

IS HORSE PHYLOGENY BECOMING A PLAYFIELD IN THE GAME OF THEORETICAL EVOLUTION?

VÉRA EISENMANN¹, PAUL SONDAAR², MARIA-TERESA ALBERDI³, and CLAUDIO DE GIULI⁴, ¹UA 12 du CNRS, Institut de Paléontologie, 8 rue Buffon, 75005 Paris, France; ²Rijksuniversiteit Utrecht, Instituut voor Aardwetenschappen, Budapestlaan 4, 3508 TA Utrecht, Netherlands; ³Museo Nacional de Ciencias Naturales, CSIC, José Gutierrez Abascal 2, 28006 Madrid, Spain; ⁴Istituto di Geologia e Paleontologia dell'Università di Firenze, Via La Pira 4, 50121 Firenze, Italy

INTRODUCTION

The following is a comment of MacFadden, B. J., 1984, *Systematics and Phylogeny of Hipparion, Neohipparion, Nannippus, and Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World.

The phylogeny of horses has been and still is one of the most satisfactory and most frequently quoted examples of evolution. That is because of the existence of an evident relation between morphological changes and functional adaptations. From a small ancestor with short and polydactyl legs and with short and bunodont teeth, they eventually developed into large long-legged monodactyl animals with hypsodont grinding teeth.

Therefore, it is logical that scholars interested in horse evolution have concentrated their attention on the two points most important for the survival of the animals: their dentition and their locomotory apparatus. This approach may have led to some oversimplification, and in fact the evolution of equids was certainly more complicated than most people think it was. As usual in paleontology, new material brought new problems; and the very extensive Frick collection has been recently made available for study at the American Museum of Natural History, where it fills most of an entire story in a special building. The very abundance of fossils (that will provide work for many researchers) could have discouraged rather than encouraged researchers. So we can only be happy that some people like MacFadden, Woodburne and others undertook revision of this tremendous material with the help of Morris Skinner, who spent his life collecting and curating the Frick collection and who is one of the persons who knows most about it in the world (Skinner and Johnson, 1984). Another exciting point is that the material was approached in a new way, by comparing the preorbital fossae of scores of skulls.

We regret, however, that the new approach was not combined with the ancient, nor extended to study of skull parts other than the jugal area. Actually the old characters were rather superficially treated or not used, and the "craniological" approach remained centered on the fossa in spite of repeated suggestions from other equid specialists. In short, we criticize MacFadden's work in that it does not take the works of previous authors enough into account, and that it is too much centered on one single anatomical feature: the preorbital fossa. On a more general plane, we think that works that try to take a short cut (by concentrating on one or a few anatomical points instead of trying to characterize a fossil

animal as a whole) are bound to be disappointing in the long run. How could one hope to achieve a valuable synthesis after having skipped part of the analysis?

Our critical comments on MacFadden's revision (MacFadden, 1984: given hereafter as MF) will successively consider the choice and treatment of tooth characters, the choice and treatment of limb bone characters, and the new "craniological" approach favoured by MacFadden and others. After that will come a few general remarks and conclusions.

TOOTH CHARACTERS

It is naturally out of the question to discuss all the tooth characters that have been found useful by equid specialists and were not considered by MacFadden. We will concentrate on the question of hypsodonty and a few other aspects of dental study.

1. Hypsodonty—One of the striking functional adaptations in horses is the acquiring of *relatively* high crowned teeth (hypsodonty) that can resist for a longer time the abrasive effect of food. The term "relatively" is here underscored because a crown of 50 mm height is hypsodont if it belongs to a small animal with small teeth like *Nannippus* but brachyodont if it belongs to a large animal with large teeth like a rhinoceros. In order that this relativity is taken into account, an hypsodonty-index was invented and used systematically by all workers, at least since Gromova's (1952) revision of hipparions. This index combines the height of the crown and one of the perpendicular diameters, usually the anteroposterior. In that way, the sizes of the teeth do not blur the comparison of their relative crown heights.

MacFadden uses the term "hypsodonty" but not the index, preferring to give absolute measures of crown heights. It leads him to surprising statements (MF, tab. 1, p. 7): *Nannippus* can be "extremely hypsodont" with crown heights of 66 mm while *Neohipparion* would be only "very hypsodont" with crown heights of 71 mm. The explanation is naturally that *Nannippus* teeth are smaller than those of *Neohipparion*. But would it not have been more informative to publish the classical hypsodonty-index (or even better, to do a bivariate analysis as suggested by Forstén [1982a] to replace indices)? The separation between the notion of hypsodonty and that of crown height is even more puzzling: on several occasions when he enumerates diagnostic characters (MF:177, 179 for example), he mentions crown height and hypsodonty as if they were unrelated characters.

In a more recent paper devoted to the patterns and rates

of evolution in fossil horses, MacFadden (1985) continues to consider independently crown heights and other tooth dimensions. He finds that different hipparion genera evolve similar crown heights at roughly the same time. One of the exceptions is *Nannippus minor*, its crown height being smaller than that of the other contemporaneous Hemphillian genera. The given explanation is that it is a matter of short potential longevity related to small body size (MF:252). *Nannippus minor* is indeed a small species with very small teeth that are nevertheless very hypsodont if their height is related to their occlusal size. If the relation between the two variables had been studied, *Nannippus minor* would probably not have appeared as an exception in the evolution of cheek tooth height in equids. Actually, MacFadden's conclusion (MF:252) that occlusal surface dimensions of equids do not evolve as rapidly as crown heights appears to re-discover the well known fact that hypsodonty increases during the evolution of horses.

Also, as pointed out to one of us by Mahito Watabe from Kyoto University (presently studying the Chinese hipparions), it would probably have been more interesting to compare the rate of increase of the crown height with the rate of increase of the occlusal surface, because these are the functionally important characters for feeding and therefore for potential longevity.

2. Teeth in General—The abundant and beautiful illustrations of cheek teeth are certainly a very positive aspect of MacFadden's work. But the biometrical descriptions fall short of what could be hoped. MacFadden has chosen to publish only the measures related to upper canines, upper second premolars and upper first molars, as well as the lengths of the complete upper cheek rows (MF:18–19). Previous works (Gromova, 1949:114–116, tab. 2) Forstén, 1968, Appendix; Alberdi, 1974, tabs. 52–56) have discussed and/or used the relative lengths of premolars and molars; it is a pity that these data are not available from MacFadden's paper. The lack of biometrical data on lower dentitions is also regrettable.

If the selection of studied characters may be discussed, so may also be their treatment. Many text descriptions are not very helpful because of their woolliness; for example, in the description of *Hipparion forcei* (MF:64, first column), the term "usually" appears seven times in two paragraphs. When precise data are given, they may be different in the text and the tables; for example, the crown heights of *Cormohipparion occidentale* are said to be "ca 37–43 mm" on unworn or little worn M¹ (MF:162) but the observed range of variation given in table 43 (MF:164) is 30.2–39.1, with one juvenile tooth measuring 39.1. Clearly the sample described in the text is not the same as the one used in the table, but the nature and reason of the difference do not appear. The significance of the statistical tables may also be questioned. What value must be attached to statistics on teeth of *Cormohipparion occidentale* if the species has existed from the early Clarendonian to the Hemphillian (MF:186, fig. 150) and if specimens of different localities of such different ages are mixed together (MF:164, tab. 43)? It may be suspected that in such tables, the variation will be rather too large. But at times, variation seems also surprising between specimens of about the same age; for example, the type teeth of *Neohipparion coloradense* (MF:82, fig. 51) are clearly hypsodont although already worn, but the teeth of the skulls referred to the same species (MF:84, fig. 53, 85, fig. 55) are not clearly so: in both specimens the protocones of the M¹ are already united to the protoloph although the M³ is scarcely worn. Moreover, the referred

dentitions differ by the presence (MF, fig. 53B) and the lack (MF, fig. 55B) of a protoconal spur. According to MacFadden's diagnosis of *Neohipparion coloradense* (MF:87) a protoconal spur may often be present in early wear; nothing is said, however, about a possible early fusion of the protocone to the protoloph (which is a merychippine character). So the question arises: do all the teeth ascribed to the same species really belong to them?

Considering the tooth features used and their description, one does understand why MacFadden has not based his supraspecific groups on dental characters. The question may even arise if "the species-level taxonomy of hipparions can be interpreted by dental differentia" (MF:47). For example, if we judge by table 7 (MF:57), *Hipparion tehonense* and *H. forcei* seem to differ only in size. In addition, MacFadden writes that "*Cormohipparion goorisi* and *Cormohipparion sphenodus* do not have diagnostic characters of size and dental pattern that would allow unambiguous specific recognition" (MF:147).

If teeth do not show good supra-specific characters, a still more awkward question arises. MacFadden accepts four genera of New World hipparions represented by 16 species. Out of these, 13 have been described by previous scholars on isolated teeth, sometimes on one single tooth. How MacFadden manages to link the skulls (the base of his generic taxonomy) to the teeth (the base of his specific-level taxonomy) when the teeth are lower (MF:99, *Neohipparion leptode*)? Or if the specimens are from uncertain localities (MF:162, *Cormohipparion occidentale*)? Why could not the "M¹?" type of *Hipparion tehonense* (MF:65) belong to a *Cormohipparion* species? Certainly, MacFadden has his reasons but they do not appear clearly in the text.

To sum up, the study of New World hipparion dentitions by MacFadden will unfortunately not be a great help for comparisons with Old World hipparions or with "old-fashioned" studies, because data on some of the more usual measures and indices were not considered or not published by MacFadden. Moreover, the parameters studied and published by MacFadden seem to lead to more questions about the New World hipparions than they give answers.

LIMB BONE CHARACTERS

Although the introduction of MacFadden's revision mentions the integration of postcranial characters in the new taxonomical approach (MF:6), the limb bones are not discussed to any extent.

From table 1 (MF:7) it appears that all the considered genera are tridactyl, that they present "so far as is known" a trapezium, with the exception of two species of *Nannippus*, and that the central metapodials may be more or less robust and more or less elongate. Barring this table and a few other synoptic ones there is no mention of limb bones except for a single species, *Hipparion shirleyi*.

For *Hipparion shirleyi*, MacFadden gives one table of measurements with two measures on five metapodials (MF:64, tab. 11), 8 lines of text description (MF:64) and one illustration of a pes (MF:61, fig. 30). The only precise statement in the text is that "terminal lateral phalanges extend distally . . . to a position lateral to the distal tip of the first medial (III) phalanx". Figure 30 (MF:61), however, is in contradiction to the text. On the medial view (not "lateral"), the digit II terminates much higher than the distal end of the central (not "medial") first phalanx. This position of the phalanges of digits II and IV is quite unusual for tridactyl horses and

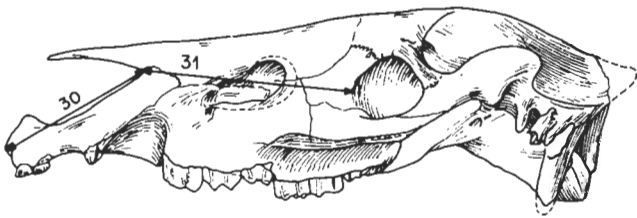


FIGURE 1. After MacFadden, 1984, fig. 132: lateral view of the skull FAM 71801 from Christmas Quarry. 30 = depth of the narial opening; 31 = distance between the naso-incisive notch and the orbit.

evokes more the litoptern *Diadiaphorus majusculus*. Probably, the illustration is a little inaccurate as is also the use of anatomical terms: "lateral" instead of medial, and "medial" instead of central or median. On the whole, all we are sure about *Hipparion shirleyi* is that it was tridactyl. But there are clear anatomical, function-related, differences between different tridactyl horses. Very important characters are the degrees of development of the sagittal keel on the distal articulations of the metapodials. In merychippine horses, the sagittal keel is faint on the dorsal side of the central metapodial but well developed on the volar side of the lateral metapodials. In hipparions, the keel is better developed on the central metapodials and lost on the lateral (Sondaar, 1968: 30, 32). If the figure 30 (MF:61) is reliable, *Hipparion shirleyi* belongs with the merychippine horses rather than in the hipparions, given the lack of a dorsal keel on the distal end of the MT III. But the figure may be inaccurate and MacFadden gives no information on the keel development on lateral metapodials. The bare mention of tridactyly when one is trying to understand the systematics of Miocene and Pliocene horses is not sufficient.

The second postcranial character appearing in table 1 (MF: 9) concerns the presence or lack of the trapezium. MacFadden does not bring any new data on this point (MF:118) which, moreover, is of a rather restricted interest. It is to be regretted that other, more important characters related to carpal and tarsal facets on the metapodials (Gromova, 1949, tab. 2; Gromova, 1952:142-156; Hussain, 1971, tab. 19) were not considered.

Robustness of limb bones and elongation of a limb segment relative to others are also important characters that may give indications to adaptations to the environment. Robustness may be related to humid conditions, elongate distal segments to open landscapes. But if these characters do appear in the MF tables, it is without precise information: no indices of robustness, no measures rendering possible their calculation or the appreciation of the relative lengths of the limb segments, and no discussion or no reference to the works of other authors (Sondaar, 1968; Forstén, 1973, 1975a; Hussain, 1975) are given.

All this seems to show a general lack of interest in postcranial anatomy and function. For the limb bones, MF's paper fails to give the information one would like to get and is still more frustrating than for the dentitions.

THE CRANIOLOGICAL APPROACH

1. The Preorbital Fossa—MacFadden is quite right when he writes (MF:29-30) that the functional morphology of the preorbital fossa is not completely understood and that its

origin and function are somewhat controversial. He is not right when he states that the fossa was not usually employed as a diagnostic taxonomic character with the exception of his own work on Siwalik hipparions (MF:29). It is certainly understandable that someone revising equids of the New World cannot be acquainted with the whole literature on equids. However, when the structure of the fossa is the main, if not the only, character thoroughly studied, one would expect a special bibliographical effort in this domain. Three of the largest works dealing with equids of the Old World (Gromova, 1949, 1952; Gabunia, 1959) have used the preorbital fossa as one of the characters distinguishing hipparions on the specific level and/or discussed its variations and possible functions; other observations and interpretations of interest are also available in the international literature (Meladze, 1967; Zhegallo, 1978).

After having studied a large sample of skulls from the MacAdams Quarry, MacFadden concludes that despite the claim to the contrary, the variation of facial fossae "within equid taxa" is not strongly controlled by either ontogeny or sexual dimorphism (MF:36). In this particular sample, males and females seem to separate beautifully on a dispersion diagram using their canine diameters (MF:33, fig. 11); they do not differ by the parameters related to the preorbital fossa. In our opinion, the generalization to other equid taxa is premature because other observations are clearly different.

Gromova (1952:63) mentions continuous variation in the size of canines of hipparions, making them hard to use as sex indicators other than in extreme cases. She also points out that when canines appear to be small, in particular on figures, it is not clear whether they belong to mature females or represent lingering lacteal teeth. Concerning the fossa, Gromova (1952:188) considers that it is a character of good specific value; the development of the fossa is roughly the same inside a given species although differences in shape and proportions seem to occur between juvenile, mature and old individuals. She also discusses the different functional interpretations (Gromova, 1949:69-70, vol. II) favouring the opinion advanced and defended by Lydekker, Gaudry and Sefve, that the fossae contained some glands probably important for the social life of the animals; Gromova regrets, however, that there is not yet any definitive evidence on the function of the fossae that would give a better insight into the ecology and ethology of primitive equids. Gabunia (1959: 18-19) agrees on the whole with Gromova. He also insists that one exceptionally stable parameter concerning the fossa is its distance from the orbit.

The evidence given by Meladze (1967:137-141) is quite different. According to this author, five skulls found in exactly the same level, and even in the same block of sediment, at Bazaleti, belong without any doubt to the same species of *Hipparion* by all their characters with the exception of the fossae. In three skulls the fossae are much more complicated, developed, better "rimmed" and "pocketed" than in the other two. Meladze considers the first ones as male and the latter as female. His interpretation is based on the assumption that the fossae accommodated glands not unlike that of modern cervids and that these glands are usually more developed or more frequently well developed in males. But Meladze points also to the fact that canines are smaller in one assumed male than in one assumed female (Meladze, 1967, pls. VII, VIII) and that the fossa is farther situated from the orbit in the assumed female (45 mm) than in the assumed male (31.5 mm). Eventually, Meladze wonders if the intraspecific variation in the shape of the fossa referred by Gromova to on-

togenetical causes may not be in fact related to a sexual dimorphism. The fact that development of canines does not appear to be a reliable sexual character in hipparions would naturally complicate the corroboration or falsification of this hypothesis.

Zhegallo (1978:35–39) has an altogether different opinion; he has proposed (Zhegallo, fig. 17) a reconstruction of the facial musculature of hipparions; he thinks that the posterior (lacrymal and malar fossae) were related to the attachment of specially developed elevators of the upper lip, while the *diverticulum nasi* was probably situated much closer to the narial opening, possibly inside the *fossa subnasalis*. In his opinion, the very well developed facial musculature of hipparions is related to the complicated movements of browsing, so that the lacrymal and malar fossae would weaken or disappear in grazers; the *diverticulum nasi* could be of some interest in the amelioration of respiratory mechanisms.

If we have emphasized the above points, it is not because we have a definitive opinion on the function or the variation of the fossa “within equid taxa”. We simply wish to show how complicated and controversial the question remains, and also to present some published observations and discussions not used by MacFadden, although Forstén (1982b) had pointed them out already and added a few personal observations. If MacFadden could not discuss Forstén’s observations because the skulls were not figured or described in detail (MacFadden and Skinner, 1982:1337), he could have found illustrations and a detailed description in Meladze’s paper.

If one has no “a priori” reason to disbelieve the evidence given by Gromova, Gabunia, Meladze, Zhegallo, Forstén, MacFadden and others, the question arises if the fossae of different equid taxa may not have possessed different functions, as MacFadden himself admits (p. 30), and different intraspecific modes of variation. In that case, the shape of the fossa does not appear as a perfect systematic tool for *all* equid taxa, whether at the specific or at the generic level; it would not be a character reliable enough to support, all by itself, a whole phylogenetic edifice. For example, if instead of generalizing from the MacAdams Quarry, one would generalize from the Bazaleti sample, the “genus” *Cormohipparion* would appear composed of males from the “genus” *Hipparion*: pocketed and anteriorly rimmed fossae in the first; smaller, simpler and anteriorly less well defined fossae in the second (MF:64).

Another question arises about horses without preorbital fossa. MacFadden writes (MF:38) that in the Old World some hipparions lack this feature and quotes three papers that deal with three African skulls belonging to two species. This is an understatement. The lack of a fossa has been mentioned in *Hipparion hippidiodum* and *Proboscideipparion sinense* by Sefve (1927), in *H. platygenys* by Gromova (1952), *H. urmiense* by Gabunia (1959), *H. rocinantis crusafonti* by Sondaar (1962) and Alberdi (1974), *H. afarensis* and *H. cf. ethiopicum* by Eisenmann (1976, not 1977 as stated in MF:188), *H. houghenense* by Qiu et al. (1980), and others. Admittedly, the lack of a fossa is interpreted as a loss and a derived character, although all the species above are not necessarily more recent in time. On the other hand, it would be difficult to consider the lack of a fossa in all the enumerated species as a synapomorphy.

What are we to do with skulls lacking fossae? What is to be done with the material in which the shape of the fossa is unknown (see for example the problems MacFadden has with “*Hippotherium plicatile*” (MF:170))? And in a more general

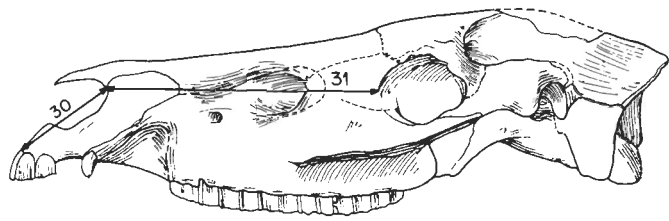


FIGURE 2. After MacFadden, 1984, fig. 133: lateral view of the skull FAM 73909 from Gidley Horse Quarry. 30 = depth of the narial opening; 31 = distance between the naso-incisive notch and the orbit.

way, how will scientists be able to synthesize a systematic approach based on the fossa in North America with approaches using teeth, limb bones, and even other cranial characters in the Old World?

2. Other Cranial Characters—Although mentioned as “cranial”, nearly all characters used by MacFadden are related to the size, shape and position of the preorbital fossa. The measures are restricted to the area situated between the naso-incisive notch and the anterior end of the orbit; exceptions are the width between the canines and the length of the postcanine diastema (MF:15, fig. 3). The fact that the number of studied characters amounts to 15 measures and five coded variables does not make up for the lack of information on the rest of the skull. These lacunae about possibly interesting dimensions are especially frustrating in consideration of such beautifully preserved material.

Let us consider Figures 1 and 2 (taken from MF figs. 132, 133) illustrating two skulls from different quarries referred by MacFadden to *Cormohipparion occidentale* (MF:165). A look at the figures shows a striking difference in the depth of the narial opening: in the first skull, the naso-incisive notch is approximately equidistant from the anterior end of the muzzle and from the posterior end of the preorbital fossa; in the second one, it is much closer to the anterior end of the muzzle.

We are not accustomed to see such intraspecific differences in the equids we have studied so far. That something is amiss in this respect is also shown by the coefficients of variation plotted by MacFadden (MF:37, fig. 12): the distance between the naso-incisive notch and the posterior end of the preorbital fossa (NNDPOF) has a relatively high coefficient of variation. If the distance between the first point and the anterior end of the muzzle had been measured, the coefficient of variation would probably have been even higher. A short narial opening, such as in Figure 2, is usual for Eocene and Oligocene equids and may therefore be considered as a primitive character, lingering in some Miocene forms (Eisenmann, 1982, fig. 3). The presence of one primitive and one evolved morphology in contemporaneous animals (both dated to the late Clarendonian) should, in our opinion, preclude their reference to the same species.

A few pages farther, MacFadden tries to invoke sexual dimorphism as an explanation for the muzzle proportions of skulls from Hans Johnson Quarry, referred also to *Cormohipparion occidentale* (MF:169, fig. 138). He also states that males of this quarry seem to show some phylogenetically advanced characters, whereas females show the relatively primitive character states (MF:170). This may or may not be an explanation for the differences in Hans Johnson Quarry sample. But if well developed canines do indicate males, no

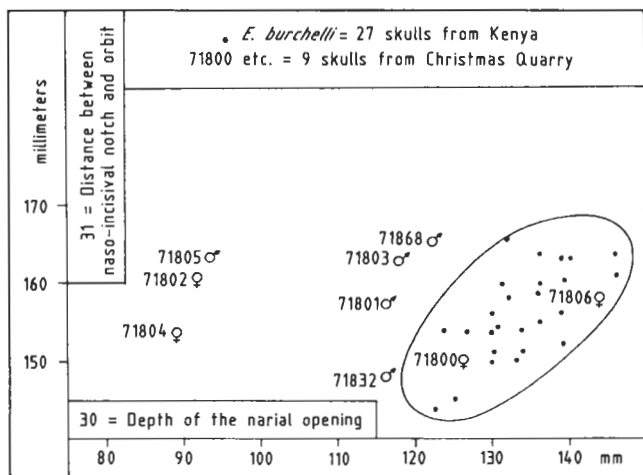


FIGURE 3. Bivariate plot for the depth of the narial opening (measure 30) and its distance from the orbit (measure 31) in 9 skulls from Christmas Quarry and 27 skulls of modern Plains Zebra. ♂ = skulls with well developed canines; ♀ = skulls with smaller canines.

sexual dimorphism can account for the differences between the narial openings of skulls on Figures 1 and 2, both specimens having large canines.

Actually, the data we have collected all together on the Christmas Quarry material (during the New York Hipparion conference in 1981) compared to a normal intraspecific variation in a modern equid (Fig. 3) show: (1) how extremely improbable is the homogeneity of the material from this quarry, the whole of which had been nevertheless referred to a single species, *Cormohipparion occidentale*; (2) how extremely improbable is a sexual-dimorphic explanation of this lack of homogeneity.

As in our discussion of the preorbital fossa, we do not pretend to give here a definitive solution to the problem but to show how uncertain MacFadden's diagnoses may appear when they are looked at independent of the "preorbital fossa model". If, as we suppose, at least two different species are mixed in the same quarry(ies) and referred to the same taxon, the question also arises as to which one is *C. occidentale*, the type species of the genus *Cormohipparion*.

If determination at the specific level of complete skulls may still be so controversial, is it not premature to propose a biochronological distribution of the New World species of hipparions (MF:186, fig. 150) and a representation of their phylogenetic relationships (MF:184, fig. 149)? What is to be thought of cladograms if primitive and derived characters may be at times sexually-dimorphic (MF:170)?

GENERAL REMARKS AND CONCLUSIONS

In spite of bringing a lot of interesting and new information, MacFadden's work is rather disappointing because of fundamental and formal flaws.

Considering the formal side, one flaw is the off-handedness with which the bibliography is treated (papers not quoted, or quoted but not discussed at all, or not enough, or wrongly quoted or discussed). Other flaws are contradictions, inaccuracies and especially imprecisions. For example, in table 1 (MF:7-9) or 29 (MF:120-121), nearly all characters (even

some that are related to the preorbital fossa) are said to vary from one extreme to another, passing through a moderate stage; nearly all characters are "usually", "moderately", or "relatively" one way or another. Although this kind of vocabulary is understandable in synoptic tables, it should be substantiated somewhere in the text or in other tables.

As we have seen, statistical tables exist only for some upper teeth characters and preorbital fossa parameters. Information on characters usually studied by equid paleontologists is not available: no study of the hypsodonty, no premolar and molar row lengths, no biometrical data on lower dentitions, no measures of limb bones. Paleontological studies cannot do without comparisons and comparisons are difficult if the same characters are not described. Actually, this question is so important that the very aim of the International Hipparion Conference in New York, in 1981, was to improve communication between paleontologists and make easier the comparison between fossils by a standardization of methodology. A whole system of measures and observations was agreed upon, but unfortunately is still not published. Possibly, MacFadden's work could not have benefitted from this international agreement because it was already nearly finished at that time. But even so, his descriptions and presented data fall rather behind the paleontological reviews of hipparions published before the Hipparion conference, like those of Gromova (1952), Gabunia (1959), Sondaar (1962), Alberdi (1974), Hooijer (1975), Forstén (1968, 1975b) and others.

From a fundamental point of view, MacFadden's work fails to convince us that a phylogeny of tridactyl horses can be based on the preorbital fossa. When other observations than those of MacFadden are taken into account, it appears that preorbital fossae may have had different functions and modes of variation within different equid taxa; they can also be lacking much more frequently than implied by MacFadden (no fossa in at least eight Old World species).

While works like those of Gromova (1952), Gabunia (1959) or Radinsky (1983) have shown how different cranial characters could help to differentiate hipparion species or understand horse evolution, MacFadden's "craniology" does not manage to get out of the jugal area. Because of this restricted approach, MacFadden may well be wrong not only at a supraspecific level but even in his species identification of hipparions; one of the few "species" (*Cormohipparion occidentale*), which we have had time to study by another craniological approach than the pure observation of the preorbital fossa, could well contain different taxa (Fig. 3).

If the basic, fundamental work at the species level is so uncertain, what is the reliability of proposed patterns of phylogeny and rates of evolution in fossil horses (MacFadden, 1985)? We do not agree that our different "taxonomic approach and phylogenetic interpretation" may be explained away as resulting from different "philosophical approaches" (MacFadden, 1985:245-246) "rather than from flaws in the (MacFadden's) data base". Philosophy has nothing to do in the matter; we just do not construct buildings before being sure of their foundations.

In our opinion, a revision of Old World as well as New World hipparions is badly needed, and could constitute a large international program, if only people could agree not to restrict themselves to the study of the jugal area. In the particular case of New World hipparions, we think that a revision should begin locality by locality, to ascertain first how many species of tridactyl horses could live at the same time at the same place. The answer to this question could

probably be easier to obtain on recently excavated sites where complete skeletons are present, so that there is no possible discussion about what limb bones, mandibles and skulls belong together (like in "Poison Ivy" quarry excavated by M. Voorhies). Such descriptions would constitute a really solid basis of comparison for other material, even if we may now suspect that everything that is true for one equid is not necessarily generalizable to all. A better knowledge of the ecology and tentative interpretations of the ethology of the tridactyl equids may help to elucidate the function(s) of the preorbital fossa(e). At that point, the usefulness of this important character may become as apparent, whether in a systematic or an ecological context (or both), as that of the teeth and locomotor system.

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