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Article XXI.— ABSENCE OF THE POLLEX IN PERISSODACTYLA.

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So far as the writer can discover there is no valid evidence for the presence of a pollex in any perissodactyl, living or extinct.

It is quite true that the pollex has been repeatedly recorded as present in descriptions of extinct Perissodactyla. In only one instance has the bone itself been identified and in this case the identification is certainly incorrect; in all others the conclusion rests upon the presence of a facet upon the inner side of the second metacarpal, supposed to be for the first metacarpal, but not so in fact.

Imprimis, there is no trace of pollex in any modern perissodactyl. The tapir, which has four fully developed digits on the manus, shows no trace of the first digit. The trapezium is present in most Perissodactyla; even in the horse a vestige of it is seen in some individuals.[1]

Among the Artiodactyla the pollex is present in *Ancodon, Oreodon, Agriochœrus* and probably in some other primitive extinct forms. It is well developed in the subungulate orders, in most unguiculate orders and in nearly all Primates, most edentates, etc.

In order to appreciate the evidence properly, a few words must be prefaced as to the relations of the trapezium, and pollex when present, to the remainder of the carpus. The primitive relations for the placental mammals are presumably shown in the Eocene and Paleocene Mammalia; the relations in all later mammals are specializations from these.

In the creodonts (excepting the later Mesonychidæ) the pollex is well developed. The trapezoid is small and rests upon mc. II. The trapezium is considerably larger, with a proximal facet for the scaphoid and a lateral facet which abuts against the trapezoid and the upper end of the mc. II; distally the trapezium rests upon mc. I which is more or less divergent and does not touch mc. II.

In *Phenacodus* the first digit is less divergent and mc. I is in contact with mc. II, although no distinct facet is developed. In *Ectoconus* and *Pantolambda,* commencing the subungulate series, the first digit is somewhat divergent, and mc. I articulates with the trapezium only, having no facet for mc. II; nor does such a facet develop in any subungulate manus so far as I have examined.

[1] Chubb, S. H., 1912, Bull. Amer. Mus. Nat. Hist., Vol. XXXI, p. 113.

In the earliest primates the pollex is larger and strongly divergent, largely opposable although not so fully as in the higher primates. In the earliest rodents (*Paramys*) the pollex is very short and small, mc. I has no facet for mc. II, but in some of the later rodents the reduction of the trapezium brings the two metacarpals into closer relation and a definite facet develops.

The same holds true in many modern Carnivora, the trapezium standing as a wedge separating the two metacarpals, but where, as in bears, the pollex has lost its divergence it develops a definite facet for mc. II.

In *Didelphis* and other primitive marsupials the manus has a strongly divergent, partly opposable pollex, and this may represent an earlier stage, from which the divergent or slightly opposable condition prevalent in primitive placentals is derived. Proof of this, however, is not at hand; all that we can properly conclude from the evidence, of which a few salient points are mentioned above, is that the primitive manus among the placental mammals had a partly divergent pollex, with large trapezium overlapping the head of mc. II and completely separating it from mc. I.

In *Ancodon, Oreodon* and *Agriochœrus,* which, although not the earliest Artiodactyla are the most primitive known genera with respect to the reduction of lateral digits, the pollex is small, and somewhat divergent, the trapezium overlaps the head of mc. II, and completely separates it from mc. I which is articulated only with the trapezium (except in *Ancodon,* fide Scott).

Among extinct Perissodactyla, we may consider first the Equidæ.

Marsh in 1876 reported the presence of the pollex in *Eohippus.* The statement was based upon fragments of the manus and pes in *E. pernix* from Black Buttes, Wyoming. Upon examination of Marsh's specimens by Mr. Granger and myself, permitted through the courtesy of Professors Schuchert and Lull, it was evident that Marsh had made this statement because of the presence, upon a fragment which he had identified and marked as the head of mc. II, of a lateral facet for another metacarpal. The bone is, however, the fourth metacarpal of the opposite side if I recall correctly; at all events it certainly is not mc. II. Consequently there is no evidence here. In the finely preserved manus of *Orohippus* in the Yale Museum there is certainly no first metacarpal. In the manus of *Eohippus* ("*Protorohippus*") *venticolus* in the Cope Collection, it appears to be absent. In other specimens of *Eohippus* collected by Mr. Granger the complete absence of the pollex is clearly demonstrated. It is certainly absent in *Mesohippus* and *Miohippus.* In early studies by Gidley and myself on the Miocene genera of Equidæ (1898–1901) we believed that we had found evidence for the existence of a small vestigial mc. I in *Merychippus* ("*Proto-*

hippus") from the Miocene of Colorado, again in the form of a lateral facet on mc. II; the trapezium in this genus is a small nodule with two facets which joined at a right angle, one of them conforming to a corresponding facet on the trapezoid, the other supposed to be for the head of mc. I. This evidence, fortunately, remained unpublished.

In 1903 Mr. Gidley in articulating the very perfect skeleton of *Hipparion whitneyi* identified as mc. I a small nodular bone very similar to the trapezium. The demonstration appeared therefore to be complete that in this far advanced equid a vestige of mc. I was retained, although it was absent in the Oligocene and Eocene Equidæ!

In the course of studies upon numerous specimens of the manus of Miocene Equidæ belonging to many species I observed several in which the trapezium was present but could never find any mc. I. It appeared moreover that the trapezium if accurately fitted to the carpus had been placed upside down by Gidley and myself; that its two facets were for the trapezoid and scaphoid, and that there was none for a mc. I. Nevertheless there remained the little facet on mc. II unaccounted for; it might well be for a vestigial mc. I that had lost its connection with the trapezium — although as might be inferred from the conditions among other placentals, the ordinary course of reduction does not in any instance follow that procedure.

Upon examining the supposed mc. I in *Hipparion whitneyi* it appeared moreover that it was not merely similar to the trapezium but identical; it was in fact the trapezium of the opposite manus.

Study of the flexed position of the carpal bones solved this puzzle. It appears that in flexure of the wrist the scaphoid pushes the trapezium downward, displacing it from its position upon the trapezoid and forcing it down upon the head of mc. II, where it fits well upon the small lateral facet and against the scaphoid above. The accuracy of these articulations of the trapezium in the extended and flexed manus was unmistakable. No one with much practical experience in the articulating of skeletons fossil or recent would, I believe, have any doubt whatever that this is the correct solution. The trapezium therefore in these Equidæ occupies two positions and has two articular connections, one with the trapezoid in extension, the other with mc. II in flexion, the former also serving the scaphoid in flexion. This facet on mc. II for the trapezoid is not present in the Oligocene and Eocene horses because on account of the difference in proportions of the carpal bones the trapezium is not pushed down by the scaphoid in flexure to a contact with mc. II beyond the small proximal facet that it has in extension. It is not present in *Equus* because on account of the extreme reduction of the trapezium it does not reach the metacarpal at all. It is not present in rhinoceroses because the carpus is not capable of the sharp flexure necessary to bring about this relation.

It appears therefore that at a certain stage in the evolution of the manus in the Equidæ the relations of the disappearing trapezium to the progressively more broad and quadrate scaphoid became such that it occupied two distinct positions on the inner side of the manus, one internal to the trapezoid the other internal to the head of mc. II, and was provided with a distinct facet on each bone.

In other Perissodactyla the following are the principal data:

In *Hyrachyus* there is no trace of mc. I. The trapezium is in form characteristically like the trapezium of the Equidæ, only less reduced; it has facets for scaphoid and trapezoid in extension and in flexion is pushed down over the head of the second metacarpal where it occupies a distinct although small facet. In *Trigonias, Cœnopus, Diceratherium, Aphelops* and *Teleoceras* the form is somewhat similar, but the trapezium relatively smaller, and has no facet on mc. II.

In the modern tapir the trapezium is small, but it takes more part in the supporting of the limb than in any other perissodactyl. It rests partly upon the proximal end of the second metacarpal, aiding the trapezoid in the support of the scaphoid, and is not excluded from the supporting series of carpals as in the preceding genera. It is larger in *Protapirus*, but its form and relations are much the same. Whether this is secondary, after the manner of adaptive reduction as observed in other carpal bones, or is its primary relation, cannot be determined from the known fossils. There is no trace of mc. I and no lateral facet on mc. II for the trapezium in flexed position. It would seem that in the tapirs, as in the rhinoceroses, the carpus is incapable of the sharp flexion of the later Equidæ, and the trapezium is not pushed down far enough to press against mc. II below its head.

In *Lophiodon* Deperet has announced the presence of a pollex, again upon the evidence of a small lateral facet upon mc. II, the bone itself not being known. It is probable that the conditions in *Lophiodon* were like those in *Hyrachyus*, a rather near relative, in which this facet is present but is for the reception of the trapezium in flexion, and not for any vestige of mc. I which is certainly not present. There is clearly a lateral facet on mc. II in *Colodon*, but the character of the trapezium is unknown.

The same conclusion, based upon the same evidence has been published in regard to *Schizotherium*, an early Oligocene chalicothere. In *Moropus* there is certainly no trace left of the first metacarpal. Nor is there any indication of a lateral facet on mc. II of the much more primitive *Eomoropus* of the Middle Eocene. Holland has based a subfamily distinction, between *Moropus* on one hand and *Schizotherium* and *Eomoropus* on the other, upon the supposed presence of a vestigial pollex in the two latter genera. The arrangement would be highly artificial even if the supposition were correct,

but the evidence for the presence of mc. I in *Schizotherium* does not appear to be valid, and there is absolutely no reason to suppose that it was present in *Eomoropus*.

There is no pollex in any of the Titanotheriidæ, so Dr. Gregory assures me.

In sum, after examining all the evidence for the presence of a pollex in Perissodactyla it appears reasonably certain that it had wholly disappeared from the order at the time when we first meet it, in the Lower Eocene. The unknown Cretaceous ancestors of the order doubtless possessed a pollex, but whether they were perissodactyls in any definable sense may be doubted. More probably they would fall within the order Condylarthra. At all events, the absence of pollex is diagnostic of all known perissodactyls, living or extinct.

Finally it is necessary to call attention to two points of general application among fossil mammals.

1. The absence of a lateral (internal) facet on mc. II does not indicate absence of the pollex, since mc. I when present is more often divergent and not in contact with mc. II.

2. The presence of a lateral (internal) facet on mc. II does not prove the presence of the pollex, since it is frequently present in forms that have no mc. I, and serves for the accommodation of the trapezium in extreme flexure of the carpus.

Failure to appreciate these two points has led a number of able palæontologists to unwarranted conclusions with regard to presence or absence of the pollex, and to equally unwarranted deductions regarding the phyletic relations of various mammalian genera and species.