3}$ nat. size, the shaded shelf in front represents the cingulum, the dotted area the dark band of dentine in the middle of the worn crests and the external shaded areas the outer surface of the teeth.

Borneo, is a little younger than the skull of *Rh. unicornis* from Kuch Behar. Its pm^4, although almost fully erupted, is quite unworn and differs noticeably from the same tooth in the Kuch Behar skull in several respects. There is no

trace of the anterior fossa opening to the exterior in front, the antero-lateral angle of the tooth is bilobate, the unworn enamel-edge of the ectoloph is much straighter and in front forms a continuous curve with the enamel-edge of the protoloph, there being no visible separation between the paracone and the protocone. The metaloph is similarly confluent with the hypocone, it is not

Text-figure 5.



A. Newly erupted and unworn pm^4 and considerably worn m^1 of a skull of *Rh. sondaicus*, the type of *nasalis*, supposed to be from Borneo, showing in pm^4 especially the continuity of the enamel-edges of the ectoloph and protoloph, the closure of the anterior fossa in front and the deep-set simple "crochet." Also the bilobed antero-lateral angle in both teeth and the absence of the accessory fossa in m^1.

B. The same two considerably worn teeth in a much older skull from the Sunderbans, showing especially the double crochet in pm^4 and the closed posterior fossa in m^1.

C. The just erupting, unworn but still imbedded pm^4 of a youngish skull from S. Tenasserim, showing its general resemblance to the same tooth in A, except that the "crochet" is bifid, its outer branch almost touching a small crest from the metaloph to form an "accessory" fossa, and the widely open posterior fossa is subdivided by a thin crest.

D. The greatly worn pm^4 of an old skull from the Malay Peninsula showing the completed "accessory" fossa, drawn a little too large, the almost complete closure of the median fossa and the complete closure of the posterior fossa.

hammer-headed in shape and carries a thin enamel-edge, rising from the ectoloph, but this is not continued on to the "crochet," which is much smaller, more deeply set and does not curve outwards towards the inner wall of the ectoloph (text-fig. 5, A, upper tooth). In the same skull m^1 resembles pm^4 in its bilobate antero-lateral angle but is considerably worn, although not to the same extent as m^1 in the skull of *Rh. unicornis* from Kuch Behar, from which, apart from the

lesser width of the worn areas, it principally differs in having a straight angular "crochet" jutting forwards into the median fossa without curving outwards to join the ectoloph and thus cut off an "accessory" fossa (text-fig. 5, A, lower tooth).

In a much older skull of *Rh. sondaicus* from the Sanderbans (76.3.30.1), with m^3 in use and a little worn, pm^4 is not so distinctly bilobate as in the two teeth of the skull from Borneo, the antero-lateral angle being more like that of several skulls of *Rh. unicornis*. The tooth is of interest from the duplication of the "crochet," which consists of a pair of subequal angular crests jutting straight forwards into the median fossa (text-fig. 5, B). It is also double in pm^3. As Flower pointed out, this is a not uncommon feature in the premolars of *Rh. sondaicus*, in which this branch of the metaloph is very variable. It may be absent as in pm^2 of the Bornean skull and in an old skull from Cochin China (81.6.30.9); its apex may be bifid or simple; quite commonly it is double, sometimes on pm^2, pm^3 and pm^4; and on pm^3 and pm^4 it may contribute to the formation of an "accessory" pit like that usually present in the teeth of *Rh. unicornis*. For instance, in a young skull from S. Tenasserim (21.5.15.1) it is double in the unworn pm^3 and the outer branch is attached to the inner wall of the ectoloph cutting off a very distinct accessory pit. A similar but smaller pit is present in pm^4 of the same skull (text-fig. 5, C) and in this tooth the "crochet" is bifid at the tip, its outer branch turning outwards almost to meet a little crest rising near the base of the anterior wall of the metaloph. A peculiarity of this tooth is the division of the fore part of the posterior fossa by a long, thin vertical crest. Remnants of "accessory" pits are also visible on pm^3 and pm^4 of an old skull (79.11.21.178), from the Malay Peninsula (text-fig. 5, D).

The skulls of this species that I have seen bear out Flower's statement that the "accessory" pits may be present on pm^3 and pm^4 of *sondaicus*, but not on m^3 and m^4 where they frequently occur in *unicornis*. That is one apparently constant difference between the cheek-teeth of the two species. Another is the more pronounced bilobation of the antero-external angle in *sondaicus*; but the most striking, not previously, I believe, taken into account, is the absence in the teeth of *sondaicus* of the open anterior fossa separating the paracone and protocone and its presence in most of the unworn teeth of *unicornis*. This differentiating character at all events is manifest in two skulls of each of the species, namely the skulls of *sondaicus* from Borneo and S. Tenasserim, in which the unworn premolars have no anterior pit opening in front, and the skulls of *unicornis* from Kuch Behar and the Nepal Tarai in which the premolars even when worn to a considerable extent have the anterior fossa opening in front.

A moderately good series of skulls of *Didermocerus sumatrensis* confirms Flower's statement that in a general way the cheek-teeth are very like those of *Rh. sondaicus*. His claim that the posterior fossa is deeper and therefore disappears later with wear may be true; but the differences observed in the series of skulls I have examined are as follows:—(1) The teeth are smaller, the length of the five varying from a little over 7 inches in youngish skulls to a little under 6 inches in old skulls with the teeth much worn, the average length in seven skulls being slightly over 6·6 inches; (2) the cingulum in front is narrower at least on the anterior teeth; (3) the "crochet" is less well developed, at least on the premolars, and never contributes to the formation of a complete "accessory" fossa; (4) the anterior fossa is widely open in front on pm^2 even when noticeably worn and on pm^3 when a little worn.

Some individual variations may be noted. In a young-adult skull from Mogok, Upper Burma (31.5.28.1), with pm^1 shed and m^3 erupted but unworn, pm^2, which is noticeably worn, has the anterior fossa widely open in front and the crochet hardly developed; in pm^3 the anterior pit is closed in front but the crochet is very low; and on the right side, but not on the left, a definite "crista" projects from the ectoloph into the median fossa but does not reach

the angular excrescence representing the crochet; in pm^4, which is a little worn, the protoloph and ectoloph touch without fusion at the antero-external angle.

A younger skull, probably from Sumatra (Raffles, 1411 *b*), with pm^4 of the milk set retained and much worn and m^3 not erupted, pm^2 resembles that of the skull from Mogok and on pm^4 there is a small "crista" which nearly reaches the thick crochet. In a skull from British North Borneo (1.8.15.1), slightly younger than the last, the anterior fossa is widely open in front on pm^2 and pm^3.

In the widely open anterior fossa of some of the premolars this species resembles *Rh. unicornis* rather than *Rh. sondaicus*.

The classification of existing Rhinoceroses

Since Flower's time it seems to have been the general opinion of systematists that the five existing species of Asiatic and African Rhinoceroses fall into three equivalent groups, one represented by the genus *Rhinoceros*, with its two species *unicornis* and *sondaicus*, a second by the Asiatic two-horned genus, *Didermocerus*, better known as *Ceratorhinus* or *Dicerorhinus*, and a third by the two African species, *Diceros bicornis* and *D. simus*, the latter sometimes being given generic status as *Ceratotherium*.

In comparatively recent years these three groups have been granted the rank of subfamilies. Abel, for example, in Weber's *Die Säugethiere*, 2, pp. 670–671, 1928, adopted for them the names *Rhinocerinæ*, *Dicerorhininæ*, which should have been rendered *Dicerorhininæ*, and *Dicerinæ*.

But this classification is, in my opinion, illogical in the sense that it does not express satisfactorily the facts to be dealt with. It attaches an unreasonable importance to the characters of *Didermocerus* and entirely obscures its obviously much closer kinship with *Rhinoceros*, the other Oriental genus, than with the African forms. It admittedly resembles the latter and differs from the former in possessing two horns and the open subaural channel in the skull; but, whatever may be said of the horns, the openness of the channel is due to the common inheritance of a primitive feature and, as such, is in itself at most an indication of remote affinity.

In the following analytical classification, which expresses my views of the affinities of the existing species of Rhinoceroses, the principal characters mentioned have long been known. The most important feature distinguishing the two subfamilies admitted is emphatically the tusk-armature and elongation of the jaws in front of the cheek-teeth in the Asiatic genera and the suppression of the tusks and abbreviation of the jaws in the African genera, this last being a highly specialized character not likely to have been independently acquired in the two.

a. The anterior part of the jaws elongated and provided with two pairs of large, functional teeth forming an offensive tusk-armature; the anterior end of the nasals narrowed and comparatively pointed. Skin with at least one fold, the scapular, passing over the back; the posterior horn, when present, more remote from the front horn, which is not used as a weapon of attack ..... Subfamily RHINOCERINÆ.

b. Channel beneath the auditory orifice in the skull closed at an early age; the occipital plane with pronounced forward slope, so that the occipitonasal length is much shorter then the condylonasal length; the orbitonasal length shorter than the orbitoaural length. A single nasal horn; the pelvic fold of skin passing over the back .... *Rhinoceros unicornis*, [*sondaicus*.

b'. Channel beneath the auditory orifice in the skull open, but very narrow inferiorly in some old skulls; the occipital plane subvertical, so that the occipitonasal and condylonasal lengths are subequal; the orbitonasal length surpassing the orbitoaural length. Two horns, the posterior on the frontals; the pelvic fold of skin not reaching the spine ..... *Didermocerus sumatrensis*.

a'. The anterior part of the jaws abbreviated, without tusk-armature, the front teeth, when present, small and functionless; the anterior end of the nasals bluntly rounded or truncated. Skin with no folds passing over the back; two horns typically set close together at the base, at least the anterior used for attack	Subfamily DICERINÆ.
c. Skull short, with the anterior end of the mandible compressed and spout-like. The upper lip pointed, prehensile, adapted for browsing; teeth simpler	*Diceros bicornis*.
c'. Skull longer, with the anterior end of the mandible expanded and spatulate. Upper lip with a straight edge adapted, like the long head, for grazing; teeth more complex	[*Ceratotherium*] *Cœlodonta* (or *simus*).

With the substitution of *Didermocerus* for *Dicerorhinus*. the generic names here used are the same as those adopted by Thomas (Proc. Zool. Soc. Lond. 1901, pp. 157–158). He did not, however, admit more than one African genus, *Diceros*, and in this he was followed by Lydekker (Cat. Ung. Brit. Mus. **5**, p. 51, 1916). But the differences between the two species in cranial and dental characters, of which one or two only are briefly referred to above, are quite sufficient to justify their generic separation. Of the two, *Diceros* is the more primitive and comes nearer the Asiatic genus *Didermocerus*.