TEETH

The many features significant in equid teeth require a special treatment to make the best use of their discriminating value. Some of them can be and should be measured, others will be counted, described, or their presence or absence merely stated. A detailed nomenclature has already been developed for the various characters of different kind of teeth. In the present paper, an effort has been made to standardize the nomenclature, to define and illustrate several patterns of protocones, double knots, and incisor morphologies in *Equus* and in *Hipparion*, and to explain how teeth should be measured, plications counted, and stages of wear taken in account.

In this paper we will consider only the permanent teeth because milk teeth are usually rarer, more difficult to observe, and less reliable for interspecific discrimination. The observations and measurements recommended for permanent teeth can however be used for milk teeth also.

When dealing with isolated teeth, the first step is to try to distinguish the different categories. No difficulties arise in separating P2 and M3 (both upper and lower). But the distinction between P3 and P4, or M1 and M2, or even between premolars (P3 and P4) and molars (M1 and M2) may prove very difficult. Not a single character of the many proposed by various authors (especially Cooke, 1950 and Gromova, 1952) is absolutely reliable when used alone, but when several of them are combined, in most cases a distinction is possible; if distinction between P3 and P4, and between M1 and M2 seem too uncertain, it should at least be tried to separate the sample in four categories: P2, P3 and P4, M1 and M2, M3. Special paragraphs deal with this question.

Since Gidley (1901) it is well known that the shape and size of equid teeth vary greaty with wear. Wear related variations have been studied in great detail by Petit (1939) and Howe (1970) in *Equus*, and by Sondaar (1961) in *Hipparion*. In order to neutralize these variations, different ways of measuring equid teeth have been proposed. Some authors recommend to distinguish several classes of wear and to submit the data on each class to a separate study; Gromova recommended to distinguish four stages of wear in *Hipparion* teeth; she was followed by Alberdi (1972, 1974). Musil (1969) proposed to distinguish three stages in *Equus*. In any case, the number of teeth in each wear-stage sample is smaller than the total number. To avoid such a reduction of the sample, other authors proposed to measure every tooth at the same height (i.e. at the same distance from the roots); Sondaar (1961) measured the teeth at 1 cm from the roots, Forstén (1968) exactly at the base of the crown, Prat (1968) and Hooijer (1975) at 2 cm from the roots. Eisenmann (1980) objected that the measurements taken too close to the roots are not really reliable because they include the cement (which is by itself very variable in thickness) and because the tooth is no longer in "normal" function; she pointed also that it is quite impossible to measure in this way teeth that are *not* isolated which is a pity since they are the only ones for which the place inside the row is absolutely certain. For *Hipparion* the New York Conference decided to recommend both occlusal (without the cement) and "1 cm from the roots" measurements on isolated teeth; occlusal measurements should be studied by stages of wear (four stages must be recognized). For *Equus*, are recommended occlusal measurements (without the cement) on not too worn or not too unworn teeth, and a set of measurements at the supposed mid-height of the crown, when possible.

Points specific to upper or lower cheeck teeth will be discussed in the corresponding chapters.

UPPER CHEEK TEETH

How to distinguish isolated premolars and molars?

Leaving aside the P^2 and the M^3, this is by no means an easy task, either in *Equus* or in *Hipparion*. A lot of characters have been proposed in the litterature. None is absolutely reliable. The best way seems to use several characters at the same time.

In the same series (and usually in the same species) molars are smaller than premolars. In the same series, molars (specially the M^1) are always more worn than premolars; in result, their occlusal shape is already quadrate when that of the premolars is still rectangular (length larger than width); later on, the occlusal shape of worn molars becomes rectangular in the other direction (width larger than length), while premolars are still quadrate. In molars, specially in M^2, the posterior width is smaller than the anterior width. Usually, the entire upper cheek row is mesio-distally convex. In result, premolars, specially P^3, have their occlusal surface tilted in the front direction; molars, specially M^2, have their occlusal surfaces tilted backwards. In premolars, the vestibulo-anterior horn of the postfossette tends to be more developed in the vestibular direction than the vestibulo-posterior horn of the prefossette; in molars, both horns reach roughly the same level.

By using the sum of these characters, one may hope to arrange at least part of a good sample of isolated teeth according to their exact position in the row and to study separately the 6 kinds of upper cheek teeth. For the rest of the sample, it may happen that only a distinction in 4 categories (P^2, P^3 or P^4, M^1 or M^2, M^3) is possible or even that the distinction between P^4 and M^1 is difficult. These problems usually arise for very worn teeth which are not very useful anyway; or for very unworn teeth in which case the best solution is to have them cut at mid-height, if it is possible.

Characters that can be measured

—Tooth height. The measurement is to be taken from the uppermost margin of the anterior root to the anterostyle in P^2 (fig. 5A), and to the parastyle in other upper cheek teeth (fig. 6B).

When possible, the maximum height of each kind of tooth (P^2, P^3, P^4, etc.) is estimated. The maximum is divided by 4 in order to distinguish 4 stages of wear for each kind of tooth. For example, if the maximum height for P^4 is 60 mm, all the P^4 the height of which is comprised between 60 and 45 mm belong to the first stage of wear, those measuring 30 to 45 mm belong to the second stage, those measuring 15 to 30 mm to the third, and those between 0 and 15 mm to the fourth. When measuring a complete tooth row, the determination of the stage of wear will usually be approximative.

—Length and breadth of the tooth, protocone length (and protocone breadth in *Hipparion*). These measurements are taken on the occlusal surface, excluding the cement (fig. 6C) and corrected separately for teeth belonging to different stages of wear.

When dealing with isolated cheeck teeth of *Hipparion*, additional measures are taken at 1 cm from the roots (they usually have to include the cement, and the measure of breadth of the protocone is naturally impossible). For *Equus*, this set of measures is replaced by one taken at the supposed mid-height. In the case of *Equus* M^3, the measurements at mid-height seem much less variable then the occlusal ones. It is recommended not to include very worn or very unworn cheek teeth in the statistics (which amounts more or less to use only the teeth belonging to the two intermediate stages of wear).

Parameters that have to be calculated

—Hypsodonty indices (HI). Very important to estimate the degree of adaptation to a rough diet, the hypsodonty index should only be calculated for unworn or very little worn teeth, i.e. using the maximal height of the crown. It must be calculated separately for each kind of tooth (P^2, P^3, P^4, etc.).

In *Hipparion*, the HI = tooth length at 1 cm above the roots × 100 / maximal height. In *Equus*, the HI = tooth length at mid-height × 100 / maximal height. So that, the more hypsodont the tooth, the smaller the HI.

—Protocone indices (PI). Important for interspecific discriminations, these indices should also be calculated separately for each kind of tooth and only for teeth normally worn. PI = occlusal length of the protocone × 100 / occlusal length of the tooth. In unworn teeth, if the cement is not too thick,

it may be possible to use the mid-height lengths for *Equus*, and the "1 cm above the roots" lengths in *Hipparion*.

Characters that have to be counted

—Enamel plications. Are counted as plications the ones situated on the anterior and posterior walls of the pre- and postfossette, and the pli(s) caballin(s); other grooves or constrictions as in the hypoconal area or on the para- and mesostyle are not counted but have to be observed (see below).

The counting may be difficult for two reasons. First, one may not know if one has to count the invaginations *inside* or *outside* the fossette (on fig. 5B, there would be 2 plis protoloph in the first case, and only one in the second). Secondly, it may be difficult to decide if one is seeing a "true plication" or just a mere "wrinkle" of the enamel. It has been decided:

1. that the plications are to be considered as invaginations *inside* the fossette and evaginations in the direction of the protocone (on the figure 5B, there are 2 plis protoloph but only one pli caballin). Note that the pli protoconule was previously defined as an evagination, i.e. in a direction opposite to that of the other plications;

2. that in a "true" plication, the length is superior to the enamel thickness (suggestion of Dr Staesche). If not, the "wrinkling" of the enamel should be merely noted.

When a plication is very broad and seems to result from the fusion of two plis, it may be counted for two (for example, the first invagination posterior to the pli protoconule in fig. 5B). When a plication is bifurcated, each branch is counted as one plication. For the tooth illustrated in fig. 5B, the plication number may be conveniently noted in the following way: plis fossette / pli(s) caballin(s) = 2-8-4-1 / 1, which means that there are 2 plis on the anterior wall of the prefossette, 8 on its posterior wall, 4 on the anterior wall of the postfossette, 1 on its posterior wall, and 1 pli caballin.

When using the terms of plis prefossette or plis postfossette, one should precise if one is speaking "sensu stricto" or including in the former the plis protoloph and protoconule, and in the latter, the plis hypostyle. When giving the total number of plications by tooth, one should precise if the plis caballins are or not included.

Characters that have to be described

—Shape of the protocone (see below and fig. 5C for *Hipparion*, 6A for *Equus*).

—Characters of the fossettes. If the fossettes communicate one with the other, of if they are opened at one or other wall, these characters may be included in the plication formula:

- if the pre- and postfossettes were united in the tooth figured in 5A, these features could be noted by inserting an "equal sign" (=) between the numbers of plications on the posterior wall of the prefossette and that on the anterior wall of the postfossette; the formula would appear as follows: 2-8 = 4-1/1;
- if, moreover, the posterior wall of the postfossette were open, a "o" could be added after the plication number for the posterior wall of the postfossette: 2-8 = 4-1o/1.

—Hypoconal area. The presence of a constriction (as in P^4 of fig. 5A) or an islet (as in M^3 of fig. 5A) should be noted.

—Development of para- and mesostyles. Their widths and the presence or absence of grooves on them should be noted.

—The occurrence of wolf teeth (dP^1) should also be noted.

This list of observations is not limitative; any observations believed to be of some interest should naturally be added.

FIGURE 5: UPPER CHEEK TEETH OF HIPPARION

A: Occlusal view of a left tooth row;

B: Occlusal view of an upper left tooth;

C: Occlusal views of selected shapes of protocones to be used as references in the descriptions.

Figures 5A and 5B illustrate the nomenclature of the different features appearing on the occlusal surfaces. The nomenclature is the same for *Hipparion* and for *Equus*.

In *Hipparion*, protocones may be described by reference to several main shapes (fig. 5C). The protocone may be more or less round (1, 2, 3 and 4), and its lingual border may be convex (1, 2, 3 and 4), flat (5), or concave (6). In addition, the protocone (whatever its shape) may be united to the protoconule (7) and/or bear a "spur" (8). Shapes vary with the degree of wear.

The enamel plications should be counted separately:

—on the anterior wall of the prefossette (they are sometimes named "plis protoloph";

—on the posterior wall of the prefossette (it may be possible to distinguish the "pli protoconule" from the plis "prefossette");

—on the anterior wall of the postfossette (sometimes named "plis postfossette");

—on the posterior wall of the postfossette (sometimes named "plis hypostyle");

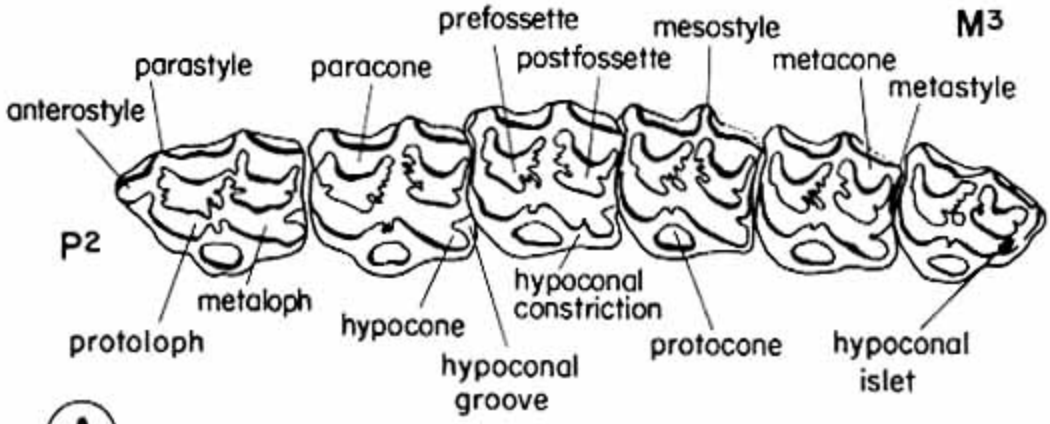
—in the lingual groove, in front of the protocone: "plis caballins".

For the way of counting plications and writing the plication formula, see above.

In the hypoconal area, the presence of a constriction (P^4 of fig. 5A) or of an islet (M^3 of fig. 5A) should be noted.

Other features to be noted are the development of the para- and mesostyle (width, presence of a groove) and the occurrence of a wolf tooth (dP^1).

Specific determinations based on lacteal teeth should be avoided because their morphology is usually similar in different species (baring size differences parallel to the size differences of the permanent teeth).


prefossette
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islet
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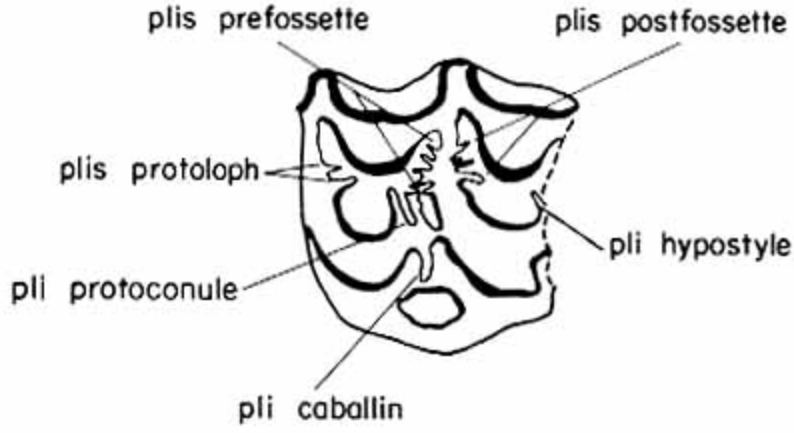
A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pli hypostyle
pli protoconule
pli caballin

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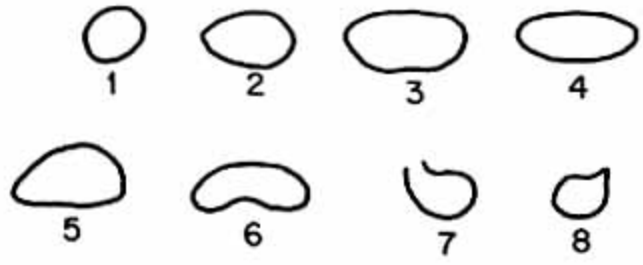
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FIGURE 6: UPPER CHEEK TEETH OF EQUUS

A: Occlusal views of selected (left) protocone shapes to be used as references in the descriptions;
B: Vestibular view of an upper left cheek tooth; 1 = tooth height;
C: Occlusal view of an upper left cheek tooth; 2 = occlusal length; 3 = occlusal length of the protocone; 4 = occlusal breadth.

Figure 6A illustrates a sample of protoconal shapes that were observed in *Equus*; as for *Hipparion*, the shape of an *Equus* protocone may be described by reference to one of these. Plications are to be counted in the same way as in *Hipparion*; presence of enamel islets and openings or communications of the fossettes should be noted; and development and shape of para- and mesostyle observed.

Figures 6B and 6C show how to measure upper cheek teeth of *Equus* and *Hipparion*.

Let us repeat that most of qualitative characters and dimensions of the teeth depend on their state of wear. When dealing with a sample of equid cheek teeth, one should measure the height of several unworn P^3 or P^4, and M^1 or M^2, and M^3 at the parastyle (fig. 6B, measure 1), or at the anterostyle for the P^2. These heights should be divided by 4, to distinguish 4 stages of wear. For example, if an unworn M^1 is 60 mm high, all the M^1 and M^2 should be classified in 4 groups:

1. 60 to 45 mm high (unworn or little worn teeth)
2. 45 to 30 mm high
3. 30 to 15 mm high
4. 15 to 0 mm high (very worn teeth).

In practice, only the teeth belonging in the stages 2 and 3 (and specially 2) give reliable occlusal observations and measurements. Anyway, all observations, measurements and indices should be accompanied by the reference to the stage(s) in which they were made.

Figure 6C shows how to measure occlusal length (2), occlusal length of the protocone (3) and occlusal width (4); the technic is the same with a tooth of *Hipparion*.


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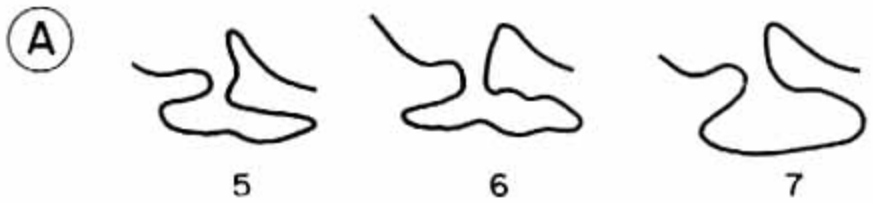
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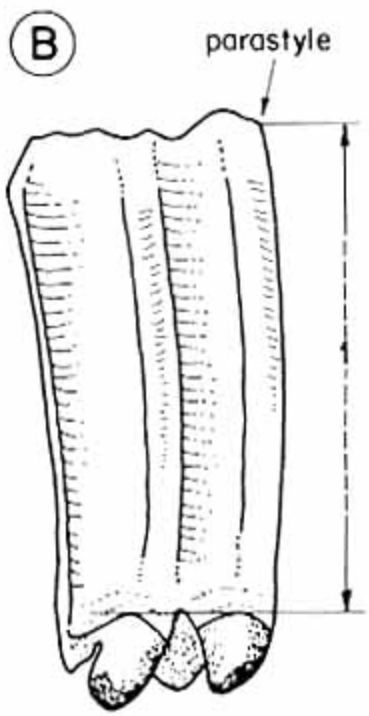
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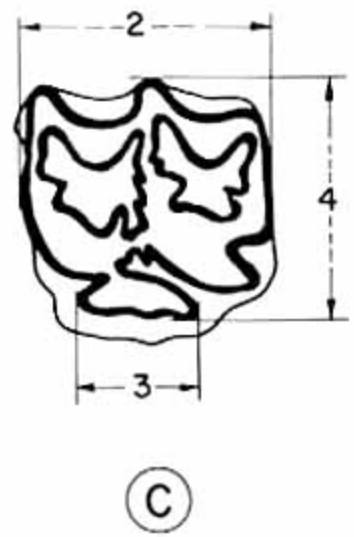
parastyle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LOWER CHEEK TEETH

Two potentially interesting measurements have been added to the "old" ones for the lower cheek teeth: measurements of the prefossette and of the double knot lengths.

Lower cheek teeth of *Hipparion* and *Equus* are much more difficult to distinguish than upper. This problem is often ignored or wrongly solved so that we decided to address it in a special paragraph at the end of this chapter.

But as for the upper cheek teeth, the first task is to try to distinguish the different teeth according to their position inside the toothrow.

How to distinguish isolated premolars and molars in general?

As for the upper cheek teeth, the distinction is difficult (with the exception of P_2 and M_3), and should be based on a conjunction of characters, some of which are similar to those used in the discrimination of upper cheek teeth.

Usually, molars are smaller than premolars, specially by their width. Since the entire cheek row is at his widest between P_4 and M_1, the molars (specially M_2) are usually wider anteriorly than posteriorly, while it is the reverse on premolars (specially the P_3). The occlusal surfaces are more or less at right angles with the crown in premolars; in molars, specially in M_2, the crown is distally incurved backwards. In premolars, the hypoconulid is usually wide and short; in molars, it tends to be thinner, elongated, and to be separated from the entoconid by a sort of "neck" (fig. 7B).

Another point is of interest but, considered alone, may well generate a vicious circle of observations and interpretations. *Usually*, the ectoflexid is relatively shallow on premolars and deep in molars. It seems, however, that the depth of the ectoflexid is a primitive character, first lost by the premolars, then by the molars. If one relies on the shallowness of the ectoflexid to identify a premolar, one will never be able to observe "evolved" molars, with shallow ectoflexids (Eisenmann, 1977).

Characters that can be measured

—Tooth height. The measurement is to be taken from the uppermost margin of the anterior root to the antero-lingual corner of the paraconid in P_2 (fig. 7A), and to the parastylid in other lower cheek teeth (fig. 8B).

As for upper cheeck teeth, the maximum height for each category of teeth must be estimated and 4 stages of wear defined (see above).

—Breadth and length of the tooth, and lengths of prefossette, double knot and postfossette. The measurements are occlusal (fig. 8C) and exclude the cement and the stylids if any. They are studied separately for each category of teeth and for each stage of wear, exactly as for the upper cheek teeth. On P_2, the width is posterior, and no prefossette length is taken.

If the tooth is isolated, one measure of width (maximal) is enough. If the tooth is included in a cheek row, anterior *and* posterior widths should be taken because it has been observed (Pr Tobien) that their relative size may change during evolution: in North-American tridactyl equids, the maximal width seems always anterior, not only in molars as usual, but also in premolars (with the exception of P_2).

For isolated cheek teeth, additional total length and breadth are taken at 1 cm above the roots in *Hipparion*, and at supposed mid-height in *Equus*.

Parameters that have to be calculated

—Hypsodonty indices. To be calculated exactly as for the upper cheek teeth (see above). For *Hipparion*, HI = Length of the tooth at 1 cm from the roots × 100 / maximal height. For *Equus*, HI = Length of the tooth at mid-height × 100 / maximal height.

—Indices for preflexid, postflexid, and double knot may be calculated in the same way as protocone indices of the upper cheek teeth.

Characters that have to be described

—Shape of the double knot (see below and fig. 7C for *Hipparion* and 8A for *Equus*).

—Depth of the ectoflexid and its position relatively to the pre- and postflexids (see below).

—Occurrences of plis caballinid and antecaballinid. Their presence, number, and development should be noted. The other enamel plications (usually on the flexids) are rare and more or less constant in number so that there is no need to give a "plication formula"; but if the enamel is wrinkled (fig. 7C:1) or if there is a pli on the linguaflexid, these characters should be recorded.

—The stylids must be carefully described. In *Equus*, the stylids are usually simple plications of the enamel; their isolation is quite exceptional. In *Hipparion*, both states can be found (fig. 7A and 7B).

Lower lacteal cheek teeth are hardly more suitable for specific determinations than upper.

FIGURE 7: LOWER CHEEK TEETH OF HIPPARION

A: Occlusal view of a left lower tooth row;
B: Occlusal view of a left lower cheek tooth;
C: Selected lower cheek teeth showing different double knots.

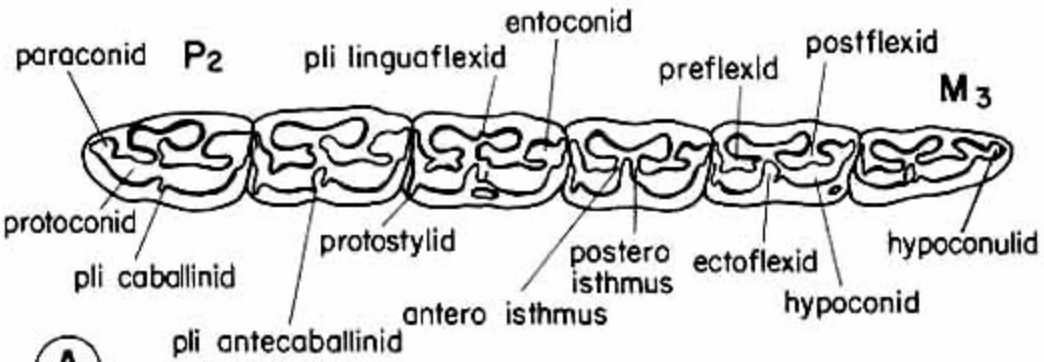
Figures 7A and 7B illustrate part of the nomenclature. Other names exist to describe different features of equid lower cheek teeth. For example, the "protolophid" is the part situated in front of the ectoflexid, while the "hypolophid" is situated behind. The linguaflexid is also named "lingual groove", and the ectoflexid is the "vestibular groove". The isthmus may also be described as the "stem" of the double knot. The pli caballinid is sometimes named "ptychostylid". When protostylids and hypostylids are not isolated as in 7B, but appear as a simple plication (protostylid on fig. 7A), some authors assimilate them, respectively, to the parastylid and the hypoconulid.

As for the upper cheek teeth, all characters depend of the stage of wear which is to be similarly defined (see fig. 8B and corresponding text).

The double knot must be carefully observed. The depth of the linguaflexid and the shape of the metaconid and metastylid must be noted. Some of the most representative shapes are illustrated on fig. 7C (1-4) and fig. 9D and E on middle-worn teeth (stage 2 of wear). One of the peculiar shapes is the "caballine" in which metaconid and metastylid are angular instead of rounded (fig. 7C:4 and fig. 9E). Caballine double knots are evolved features in *Hipparion* found in the last species of the genus in Eurasia and Africa.

The depth of the ectoflexid and its position relatively to the isthmus, the preflexid, and the postflexid are other very important characters. They are illustrated on *Equus* teeth in figure 8A. The ectoflexid may be shallow and not penetrate the isthmus (1, 2, 3); it may be deeper and reach the level of the preflexid but remain on the vestibular side of the postflexid (4); it may penetrate the isthmus (5) and even come in contact with the linguaflexid (6). The depth of the ectoflexid may help to distinguish between premolars and molars but it is also a character modified by evolution in *Hipparion* and *Equus*.

The occurrence, shape, size, number, and height of stylids must be carefully noted. When the ectostylids are very well developed (as in some African *Hipparion*), their maximal occlusal diameter should be measured as well as their heigth from the base of the crown (do they reach the occlusal surface? What is their maximum height, absolutely and relatively to the maximal height of the tooth?). Let us remind that although ectostylids are frequently present and well developed in Plio-Pleistocene African *Hipparion* with caballine double knots, the two characters are independent. In Eurasia (and even in Africa) caballine teeth of *Hipparion* without ectostylids do occur. This means that the lack of ectostylid should never to be considered as enough to discriminate *Hipparion* and *Equus* lower cheek teeth, in spite of what has too often been believed.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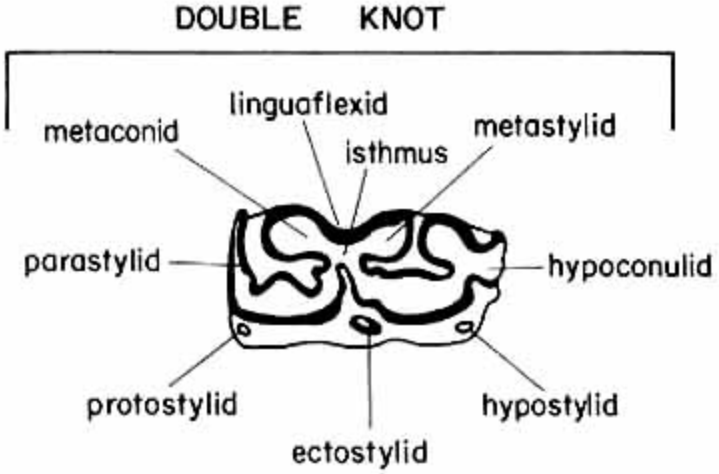
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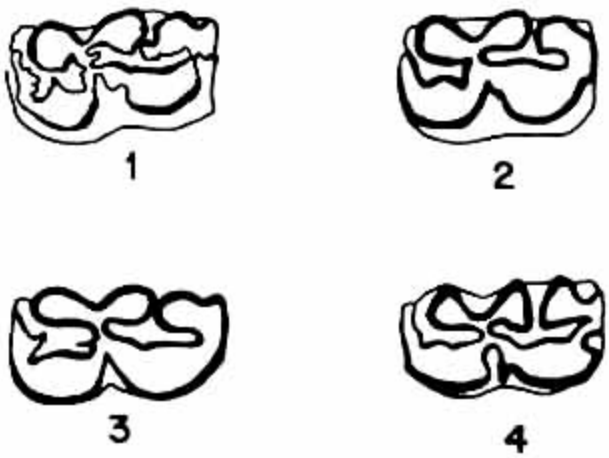
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FIGURE 8: LOWER CHEEK TEETH OF EQUUS

A: Occlusal views of selected left lower cheek teeth showing different shapes of double knots and different degrees of development of the ectoflexid;

B: Lingual view of a right lower cheek tooth; 1 = tooth height;

C: Occlusal view of left lower cheek tooth; 2 = tooth length; 3 = length of the preflexid; 4 = length of the double knot; 5 = length of the postflexid; 6 = maximal breadth.

Figure 8A illustrates different shapes of double knots and different states of depth of the ectoflexid. The two characters must be studied separately although the interpretation of an *Equus* tooth must consider the combination of both.

Figures 1 and 2 show double knots with clearly pointed, "V-shaped", linguaflexids. In 5, the linguaflexid appears more blunted; it is quite flattened and angular, "U-shaped', in 3, 4 and 6. In 7, the linguaflexid is rounded and shallow.

In figures 1, 2, 3, and 7, the ectoflexid is shallow and does not enter inside the isthmus. In 5 and 6, the ectoflexid is deep and penetrates the isthmus. In 4, its developement and position relatively to the pre- and postflexid are intermediate.

Among the 7 figures, only 3 and 4 should be described as "caballine", because of the angulation of the linguaflexid. In 6, the linguaflexid is flattened by the contact with the ectoflexid; it is not angulated by itself.

Other characters to be observed are the occurrence and the development of the wolf tooth (dP_1), of the protostylid on P_2 and dP_2, and of plis caballinid.

Figures 8B and 8C show how to measure an equid lower cheek tooth. The height is measured at the antero-lingual corner of the paraconid on P_2 and at the parastylid on all other teeth. The stages of wear are to be defined as for upper cheek teeth (see text corresponding to fig. 6).

Figure 8C shows how to measure the occlusal length (2), the lengths of the preflexid and postflexid (3 and 5), the length of the double knot (4) and the maximal width, which is here anterior (6).

The hypsodonty index should be calculated on unworn or little worn P_3-P_4 and M_1-M_2, exactly as for the upper cheek teeth:

HI = Length at mid-height × 100 / heigh at the parastylid. Postflexid, preflexid and double knot indices may be calculated in the same way as the protocone index of the upper cheek teeth.

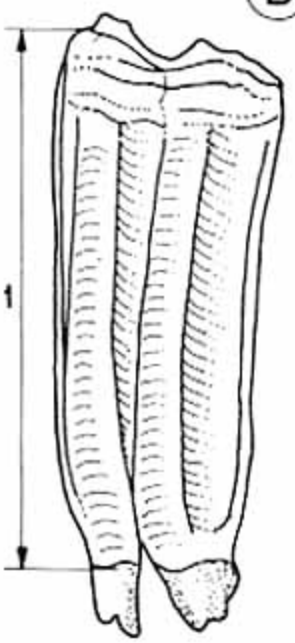
How to discriminate lower cheek teeth of Equus and Hipparion?

Usually, the linguaflexid of *Hipparion* is rather shallow and rounded (fig. 7B and 9D). Most of *Equus* linguaflexids (fig. 8A) are either angular (3, 4, 6) or pointed (1, 2). So that the problem arises with "caballine" teeth of *Hipparion*, which (if they lack an ectostylid) could be confused with caballine teeth of *Equus*. And also with *Equus* teeth where the linguaflexid is shallow and rounded (7) or not very clearly pointed (5); these patterns could be confused with the usual pattern of *Hipparion*.

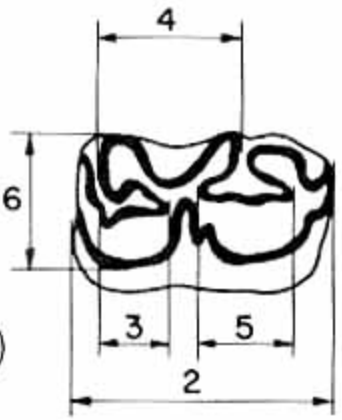
In these cases, one character observed by Gromova, is of major help. In most *Hipparion* (fig. 7B, 9D, and 9E) the preflexid bears two symmetrical "horns" pointing in the vestibular direction. In most *Equus* (fig. 8A); the preflexid is asymmetric and only the anterior horn is well developed.

A

B



C



INCISORS

FIGURE 9: LOWER INCISORS AND CHEEK TEETH OF HIPPARION

(Not to scale)

Lower incisors, occlusal views
A: Vallesian, Bou Hanifia
B: Pliocene, Hadar
C: Pleistocene, Olduvai

Lower cheek teeth series, occlusal views
D: Turolian, Samos
E: Pliocene, Omo

The International Equid Conference did not recommend any definite measurement for incisors. These are indeed difficult because of the curvature of the crown and because the shape and dimensions of the incisors vary even more with the stage of wear than do shape and dimensions of the cheek teeth. Naturally, no index of hypsodonty has been defined but it is obvious that the observation of the crown height is as important in incisors as in cheek teeth.

Characters that should be observed and described are:
—the occurrence and development of the infundibula;
—the degree of plication of the corresponding enamel marks on the occlusal surfaces;
—the occurrence of longitudinal crenulations on the crown (fig. 9B and C).

Other interesting features are the shape of the whole incisival series and the possible involution of the third incisors.

The incisival row may be rounded as in 9A, straight as in 9C, or intermediate as in 9B. The third incisors may be perfectly developed as in 9A, or atrophied as in 9C. In 9B, the third incisors are not entirely erupted but they are not atrophied.

When the third incisors are atrophied as in 9C, they are placed at the rear of the second incisors, the latter being on the same line as the first. All these changes contribute to give a quadrate aspect to the incisival row so that reduction of third incisors and quadrate shape appear linked. Figure 9B shows that it is not always so: third incisors not reduced but placed posteriorly to the second.

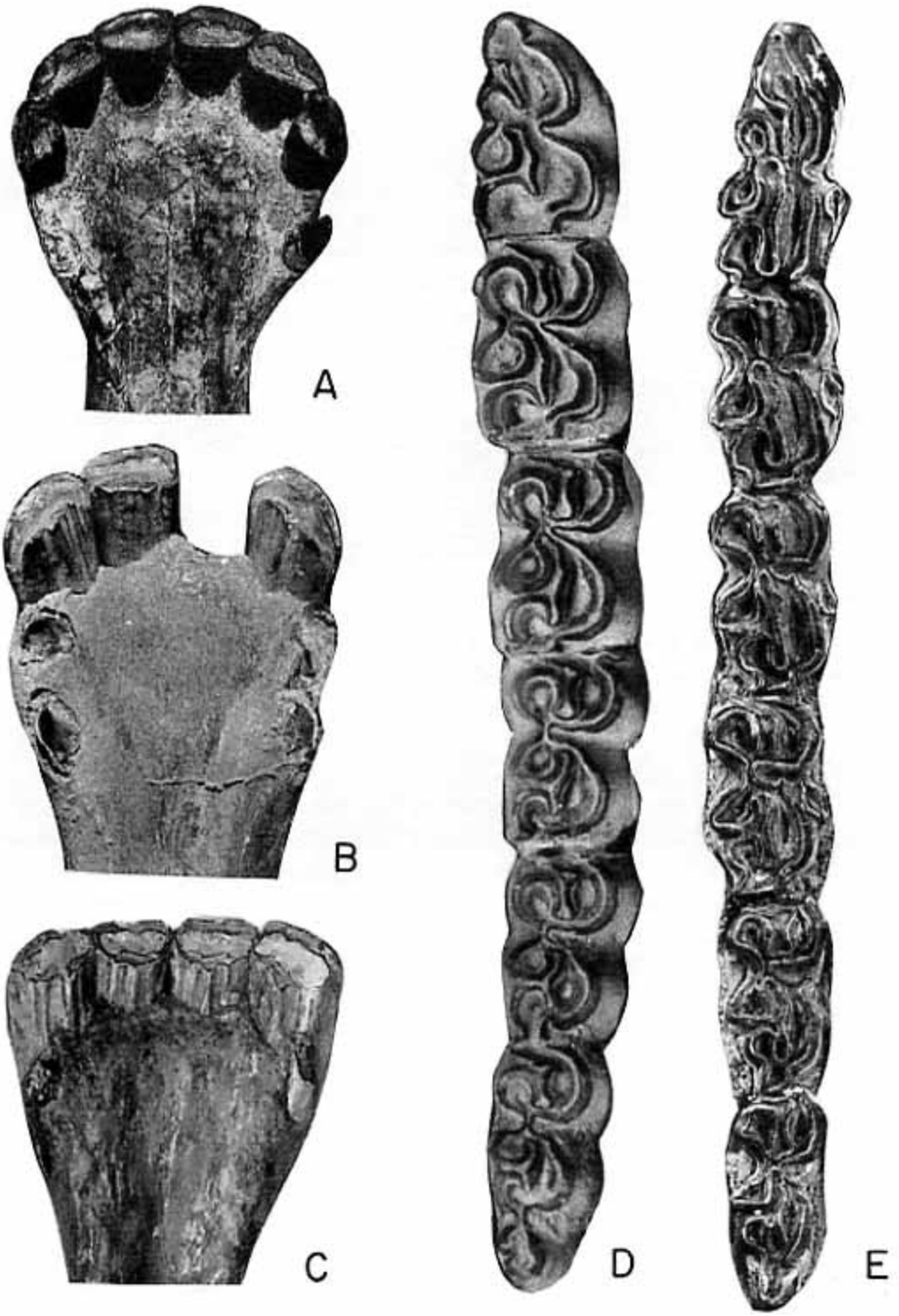

A
B
C
D
E

FIGURE 10: LOWER INCISORS OF EQUUS

Occlusal views of:
Little worn incisors: A, D, E, F and G
Moderately worn incisors: B and H
Very worn incisors: C and I.

The main characters to be studied are the frequency and degree of development of the infundibula on the lower incisors (infundibula are constant on upper incisors).

Figures 10A, B and C show the usual conditions in *Equus*, where infundibula are present and well developed on all incisors but wear completely off in old animals. In A, the marks (rings of enamel formed by cross sections of the infundibula) are elongated. In B, they are less elongated in I_2 and tend to be round in I_1. In C, they have completely disappeared: the sort of circles appearing on the occlusal surfaces are *not* enamel marks but patterns formed by the secondary ivory deposited in the pulpar cavity.

In some *Equus*, infundibula are totally lacking in every stage of wear. Compare the similar stages of wear of A-G, B-H, and C-I.

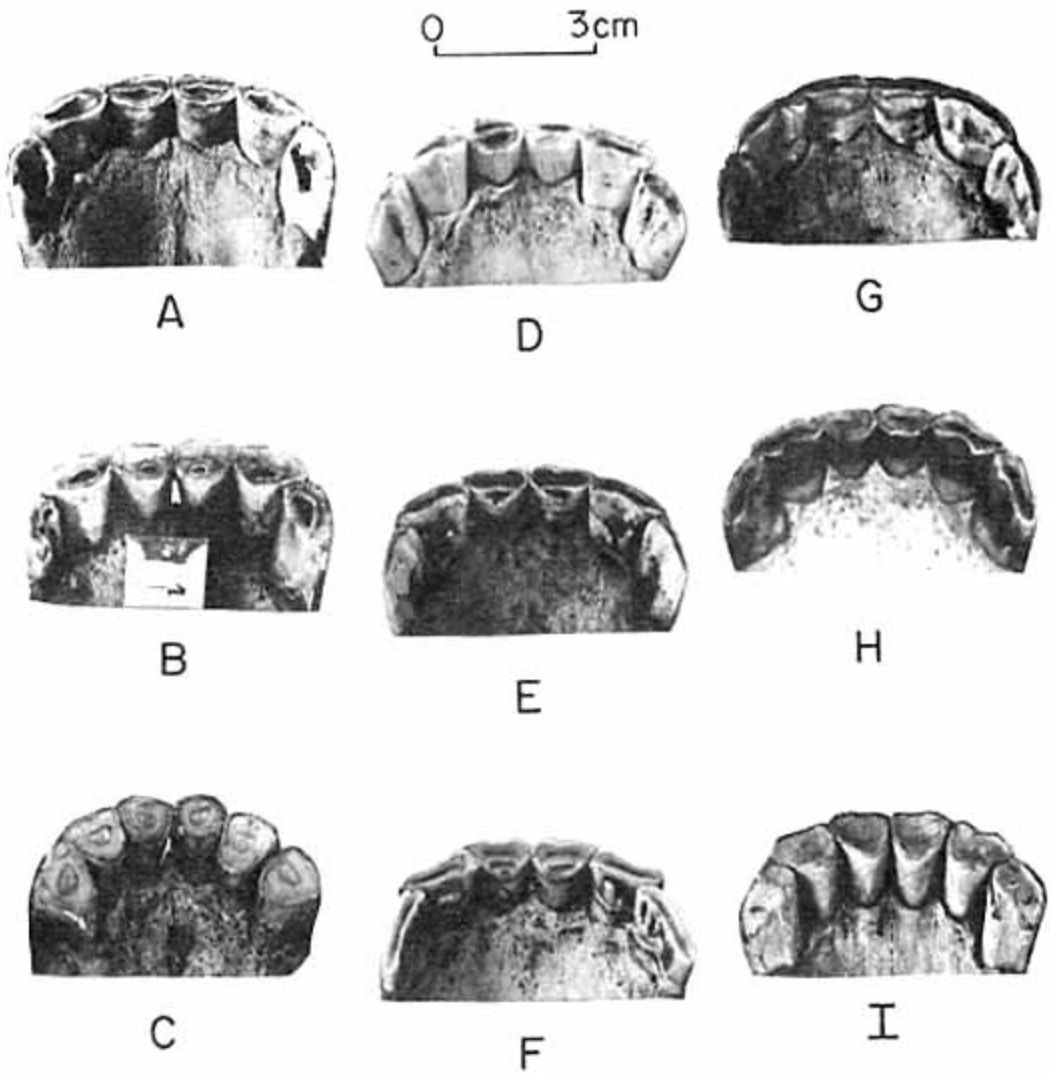
Between these extremes, all kind of intermediate conditions exist: infundibulum on a single I_1 (D); rudimentary infundibula in both I_1 and enamel outgrowths on I_2 (E), or in I_2 and I_3 (F).

Incisors in general

The distinction between lower and upper incisors may be difficult. Upper incisors are usually larger and have more curved crowns. The infundibula are always present; they are more central, while they tend to be more lingual in lowers.

Hipparion incisors have usually shorter crowns than those of *Equus*. In evolved, Pio-Pleistocene forms, the crowns may be as high as in *Equus*, but they may nearly always be distinguished by the occurrence of crenulations on the crowns and of plications inside the marks.

The distinction between isolated first, second and third incisors may be helped by the fact that, at the same stage of wear, third incisors have larger occlusal surfaces than second, and second than first, and also by the angulation of the occlusal surface to the crown. But the discrimination may prove very difficult and, at times, impossible between first and second or between second and third.


0 3cm
A
D
G
B
E
H
C
F
I