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Chapter 16

A Revised Dental Nomenclature for Fossil Horses

ROBERT L. EVANDER

ABSTRACT

A revised nomenclature for the description of fossil horse teeth is proposed. Wherever possible, names used exclusively by horse paleontologists are abandoned in favor of terms that enjoy wide usage by most mammalian paleontologists. Each of the names adopted is defined in terms of the three-dimensional structure represented.

INTRODUCTION

The upper cheek teeth of horses are among the largest and the most complex of mammalian teeth. Paleontologists have studied the historical development of these complex forms and have achieved notable successes in our understanding of them (Osborn, 1907, 1918; Stirton, 1941). The evolutionary history of horse teeth is characterized by the progressive and steady accumulation of dental elaborations. The complex form of the modern horse molar can be deciphered as a series of progressive complications, some of which originated several tens of millions of years ago and others of which are relatively more recent.

The literature contains an extensive dental nomenclature that can be employed to describe the teeth of fossil horses. Osborn (1918) and Stirton (1941) both presented important reviews on horse tooth nomenclature. During the past 40 years, however, new terms have been introduced in a piecemeal manner. Terms introduced by one author have not always enjoyed acceptance by others. As a result, some lower molar structures have been given as many as five different names. In 1981, a multinational panel of hipparion experts met at the American Museum of Natural History and considered, along with other issues, the problem of horse tooth nomenclature. This Hipparion Symposium adopted a series of terms for describing the teeth of hipparions (Eisenmann et al., 1988); a modern standard for horse tooth nomenclature will undoubtedly coalesce around these terms. I endorse the use of the symposium's terminology and have incorporated it whenever possible throughout this report. Nonetheless, because of concerns voiced below, I present an independent dental nomenclature.

At the same time that a complex terminology was developing for horse teeth, a parallel nomenclature was developing for mammals in general. In particular, an important consolidation of the Cope-Osborn theory of tritubercular molars occurred (MacIntyre, 1966; Van Valen, 1966; Szalay, 1969). Patterson (1956) clarified the homologies between the single cusp of lower vertebrates and the tricuspate therian molar, and Butler (1952) and Hershkovitz (1971) reviewed premolar-molar analogies throughout Mammalia. An appropriate dental nomenclature developed at the same time.

Unfortunately, the nomenclature developed for horse teeth does not entirely correspond to the nomenclature for mammals in general. For the most part, differences in the nomenclature arise from the specializations of horse molars. The general mammalian terminology is designed to describe morphology of the observed enamel surface, a three-dimensional entity. Some horse terms describe the worn occlusal surface, which is a two-dimensional cross section of the enamel surface. Horse paleontologists rarely observe the three-dimensional folding of the surface

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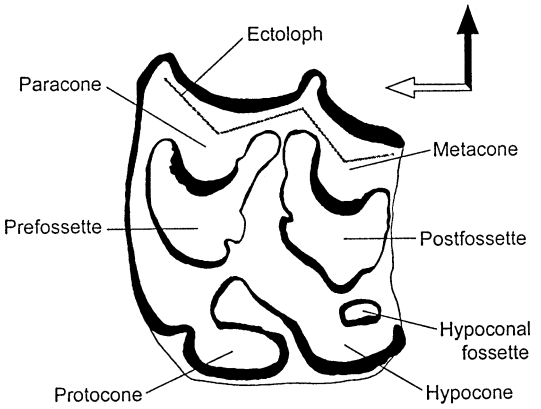


Fig. 16.1. The four main cusps and three fossettes of an upper cheek tooth, demonstrated on a molar of *Pliohippus*. Note also the W-shaped ectoloph. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis.

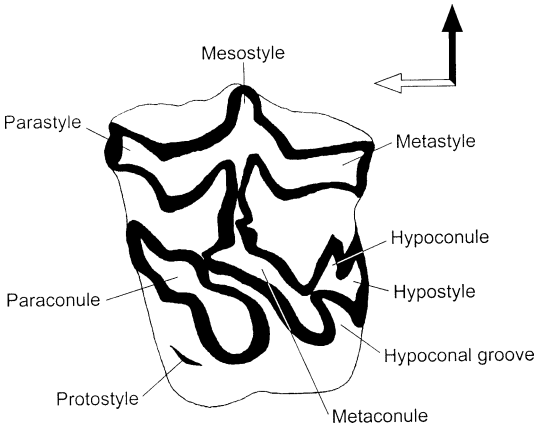


Fig. 16.3. The five styles and three conules of an upper cheek tooth, demonstrated on a molar of *Parahippus*. The hypoconal groove is also labeled. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis. After Osborn (1918).

enamel of late Tertiary horse molars, for the enamel surface is covered with cement. Terms for occlusal patterns with clear meanings in the two-dimensional sense in which they were defined (for example, *isthmus*, *plica*, or *spur*) often fail to preserve clear meanings in translation to the three-dimensional structures that they represent.

The present nomenclature attempts to describe the three-dimensional form of the enamel surface of the cheek teeth in fossil horses. I accomplish this goal by the use of a dental terminology that is itself defined entirely in terms of three-dimensional dental structures. The surest generalization concerning the occlusal patterns of horse teeth is that they change with the wear of the tooth. A complete tooth description must transmit the occlusal pattern of all wear stages, not just the occlusal pattern at a particular wear stage.

LEXICON OF HORSE TOOTH STRUCTURES

The following definitions of horse tooth structures will refer to the main cusps illustrated in figures 16.1 and 16.2. They will also refer to the styles and conules illustrated in figure 16.3.

Anterior Accessory Rib on P^2, (new name): A labially convex bulge between the parastyle and paraconal rib of P^2 (fig. 16.4). Skinner and Taylor (1967) termed the occlu-

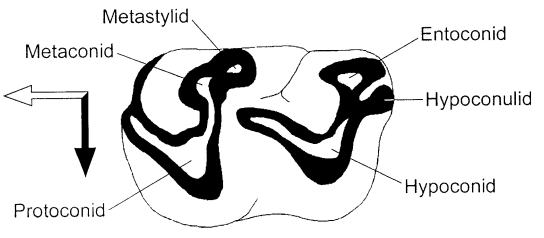


Fig. 16.2. The five main cusps of a lower cheek tooth, demonstrated on a molar of *Miohippus*. The metastylid is also labeled. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis. After Osborn (1918).

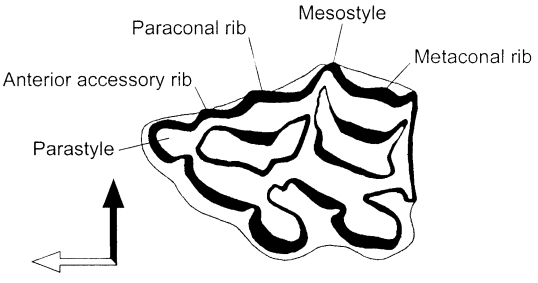


Fig. 16.4. Special nomenclature for the labial side of a P2, demonstrated on a premolar of *Calippus*. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis.

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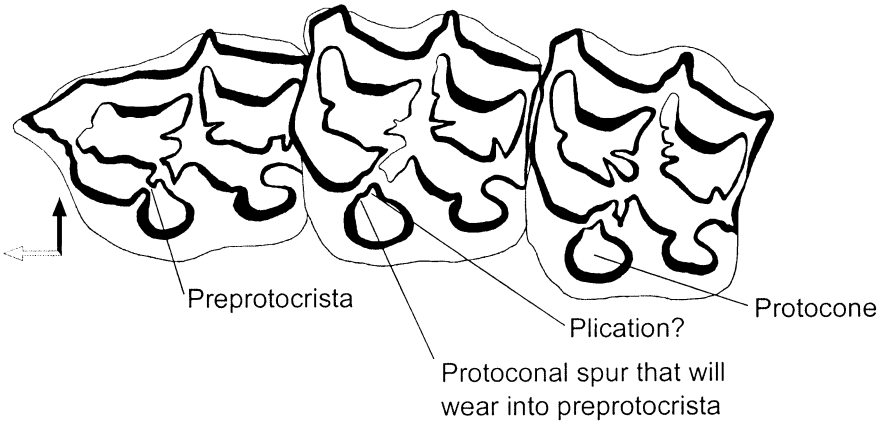


Fig. 16.5. Occlusal aspect of the premolars of F:AM 71115. The protocone of the P3 and the P4 each bear double protoconal spurs. The protocone of the P2 is linked with the paraconule in the position of one of these protoconal spurs, suggesting by serial homology that one of the pair of spurs is a preprotocrista. The other spur might be a plication. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis.

sal representation of this structure the pseudoparastyle. I have inspected numerous P^2s possessing this anterior accessory rib, and in all cases examined, the labial cingulum continues uninterrupted between the parastyle and the mesostyle and does not involve the anterior accessory rib. The term pseudoparastyle is incorrect because the structure named is not a style, in that it does not originate from the cingulum. The term anterior accessory rib, which conveys no genetic implication, is preferred.

Cingulum: A narrow ledge at the base of the crown of upper cheek teeth. Cingula circled virtually the entire crown of *Hyracotherium*, but the lingual cingulum soon became discontinuous, appearing for only a short distance between the protocone and hypocone. The posterior (post-) and labial cingula persist in all equids studied, but development of the anterior (pre-) cingulum is variable. Small cusps developing as upgrowths of the cingula are termed styles.

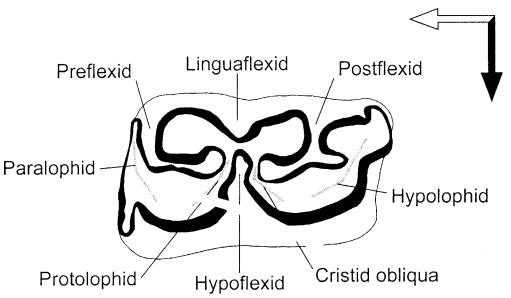


Fig. 16.6. The four lophids and four flexids of a lower cheek tooth, demonstrated on a molar of *Cormohipparion*. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis.

Cingulid: A narrow ledge at the base of the crown of lower teeth. Anterior (pre-), labial, and posterior (post-) cingulids characterize the lower cheek teeth of all horses; the lingual cingulid is absent. Upgrowths of the cingulids are termed stylids.

Crista: A crest or ridge. Where they are present, crests perform an important shearing function in teeth, and thus are structures deserving of distinctive names. Generally, cristae extend anterolabially or posterolabially from cusps, and Szalay (1969) has initiated the convention of naming these the pre-(cusp name)-crista and the post-(cusp name)-crista, respectively. Thus the preprotocrista (shortened from preprotoconecrista) is a crest extending anterolabially from the protocone (fig. 16.5). Cristae not directed anterolabially or posterolabially from cusps present a special problem, and must be expansively described.

Cristid obliqua: The crest extending anterolingually from the hypoconid (fig. 16.6).

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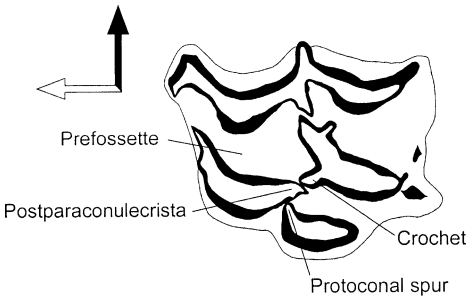


Fig. 16.7. Special structures of an upper cheek tooth of a mesodont horse, demonstrated on a molar of *Protohippus*. Note that both the postparaconulecrista of the paraconule and the crochet contribute to the closure of the prefossette. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis.

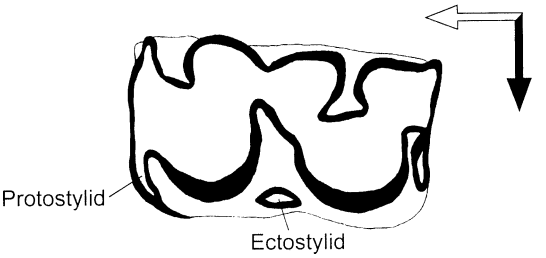


Fig. 16.8. Special structures on the labial side of a lower cheek tooth, demonstrated on a deciduous premolar of *Pseudhipparion*. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis.

At its lingual end, the cristid obliqua may simply terminate, or may be linked to the protolophid, metaconid, metacristid, or metastylid. This crest was named the metalophid by Stirton (1941), but that term was already in use with definitions given in Osborn (1907, 1918). Both Van Valen (1966) and MacIntyre (1966) used the term crista obliqua for this structure. The term crista obliqua also has been used for an upper molar structure (Szalay and Delson, 1979). Szalay (1969) modified the noun to suggest that a lower tooth structure was involved, and that name is adopted here.

Crochet: A crest projecting from the metaloph into the sulcus between the metaloph and the protoloph (fig. 16.7). The crochet first appeared in some Oligocene specimens of *Mesohippus*, and became common in the Miocene form *Parahippus*.

Ectoloph: The joined preparacrista, paracone, postparacrista, premetacrista, metacone, and postmetacrista (fig. 16.1 and discussion of cristae above). The ectoloph is a composite crest extending across the labial border of all upper cheek teeth. It joins the parastyle, mesostyle (when present), and metastyle labially. The protoloph of horses always joins the ectoloph at the parastyle. In some forms the metaloph joins the ectoloph at the mesostyle.

Ectostylid: An upgrowth of the labial cingulid between the protoconid and the hypoconid (fig. 16.8). Osborn (1918) introduced and defined this usage. It is clear from Osborn's figures that he recognized two structures, the ectostylid and the pli caballinid, as homologous. Osborn first published this mistaken homology in 1907, when he termed both structures the protostylid, then repeated the mistake in 1918 using the name ectostylid. Stirton (1941) attempted to rectify the resulting nomenclatural problems, but failed to recognize Osborn's mistaken homology. In this review, I accept Osborn's (1918: 7) written definition of the term ectostylid as an ''accessory column between trigonid and talonid in cleft of outer wall''. Stirton (1941) used the term protostylid to refer to the ectostylid.

Entoconid: The major posterolingual cusp on a lower cheek tooth (fig. 16.2).

Hypoconal fossette: A small basin generated by closure of the posterior opening of the hypoconal groove by a narrow upgrowth of the postcingulum (fig. 16.1). The condition of the hypoconal groove (fig. 16.3) is one of the most variable features of late Tertiary horse teeth. At least three separate conditions are common: First, the hypoconal groove may remain as a short, deep valley at the rear of the tooth. Second, the hypoconal groove may be squeezed up to the top of the crown by enlargement of the bases of the hypocone, hypoconule, and/or hypostyle. Third, a narrow crista stretching lingually from the hypostyle (actually a remnant of the postcingulum from which the hypostyle originated) closes off the posterior opening of the hypoconal groove, but the valley of the groove remains deep.

Hypoconal groove: The narrow valley be-

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tween the metaloph and the postcingulum (fig. 16.3). In Eocene horses, the hypoconal groove was open to the postfossette, but in Oligocene forms this opening was restricted by development of the hypoconule. In forms where the postfossette is closed off, the valley between the metaloph and postcingulum becomes quite short, although it may remain quite deep vertically. Primitively, the hypoconal groove opened at the posterolingual corner of the tooth. In mesodont forms, the hypoconal groove changed its orientation and opened on the posterior face of the tooth. Cooke (1950) introduced the term hypoglyph as a substitute for the term hypoconal groove.

Hypocone: The major posterolingual cusp on an upper cheek tooth (fig. 16.1). The hypocone of equid molars appears to be a true hypocone (Hershkovitz, 1971). That is, it appears to be of stylar origin rather than a posteriorly shifted metaconule. Primitive therian premolars are either unicuspate or consist of a single (labial) row of cusps. A cusp developing on the lingual side of this row may the termed the protocone, but the basis for this terminology is serial homology rather than phylogenetic homology. Whatever the origin of the first lingual cusp on the premolars of horses may be, Granger (1908) has shown that the second lingual cusp was added posterior to the protocone in P^4, whereas the second lingual cusp was added anterior to the protocone in P^3. My own observations on *Epihippus* suggest that, in P^2 as well as in P^3, the second lingual cusp was added anterior to the protocone. Here, I name the protocone and hypocone of P^2 and P^3 by serial homology to the similarly named structures in P4–M3, and note that the named structures are not structurally homologous.

Hypoconid: The major posterolabial cusp on a lower cheek tooth (fig. 16.2). A distinct hypoconid is known only in the earliest equids; in all later forms it is considered to occupy the labial apex of the posterior selenid (a crescent-shaped prominence).

Hypoconule (new name): A minor cusp located posterolabially to the hypocone and anterior to the posterior cingulum (fig. 16.3). A hypoconule first appeared in some specimens of early Eocene *Hyracotherium*, and became a constant feature in Oligocene *Mesohippus*. This cusp was termed the hypostyle by both Osborn (1918) and Stirton (1941). But this usage seems poorly chosen, as the hypoconule is not of cingular origin, as are all other styles. Additionally, some horses possess both a hypoconule and a true hypostyle. Eisenmann et al. (1988) suggested the term hypoconal islet for the hypoconule.

Hypoconulid: The posterior or posterolingual cusp on a lower cheek tooth (fig. 16.2). Primitively, the hypoconulid is one of three major cusps defining the talonid basin of therians. In the earliest horses, a hypolophid connects the hypoconid with the entoconid, excluding the hypoconulid from the basin margin. The hypoconulid remained at the center-posterior of the tooth only in early Eocene horses. Later, it shifted lingually to a position just posterior to the entoconid, and became greatly reduced in size. Osborn (1907: 174) termed the hypoconulid an entostylid, but he corrected his mistake in Osborn (1918). Skinner (1972) used the term hypostylid to describe the hypoconulid. However, this is the primitive therian position for the hypoconulid (Szalay, 1969). The hypoconulid of m3 is distinct in that it does not undergo involution following the formation of the hypolophid. Instead it remains a major cusp. In many species, the hypoconulid forms a third selenid (crescent-shaped prominence) at the back of m3.

Hypoflexid: The labially opening valley between the protolophid and cristid obliqua (fig. 16.6). In later Tertiary forms, the hypoflexid is often cement filled. Like other lower tooth flexids, the hypoflexid has been given a variety of names by earlier authors: median valley (Quinn, 1955), outer groove (Forstén, 1968), ectoflexid (Skinner, 1972), and vestibular groove (Eisenmann, 1977). The term hypoflexid, recommended by Szalay (1969) is used here.

Hypolophid: The crest extending from the hypoconid to the entoconid (fig. 16.6).

Hypostyle: An upgrowth of the middle of the postcingulum (fig. 16.3). Use of the term hypostyle is greatly restricted in this nomenclature. Previous authors (Osborn, 1918; Stirton, 1941) used the term hypostyle to encompass the concepts of the hypostyle and hypoconule as they are defined here.

Linguaflexid: The vertical groove be-

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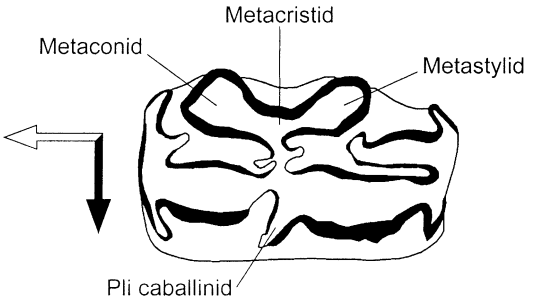


Fig. 16.9. Special structures on the lingual side of a lower cheek tooth, demonstrated on a premolar of *Neohipparion*. The metacristid is a crest connecting a well-separated metaconid and metastylid. A pli caballinid is also labeled. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis. After a drawing in the archives of the Frick Laboratory.

tween the metaconid and the metastylid on the lingual side of a lower tooth (fig. 16.6). This is a specialized term whose use in this sense is restricted to horse paleontologists. It was first introduced by Skinner (1972).

Mesostyle: An upgrowth of the middle of the labial cingulum, between the paracone and the metacone (figs. 16.3 and 16.4). The mesostyle of horses first appeared in the middle Eocene genus *Orohippus*. When present, the mesostyle joins the center of the ectoloph. In those forms where the metaloph joins the ectoloph, the junction occurs at the mesostyle.

Metacone: The major posterolabial cusp on an upper cheek tooth (fig. 16.1).

Metaconid: The major lingual cusp in the middle of a lower cheek tooth (figs. 16.2 and 16.9). If the metaconid has twinned into two cusps, then the anterior cusp retains the name metaconid, and the posterior cusp becomes the metastylid.

Metaconule: A major cusp located between the protocone and metacone (fig. 16.3).

Metacristid (new name): The crest joining the metastylid and metaconid when these two cusps become widely separated (fig. 16.9). Skinner (1972) named several occlusal patterns in modern equids: isthmus, antroisthmus, postisthmus, and meta-isthmus. Hulbert (1988) and Eisenmann et al. (1988) modified some of Skinner's names. Most of these terms are two-dimensional patterns generated by previously named three-dimensional structures. The only unnamed structure underlying this complex terminology is the metacristid. A meta-isthmus is generated by wear of a metacristid.

Metaloph: The joined hypocone, prehypocrista, metaconule, and premetaconulecrista (see discussion of cristae). A true metaloph as defined by Osborn (1907: 72) includes the metacone. The metaloph of horses excludes the metacone, but use of the term metaloph in fossil horse literature is widespread. Use of the term is continued here, with the note that the metaloph of horses is not homologous to the metaloph of other ungulates because it excludes the metacone.

Metastyle: An upgrowth of the labial cingulum at the posterolabial corner of the tooth (fig. 16.3). Both the ectoloph and the postcingulum join the metastyle in horses.

Metastylid: The posterior cusp developed by the twinning of the metaconid (figs. 16.2 and 16.9). The anterior cusp retains the name metaconid. As was pointed out by Stirton (1941), the metastylid is clearly not of cingular origin, making the suffix ''-stylid'' technically incorrect. This cusp originates by a process that Morris Skinner (personal commun., 1978) termed ''cusp fission''. In selected unworn specimens of *Miohippus*, a metastylid apex can be seen separating from a metaconid apex, but these two apices are both part of a single cusp. The term metastylid has been widely accepted in both the horse and nonequid literature (Van Valen, 1966; Hutchison, 1968) for a cusp developing in this manner from the metaconid. Froehlich (2002) named the metastylid a twinned metaconid.

Paracone: The major anterolabial cusp on an upper cheek tooth (fig. 16.1).

Paraconule: A major cusp located between the protocone and paracone (fig. 16.3). The paraconule of mesodont horses is often seleniform, with strong pre- and postparaconulecristae. The posterior crest originating at the paraconule (the postparaconulecrista) serves a major role in the closure of the prefossette of mesodont and hypsodont horses (fig. 16.7). In the horse literature this cusp has been termed the protoconule (Osborn, 1918; Stirton, 1941). In the nonequid litera-

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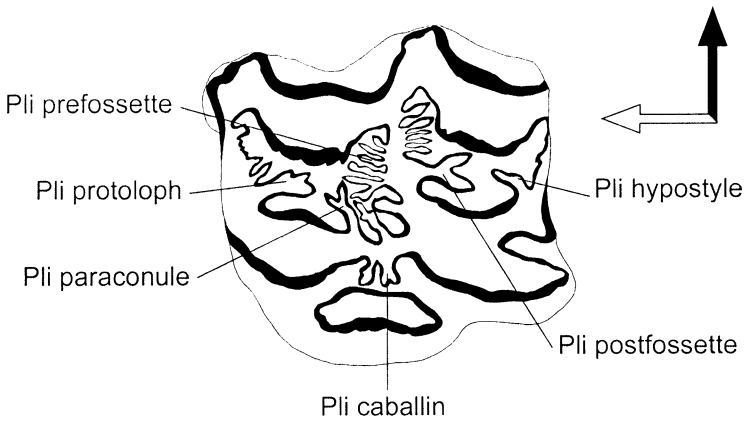


Fig. 16.10. Six types of plicae of an upper cheek tooth, demonstrated on an upper premolar of *Cormohipparion*. The solid arrow points toward the cheek; the hollow arrow points forward toward the symphysis. After a drawing in the archives of the Frick Laboratory.

ture the term paraconule has found wide acceptance (MacIntyre, 1966; Van Valen, 1966; Szalay, 1969). This acceptance has recently extended to horse paleontologists (Hooker, 1989; Froehlich, 2002). Hulbert (1988) introduced the name protoselene for the paraconule.

Paralophid: A crest extending anterolingually from the protoconid of a lower cheek tooth (fig. 16.6). Osborn (1907) noted that the paraconid is lost in horses, making the term paralophid, first introduced by Stirton (1941), somewhat awkward. However, a homologous relationship to the paralophid of other therians (Szalay, 1969) seems clear and the term is retained.

Parastyle: An upgrowth of the labial cingulum at the anterolabial corner of the tooth (figs. 16.3 and 16.4). The ectoloph and protoloph both join the parastyle in horses.

In the P2 of fossil horses, the labial cingulum continues uninterrupted between the mesostyle and the cusp at the front of the tooth. This observation supports the recognition of the cusp at the front of the P2 as the true parastyle, for it is the only stylid anterior to the mesostyle. Skinner and Taylor (1967: 29) define the anterocone as ''a conelike structure developed on the DP2 of equids between the true parastyle and the paracone''. Several modern authors, beginning with MacFadden (1984), have mistakenly recognized the P2 paracone as an anterocone.

Plica: Any corrugation of the enamel pattern of an upper cheek tooth. Plicae are well understood as folds of enamel on the occlusal pattern of horse teeth, but their three-dimensional form is little appreciated. Plicae first appear in the upper cheek teeth of mesodont horses, where they appear in the occlusal pattern very early in wear, then disappear quickly before much of the crown is worn away. These plicae must hang, like so many tall, narrow banners, from the steep enamel walls of the crests from which they develop. The plicae of later Tertiary horses, which persist in the occlusal pattern through much of the wear of the tooth, must represent an evolutionary expansion of these flaglike plicae downward, toward the depths of the fossette. In other words, plicae originate at the top of the crown then extend down toward the base of the tooth.

Specific types of plicae include the pli hypostyle, the pli protoloph, the pli prefossette, the pli postfossette, the pli paraconule (new name) and the pli caballin (fig. 16.10). What is here termed the pli paraconule was called the pli protoconule by Osborn (1918) and Stirton (1941). The new name reflects the use of paraconule rather than protoconule.

Plicid: Any corrugation of the enamel pattern of a lower cheek tooth. Plication of the lower dentition is never so marked as in the upper, and only pli caballinid is so characteristic as to merit naming. The pli caballinid (Stirton, 1941) is a labial fold of the cristid

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obliqua (fig. 16.9). Eisenmann (1977) used the term ptychostylid to refer to the pli caballinid.

Postflexid: The lingually opening valley between the cristid obliqua and the hypolophid (fig. 16.6). The postflexid of fossil horses has been given several names by previous authors: entoflexid (Stirton, 1941), posterior fossetula (Forstén, 1968), postflexid (Skinner, 1972), postfossette (Eisenmann, 1977), and metaflexid (Hulbert, 1988). The term postflexid, recommended by Eisenmann et al. (1988), seems appropriate in mesodont to hypsodont horses.

Postfossette: An enamel basin, often cement filled, formed by the lingual closure of the valley between the metaloph and the postcingulum (fig. 16.1). Closure of this basin results from upgrowth and expansion of the postcingulum and the development of cristae that extend from the metaloph to the hypoconule and from the hypoconule to the hypostyle on the postcingulum. Closure of the postfossette is not clearly demonstrable in brachydont forms, but the elements involved can be identified in selected mesodont specimens from individuals that died with fully formed tooth germs on which cement had not been deposited.

Preflexid: The lingually opening valley between the paralophid and the protolophid (fig. 16.6). In later Tertiary horses, this valley is often cement filled. The preflexid of fossil horses has been given a plethora of other names: metaflexid (Stirton, 1941), anterior fossetula (Forstén, 1968), preflexid (Skinner, 1972), prefossette (Eisenmann, 1977), and entoflexid (Hulbert, 1988). The term preflexid was recommended by Eisenmann et al. (1969).

Prefossette: An enamel basin, often cement filled, formed by the lingual closure of the valley between the protoloph and metaloph (figs. 16.1 and 16.7). Classically, closure of the prefossette has been attributed to the linkage of the crochet to the protoloph at the level of the paraconule. The crochet can be seen to close off the prefossette in selected specimens of ''*Parahippus*'' and individual uncemented molars of some later Tertiary forms. However, mesodont forms suggest a major reorganization of the protoloph, in which the paraconule expands and develops strong crests, effectively becoming seleniform. In these forms, the contribution of the expanded paraconule to the closure of the prefossette is as important as the contribution of the crochet.

Protoconal spur: Any crest or plication originating on the protocone (fig. 16.7). This usage is generally restricted to mesodont forms.

The protoconal spur has generally been regarded as a tall remnant of the preprotocrista originating from the top of an isolated protocone. There are several specimens in the American Museum collections that support this interpretation of the protoconal spur by serial homology.

However, Skinner and Taylor (1967) treated the protoconal spur as a plica of the protocone. The existence of double spurs on some specimens suggests some validity to the hypothesis that protoconal spurs are simply plications. Protoconal spurs tend to appear early in the wear of teeth, then subsequently disappear in mature specimens. This tendency is also seen in the wear pattern of plications.

Specimens supporting the dual origin of protoconal spurs are rare. The premolars of F:AM 71115 (fig. 16.5) demonstrate a serial homology between one of a pair of protoconal spurs and the preprotocrista, but not the other. The second spur is most easily explained as a plication.

Protocone: The major anterolingual cusp on an upper cheek tooth (fig. 16.1).

Protoconid: The major anterolabial cusp on a lower cheek tooth (fig. 16.2). The protoconid exists as a distinct cusp only in Eocene horses. In all later forms the protoconid occupies the labial apex of the anterior selenid (crescent-shaped prominence).

Protoloph: The joined protocone, preprotocrista, paraconule, and preparaconulecrista (see discussion of cristae above). The equid protoloph joins the ectoloph at the parastyle. Osborn (1907: 13) specified that a protoloph included the paracone. Nonetheless, the term protoloph enjoys wide use in the horse literature (including Osborn, 1907, 1918), and its use is perpetuated here. However, it should be noted that the protoloph of equids is not homologous to the protoloph of other ungulate families.

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Protolophid: The crest extending between the protoconid and the metaconid (fig. 16.6). Osborn (1907, 1918) termed this crest the metalophid, a term that was unfortunately used for another crest by Stirton (1941). The term protolophid, endorsed by Szalay (1969) and advocated by Van Valen (1966), is adopted here.

Protostyle: An upgrowth of the precingulum at the anterolingual corner of the tooth (fig. 16.3). The protostyle is a common development of the deciduous molars in later Tertiary forms. It is never seen in the permanent dentition.

Protostylid: An upgrowth of the precingulid at the anterolabial corner of the tooth (fig. 16.8). Stirton (1941) named this structure the parastylid, a term that had been used in a different sense by Osborn (1918). Because a labial structure is being named, the term parastylid seems singularly inappropriate. MacFadden and Skinner (1981) used the awkward term ectoparastylid to refer to the protostylid. European workers (Eisenmann et al., 1988) have adopted the term protostylid, and that usage is followed here. Unfortunately, the term protostylid has a checkered history (Osborn, 1907; Stirton, 1941; see also ectostylid above). The usage of the term by Osborn (1907) and Stirton (1941) is not endorsed here.

Rib: Any labially convex structure between the labial styles of an upper cheek tooth (fig. 16.4). As the labial styles become the predominant positive features on the labial face of the tooth, the primitive curvatures of the paracone and metacone become less conspicuous. We denote their persistent expression as ribs. Thus two ribs are present primitively, and continue to be expressed on all horse teeth except those of the anchitheriine genera *Anchitherium*, *Hypohippus*, and *Megahippus*. Also see the definition of the anterior accessory rib.

CONCLUSION

Classic mammalian tooth nomenclatures suggest that novel structures originate at the base of the crown and grow upward toward the crown top. The origin of styles from cingula and conules from crests are examples of this ''bottom-up'' nomenclature. The evolution of mesodont horse teeth demonstrates several structures that originate near the occlusal surface and later grow down to include the entire crown height. The origin of the metastylid by crown fission of the metaconid and the origin of molar plicae are both examples of these crown-top origins. These crown-top origins are a distinct class of structures. Structures with crown-top origins are common enough in horse tooth evolution so that ontogenetic wear of molars results in a reversal of the phylogenetic increase in molar complexity. As a horse tooth wears down, these novel structures are erased from the occlusal surface, and a more primitive occlusal pattern is revealed.

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Malcolm McKenna required a revision of horse tooth nomenclature in my dissertation. He simply was not going to tolerate page after page of tooth description couched in terms with which he was not fully familiar. Malcolm felt that ''horsifers'' were becoming self-indulgent, and that their specialized nomenclature was degenerating into a jargon.

Dr. McKenna was correct about horse paleontologists becoming self-indulgent. I found few precise definitions for several terms freely employed in the literature, and where a definition existed, that definition was often ignored. New structures and redefinitions were typically introduced into the literature in an illustration. Few of these illustrations bore satisfactory explanations or any sense of the historical development of the structure they were naming. This shortcoming was not all that difficult to resolve. It just took a little nudge from my mentor.

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