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Critical comments on the genus *Propachynolophus* Lemoine, 1891 (Mammalia, Perissodactyla, Equoidea)

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Abstract: The validity of *Propachynolophus* Lemoine, 1891, supposedly an intermediate between *Hyracotherium* Owen, 1841 and *Pachynolophus* Pomel, 1847, has been questioned for a long time. A detailed analysis of features on which this genus is based further supported by a formal cladistic analysis demonstrates that *Propachynolophus* is not a valid taxon. The type species, "*Propachynolophus gaudryi* Lemoine, 1891" shall be assigned to *Propalaeotherium* Gervais, 1849, under the new combination *Propalaeotherium gaudryi* (Lemoine, 1891). "*Pachynolophus maldani* Lemoine, 1878", later assigned to *Propachynolophus*, typifies the new genus *Orolophus*, under the binomen *Orolophus maldani* (Lemoine, 1878). The other referred species, "*Propachynolophus levei* Hooker, 1994" and "*P. remyi* Checa-Soler, 1997" are poorly documented, and both species shall be provisionally referred to as "*Hyracotherium*" *levei* (Hooker, 1994) and "*Hyracotherium*" *remyi* (Checa-Soler, 1997), pending new discoveries.

Keywords: Eocene, tooth morphology, *Pachynolophus*, *Propalaeotherium*, *Eurohippus*

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INTRODUCTION

By their diversity and abundance, perissodactyls have played a crucial role in the European Eocene mammalian faunas. During the early and middle Eocene, these assemblages were dominated by the Lophiodontidae, a family of large tapir-like perissodactyls, later replaced by the Palaeotheriidae equoids, of which the last offshoots became extinct by the early-late Oligocene transition (Remy, 1995).

Besides these large-sized taxa, there was a profusion of relatively small-sized equoids, formerly gathered within Pachynolophidae Pavlow, 1888, "Hyracothéridés" (Depéret, 1901), or "paléohippidés" (Stehlin, 1905). Depéret (1901) was the first to put some order in the systematics of this group by giving a clear definition of generic diagnoses that would be long accepted. His views have been followed in particular by Stehlin (1905, 1941).

The oldest of these Equoidea are represented by the "hyracotheres" *Hyracotherium* Owen, 1841 (with *H. leporinum* Owen, 1841) and *Pliolophus* Owen, 1858 (with *P. vulpiceps* Owen, 1858) from the London Clay (lower Ypresian, MP 8-9 in the biochronologic scale of Paleogene mammals, BiochroM'97). Both genera were often synonymized (Depéret, 1901; Cooper, 1932; Simpson, 1952; McKenna & Bell, 1997). They have been considered close to the stem group of all perissodactyls (Simpson 1945: 253), or at least of hippomorph perissodactyls (Rose *et al.* 2014).

The genus *Propachynolophus* Lemoine, 1891 which is the main subject of the present work, was subsequently erected for a species larger and slightly younger than the hyracotheres, i.e., *Pachynolophus gaudryi* Lemoine, 1878. Three other species were subsequently assigned to *Propachynolophus*: *P. maldani* (Lemoine, 1878), *P. levei* Hooker, 1994, and *P. remyi* Checa-Soler, 1997.

Propachynolophus gaudryi was "based upon miscellaneous isolated teeth and jaw fragments constituting a part of the fossil vertebrate sample collected in the vicinity of Epernay (Marne)" (Savage *et al.*, 1965: 16), a sample known as the "Ageian fauna". This fauna was diachronic, but the material referable to *Propachynolophus* is restricted to Ypresian levels of the Paris Basin, namely from the "*Sables à unios et térédines*". Better-calibrated localities have since been discovered, such as Mancy, Grauves, or Monthelon (Louis, 1996). They allow for assigning a Late Ypresian age to the hypodigm of both *P. gaudryi* and *P. maldani*, around the reference level MP 10 (BiochroM'97).

No holotype has been explicitly chosen by Lemoine (1891). Accordingly, Savage *et al.* (1965) have designated a lower jaw fragment with M/1-M/3 (MNHN AL-5210) as the lectotype of *P. gaudryi* (Savage *et al.*, 1965: fig. 8). MNHN AL-5210 is the posterior part of the mandible figured by Teilhard de Chardin (1922: pl. 8, fig. 8); its anterior part (MNHN AL-6685) might belong to another unidentified taxon, following Savage *et al.* (1965: 16). Quite a lot of jaw fragments and isolated teeth referred to *P. gaudryi* are notably deposited in the FSL, MNHN and NMB collections. Several of these specimens were published and figured by Savage *et al.* (1965: fig. 7, 10, 11).

Other species assigned to *Propachynolophus* are less well documented. *Propachynolophus maldani* and *P. remyi* are mostly known by isolated teeth and fragmentary jaws. *Propachynolophus levei* is based on a single maxilla fragment with P3/-M3/ (Figures 1, 2).

The Geiseltal specimens which were first reported to *P. gaudryi* (see Matthes, 1977) must be dissociated from that taxon. They have led to the definition of *Hallensia* Franzen & Haubold, 1986, considered by them as more archaic than basalmost hyracotheres and close to phenacodontid condylarths. Eversince, *Hallensia* has been positioned at the base of the Equoidea by Holbrook (2009) and is beyond the scope of the present work.

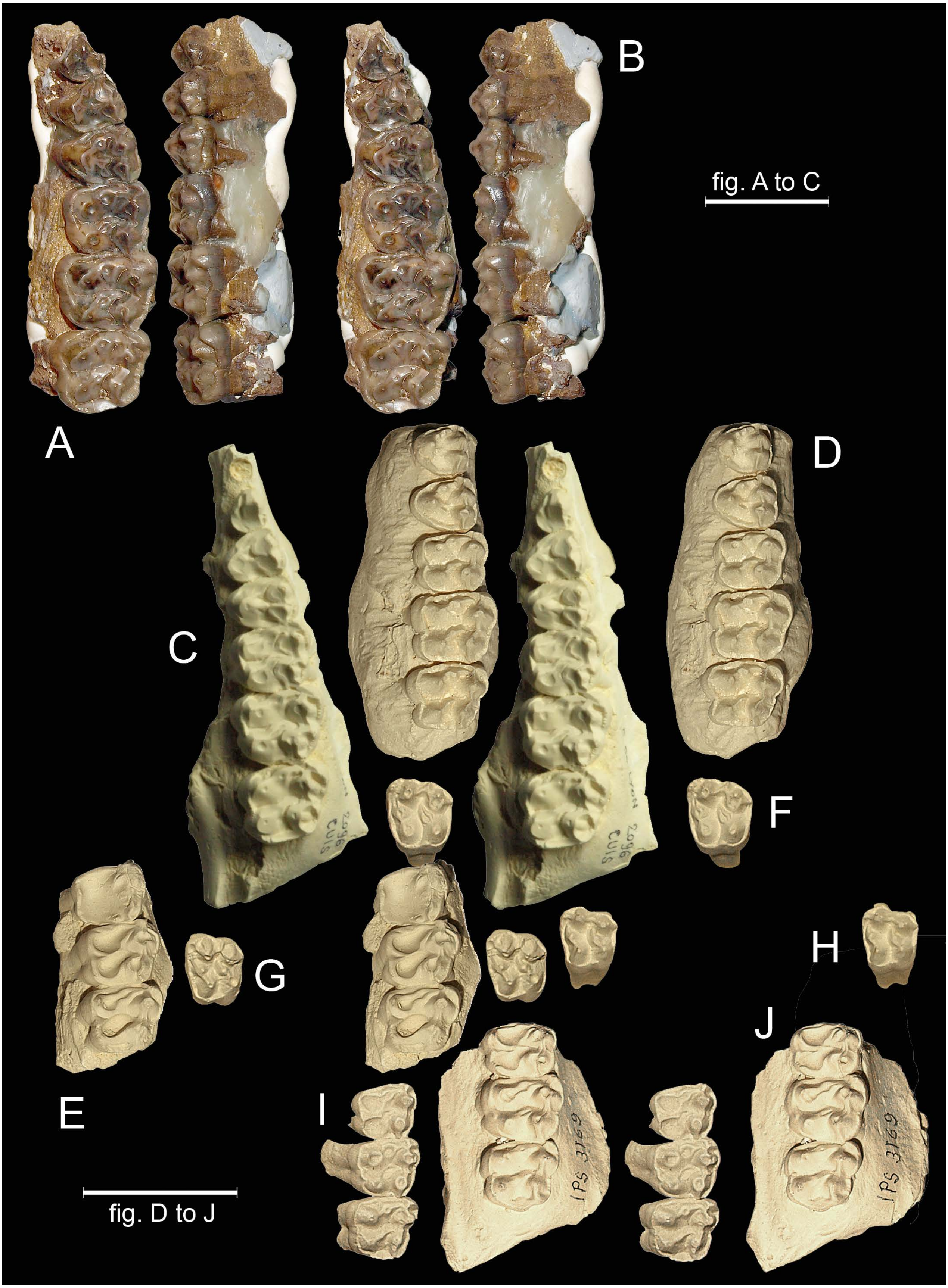

Figure 1. Upper cheek teeth of "*Propachynolophus*" (stereopairs). **A-B**, "*P.*" *gaudryi*, NMB TS-83, left maxilla with P2/-M3/; A, occlusal view, B, labial view. **C**, "*P.*" *gaudryi*, FSL 2096, left maxilla with P2/-M3/ (cast), occlusal view. **D**, "*P.*" *levei*, NHML M49399 (holotype), left maxilla with P3/-M3/ (cast), occlusal view. **E**, "*P.*" *maldani*, FSL 1971, left maxilla with M1/-M3/ (cast), occlusal view. **F-H**, "*P.*" *maldani*, left molars in occlusal views (casts); F, MNHN AL-6564, M2/; G, MNHN AL-6563, M1/; H, MNHN AL-6561, M1/. **I**, "*P.*" *remyi*, ICP 3114, right M1/-M3/ (cast, reversed), occlusal view. **J**, "*P.*" *remyi*, ICP 3169, left maxilla with M1/-M3/ (cast), occlusal view. Scale: 2 cm.

Figure 2. Lower cheek teeth of "*Propachynolophus*" (stereopairs). **A-B**, "*P.*" *gaudryi*, NMB TS-628, left mandible with P/2-M/3; A, occlusal view, B, labial view. **C-D**, "*P.*" *gaudryi*, MNHN AL-5210 (lectotype), left mandible with M/1-M/3 (cast); C, occlusal view, D, labial view. **E**, "*P.*" *maldani*, MNHN AL-5199 (holotype), right mandible with P/4, M/1-M/3 (cast, reversed), occlusal view. **F-G**, "*P.*" *remyi*, right mandibles with M/1-M/3 (casts, reversed), occlusal views; F, ICP 3120; G, ICP 3116. Scale: 2 cm.

The systematic status of all other small Eocene European Equoidea is still debated. They are either assigned to the Equidae Gray, 1821 by some authors (Savage *et al.*, 1965; Franzen, 1995), split between several super-families (McKenna & Bell, 1997) or assigned to Pachynolophinae Pavlov, 1888 (Remy, 1967, 1976) within Palaeotheriidae Bonaparte, 1850 *s. l.* (Simpson, 1945; Butler, 1952).

However, as supported by formal parsimony analyses, "Pachynolophinae" is a paraphyletic ensemble (Hooker, 1989; Danilo *et al.*, 2013).

Among Equoidea, *Hyracotherium* is considered as an early diverging representative of "Pachynolophinae" and more generally of all Palaeotheriidae (Hooker, 1989; Froehlich, 1999, 2002), excluding *Pliolophus* which is rather a primitive equid (Froehlich, 1999, 2002).

Beside *Hyracotherium* and *Propachynolophus,* Eocene "Pachynolophinae" also include *Pachynolophus* Pomel, 1847, *Propalaeotherium* Gervais, 1849, *Anchilophus* Gervais, 1852, *Lophiotherium* Gervais, 1852, *Paranchilophus* Casanova & Santafe, 1989, *Bepitherium* Checa & Colombo, 2004, *Eurohippus* Franzen, 2006, and *Metanchilophus* Remy, 2012. Other Palaeotheriidae, gathered as a subfamily Palaeotheriinae, aggregate the genera *Palaeotherium* Cuvier, 1804, *Plagiolophus* Pomel, 1847, *Paraplagiolophus* Depéret, 1917, *Leptolophus* Remy, 1965, *Pseudopalaeotherium* Franzen, 1972, *Cantabrotherium* Casanovas & Santafé, 1987, *Franzenium* Casanovas & Santafé, 1989, *Metaplagiolophus* Checa-Soler, 1993, *Mekodontherium* Remy, 2000, *Iberolophus* Badiola & Cuesta, 2008.

Propachynolophus has often been considered as an intermediate between hyracotheres (*Hyracotherium* and *Pliolophus*) and *Pachynolophus* (Depéret, 1901; Froehlich, 1999), though it would be closer to the latter (Depéret, 1901). Although it is still mentioned as a formal genus in the literature, its validity has long been questioned (Cooper, 1932) and most authors use it with caution and add quotation marks in some papers (Franzen, 1995: 34; Hooker, 1994 [for *P. maldani*]).

A description of the Equoidea of the Aumelas Middle Eocene locality in progress (Remy *et al.*, 2016) highlighted the interest of revising *Propachynolophus* and its definition. This is the aim of the present paper.

Institutional abbreviations

FSL, Université Claude Bernard, Lyon; GMH, Geiseltal Museum, Halle; ICP, Instituto Catalán de Paleontología Miquel Crusafont, Barcelona; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; MCZH, Museum of Comparative Zoology, Harvard; MNHN, Muséum National d'Histoire Naturelle, Paris; NHML, Natural History Museum, London; NMB, Naturhistorisches Museum, Basel; UCMP, University of California Museum of Paleontology, Berkeley; UM, Université de Montpellier.

Anatomical abbreviations and indexes

Dental nomenclature follows that of Froehlich (1999). Upper and lower cheek teeth are designated as follows, respectively: C/, P1/, DP1/, M1/... and /C, P/1, DP/1, M/1...

DPC: post-canine diastema = distance C-P2 (upper or lower) at bone level; %DPC: DPC/LRDJ x 100; H_{cing}: cingulum height / crown height x 100; $I_{H:}$ hypsodonty index = crown height / width x 100; LRDJ: length P2-M3 (upper or lower); PMI: premolar-molar index ($L_{P2\text{-}P4}/L_{M1\text{-}M3}$); S_P/S_M: area of (P2/-P4/) on area of (M1/-M3/) x 100; S_{P4}/S_{3M}: area of P4/ on area of (M1/-M3/) x 100.

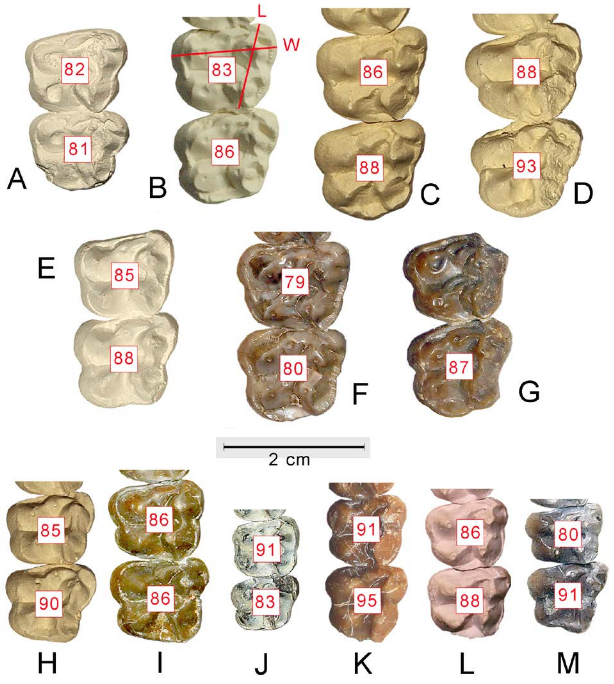

Figure 3. Relative width of upper molars in "*Propachynolophus*" and *Pachynolophus* species. Ratios **L/W** in percentage. To avoid misinterpretation of the rank of the teeth, only series with M2/-M3/ were retained. **A-G**, "*Propachynolophus*" *gaudryi*; A, MNHN L61-GR (reversed); B, FSL 2096; C, FSL 1960 (reversed); D, FSL 1961; E, MNHN L62-GR; F, NMB TS-83; G, NMB TS-742; **H-M**, *Pachynolophus*; H, *P. boixedatensis* ICP 2059; I, *P. cesserasicus* FSL 2977b; J, *P. eulaliensis* UM-SEL 101; K, *P. garimondi* UM-F1 290; L, *P. lavocati* MNHN Qu-7371; M, *P. livinierensis* FSL 3068.

Rationale

Propachynolophus was originally diagnosed as having brachydont and bunodont cheek teeth surrounded by rather well marked cingula. The premolars, hardly molarized, are devoid of hypocone or entoconid. Differential characteristics with *Pachynolophus*, to which it is usually compared, are actually very difficult to find. So we first need to critically revise the characters that were invoked in this purpose by authors (Depéret, 1901; Teilhard, 1922; Savage *et al.*, 1965), before performing an original cladistic analysis and comparing the results with previous ones (Hooker, 1989, 1994; Froehlich, 1999; Hooker & Dashzeveg, 2004; Danilo *et al.*, 2013).

Shape of upper molars. *Propachynolophus* was first defined as having upper molars squarer than those of *Pachynolophus* (Depéret, 1901; Hooker, 1989: character 67; Hooker, 1994: character 21). This assertion is in fact absolutely not verified when considering a sufficient sampling; the ranges of variation are largely overlapping (Supp-data 1, Figure 3). Among "Pachynolophinae", the correlation is strong between molar length and width ($r^2 = 0.92$) and there is no outlier: *Propachynolophus gaudryi* is distinguished only by its larger size (Figure 4).

Development, continuity and height of the cingula. *Propachynolophus* supposedly has thicker and more continuous cingula than *Pachynolophus* (Teilhard, 1922; Savage *et al.*, 1965), especially on upper premolars. Hooker (1994; character 20) noted also that the ectocingulum is always unbroken in upper molars, unlike *Pachynolophus* in which it can be interrupted at the level of the paracone. The thickness of upper molar lingual cingulum is also quoted in Danilo *et al.* (2013: character 48), as

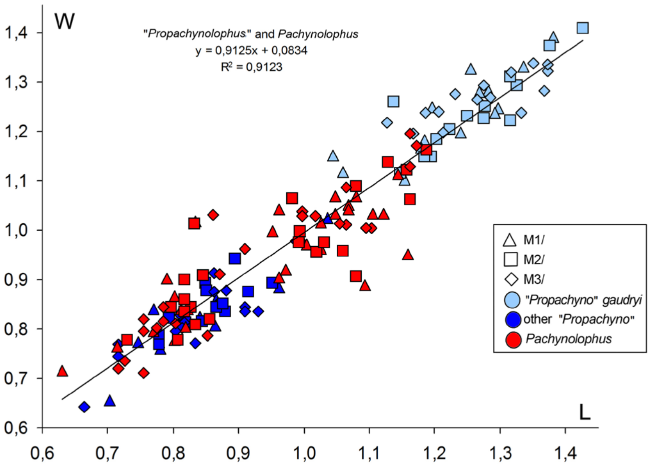

Figure 4. Relative width of upper molars in "*Propachynolophus*" and *Pachynolophus* species. Ratios **L/W** in percentage. To avoid misinterpretation of the rank of the teeth, only series with M2/-M3/ were retained. **A-G**, "*Propachynolophus*" *gaudryi*; A, MNHN L61-GR (reversed); B, FSL 2096; C, FSL 1960 (reversed); D, FSL 1961; E, MNHN L62-GR; F, NMB TS-83; G, NMB TS-742; **H-M**, *Pachynolophus*; H, *P. boixedatensis* ICP 2059; I, *P. cesserasicus* FSL 2977b; J, *P. eulaliensis* UM-SEL 101; K, *P. garimondi* UM-F1 290; L, *P. lavocati* MNHN Qu-7371; M, *P. livinierensis* FSL 3068.

being “strong to weak” in *Propachynolophus* whilst moderately developed and restricted to the medivallum in *Pachynolophus*. In fact, some upper cheek teeth of *Propachynolophus,* notably of *P. gaudryi,* have interrupted or almost absent labial cingula (e.g., FSL 1997, MNHN AL-6536) or show an interrupted lingual cingulum (e.g., FSL 6385, MNHN AL-6533 [Savage *et al.*, 1965, fig. 7c-e]).

The same situation occurs regarding the labial cingulum on lower molars. Likewise, the difference between both genera is not clear-cut. While considered as continuous in *Propachynolophus* (character 60 in Danilo *et al.*, 2013), the labial cingulum is very narrow and more or less interrupted on some molars of *P. gaudryi* (e.g., the holotype MNHN AL-5210), but also interrupted on some molars of *P. remyi* (e.g., ICP 3159). On the contrary, it can be almost complete to continuous in *Pachynolophus* specimens, such as UM-SEL 2, 5, 8 (*P. eulaliensis*) or UM-AUM 161 (*Pachynolophus* sp. 1, Aumelas).

Moreover, Danilo *et al.* (2013: character 61) noted that the lower molar cingula of *Propachynolophus* were higher than those of most *Pachynolophus* (except for *Pachynolophus eulaliensis*). This character is difficult to objectify. Accordingly, I have measured the percentage ratio between the cingulum height and the crown height at the paracone (or respect. at the protoconid) (Figure 5). The variation ranges do not show any clear-cut separation between the representatives of both genera.

In fact we can only observe a gradual reduction in height of the cingula through time on upper and lower cheek teeth (r^2 = 0.72 and 0.73 respectively), and *Propachynolophus* fits well into this scheme according to its biochronological situation (Figure 6; Supp-data 2, 3).

In this regard, it is worth noting that the specimen FSL 2977 from La Livinière, neotype of “*Pachynolophus cesserasicus* Gervais, 1849”, presents almost continuous cingula on premolars and had been considered as belonging to a species hypothetically related to *Propachynolophus gaudryi* (Savage *et al.*, 1965: 56).

Crown height and convergence of labial sides of cusps. One may also wonder if the crown height increase observed through time within Equoidea would distinguish *Propachynolophus* from *Pachynolophus*. Unfortunately, this parameter is difficult to quantify in brachydont forms; the plan of the neck which is the basis for that measure is an imprecise concept and its determination more or less subjective (Savage *et al.*, 1965: 67). As a result, the index I_H may be highly variable within a given species (V = 10.6 in *P. gaudryi* and 12.6 in *Pachynolophus* sp.1

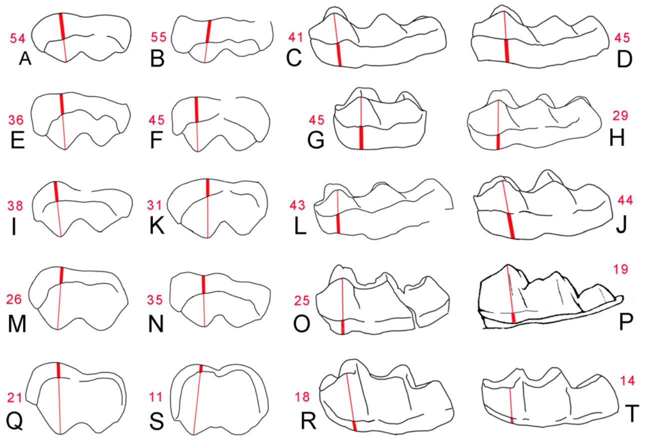

Figure 5. Relative height of cheek teeth cingula, in “*Propachynolophus*” and other equoid species, as it has been quantified (Supp-data 2, 3). The percentage ratio retained is the cingulum height (heavy red line) on the total crown height, measured at the paracone (upper teeth) or at the protoconid (lower teeth). **A**: *Hallensia matthesi*, right M3/ (reversed) from GMH 14-439; B-C: *Hyracotherium leporinum*, **B**, right M3/ (reversed) from NHML 16336; **C**, left M/3 from NHML M51682; **D**: *Pliolophus barnesi*, right M/3 (reversed) from NHML M44910; E-H: “*Propachynolophus*” *gaudryi*, **E**, right M3/ (reversed) from FSL 1960; **F**: right M3/ (reversed) MNHN AL-6532; **G**, left M/2 from FSL 2043; **H**, left M/3 from MNHN L10Ma; I-J: “*Propachynolophus*” *remyi*, **I**, left M3/ from ICP 3374; **J**, right M3/ (reversed) from ICP 3092; **K**: “*Propachynolophus*” *levei*, left M3/ from NHML M49399 (cast); **L**, “*Propachynolophus*” *maldani*, right M/3 (reversed) from MNHN AL-5199; **M**: *Pachynolophus* sp., left M1/ from UM-AUM 321; **N**: *Pachynolophus boixedatensis*, left M3/ from ICP 2059; **O**: *Pachynolophus livinierensis*, right M/3 (reversed) from NMB Liv-28; **P**: *Pachynolophus garimondi*, left M/3 from UM-F1 290; Q-R; *Pachynolophus lavocati*, **Q**, left P4/ from MNHN Qu-7371; **R**, left M/3 MNHN Qu-7372; S-T, *Pachynolophus zambranensis*, **S**, right M2/ (reversed) MCNA 10666; **T**, right M/3 (reversed) MCNA 10668. Not to scale.

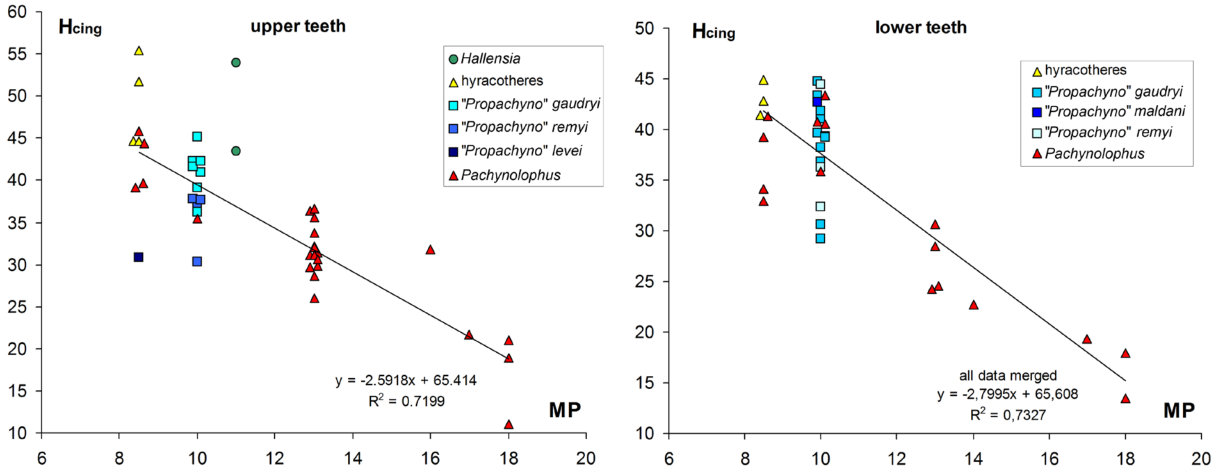

Figure 6. Evolution of the relative height of the check teeth labial cingulum (Hcing) in hyracotheres, “*Propachynolophus*” and *Pachynolophus* (measured at level of paracone or protoconid), according to admitted biochronological data (BiochroM’97). Some data were slightly staggered to mitigate overlaps.

from Aumelas [Supp-data 4]). In this context, the indexes of *Pachynolophus* largely overlap with those of *Propachynolophus* as well as with those of hyracotheres and the character I_H can not be used either to differentiate these genera (Figure 7).

In order to estimate and compare crown height on upper molars, Hooker (1994: character 12) also suggested to consider the angle formed by the external sides of labial and lingual cusps. He then asserted that this angle was ranging between 90° and 100° in *Propachynolophus* and less than 90° in less brachyodont taxa. In fact, this parameter is difficult to assess because of strong intraspecific variation, even on a single tooth depending on the cusps considered. I have however tested it (Supp-data 5, Figures 8, 9). In this case too, the data greatly overlap, and although the mean value for *Propachynolophus* slightly exceeds that for *Pachynolophus*, the difference does not seem to be significant. In any case it can not be considered as a discriminant character.

Individualization of the conules in upper cheek teeth. In terms of morphological characters, Savage *et al.* (1965) noted that the genus *Propachynolophus* was characterized by upper molars showing highly developed and well individualized paraconules and metaconules, as in *Hyracotherium*. Moreover, the paraconule would be slightly more offset distally from the preprotocrista than on *Pachynolophus* (Froehlich, 1999: character 44). Likewise, the presence of a groove separating the metaconule from the hypocone (Hooker, 1989: character 40; Danilo *et al.*, 2013: character 31), resulting in a metaloph more stepped than in *Pachynolophus* (Froehlich, 1999: characters 49 and 56) would be typical of *Propachynolophus*. But these characters, often difficult to objectify, mostly reflect the persistence of a certain degree of bunodonty. They are also found at some extent in representatives of *Pachynolophus* (e.g. *P. duvali*, *P.* sp.1 in Aumelas, *P. garimondi*, or *P. cesserasicus* [Figure 10]), and very lophodont species of *Pachynolophus* where conules are totally fused into lophs, such as *P. lavocati*, may then be considered as derived forms.

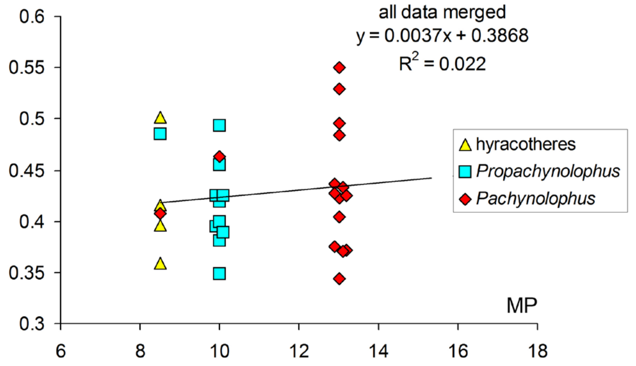

Figure 7. Evolution of height of upper molars in hyracotheres, "*Propachynolophus*" and *Pachynolophus* according to admitted biochronological data (BiochroM'97).

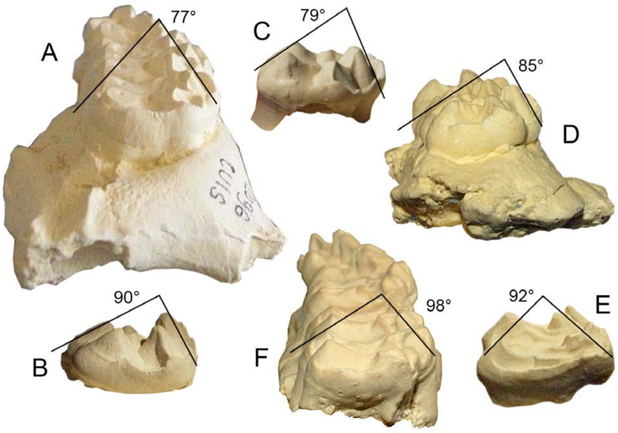

Figure 8. Examples of convergence angles between outer walls of paracone and protocone in "*Propachynolophus*" and *Pachynolophus* (see Supp-data 5). **A-C**, "*Propachynolophus*" *gaudryi*; A, left M3/ from FSL 2096; B, right M3/ (reversed) FSL 2047; C, left M3/ FSL 1997. **D-F**, *Pachynolophus*; D, *P. boixedatensis*, left M3/ from ICP 3059; E, *P. duvali*, left M3/ MNHN PS-11487; F, *P. duvali*, left M3/ from MCZH 5464. Not to scale.

Relations between protoloph and ectoloph. The protoloph-preparacrista relation on upper molars, rather subtle to objectify, also presents some variability. Although scored as notched in *Propachynolophus* (Hooker, 1989: character 41; Froehlich, 1999: character 57; Danilo *et al.*, 2013: character 36), the junction seems to be complete on some specimens of *P. gaudryi* (Hooker, 1994: character 2), e.g. NMB TS-83, MNHN AL-1973, MNHN AL-6549, and FSL 1997. Instead of being connected in *Pachynolophus*, it is conversely interrupted on some molars such as MNHN CGR-90 (*P. duvali*), FSL 2977b (*P. cesserasicus*), FSL 3068 (*P. livinierensis*), and UM-AUM 176, 194, 231 (*P.* sp.1, Aumelas), contrary to Froehlich's (1999: character 55) assertion.

Alignment of the metastyle. The supposed alignment of the metastyle with the labial cusps in *Propachynolophus* (Danilo *et al.*, 2013: character 53) is difficult to observe because the former is lower than main cusps and often barely prominent. A statement about this parameter is therefore fairly subjective. Moreover, there is a noticeable variability in some taxa: the metastyle is labially shifted in some specimens of *P. gaudryi* (NMB TS-83, MNHN AL-6532, AL-6534, and FSL 1997). Conversely, it is sometimes aligned in *Pachynolophus* (e.g., MNHN CGR-90 [*P. duvali*], UM-SEL 87 [*P. eulaliensis*], and UM-F1 290 [*P. garimondi*]) and in most specimens of *P.* sp. 1 from Aumelas.

Relative distance between protocone and hypocone. The relative length of the gap between protocone and hypocone was also used to distinguish both genera. This gap was estimated as subequal to the paracone-metacone gap in *Propachynolophus gaudryi* (Hooker, 1994: character 22), while it would often exceed it in *Pachynolophus* (Danilo *et al.*, 2013: character 56). My measurements show a wide variability for this parameter and do not confirm such assertions (Supp-data 6). Indeed, the

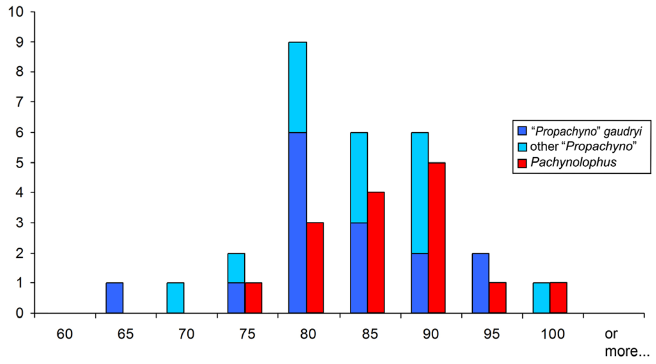

Figure 9. Convergence angles (in degrees) observed between the outer sides of paracone and protocone of upper cheek teeth in "*Propachynolophus*" and *Pachynolophus* (see Supp-data 5).

mean value of the protocone-hypocone gap is slightly higher in *Propachynolophus* than in *Pachynolophus*, according to the available sample, but data overlap too much for a significant difference to be demonstrated between both genera (Figure 11).

Shape of P4/. Concerning the premolars, P4/ is considered as always triangular in *Propachynolophus*, contrary to *Pachynolophus* (Danilo *et al.*, 2013: character 20) and a posterior-lingual expansion of the distal cingulum of P4/ is supposedly characteristic of *Pachynolophus* (Danilo *et al.*, 2013: character 22). But if a fair number of specimens are taken into account, these differences are vanishing. Actually, some species of *Pachynolophus* retain triangular P4/ (*P. duvali, P. garimondi*, P. *cesserasicus*, and P. *livinierensis*) while some representatives of *Propachynolophus* have subquadratic P4/ with a large lingual outline (e.g., FSL 2048, 2096 [*P. gaudryi*], ICP 3374 [*P. remyi*], and NHML M49399 [*P. levei*]). In the same way the posterior expansion of the distal cingulum which characterizes some *Pachynolophus* species is also present on some teeth of *Propachynolophus* (e.g., MNHN L31-GR and FSL 2048 [*P. gaudryi*] or ICP 3374 [*P. remyi*]; [Figure 12]).

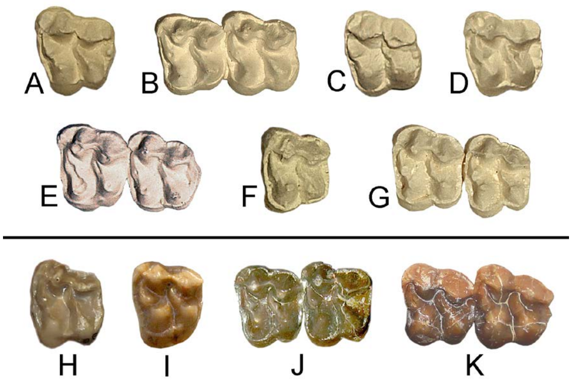

Figure 10. Some examples of upper molars of "*Propachynolophus*" with protoloph and metaloph grooves no more stepped than in *Pachynolophus* and with paraconule not distally offset, facing molars of *Pachynolophus* with deep protoloph and metaloph grooves. Not to scale. **A-G**: "*Propachynolophus*"; A-B, "*P.*" *gaudryi*; A, left M1/ FSL 1973; B, left M2/-M3/ MNHN L62-GR; C-D, "*P.*" *maldani*; C, left M3/ MNHN AL-6552; D, right M3/ (reversed) MNHN AL-6547; E-F, "*P.*" *remyi*; E, left M2/-M3/ from ICP 3169; F, left M2/ ICP no n°; G, "*P.*" *levei*, left M2/-M3/ from NHML M49399. **H-K**: *Pachynolophus*; H, *P. duvali*, right M3/ (reversed) MNHN CGR-90; I, *P.* sp. (Aumelas), left M1/ UM-AUM 194; J, *P. cesserasicus*, right M2/-M3/ (reversed) from FSL 2977b; K, *P. garimondi*, left M2/-M3/ from UM-F1 290.

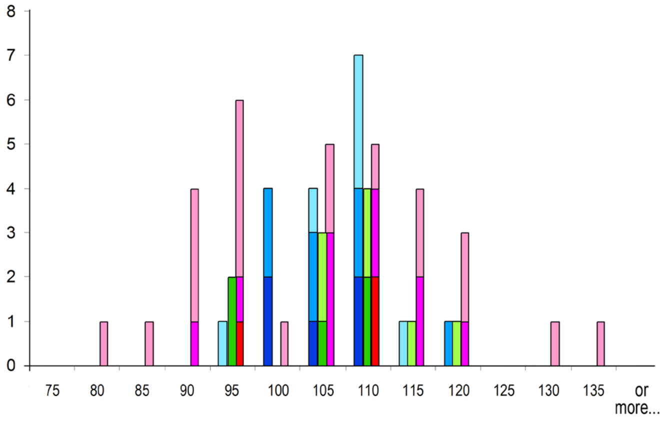

Figure 11. Spacing index protocone - hypocone / paracone - metacone on upper molars of "*Propachynolophus*" and *Pachynolophus* (see text). **Blue**: "*Propachynolophus*" *gaudryi*; **green**: other "*Propachynolophus*"; **red or pink**: *Pachynolophus*. **Dark** color: M1/; **medium**: M2/; **light**: M3/.

Consequently, the shape of P4 / in *Propachynolophus* is not significantly different from that of *Pachynolophus*.

Shape of P3/. A distal enlargement of the occlusal surface is sometimes observed on P3/ of *Propachynolophus* (NMB Ts-83 and MNHN AL-6538), with a weakly developed protoloph, as in *Pachynolophus* (Hooker & Dashzeveg, 2004: character 30). Contrary to the assertion of Froehlich (1999: character 24), the paraconule of this tooth is not always distal to the protocone-parastyle line on *Pachynolophus* (e.g., UM-AUM 199 [*P.* sp.2, Aumelas]; UM-F1 290 [*P. garimondi*]; MNHN Qu-7371 [*P. lavocati*]; FSL 3068 [*P. livinierensis*]). It could even have been more mesial (see the P4/ ICP 3059, Fig. 12N [*P. boixedatensis*]).

Diastemata between P1 and P2. Contrary to Hooker (1989: character 14), *Propachynolophus* is also described as having a diastema between upper and lower P1 and P2. This feature is poorly documented and likely inconstant: the maxilla assigned to *P. gaudryi* FSL 6385 (Savage *et al.*, 1965, fig. 7c) has such a diastema, but this diastema is not inferred in NMB Ts-83 (a concavity at the front edge of the specimen appears to be the alveolus of P1/ closely appressed to P2/).

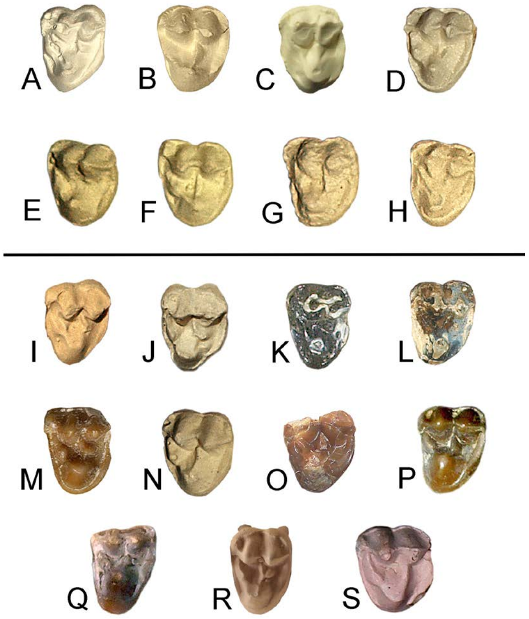

Figure 12. Shape variability of P4/ in "*Propachynolophus*" and *Pachynolophus* species. **A-H**: "*Propachynolophus*"; A-C, "*P.*". *gaudryi*; A, left P4/ MNHN L31-GR; B, right P4/ (reversed) FSL 2048; C, left P4/ from FSL 2096; D, "*P.*" *levei*, left P4/ from NHML M49399 (cast); E-H, "*P.*" *remyi*; E,F, two left P4/ ICP no n°; G, left P4/ from ICP 3374; H, left P4/ ICP 3146. **I-S**: *Pachynolophus*; I-J, *P. duvali*; I, left P4/ from MCZH 5464; J, left P4/ MNHN Ps-11484; K-L, *P. eulaliensis*; K, left P4/ from UM-SEL 25; L, right P4/ (reversed) from UM-SEL 10; M, *P.* sp. (Aumelas) left P4/ from UM-AUM 231; N, *P. boixedatensis*, left P4/ from ICP 3059; O, *P. garimondi*, left P4/ from UM-F1 290; P, *P. cesserasicus*, left P4/ from FSL 2977a; Q, *P. livinierensis*, left P4/ from FSL 3068; R, *P. cayluxi*, right P4/ (reversed) from MNHN QU-8225; S, *P. lavocati*, right P4/ (reversed) from MNHN QU-7371. Not to scale.

Likewise, whereas hyracotheres are assumed to bear such a diastema, it is lacking in the skull of *Pliolophus vulpiceps* NHML M10657 (Simpson, 1952, fig. 1b ["specimen 3"]) as well as in the mandible of *Pliolophus barnesi* NHML M44910 (Hooker, 2010, text-fig. 54 b). Although missing in *Pachynolophus duvali* (Savage *et al.*, 1965, fig. 16a, 17b) and in the mandible of *P. livinierensis* NMB Liv-28 (Savage *et al.*, 1965, fig.19) this diastema occurs in the skull of *P. cesserasicus* FSL 2977 and in those of *P. eulaliensis* (Danilo *et al.*, 2013: 202, table 2). There is no diastema on the maxilla UM-AUM 231 (*P.* sp.1, Aumelas), whereas it is probably present in the mandible UM-AUM 161, referred to as the same taxon.

Length of post-canine diastemata (DPC). Could the relative length of DPC (gap between upper or lower C and P2 at the bone level) be more relevant, since short diastemata have been considered as archaic (Franzen 1968, 1972)? The DPC is assumed to be short in *Propachynolophus* (less than 30% of LRDJ) and longer in *Pachynolophus* (Hooker, 1989: character 16; Danilo *et al.*, 2013: character 7). Similarly, Froehlich (1999: character 17), considering the diastema C-P1 (upper or lower), noted that it was much longer in *Pachynolophus* than in *Propachynolophus*. But, to my knowledge, the DPC is measurable only on one specimen of *Propachynolophus*, the mandible of *P. gaudryi* UCMP 64904 (Savage *et al.*, 1965: fig.10). Moreover, this parameter presents a great intraspecific variability in some Equoidea, such as the well documented *Propalaeotherium hassiacum* Haupt, 1925, where the coefficient of variation of the relative length of the DPC ($\%_{DPC}$) reaches 11.5 at the maxilla (Supp-data 7) and 12.4 at the mandible (Supp-data 8). The DPC of the lower jaw UCMP 64904 (*P. gaudryi*) is barely shorter than the limits of variation observed on *Pliolophus vulpiceps*, *Propalaeotherium hassiacum*, or *Pachynolophus eulaliensis* (Supp-data 8, Figure 13). Consequently, and pending more available data, this character cannot be retained to characterize *Propachynolophus*.

Posterior wall of the trigonid of lower cheek teeth. Upper and lower molar morphologies are widely correlated, which led Hooker (1989) to amalgamate some features of these molars in his cladistic analysis. Several features specifically observed on the lower molars are however to be considered. Thus, the posterior wall of the trigonid is mentioned as shallow in *Propachynolophus* (Hooker, 1994 character 19; Froehlich, 1999: character 90), but steep in *Pachynolophus* (Hooker & Dashzeveg, 2004: character 19). But this feature is somewhat variable and I have found no significant difference between both genera.

Paracristid orientation on lower cheek teeth. The orientation of the paracristid has also been considered for discriminating *Propachynolophus* from *Pachynolophus*. The angle between this ridge and the longitudinal axis of the tooth would be 40° instead of 20° (Froehlich, 1999: character 87). It could even be lowered up to 10° in *Pachynolophus* according to Hooker & Dashzeveg (2004: character 17). My measurements in no way confirm these assertions: within the considered sample, this angle is fairly variable and it fully overlaps between both taxa (Supp-data 9, Figures 14, 15).

Orientation of the cristid obliqua on lower cheek teeth. Froehlich (1999: character 80) considers the cristid obliqua (or metalophid) of lower molars to be less lingual in *Propachynol-*

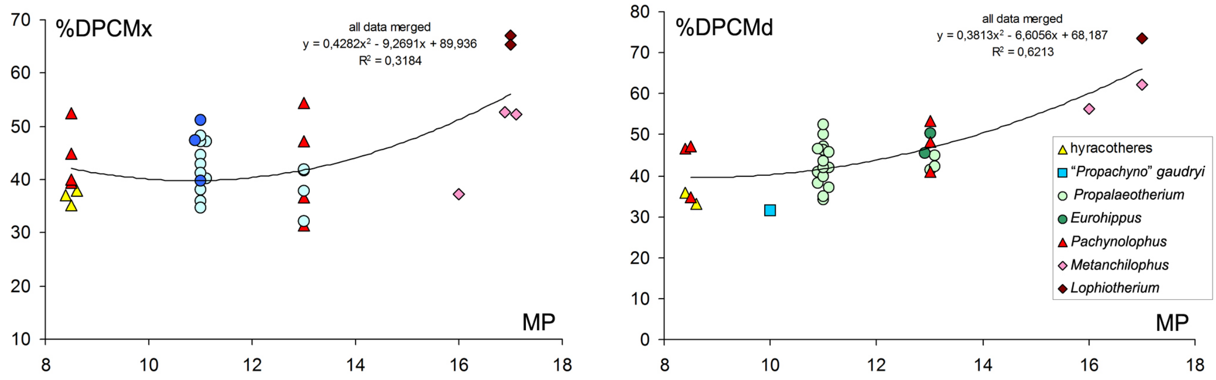

Figure 13. Evolution of relative lengths of the DPC (at the maxilla and the mandible) in hyracotheres and "Pachynolophinae" according to admitted biochronological data (BiochroM'97). Regression lines of the available data fit better with a polynomial model (r^2 resp. 0.32 and 0.62) than with linear ones (r^2 resp. 0.19 and 0.53); it seems therefore not have been any evolution during early and middle Eocene perhaps followed by some progress during the late Eocene.

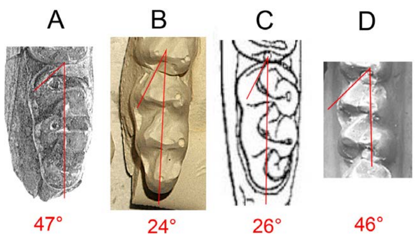

Figure 14. Examples of paracristid angle in "*Propachynolophus*" and *Pachynolophus*. **A-B**, "*Propachynolophus*" *gaudryi*; A, right M/3 (reversed) from MNHN AL-5213, Teilhard, 1922, pl.8 fig.9a; B, left M/3 from FSL 2042. **C-D**, *Pachynolophus*; C, *P. garimondi*, left M/3 from UM-F1 183, Remy, 1967, fig. 19; D, *P. livinierensis*, left M/2 from FSL 2943. Not to scale.

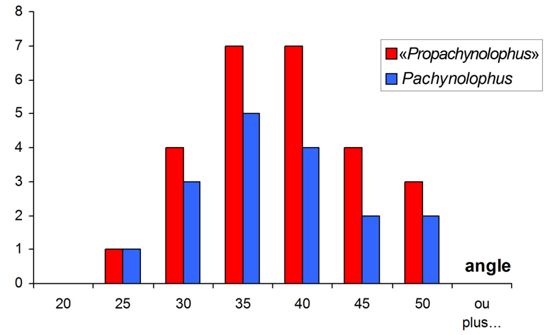

Figure 15. Angles (in degrees) between the paracristid of lower molars and the parasagittal plane. (See Supp-data 9).

ophus than in *Pachynolophus*. From a large sample, I did not find any significant difference between both genera, no more than about the relative size and position of the metaconulid (distal splitting of the metaconid), contrary to Froehlich (1999: character 83) (Supp-data 10).

Development of the hypolophid of M/3. The hypoconulid of M/3 is supposedly larger in *Propachynolophus* than in *Pachynolophus* (Froehlich, 1999: character 100), with an anterior cristid pointing toward the middle of the hypolophid, not toward the entoconid as in *Pachynolophus* (Teilhard de Chardin, 1922). The surface of the hypoconulid, anyway difficult to quantify, presents some variability and no significant difference can be detected between *Propachynolophus* and *Pachynolophus* (Danilo *et al.*, 2013: character 67). Likewise the orientation of the hypolophid toward the mid-hypoconulid is also found in some representatives of *Pachynolophus*: *P. duvali* (MNHN MP-2 [Savage *et al.*, 1965: fig. 17a]), *P. boixedatensis* (ICP 3053, 3058, BX-32), *P. livinierensis* (NMB Liv-28 [Savage *et al.* 1965: fig. 19]) and *P. eulaliensis* (UM-SEL 28) (Figure 16). Thus, these features cannot be used to define *Propachynolophus*.

Other morphological features. Several other dental traits, such as: (a) tilting of parastyle or paracone of upper molars (Hooker, 1989: character 57; Hooker & Dashzeveg, 2004: character 45), (b) hypolophid of lower molars less lophoid (Froehlich, 1999: character 91), (c) more median and discrete position of hypoconulid of M/1-2 (Froehlich, 1999: character 95; Hooker & Dashzeveg, 2004: 37), and (d) cristid uniting hypoconid to entoconid always missing on P/4 (Froehlich, 1999: character 76) have also been invoked to distinguish *Propachynolophus*. All these features are shared by *Pachynolophus* in the context of intra- and/or interspecific variation. They widely overlap and never constitute reliable discrete characters.

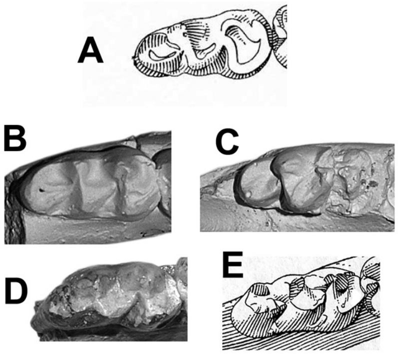

Figure 16. Some third lower molars of *Pachynolophus*, on which a junction of the labial cristid of the hypoconulid to the middle of the hypolophid is conspicuous. **A**: *P. duvali*, right M/3 from MNHN MP-2 in Savage *et al.* (1965, fig.17a); **B-C**: *P. boixedatensis*, left M/3 reversed: B, from ICP 3053, C, from ICP 3058; **D**: *P. eulaliensis*, right M/3 from UM-SEL 28; **E**: *P. livinierensis*, right M/3 from NMB Liv-28 in Savage *et al.* (1965, fig. 19). Not to scale.

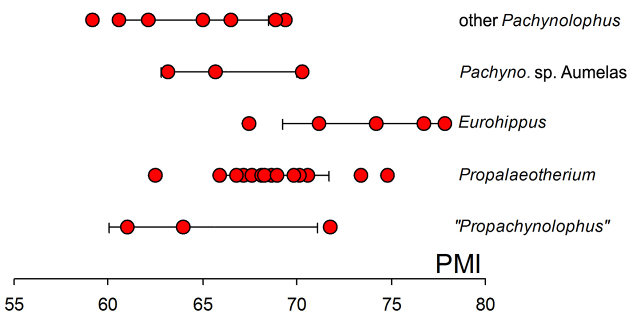

Figure 17. PMI indexes of upper cheek teeth in "Pachynolophinae". The lines equate to 1 standard deviation.

Finally, I do not know on what basis Froehlich (1999: character 115) founded his observation that the metacarpals would be relatively longer than the metatarsals in *Pachynolophus*, unlike *Propachynolophus*. To my knowledge, no postcranial remain can be assigned to *Pachynolophus* with certainty.

If we add that the cranial and postcranial morphology of *Propachynolophus* is unknown, we come to an unequivocal conclusion. This taxon has never been defined based on discrete and exclusive features, but mostly on characters shared with *Pachynolophus* under high variability and broad overlaps, or exhibiting simple differences of degree often difficult to objectify. Consequently, these features are not relevant to define a genus.

In that context, we must search what might be the systematic status of species assigned to "*Propachynolophus*". At the species level, although the characters that led to the definition of the type species *gaudryi* were not discriminating, the fact remains that this one is however distinguished by its large size and the occasional presence of a mesostyle on upper molars. It therefore presents characters expected in a basal *Propalaeotherium* as already suspected by Stehlin (1941: 295) and Savage *et al.* (1965: 26).

At this step of the discussion, one should consider the relative development of the premolar area in "Pachynolophinae". The PMI length ratio does not give satisfactory results since the variability ranges of *Pachynolophus*, *Propachynolophus*, and *Propalaeotherium* are widely overlapping (Supp-data 11; Figure 17). Moreover, one cannot find any significant change through time. Yet, regarding the area ratios (Supp-data 12), the premolar area seems to get reduced over time (in continuity with hyracotheres) within *Pachynolophus* whether we consider the ratio S_P/S_M or the ratio S_{P4}/S_{3M}. There seems to be an opposite trend in propalaeotheres (*Propalaeotherium* + *Eurohippus*; Figure 18).

"Propachynolophus" *gaudryi* is positioned away from the regression lines of these two trends, with intermediate values between *Pachynolophus livinierensis* and *P. cesserasicus* but with a temporal gap between them considered as long (BiochroM'97). The inclusion of "*P*". *gaudryi* within pachynolophs reduces the coefficient of determination r^2 of their regression line (from 0.63 to 0.39 for S_P/S_M; from 0.61 to 0.38 for S_{P4}/S_{3M}). It has been tested that even if the temporal gap between these taxa were not as long than suspected, the decrease of the r^2 coefficient when the genus *Pachynolophus* is gathered with "*Propachynolophus*" *gaudryi*, remains unchanged. On the contrary if that last one is associated with propalaeotheres, the r^2 coefficient rises from 0.16 to 0.30 for S_P/S_M and from 0.21 to 0.36 for S_{P4}/S_{3M} (Figure 18). Although these comparisons could not evidently been considered as conclusive, they suggest that the affinities of "*P*." *gaudryi* would lie nearer to propalaeotheres than to pachynolophs. Which tends to confirm the intuition of Stehlin (1905, 1941) and Savage *et al.* (1965).

CLADISTIC ANALYSIS

In order to test the phylogenetic background and to infer taxonomic considerations regarding the representatives of

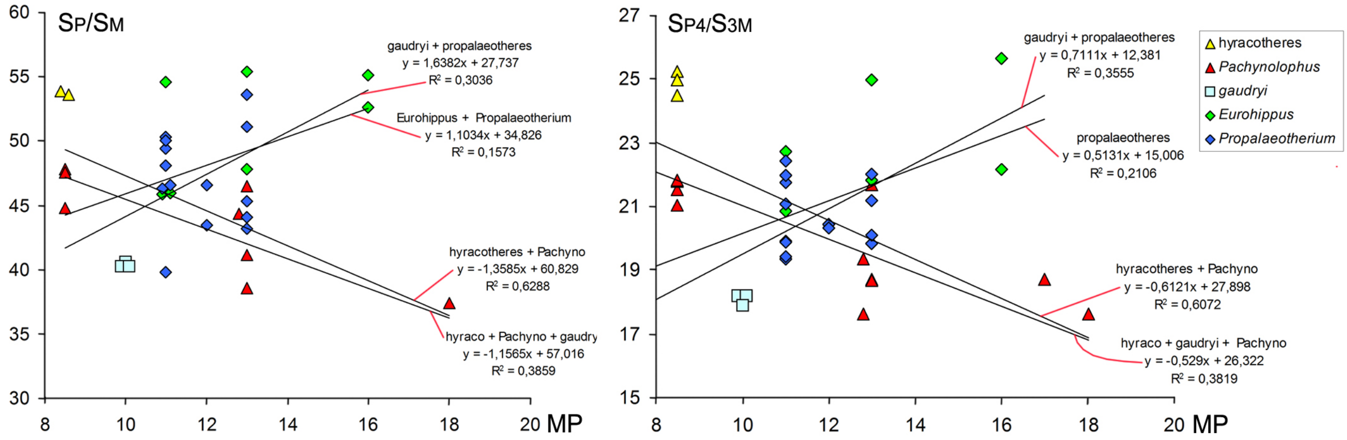

Figure 18. Evolution of ratios of the relative surfaces of upper cheek teeth in hyracotheres and Pachynolophinae", according to admitted biochronological data (BiochroM'97).

Propachynolophus, a cladistic analysis has been performed on the basis of the characters from Danilo *et al.* (2013), with further references to Hooker (1989, 1994) and Froehlich (2002). Some adjustments have been made to bring a special emphasis on species referred to as *Propachynolophus* and potentially related species among Palaeotheriidae.

Keeping in mind the caveats previously expressed, due to individual variability and interspecific overlaps of some features, I have tried to bring out a series of sufficiently well established parameters, and to quote the state that seems the best representative of a given taxon, for the apparently most variable features. Consequently I was led to significantly amend the set of characters considered by Danilo *et al.* (2013). Some original characters were also added, and some characters have been reconsidered (see characters description in Annex 1).

Then, several taxa have been removed either a priori (for being irrelevant in the current analysis or too poorly documented) or a posteriori as they were generating too much noise in the analysis: "*Pachynolophus*" *hookeri*, *Cymbalophus cuniculus*, "*Hyracotherium*" cf. *cuniculus*, *Pachynolophus garimondi*, *P. lavocati*, *P. zambranensis*, *P. boixedatensis*, *P. bretovensis*, *Anchilophus* (*Paranchilophus*) *remyi*, and *Metanchilophus dumasi*. On the contrary, three species of *Propalaeotherium* (*P. hassiacum*, *P. sudrei*, and *P. isselanum*) have been added, as well as an early representative of *Lophiotherium* (*L. pygmaeum*) and *Leptolophus nouleti* (thus allowing for enhancing the palaeotheriine sample). Following Danilo *et al.* (2013) the archaic tapiromorph *Cardiolophus radinskyi* was included in the outgroup, for which I have also considered the basal equoid *Hallensia matthesi*, and the only recognized European equid, i.e. *Pliolophus vulpiceps*.

The resulting matrix gathers 66 unweighted cranial and dental characters scored in 21 terminal taxa. The analysis of this matrix was performed with PAUP 4.0b.10 by means of a heuristic search with 1000 random replications, random stepwise addition procedure and default values for other PAUP parameters. A single most parsimonious tree was generated, with a length of 282 steps (CI = 0.38 and RI = 0.50). Of 17 nodes concerning the ingroup, 11 have a Bremer Index (BI) equalling 1, but six nodes are more robust with BI ranging from 2 to 7.

Description

The single most parsimonious tree is illustrated on Fig. 19, with all character states established from the matrix (Annex 2); temporal range of each taxon is indicated by wider lines on Fig. 20. This topology leads to the following comments.

The **node 1** (BI=1) individualizes Palaeotheriidae, with *Hyracotherium leporinum* as a first offshoot. Palaeotheriidae, monophyletic in the present analysis, are essentially characterized by two homoplastic unambiguous synapomorphy (HUS) (34[1] upper molar protoloph-ectoloph junction notched; 51[1] distal outline straight on M3/). *Hyracotherium leporinum* is discriminated by seven autapomorphies (15[2] complete postprotocrista on P3/; 19[1] presence of an accessory distal crest on the protocone of P3/-P4/; 26[1] protocone mesially shifted on P4/; 35[1] preparaconule crista directed towards the parastyle on upper molars; 39[2] parastyle large and protruding on upper molars; 50[1] metastyle oblique towards the labial side on Ml-2/; 55[2] high relative surface of P4/).

The **node 2** (BI=1) separates *Propachynolophus levei* from remaining palaeotheriids. It is supported by two non homoplastic unambiguous synapomorphies (NHUS) (32[2] metaloph grooves weak on upper molars; 38[1] metacone labial ripple weak on upper molars) and three HUS (31[1] protoloph grooves moderately developed on upper molars; 39[1] parastyle small but high on upper molars; 47[1] cingula/-ids moderately high on molars). Furthermore, *Propachynolophus levei* is individualized by one homoplastic autapomorphy (HA) (15[0] postprotocrista absent on P3/).

The **node 3** (BI=1) sets *Propachynolophus remyi* as the sister taxon to more derived palaeotheriids. It is only supported by one HUS (22[1] lingual cingulum reduced on the protocone of P4/). *Propachynolophus remyi* is individualized by six autapomorphies, i.e. one non homoplastic (24[1] missing P4/ postprotocrista) and five HA (23[1] important distal expansion of the posterolingual cingulum on P4/; 46[0] distal cingulum expansion of upper molars only observed on M3/; 51[0] distal outline convex on M3/; 54[1] weak surface difference between M3/ and M2/; 56[0] entoconid missing on P/4).

The **node 4** (BI=1) based on two HUS (8[1] buno-lophodont dentition, 44[1] lingual cingulum interrupted on upper molars), sets apart *Pachynolophus* from the remaining taxa [*Propachynolophus maldani* [*Lophiotherium* ["propalaeotheres", *Palaeotheriinae*]]].

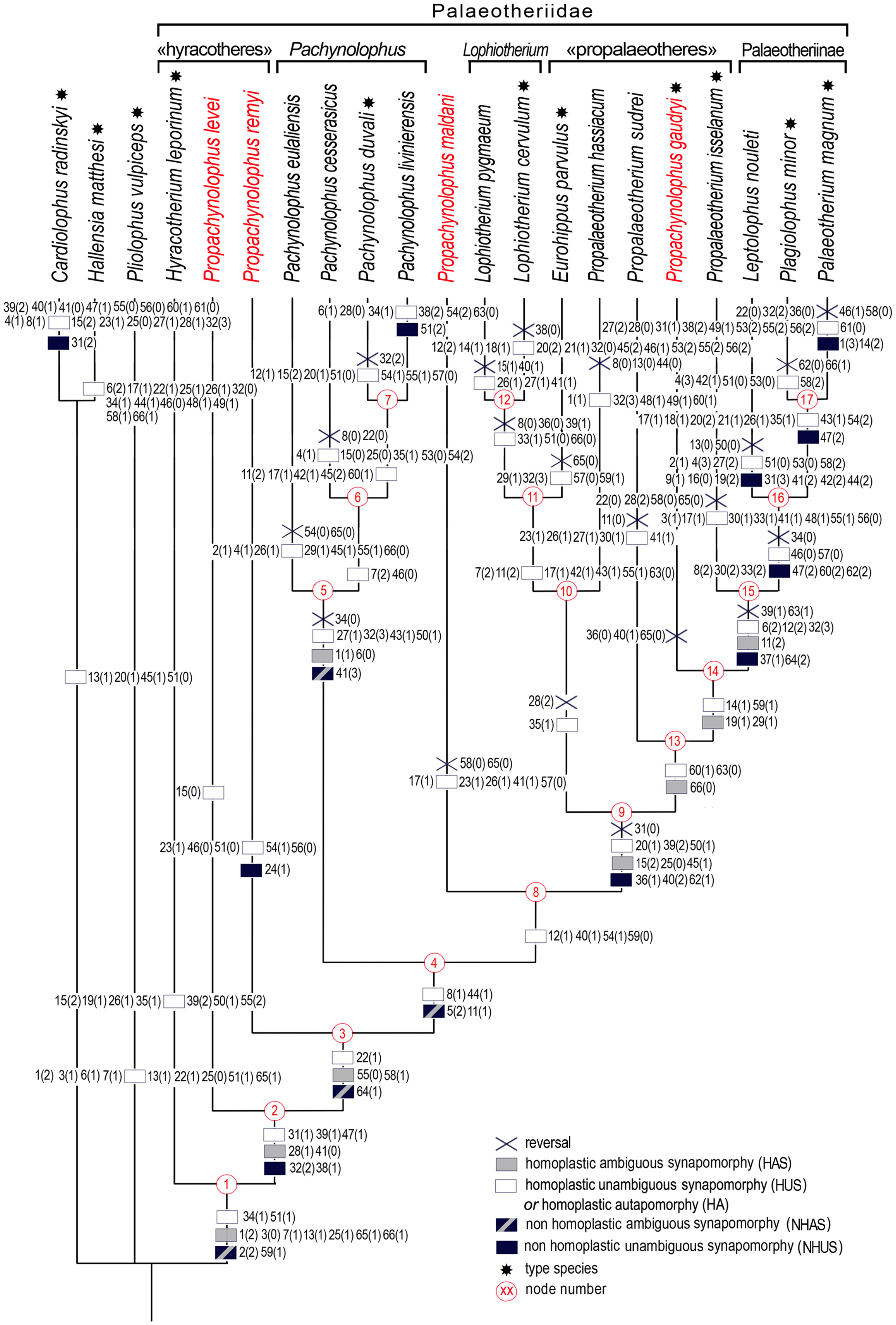

Figure 19. Most parsimonious tree of the cladistic analysis.

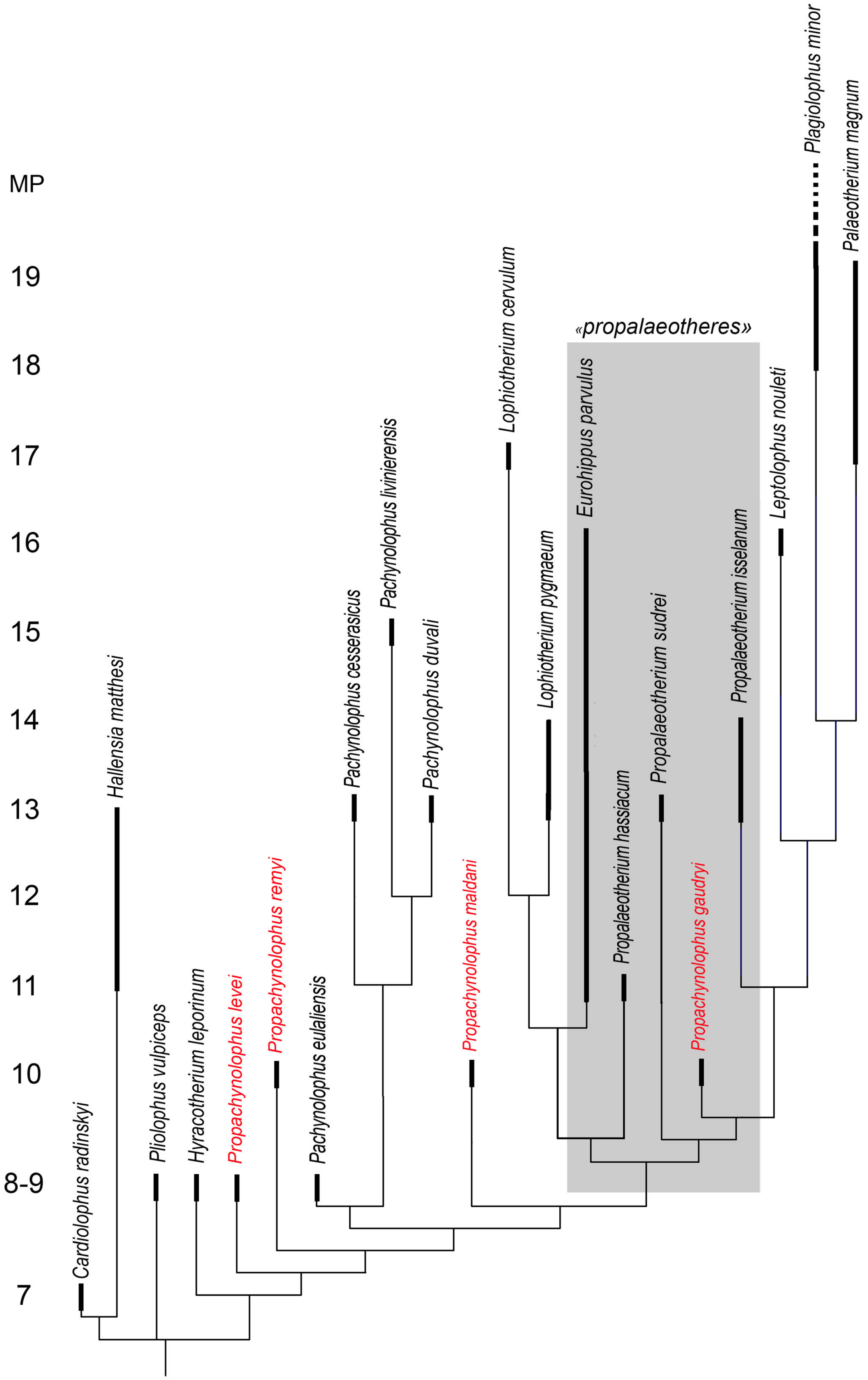

Figure 20. Chronologic distribution of the taxa considered in the cladistic analysis.

The **node 5** (BI=2) supports the monophyly of *Pachynolophus* on the basis of four HUS (27[1] paraconule moderately developed on P4/; 32[3] metaloph missing on upper molars; 43[1] labial cingulum medium to weak on upper molars; 50[1] metastyle oblique towards labial side on Ml-2/) and one reversal (34[0] protoloph-ectoloph junction unnotched on upper molars).

Other Palaeotheriidae are united at the **node 8** [BI=1] through four HUS (12[1] P2/ triangular, tapering forward; 40[1] occasional mesostyle on upper molars; 54[1] weak surface difference between M2/ and M3/; 59[0] protolophid and hypolophid transversely oriented on lower molars). *Propachynolophus maldani* has seven autapomorphies, i.e. five HA (17[1] metaconule more or less conspicuous on P3/; 23[1] posterolingual cingulum distally expanded on P4/; 26[1] protocone mesially shifted on P4/; 41[1] mesostyle strong and separated from the ectocingulum on upper molars; 57[0] lower molars narrow) and two reversals (58[0] labial cingulid thick and continuous on lower molars; 65[0] accessory crest missing on M/3).

The **node 9** (BI=1) gathers the *Lophiotherium* and Palaeotheriinae clades (**node 10** and **node 16**, respectively), plus a paraphyletic ensemble, here termed "propalaeotheres" and detailed hereafter. The **node 9** is supported by three NHUS (36[1] metaloph oriented towards the centrocrista on upper molars; 40[2] mesostyle always present on upper molars; 62[1] hypoconulid weak on M/1-M/2), three HUS (20[1] P4/ with a subquadrangular occlusal outline; 39[2] parastyle large and protruding on upper molars; 50[1] metastyle oblique towards labial side on Ml-2/) and one reversal (31[0] protoloph groove strong on upper molars).

The **node 10** (BI=1) defines the clade [*Propalaeotherium hassiacum* [*Eurohippus parvulus* [*Lophiotherium cervulum*, *L. pygmaeum*]]]. It is supported by one HUS (35[1] preparaconule crista directed towards the parastyle on upper molars) and one reversal (28[2] metaconule strong on P4/).

The **node 13** (BI=2) is characterized by two HUS (60[1] protolophid slightly notched on lower molars; 63[0] hypoconulid basin large on M/3). The first offshoot is *Propalaeotherium*s *sudrei*, with six autapomorphies, i.e. five HA (23[1] posterolingual cingulum distally expanded on P4/; 26[1] protocone mesially shifted on P4/; 27[1] paraconule moderately developed on P4/; 30[1] upper molar crowns moderately high; 41[1] mesostyle strong and separated from the ectocingulum on upper molars) and one reversal (11[0] presence of a post-P1 diastema).

More derived taxa are united at the **node 14** (BI=1) by two HUS (14[1] molarization incipient on P2/; 59[1] protolophid and hypolophid slightly inclined on lower molars), under the topology [*Propachynolophus gaudryi* [*Propalaeotherium isselanum*, Palaeotheriinae]]. *Propachynolophus gaudryi* is characterized by three reversals (36[0] metaloph directed towards the metacone on upper molars; 40[1] mesostyle occasionally present on upper molars; 65[0] accessory crest missing on M/3).

The clade including *Propalaeotherium isselanum* and the Palaeotheriinae is defined robustly at the **node 15** (BI=3) by two NHUS (37[1] paracone labial ripple weak on upper molars; 64[2] prehypocristulid oriented towards the entoconid on M/3), three HUS (6[2] high braincase index; 12[2] occlusal outline almost rectangular on P2/; 32[3] metaloph grooves missing on upper molars) and one reversal (39[1] parastyle not protruding but high on upper molars).

The **node 16** coincides with the best supported clade of the current analysis (BI=7), with *Leptolophus nouleti* as a sister taxon to the [*Plagiolophus minor*, *Palaeotherium magnum*] clade. Palaeotheriinae are diagnosed by the presence of six NHUS (8[2] dentition lophodont, 30[2] hypsodonty index I_H of upper molars usually higher than 0.70, 33[2] centrocrista of the ectoloph moderately notched on upper molars, 47[2] cingula/ids of molars low, 60[2] protolophid of lower molars almost lophodont, 62[2] hypoconulid missing on M/1-2), two HUS (46[0] expansion of the distal cingulum only on M3/, 57[0] lower molars narrow) and one reversal (34[0] protoloph-ectoloph junction unnotched on upper molars).

Systematic inferences

Along with the topology of the tree, character distribution and Bremer support as detailed here above lead to the following inferences:

- *Hyracotherium leporinum* is sister group to all other Palaeotheriidae within the studied sample, apart from the outgroup.
- *Pachynolophus* (node 5; BI=2) is a monophyletic genus, with the topology [*P. eulaliensis* [*P. cesserasicus* [*P. duvali*, *P. livinierensis*]]].
- *Eurohippus* and *Propalaeotherium* constitute a paraphyletic group, which for convenience will be herein referred to as "propalaeotheres". They are diverging in two paraphyletic sets at the node 9, related to *Lophiotherium* (node 12; BI=4) and Palaeotheriinae (node 16; BI=7), respectively. This group would need a complete systematic revision, which is beyond the aim of the present paper.
- *Propachynolophus* is polyphyletic, with all four referred species scattered in the tree (stemming from the nodes 2, 3, 8, and 14). *Propachynolophus gaudryi* (type species) is located between *Propalaeotherium sudrei* and the type species of *Propalaeotherium*, *P. isselanum* (nodes 13-15), all of them being closely related to Palaeotheriinae. It should therefore be assigned to *Propalaeotherium*. *Propachynolophus levei* and *P. remyi* form an early diverging paraphyletic ensemble close to *Hyracotherium leporinum*. Therefore, they are to be considered as "hyracotheres". *Propachynolophus maldani*, more derived than the latter species, is sister group to the [*Lophiotherium*, "propalaeotheres", Palaeotheriinae] clade.
- *Lophiotherium* is monophyletic and well supported as a genus.
- Palaeotheriinae are monophyletic, under the topology [*Leptolophus nouleti* [*Plagiolophus minor*, *Palaeotherium magnum*]].

CONCLUSION

Dental features (and their variability as discussed in the first section) and the topology of the most parsimonious tree (Figure 19) lead to discard *Propachynolophus* as a valid genus.

The type species "*Propachynolophus gaudryi*" is bracketed between two *Propalaeotherium* species, i.e. *P. sudrei* and the type-species *P. isselanum* (Figure 19). As a consequence, it should be assigned to *Propalaeotherium*, as suggested by Stehlin (1905, 1941), Savage *et al.* (1965) and according to my own morphological observations (see above), under the new combination *Propalaeotherium gaudryi* (Lemoine, 1891). Moreover, this species is remote from the monophyletic genus *Pachynolophus*, unlike the often accepted concept.

Consequently, the earliest attested occurrence of *Propalaeotherium* known so far from the Geiseltal uUK and Messel (MP11), with *P. hassiacum* and *P. voigti*, would date back to the MP10 with *P. gaudryi*. As already noticed, the topology of the parsimonious tree highlights again that the genus *Propalaeotherium* is close to the original stem of the Palaeotheriinae (=Palaeotheriidae *s.s.* for some authors), which appear around the MP 12 level and begin to diversify near the MP 13. This assumption which is at the origin of the name chosen by Gervais (1849), was discussed and supported several times (see for example Hooker, 1986: 371; Remy, 2004: 172).

The two species "*Propachynolophus*" *levei* and "*P.* " *remyi* fall among hyracotheres and they are basal to other Palaeotheriidae. The specimens recorded under the name "*Propachynolophus*" *remyi* come from a number of Spanish deposits in various South Pyrenean basins (Checa-Soler, 1997). They show a relatively high dimensional and morphological variability, suggesting that they might represent more than one taxon, as it had been already assumed (Crusafont & Remy, 1970). So the species name "*P.*" *remyi* would apply only to the type series, i.e. from the Las Badies deposits (Cuenca del Isàvena), including the holotype ICP 3206, a left maxilla with M1/-M3/ (Checa-Soler, 1997, pl. 1, fig. 1). Coeval specimens from Les Saleres (Cuenca de Ager; Checa-Soler, 1997), might belong to a smaller form, the upper cheek teeth of which have more complete and thick cingula, and less expanded parastyles. In any case, the complex "*P.*" *remyi* documents hyracotheres among Palaeotheriidae.

Finally, considering the overall *Hyracotherium*-like pattern of "*P.*" *levei* and "*P.*" *remyi*, and pending more complete data, I suggest to refer to them as ' "*Hyracotherium*" *levei* (Hooker, 1994)' and ' "*Hyracotherium*" *remyi* (Checa-Soler, 1997)'.

Lastly, whereas "*Propachynolophus*" *maldani* was originally defined as "*Pachynolophus Maldani* Lemoine, 1878", several features such as the occasional occurrence of mesostyles on upper molars are hardly compatible with this assignment, which moreover would break the monophyly of this genus and make it inaccurately paraphyletic.

Otherwise, compared with propalaeotheres, "*P.*" *maldani* is significantly smaller than *Eurohippus parvulus* from Messel or the Geiseltal uUK, probably one of the reasons that led Stehlin (1941: 295) to preferentially rank this species closer to *Lophiotherium pygmaeum* rather than to "*Propalaeotherium parvulum*". *Lophiotherium pygmaeum* was defined at Lissieu, but it is mostly known by the material from Egerkingen (chiefly Egerkingen a, MP 14 level). The specimens referred to as "*P.*" *maldani*, earlier in age, present indeed some morphological similarity with that species, but also many conspicuous divergences highlighted on the parsimonious tree.

We must also remind that another species referred to *Lophiotherium* is known, *Lophiotherium sondaari* Franzen, 1999, which was described in the Geiseltal oUK (younger than MP 11). It is older, although closer in age to "*P.*" *maldani*, and smaller than *L. pygmaeum*. It has not been integrated in the analysis due to its meager record and an ambiguous status, its strong bunodonty being the leading argument to assign it to *Lophiotherium*. This last feature discards any relationship with "*P.*" *maldani*.

Given its features and inferred phylogenetic position, aside from *Pachynolophus* as well as all other palaeotheriid genera (Figure 19), I propose to consider the species "*P.*" *maldani* as typifying a new monotypic genus, closely related to the [*Lophiotherium*, "propalaeotheres", Palaeotheriinae] clade:

Orolophus n. gen.

lsid:zoobank.org:act: 99CBA05F-69B1-449C-BD8F-41BFB8141C77

Type and only species: *Orolophus maldani* (Lemoine, 1878).

Etymology: By reference to *Orotherium* Marsh, 1872, a North American equid genus, valid but now disused, to which Lemoine (1891) compared "*Pachynolophus Maldani*".

Diagnosis (same as for the type and only species - see below).

Orolophus maldani **(Lemoine, 1878), new combination**

Holotype: a fragment of a right lower jaw with P/4, roots of M/1, and M/2-M/3, MNHN AL-5199 (Lemoine, 1891, fig. 117; Savage *et al.*, 1965, fig. 15a, 15b).

Diagnosis: Small palaeotheriid Equoidea, with an estimated P2/-M3/ length of about 40 mm, a buno-lophodont and brachydont dentition, an occasional mesostyle and a parastyle not very protruding on upper molars, a protocone mesially shifted on P4/, a distal expansion of the postero-lingual cingulum on P3/ P4/, and narrow lower molars with thick and continuous labial cingulids. Differs from species of *Pachynolophus* in having a wider P2/ and an occasional mesostyle on upper molars. Further differs from more advanced Palaeotheriidae (*Lophiotherium*, "propalaeotheres", and Palaeotheriinae) in possessing an inconstant mesostyle on upper molars, a parastyle less protruding and a shallower protoloph groove on upper molars, a lingual cingulum on these teeth stronger than in most of them, a P4/ triangular (instead of being subquadrangular), and a hypoconulid more developed on M/1-M/2.

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Appendices

(1) Nasal notch: mesially to the canine (0); above the DPC, close to the canine (1); above the DPC, close to the premolars (2); distally to the first premolar (3). (Character 1 in Danilo *et al.* [2013]).

(2) Bones surrounding the nasal notch: premaxilla enlarged upward and nasal (0); premaxilla reduced upward and nasal (1); premaxilla, maxilla, and nasal (2). (Character 2 in Danilo *et al.* [2013]).

(3) Lacrimal tubercle: present (0); missing (1). (Character 3 in Danilo *et al.* [2013]).

(4) Orbital border: reaches Ml/ (0); reaches the limit between Ml/ and M2/ (1); reaches M2/ (2); reaches the limit between M2/ and M3/ (3). (Character 4 in Danilo *et al.* [2013]).

(5) Position of basicranial foramina: foramen ovale and middle lacerate foramen distant (0); separated only by a narrow bridge of bone (1); confluent (2). (Character 5 in Danilo *et al.* [2013]).

(6) Braincase index (measure from the mesial side of P2/ to the orbital border/measure from the orbital border to the midway of the distal line of the occipital): from 0.25 to 0.30 (0); from 0.35 to 0.40 (1); more than 0.45 (2). (Character 6 in Danilo *et al.* [2013]).

(7) Postcanine diastem length (C-P2 at the bone level): short (less than 25% of the P2-M3 length) (0); 25-45% (1); longer than 45% (2). (Modified from character 7 in Danilo *et al.* [2013]).

(8) Degree of lophodonty: dentition very bunodont (0); buno-lophodont (1); lophodont (2).

(9) P1: present (0); missing (1). (Character 8 in Danilo *et al.* [2013]).

(10) P1 elongation: shorter than P2 (0); as long as or longer than P2 (1). (Character 9 in Danilo *et al.* [2013]).

(11) Post-P1 diastem: constant (0); occasional (1); missing (2). (Modified from character 10 in Danilo *et al.* [2013]).

(12) P2/ occlusal outline: triangular, tapering forward (0); wider but mesial side slanted (1); almost rectangular (2). (Character 11 in Danilo *et al.* [2013]).

(13) P2/ labial cusps: one cusp (0); two cusps (1). (Character 12 in Danilo *et al.* [2013]).

(14) P2/ molarization: missing (0); incomplete (1); complete (2). (Character 13 in Danilo *et al.* [2013]).

(15) P3/ postprotocrista morphology: missing (0); incomplete (1); complete (2). (Modified from characters 14-15 in Danilo *et al.* [2013]).

(16) P3/ paraconule: indistinct (0); conspicuous, well defined (1). (Character 16 in Danilo *et al.* [2013]).

(17) P3/ metaconule: indistinct (0); conspicuous more or less separated from the protocone (1). (Character 17 in Danilo *et al.* [2013]).

(18) P3/-P4/ molarization: hypocone missing (0); present (1). (Character 18 in Danilo *et al.* [2013]).

(19) P3/-P4/ accessory crest from the protocone (additionally of the postprotocrista): missing (0); present (1); present and joining the cingulum (2). (Character 19 in Danilo *et al.* [2013]).

(20) P4/ occlusal outline: triangular (0); subquadrangular (1); square or rectangular (2). (Character 20 in Danilo *et al.* [2013]).

(21) P4/ mesostyle: never (0); occasionally or always (1).

(22) P4/ lingual cingulum: strong and continuous (0); reduced on the protocone (1); missing (2). (Modified from character 21 in Danilo *et al.* [2013]).

(23) P4/ posterolingual cingulum: no thicker than the anterior cingulum (0); important distal expansion (1). (Character 22 in Danilo *et al.* [2013]).

(24) P4/ postprotocrista: present (0); missing (1). (Character 23 in Danilo *et al.* [2013]).

(25) P4/ postprotocrista morphology: lophoid, joining ectoloph (0); incomplete, not joining ectoloph (1). (Character 24 in Danilo *et al.* [2013]).

(26) P4/ protocone position: central (0); mesially shifted (1). (Character 25 in Danilo *et al.* [2013]).

(27) P4/ paraconule: strong (0); average (1); weak (2). (Character 26 in Danilo *et al.* [2013]).

(28) P4/ metaconule: weak (0); average (1); strong (2). (Character 27 in Danilo *et al.* [2013]).

(29) P4/ metaconule position: fused with the postprotocrista (0); distal to the postprotocrista.

(30) Upper molar hypsodonty ($I_H = H/W$): I_H mostly <0.50 (0); mostly >0.50 up to 0.70 (1); mostly >0.70 (2). (Modified from character 28 in Danilo *et al.* [2013]).

(31) Upper molar protoloph grooves size: strong (0); average (1); weak (2); missing (3). (Modified from characters 29-30 in Danilo *et al.* [2013]).

(32) Upper molar metaloph grooves size: strong (0); average (1); weak (2); missing (3). (Modified from characters 31-32 in Danilo *et al.* [2013]).

(33) Upper molar ectoloph centrocrista: deeply notched (0); moderately (1); shallow (2). (Character 52 in Froehlich [2002]).

(34) Upper molar protoloph-ectoloph junction: unnotched (0); notched (1). (Character 36 in Danilo *et al.* [2013]).

(35) Direction of the upper molar preparaconule crista-ectoloph junction: directed towards the preparacrista (0); towards the parastyle (1). (Character 37 in Danilo *et al.* [2013]).

(36) Upper molar metaloph-ectoloph junction: towards the metacone or interrupted (0); towards the centrocrista (1). (Character 38 in Danilo *et al.* [2013]).

(37) Upper molar paracone labial ripple on the ectoloph: strong (0); weak (1); missing (2). (Character 39 in Danilo *et al.* [2013]).

(38) Upper molar metacone labial ripple on the ectoloph: strong (0); weak (1); missing (2). (Modified from character 40 in Danilo *et al.* [2013]).

(39) Upper molar parastyle: low (0); small but high (1); large and protruding (2). (Modified from characters 41-42 in Danilo *et al.* [2013]).

(40) Upper molar mesostyle: missing (0); occasional (1); constant (2). (Modified from character 43 in Danilo *et al.* [2013]).

(41) Upper molar mesostyle morphology: strong rib up to the occlusal level, bulging with ectocingulum (0); strong but separated from ectocingulum (1); thin and not bulging at the collar (1); pseudomesostyle, i.e., thin rib on the superior edge of the labial side (2). (Modified from character 44 in Danilo *et al.* [2013]).

(42) Upper molar labial cingulum: continuous (0); usually interrupted on the paracone (1); almost missing (2). (Character 45 in Danilo *et al.* [2013]).

(43) Upper molar labial cingulum thickness: strong (0); medium to weak (1).

(44) Upper molar lingual cingulum morphology: continuous (0); interrupted (1); missing (2). (Modified from characters 46-47 in Danilo *et al.* [2013]).

(45) Upper molar lingual cingulum thickness: strong (0); medium to weak (1); restricted to the medivallum (2). (Character 48 in Danilo *et al.* [2013]).

(46) Localisation of the distal cingulum expansion: only on M3/ (0); on all upper molars (1); missing (2). (Modified from characters 49-50 in Danilo *et al.* [2013]).

(47) Average height of (upper or lower) molar cingula (CH = $H_{cingulum}/H_{crown}$): high, >45 (0); moderate, 30-45 (1); low <30 (2). (Modified from character 61 in Danilo *et al.*, 2013).

(48) Upper molar lingual cusps position: hypocone and protocone at the same level (0); hypocone more labial (1). (Character 51 in Danilo *et al.* [2013]).

(49) Upper molar lingual cusps size: protocone and hypocone similar in size (0); protocone larger than the hypocone (1). (Character 52 in Danilo *et al.* [2013]).

(50) Ml-2/ metastyle orientation: in line with the ectoloph (in the alignment of the paracone and metacone) (0); oblique (towards labial side) (1). (Character 53 in Danilo *et al.* [2013]).

(51) M3/ distal outline: convex (0); straight (1); concave (2). (Character 55 in Danilo *et al.* [2013]).

(52) M3/ relative distances between paracone-metacone and protocone-hypocone: subequal to equal (0); larger between protocone and hypocone (1). (Character 56 in Danilo *et al.* [2013]).

(53) Relative surface of the premolar series (following S_P/S_M index): low (<41) (0); intermediate (41-55) (1); high (>55) (2).

(54) Relative surface of M3/ on M2/ (following S_{M3}/S_{M2} index): M3/ smaller than M2/ (<0.95) (0); weak difference (>0.95 and <1.05) (1); M3/ larger than M2/ (>1.05) (2). (Character 54 in Danilo *et al.* [2013]).

(55) Relative surface of P4/ (following S_{P4}/S_{3M} index): low (<20) (0); intermediate (20-25) (1); high (>25) (2).

(56) P/4 entoconid: missing (0); incipient and low (1); fully developed (2). (Modified from character 58 in Danilo *et al.* [2013]).

(57) Lower molar relative width: narrow (L/l [M/l-2] >1.45 and L/l [M/3] >2) (0); wide (1). (Character 59 in Danilo *et al.* [2013]).

(58) Lower molar labial cingulum: always thick and continuous (0); generally narrow and more or less interrupted (1); almost missing or limited to the medivallum (2). (Modified from character 60 in Danilo *et al.* [2013]).

(59) Lower molar orientation of the protolophid and hypolophid: transversal (0); slightly inclined (1). (Character 62 in Danilo *et al.* [2013]).

(60) Lower molar protolophid morphology: deeply notched (0); slightly notched (1); almost lophodont (2). (Modified from character 89 in Froehlich [2002]).

(61) Lower molar twinned metaconid: missing (0); present (1). (Character 64 in Danilo *et al.* [2013]).

(62) M/1-M/2 hypoconulid: developed (0); weak (1); missing (2). (Character 66 in Danilo *et al.* [2013]).

(63) M/3 hypoconulid basin: large (0); reduced (1). (Character 67 in Danilo *et al.* [2013]).

(64) M/3 prehypocristulid orientation: towards the hypoconid (0); towards the midpoint of the hypolophid (1); towards the entoconid (2). Character 70 in Danilo *et al.* [2013]).

(65) M/3 accessory crest: missing (0); present (1). (Character 71 in Danilo *et al.* [2013]).

(66) M/3 hypoconulid position: labial (0); medial (1); lingual (2). (Character 72 in Danilo *et al.* [2013]).

Appendix 1 - Description of characters used in the cladistic analysis.
All characters are treated as unweighted.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Cardiolophus radinskyi	0	0	?	1	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	3	0
Hallensia matthesi	0	0	0	2	?	2	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	1	1	0	2	0	0	0	0	0
Pliolophus vulpiceps	2	0	1	2	?	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	0
Hyraco leporinum	2	2	0	2	?	?	1	0	0	0	0	0	1	0	2	1	0	0	1	0	0	0	0	0	1	1	0	2	0	0	0	1	0
Propachyno gaudryi	?	?	?	?	?	?	1	1	0	0	1	1	1	1	2	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	2	0
Propachyno maldani	?	?	?	?	?	?	?	1	?	?	?	1	?	?	?	1	1	0	0	0	0	1	1	0	1	1	0	1	0	0	1	2	0
Propachyno levei	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	0
Propachyno remyi	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0	0	0	1	1	1	-	0	0	?	-	0	1	2	0
Pachyno duvali	?	?	?	?	?	?	2	1	0	0	2	1	1	0	2	1	1	0	0	1	0	1	0/1	0	1	0	1	1	-	0	1	2	0
Pachyno cesserasicus	1	2	0	1	?	0	2	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	3	0
Pachyno eulaliensis	1	1	0	1	2	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0/1	1	1	1	1	0	1	3	0
Pachyno livinierensis	?	?	0	2	2	1	2	1	0/1	0	2	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	3	0
Eurohippus parvulus	2	2	?	0	?	?	2	1	0	0	2	1	1	0	2	1	1	0	0	1	0	1	0	0	0	0	0	2	1	0	0	3	0
Propal hassiacum	1	2	?	2	?	?	1/2	0	0	0	1	1/2	0	0	2	1	0	0	0	1	0	1	0	0	0	0	0	2	0	0	0	3	0
Propal isselanum	2	?	1	2	2	2	1	1	0	0	2	2	1	1	2	1	1	0	1	1	0	0	0	0	0	0	0	2	1	1	0	3	1
Propal sudrei	2	2	?	2	?	?	?	1	0	0	0	1	?	?	?	1	?	0	0	1	0	1	1	0	0	1	1	1	?	1	0	2	0
Lophiotherium pygmaeum	?	?	?	?	?	?	2	0	0	0	2	1	1	0	1	1	1	0	0	1	0	1	0	0	0	1	1	2	0	0	0	2	1
Lophiotherium cervulum	2	2	?	0	?	?	2	0	0	0	2	2	1	1	-	1	1	1	-	2	1	1	-	-	-	0	0	2	-	0	0	0	1
Palaeotherium magnum	3	2	0	2	2	2	0	2	0	0	2	2	1	2	-	1	1	1	-	2	1	0	-	-	-	1	2	0	-	2	1	2	2
Plagiolophus minor	2	2	0	3	2	2	1	2	0	0	2	2	1	1	2	1	1	1	-	2	1	1	-	-	-	1	0	1	-	2	0	3	2
Leptolophus nouleti	2	1	0	3	2	2	1	2	1	-	-	2	0	1	2	0	0	0	2	1	0	2	-	0	0	0	2	1	-	2	3	3	2

	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Cardiolophus radinskyi	0	0	0	0	0	2	1	0	0	0	0	1	2	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0
Hallensia matthesi	1	0	0	0	0	0	0	-	0	0	1	1	0	0	1	1	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0	1
Pliolophus vulpiceps	0	0	0	0	0	0	0	-	0	0	0	0	2	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	0
Hyraco leporinum	1	1	0	0	0	2	0	-	0	0	0	0	2	0	0	0	1	1	0	1	0	2	?	1	0	1	0	1	0	1	0	1	1
Propachyno gaudryi	1	0	0	0	1	2	1	0	0	0	1	1	2	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	0	0
Propachyno maldani	1	0	0	0	1	1	1	1	0	0	1	0	2	1	0	0	0	1	0	?	1	?	1	0	0	0	0	1	0	1	1	0	1
Propachyno levei	1	0	0	0	1	1	0	-	0	0	0	0	2	1	0	0	0	1	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?
Propachyno remyi	1	0	0	0	1	1	0	-	0	0	0	0	0	1	0	0	0	0	0	?	1	0	0	1	1	1	0	1	0	1	1	1	1
Pachyno duvali	0	0	0	0	1	1	0	3	1	1	1	2	0	1	0	0	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1
Pachyno cesserasicus	0	1	0	0	1	1	0	3	0	1	1	0	0	1	0	0	1	1	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?
Pachyno eulaliensis	0	0	0	0	1	1	0	3	0	1	1	1	2	1	0	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0/1	1	0	0
Pachyno livinierensis	1	0	0	0	2	1	0	-	1	1	1	2	0	1	0	0	1	2	0	1	2	0	1	1	1	1	1	1	0	0	1	1	1
Eurohippus parvulus	1	1	1	0	1	2	2	0	1	1	1	1	2	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	1	0	1	0	1
Propal hassiacum	1	1	1	0	1	2	2	0	0	0	0	1	2	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1
Propal isselanum	1	0	1	1	1	1	2	1	0	0	1	1	2	1	1	0	1	1	0	1	1	1	0	1	0	1	1	1	1	1	2	0	0
Propal sudrei	1	0	1	0	1	2	2	1	0	0	1	1	2	1	0	0	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	0
Lophiotherium pygmaeum	1	1	0	0	1	1	1	1	1	1	1	1	2	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0	1	1	0
Lophiotherium cervulum	1	1	0	0	0	1	2	0	1	1	1	2	1	1	0	0	1	0	0	2	1	2	2	1	1	0	0	1	1	0	1	1	0
Palaeotherium magnum	0	1	0	1	2	1	2	0	0	1	1	1	1	2	0	1	1	1	0	2	2	2	2	0	0	1	2	0	2	1	2	1	0
Plagiolophus minor	0	1	1	1	1	1	2	0	1	1	1	1	0	2	0	0	1	0	0	0	2	0	1	0	2	1	2	1	0	1	2	1	1
Leptolophus nouleti	0	0	1	1	1	1	2	2	2	-	2	-	0	-	0	0	0	0	0	0	1	0	?	0	2	1	2	?	2	1	2	1	?

Appendix 2 - Matrix drawn up for the cladistic analysis.