

The status of *Conohyus giganteus* (Nyanzachoerini, Tetraconodontinae, Suidae) – Reply to Pickford (2001)

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ABSTRACT: The recently published model of evolution and biogeography and the resulting classification of the Tetraconodontinae (Van der Made 1999) were criticised by Pickford (2001) on eight points. It was claimed that *Conohyus giganteus* is a suine, and that this ‘radically modifies tetraconodont systematics’. However, Pickford failed to demonstrate that the type specimen is a suine, and even if it were a suine, this would affect only one of over twenty species names; not a radical change of the proposed evolutionary model.

KEY WORDS: Biogeography, evolution, morphology, morphometrics.



Pickford (2001) objected to various aspects of a recent study of the Tetraconodontinae (Van der Made 1999). The objections made by Pickford are the following:

- (1) The P⁴ of the lectotype of *Conohyus giganteus* has the morphology of a suine and therefore the species cannot belong to the Tetraconodontinae.
- (2) The lectotype of *C. giganteus* has thin enamel, like Suinae and unlike Tetraconodontinae, and therefore the species is more likely to be a suine than a tetraconodontine.
- (3) Skull morphology indicates that the lectotype of *C. giganteus* belongs to the Suinae and not to the Tetraconodontinae.
- (4) The lectotype of *Conohyus giganteus* is much larger than the European and African material and therefore that material cannot be included in *C. giganteus*.
- (5) The diagnosis of *C. giganteus* does not refer to the Indian material and therefore needs revision.
- (6) Since *C. giganteus* is a suine, the derivation of the *Nyanzachoerus*–*Notochoerus* lineages needs revision.
- (7) There are no fossils from the Indian Subcontinent that can be assigned to *Sivachoerus* with an age of between 9 and 4.5 Ma, and therefore *Sivachoerus prior* is more likely to have originated in Africa and dispersed into the Indian Subcontinent.
- (8) A biogeographical model with a single dispersal of Tetraconodontinae into Africa and one from Africa into the Indian Subcontinent is more parsimonious than a model with four dispersals into Africa.

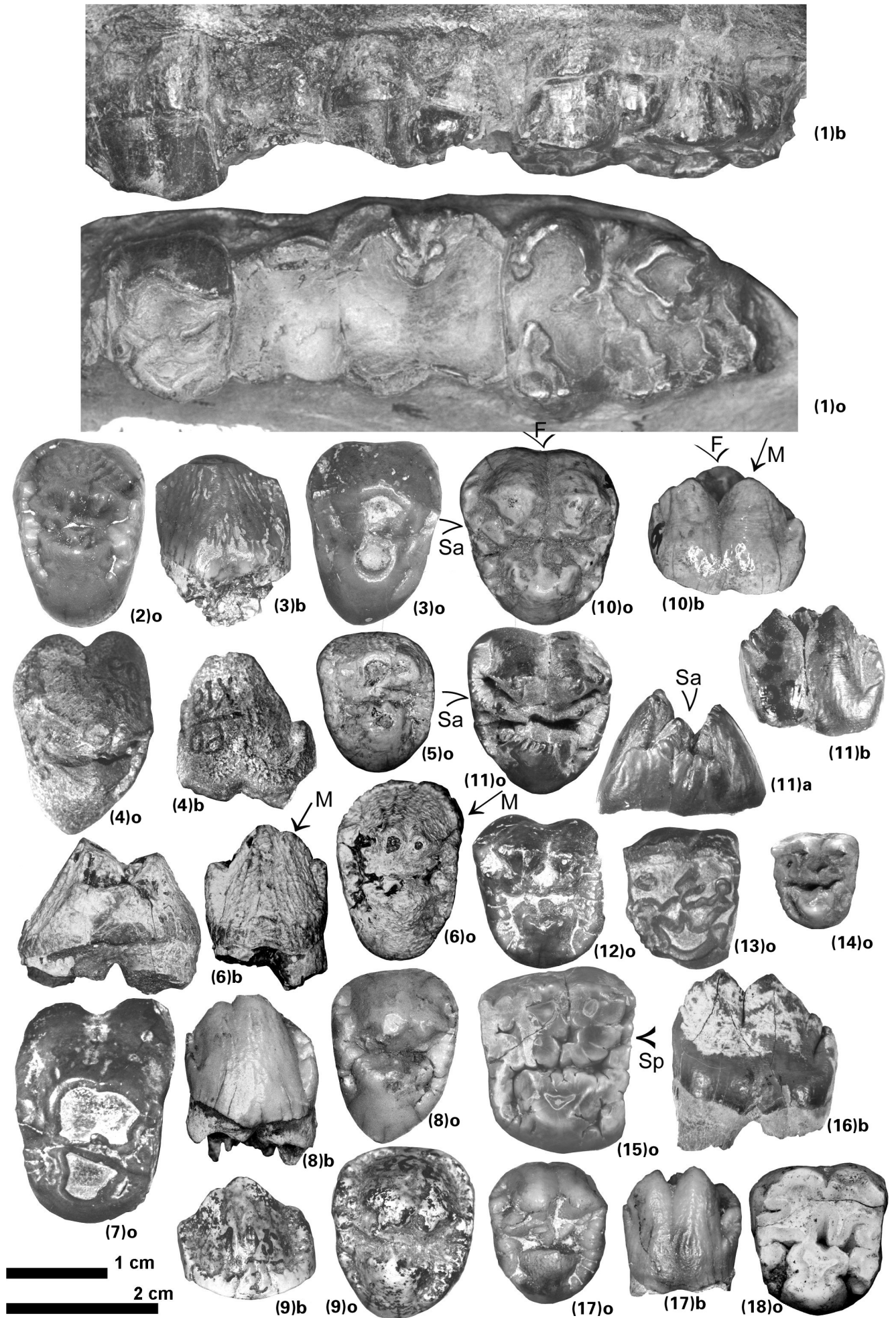
In the following sections (2.1–2.8), these points will be discussed one by one.

1. Material and methods

The methods applied here are the same as those applied by Van der Made (1999) and the measurements are taken as indicated by Van der Made (1996). The way of measuring enamel thickness in upper molars is defined here as being taken in the same way as in the lower molars (Van der Made 1996), but, in this case at the buccal side: Ta is thickness measured at the paracone, and Tp is measured at the metacone.

Material used in this paper was studied in, or is kept in, institutions or collections indicated by the following abbreviations:

AFS	Accademia dei Fisiocritici, Siena.
BSPHGM	Bayerische Staatssammlung für Paläontologie und historische Geologie, München.
DPZ	Departamento de Paleontología, Universidad de Zaragoza.
DSTUSR	Dipartimento di Scienze della Terra, Università ‘La Sapienza’, Roma.
DSTUST	Dipartimento di Scienze della Terra, Università degli Studi di Torino.
EBD	Estación Biológica de Doñana, Sevilla.
FISF	Forschungsinstitut Senckenberg, Frankfurt.
GML	Geological Museum of Lisbon.
GSP	Geological Survey of Pakistan, Islamabad.
HGSB	Hungarian Geological Survey, Budapest.
HLD	Hessisches Landesmuseum, Darmstadt.
HUJ	The Hebrew University of Jerusalem.
IGF	Istituto di Geologia, Firenze.
IGGML	Institut für Geowissenschaften/Geologie der Montanuniversität, Leoben.
IM	Indian Museum, Calcutta.
IPS	Instituto de Paleontología, Sabadell.
IPUW	Institut für Paläontologie der Universität, Wien.
ISEAK	Institute of Systematics and Evolution of Animals, Kraków.
IVAU	Instituut Voor Aardwetenschappen, Utrecht.
JGUM	Johannes Gutenberg Universität, Mainz.
LPUMM	Laboratoire de Paléontologie, Université de Montpellier II, Montpellier.
MGL	Museum Guimet, Lyon.
MNCN	Museo Nacional de Ciencias Naturales, Madrid.
MNHN	Muséum National d’Histoire Naturelle, Paris.
MPZ	Museo Paleontológico de la Universidad de Zaragoza.
MSNO	Muséum des Sciences Naturelles, Orléans.
MSNTUPC	Museo di Storia Naturale e del Territorio, Università di Pisa, Calci.
MTA	Maden Tetkik ve Arama, Ankara.



NHM	Natural History Museum, London.
NMB	Naturhistorisches Museum, Basel.
NMM	Naturhistorisches Museum, Mainz.
NMNHK	National Museum of Natural History, Kiev.
NMW	Naturhistorisches Museum, Wien.
NNML	Nationaal Natuurhistorisch Museum, Leiden.
PDTFAU	Paleoantropoloji, Dil ve Tarih Cografya Facultesi, Ankara Universitesi.
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich.
PMNH	Pakistan Natural History Museum, Islamabad.
SLJG	Steiermärkisches Landesmuseum Joanneum, Graz.
UCM	Universidad Complutense, Madrid.
UL	University of Lahore.
UPVB	Universidad del Pais Vasco, Bilbao.
VMM	Vernadzki Museum, Moscow.
ZMA	Zoologisch Museum, Amsterdam.

2. Points of divergence

2.1. Morphology of the premolars

Pickford (2001, p. 41, section 4) stated that the P⁴ of the lectotype of *C. giganteus* has the morphology of a suine and that therefore the species '*giganteus*' does not belong to the Tetraconodontinae, but to the Suinae, and may belong to the genus *Propotamochoerus*. The specimen is figured only by Falconer and Cautley (1847, plate 69, fig. 1) and since most readers will not have this publication at hand, the specimen is figured here (Fig. 1(1)). In this section, eight characters of the P⁴ are discussed.

- (1) Pickford (2001, section 3) claimed the presence of two distinct buccal cusps in the P⁴ in the type of *C. giganteus* to be indicative of it belonging to the Suinae.

The Suinae always have a P⁴ with two well-developed buccal cusps, here called paracone and metacone (arrow 'M' in Fig. 1(10)). The two cusps are generally (e.g. Fig. 1(10), (11), (14), (15), (17)), but not always (Fig. 1(16)) separated by a sharp furrow at the buccal side (arrow 'F' in Fig. 1(10)). In the Tetraconodontinae, a small metacone is often present (eg. arrow 'M' in Fig. 1(6); visible as a dentine island in occlusal view), and sometimes it is relatively large. A furrow at the buccal side of the tooth may be present but rapidly disappears with wear. Such a furrow is visible because of the shape of the enamel dentine junction in Figure 1(7).

Pickford claimed the presence of such a groove in the type of *C. giganteus*. The enamel dentine junction in this specimen can be seen to turn lingually behind the paracone, but does not curve buccally again, showing that there is no groove (Fig. 1(1)). The course of the enamel–dentine junction shows very clearly that no

well-developed metacone can have existed in this specimen. All suine P⁴ have a metacone with a tip that is placed more buccally than the enamel–dentine junction is in the type of *C. giganteus* (eg. Fig. 1(10)–(17)). Thus, contrary to Pickford's statement, the type of *Conohyus giganteus* does not have a P⁴ with a clear postero–buccal cusp, and therefore resembles the Tetraconodontinae, and not the Suinae.

- (2) Pickford (1988) indicated as one of the characters of the Suinae '2 cusplets in sagittal valley of P⁴'; elsewhere they are called '2 sagittal cusplets'.

The sagittal cusps in the P⁴ of the Suinae can be seen in Figure 1(10)–(17) (arrows 'S' indicate the anterior cusplet). Whilst *Hippohyus* has two very well-developed sagittal cusps (Fig. 1(13)), the posterior cusplet may be very small in *Propotamochoerus* (Fig. 1(10)–(17)). However, such cusplets are occasionally also seen in the later Tetraconodontinae. The buccal dentine island in Figure 1(7) (*Sivachoerus* aff. *prior*) hints of two small sagittal cusplets: the enamel–dentine junction is not an oval, but turns inward, more or less at the middle of the lingual side and just lingually of the middle of the anterior and posterior sides. These three curves coincide with three vertical furrows that separate the sagittal cusplets from each other and from the buccal cusps. Sagittal cusps are thus not unique to Suinae, and their presence in a species cannot be used to exclude that species from the Tetraconodontinae.

The wear in the type of *Conohyus giganteus* (Fig. 1(1)) is comparable to that in the specimen of Figure 1(7), however, no hint of a sagittal cusp is seen, and the enamel–dentine junction does not curve inward. Contrary to Pickford's claim, the type of *Conohyus giganteus* does not have sagittal cusps, and even if it had, this would not mean that it is a suine.

- (3) Pickford (2001, section 3) interpreted as a suine character that, even though wear is advanced, the antero–posterior valley of the P⁴ of the type of *C. giganteus* separates the buccal and lingual cusps from each other. This character is interesting and can be observed well in anterior view (Fig. 1(6)). In the type of *C. giganteus*, the antero–posterior valley is almost worn away but the remaining crown height is more than in some unworn suine P⁴ (Fig. 1(10) (taking difference in scale and size into account)). This implies that the base of the antero–posterior valley is high above the crown base, as in Tetraconodontinae, and unlike that in Suinae.
- (4) Van der Made (1999) mentioned the high crown of the P⁴, which is seen in that its base is much lower than that of the M¹. Pickford (2001, section 3) stated that the crown of the P⁴ is not so much lower than that of the M¹ as usually seen in Tetraconodontinae and suggested that the M¹ is forced occlusally by the pressure of the posterior molars. However, it can be seen clearly in

Figure 1 *Conohyus giganteus* (1) compared to other Tetraconodontinae ((2)–(9)) and to Suinae ((10)–(17)): (1) IGF 1470v (NHM M13385): left P⁴ - M³ of the lectotype of *Conohyus giganteus*; (2) PDTFAU V69: right P⁴ of *Conohyus simorrensis* from Pasalar, Turkey; (3) PIMUZ BP276: right P⁴ of *C. simorrensis* from Pasalar; (4) IM B668 (K19/60): right P⁴ of *Sivachoerus sindiense* from Bhagothoro; (5) HLD Din 64: right P⁴ of *Parachleuastochoerus huenermanni* from Wissberg; (6) BSPHGM 2585 (field number): right P⁴ of *S. sindiense* from Marianwala Kas; (7) IM B676: right P⁴ of *Sivachoerus* aff. *prior* from the Irrawady Series at Yenangyoung; (8) MGL LGr1654: right P⁴ of *Parachleuastochoerus steinheimensis* from La Grive; (9) NMM 1954/12: right P⁴ of *P. steinheimensis* from Wissberg; (10) NMM 1934–869: left P⁴ of *Propotamochoerus palaeochoerus* from Wissberg; (11) GSP 10967: left P⁴ of *Propotamochoerus hysudricus* from Pakistan; (12) NMB JH 119: right P⁴ of *Propotamochoerus* sp. from Baccinello V3; (13) IM B62: right P⁴ of *Hippohyus lydekkeri* from the Potwar Plateau; (14) IM B730: left P⁴ of *Sivahyus punjabiensis* from Hasnot; (15) GSP 11185: right P⁴ of *Hippopotamodon sivalensis* from locality 202, Pakistan; (16) GSP 4226: right P⁴ of *H. sivalense* from Pakistan; (17) NMB VJ160: left P⁴ of *Sus arvernensis* from Villafranca; (18) IM no number: left P⁴ of *Sus* from the Karnool Caves. o=occlusal view, b=buccal view, a=anterior view. The upper bar indicates the scale for (2)–(6), (8)–(14), (16) and (17). The lower bar indicates the scale for (1), (7) and (15). The right specimens are figured in mirror image for comparison.

buccal view (Fig. 1(1)) that the occlusal surface of the M^1 is much lower than that of the other cheek teeth, and this leaves no doubt that the M^1 is not forced occlusally. In fact, the M^1 is so worn that nothing of its crown is left and the distance of the base of the P^4 below the occlusal surface of the M^1 is thus an infra-estimation of its distance below the crown of the M^1 . The base of the crown of the M^1 must thus have been well below that of the P^4 , which, as Pickford admits, is a Tetraconodontine character.

- (5) Pickford (2001, section 3) takes the presence of strong buccal styles in the type of *C. giganteus* as a suine morphology. It can, however, be seen that the specimen does not have a particularly strong posterior style (Fig. 1(1)). It can also be observed that postero-buccal styles of similar development as in *C. giganteus* may occur in Tetraconodontinae (Fig. 1(2), (3), (8), (9)), whilst Suinae may have a feebler or no postero-buccal style (eg. Fig. 1(17), (18)). Suinae tend to have strong and high antero-buccal styles, but so do some Tetraconodontinae (eg. Fig. 1(8)), whilst others may have strong and low styles (eg. Fig. 1(4), (6) (see in particular the buccal sides)). The development of the buccal styles is thus no argument in favour of suine affinities of *Conohyus giganteus*.
- (6) Pickford (2001, section 3) suggests that the anterior position of the lingual cusp (protocone) of the P^4 , flanked by strong cingula in the holotype of *Conohyus giganteus*, is typical of the Suinae. The exact position of the tip is not known because of wear, but was probably about in the middle of the tooth as in any suine and tetraconodontine (Fig. 1). Cingula flanking the protocone tend to be better developed in the Suinae, but may be wide in the Tetraconodontinae as well (eg. Fig. 1(7)). These characters thus do not necessarily indicate suine affinities for *Conohyus giganteus*.
- (7) Tetraconodontinae tend to have large and wide premolars. Though the very large *Tetraconodon* is not included in Figure 2, it can be observed that the Tetraconodontinae tend to have P^4 that are larger and wider than those of the Suinae (width being measured at the base of the crown). The P^4 of *Conohyus giganteus* is as long as the very longest *Propotamochoerus* P^4 , but is much wider; it is far outside the range of *Propotamochoerus*. *Hippopotamodon* is dentally similar to *Propotamochoerus* and has the largest P^4 of the Suinae, but again, the P^4 of *Conohyus giganteus* is wider than any of the *Hippopotamodon* P^4 of the same length. The type of *Conohyus giganteus* thus resembles many other Tetraconodontinae in its very wide P^4 , and differs in this character from the Suinae.
- (8) The tetraconodontine premolars do not only tend to be wide or large in absolute terms, but also in comparison to the molar teeth. Preferentially, the M^1 is used as a standard for the size of the other teeth (Van der Made 1999). However, the M^1 of the type of *Conohyus giganteus* is much too worn to be used as a standard, and therefore the M^2 is taken here. In Figure 3, the size of the P^4 is expressed as a percentage of the width of the first lobe of the M^2 . It can be observed that the Tetraconodontinae may have very wide and large P^4 in comparison to the size of their molars, though some of them (eg. *Nyanzachoerus*) have small and narrow P^4 . The Suinae tend to have narrow P^4 . In particular, in *Sus*, *Hippohyus*, *Sivahyus* and *Kolpochoerus* the P^4 is narrow, whilst *Propotamochoerus* and *Hippopotamodon* tend to have wider P^4 . However, the P^4 of *Conohyus giganteus*

is still wider, and is well within the ranges of the Tetraconodontinae.

Of the six characters of the P^4 used by Pickford to exclude the type of *Conohyus giganteus* from the Tetraconodontinae and include it in the Suinae, two are not indicative of its affinities (characters 5 and 6), whilst four others (1–4) and two additional characters (7 and 8) indicate that it belongs to the Tetraconodontinae.

2.2. Enamel thickness

According to Pickford (2001, p. 40): 'It long has been known that molar enamel of bunodont tetraconodonts tends to be thicker than that of suines. The molar enamel in M 15385 is thin and thus suine-like rather than tetraconodontine-like . . .' Contrary to this statement, earlier authors did not give great importance to enamel thickness in suids. The two first measurements for suids may well have been published by Pickford (1988, p. 48) himself, when he used a thickness of 3 mm to assign a molar to *Tetraconodon magnus* and gave for comparison the thickness of 2.2 mm for a specimen of *Hippopotamodon sivalense*.

A standard way of measuring enamel thickness was defined, as well as an index that allows comparison of enamel thickness in teeth of different sizes, and the character was studied in larger numbers of Suoidea (Van der Made 1996). Unfortunately, this study involved few Tetraconodontinae. Enamel thickness indices are given in Figure 4. *Hyotherium meisneri* and the endemic *Sus sondaari* from the Plio-Pleistocene of Sardinia are examples of thick-enamelled suids, whilst the Listriodontinae are thin-enamelled, and the rest, including the tetraconodontines *Conohyus* and *Parachleuastochoerus*, form a group that has an intermediate enamel thickness. There is much overlap of the values of the thin, normal and thick-enamelled suids, and it is thus obvious that 'thin' enamel cannot be used as an argument that a specimen does not belong to the Tetraconodontinae.

Neither the study mentioned above, nor Figure 4, consider measurements taken on upper molars, because the data were collected for their ecological and evolutionary information, not for identification. It was considered sufficient to characterise a species by enamel thickness of the lower molars, since the general patterns are the same in both lower and upper molars. Additional observations I made suggest that enamel thickness of the upper and lower molars of the same position (eg. M_3 and M^3) have similar values for absolute enamel thickness, although the index values tend to be lower due to the greater width of the upper molars. The left M^3 of the type of *C. giganteus* has $Ta=1.7$ and $Tp=2.3$. Other teeth are too worn or broken to be measured for T. The two values are rather different, but in any case are not particularly high and are comparable to values in suids of intermediate enamel thickness and comparable size.

2.3. Skull morphology

The narrow parietal area, thin zygomatic arches and lack of protuberances on the zygomatic arch of the lectotype skull of *Conohyus giganteus* were discussed, and led to the conclusion that the skull probably does not belong to the Tetraconodontini (note that reference was made to the tribe (Van der Made 1999, p. 212). Pickford (2001, section 4) cited this and proceeded: 'These statements . . . reinforce the view that the lectotype of *Sus giganteus* does not fit comfortably within the tetraconodonts. On the contrary, all of these features reinforce its affinities with Suinae . . .' My statement that the skull does not fit Tetraconodontini, is changed into a statement that it does not fit Tetraconodontinae, but Suinae, suggesting that I

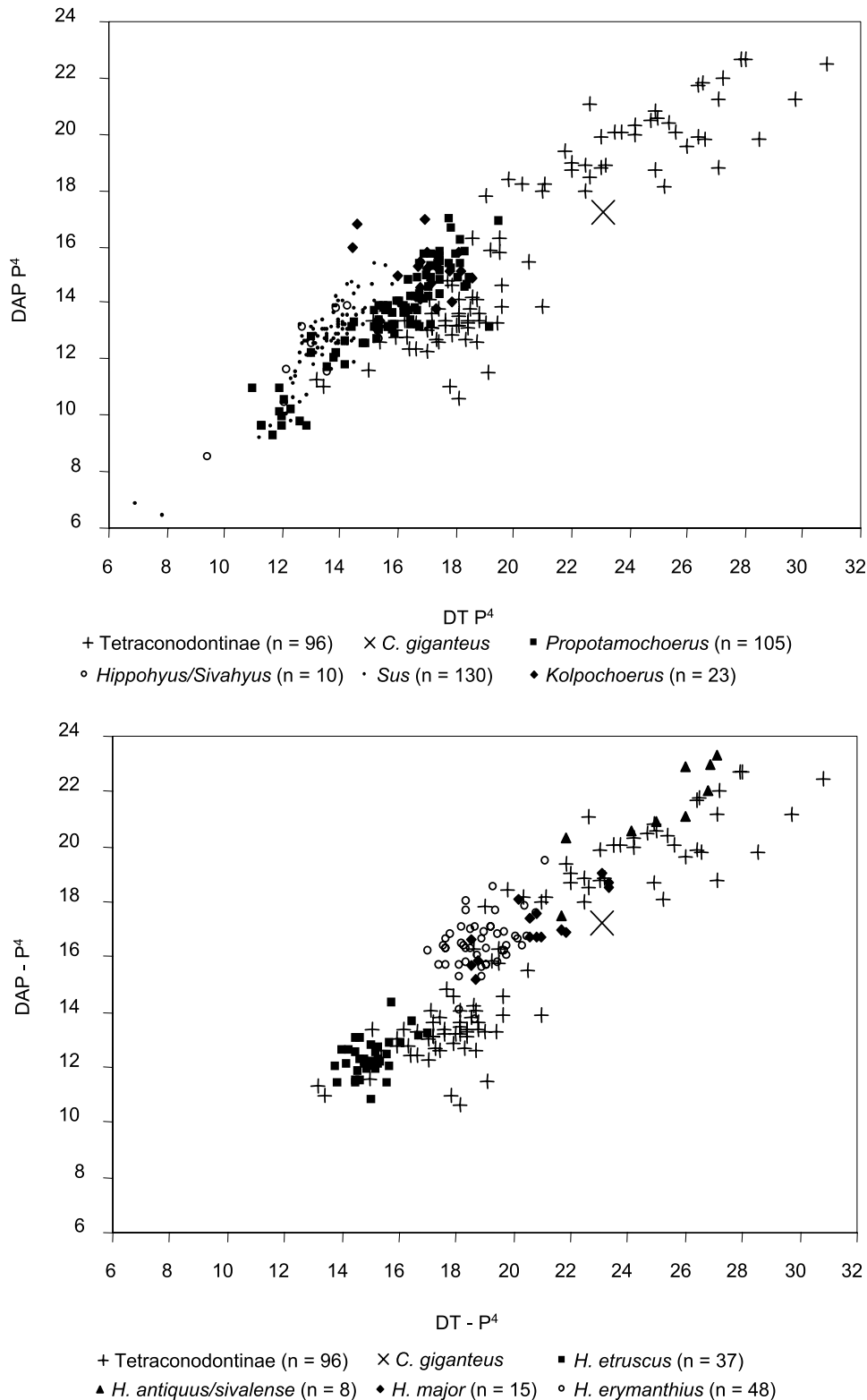


Figure 2 Bivariate plots of the P⁴. The Tetraconodontinae are largely (but not exactly) the same as those figured by Van der Made & Tuna (1999, fig. 4) and include: *Parachleuastochoerus huenermanni*, *P. steinheimensis*, *Conohyus simorrensis*, *Nyanzachoerus kanamensis waylandi*, *N. cookei*, *N. jaegeri*, *Notochoerus*, *Sivachoerus sindiense*, *S. indicus*, *S. aff. prior*, *S. tulotos*, *S. pattersoni* and *S. australis*. *Conohyus giganteus* is the type specimen. *Propotamochoerus* includes: *P. wui* from Lufeng (Van der Made & Han, 1994); *P. hysudricus* from the Indian Subcontinent (IM, GSP, BSPHGM, NMB, PMNH); *Propotamochoerus* sp. from Baccinello V3, Samos and Maramena (NMW, NMB, JGUM); *P. hyotherioides* from Lufeng (Van der Made & Han 1994); *P. provincialis* from Venta del Moro, Montpellier, Casino (MNCN, LPUMM, IGF, AFS); and *P. palaeochoerus* from Eppelsheim, Wissberg, Johnsdorf, Castell de Barberá, Münchener Flinz/Isarbett, Pyrrha, Inzersdorf, Barót-Kőpec, Mariathal, Grytsev and Doué-la-Fontaine (HLD, BSPHGM, NMB, SLJG, IPS, MNHN, HGSB; Van der Made *et al.* 1999). *Kolpochoerus* from Kobi Foorá (Harris 1987). *Sus* includes: Recent *S. scrofa* from Syria, Estonia, Germany, The Netherlands, Spain, Japan, Pakistan (HUJ, ZMA, NNML, MNCN, UPVB, UCM, UL); *S. salvanus* (MNHN, NHM); *Sus celebensis* (ZMA, FISF); *Sus barbatus* (ZMA); *Sus verrucosus* (ZMA, NNML); and fossil *Sus brachygnathus* from Trinil (NNML), *Sus falconeri/S. karnoolensis* from the Indian Subcontinent (IM, NHM). *Hippohyus* and *Sivahyus* from the Indian Subcontinent (IM, NMB). *Hippopotamodon*: *H. antiquus* and *H. sivalense* from Uşak and the Indian Subcontinent. *H. major* from Europe, Asia and the Indian Subcontinent (NMW, IVAU, IGF, Van der Made *et al.* 1992). *H. etruscus* from Monte Bamboli (IGF, NMB, MSNTUPC, DSTUST, NHM). *H. erymanthius* from Dorn Dürkheim, Kerassia, Chomateri, Ano Metochi, Samos and Polgardí (IVAU, FISF, HGSB, HLD, NMB, NMW, IPUW, NHM; Van der Made 1997b).

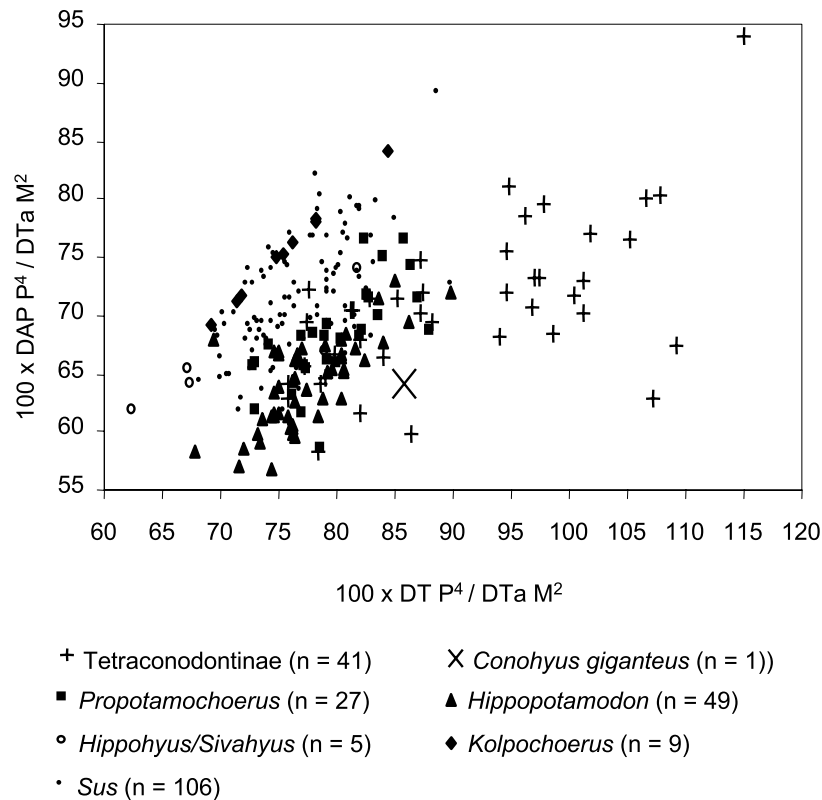


Figure 3 Bivariate plot of the length (DAP) and width (DT) of the P⁴ expressed as a percentage of the width of the anterior lobe (DTa) of the M¹. The Tetraconodontinae are largely (but not exactly) the same as those figured by Van der Made & Tuna (1999, fig. 4) and include: *Parachleuastochoerus steinheimensis* from La Grive and Hollabrunn (MGL, IPUW); *Conohyus simorrensis* from Göriach and Elgg (SLJG, IPUW, PIMUZ); *Nyanzachoerus cookei* from Sahabi (DSTUSR); *N. jaegeri* from Kanapoi (Cooke & Ewer, 1972); *Notochoerus* from Koobi Fora (Harris, 1987), *Sivachoerus sindiense* from the Indian Subcontinent (IM, GSP, NMB); *S. indicus* from the Indian Subcontinent (NMB); *S. aff. prior* from Yenangyoung (IM); *S. tulotos* from Lothagam (Cooke & Ewer 1972); *S. pattersoni* from Kanapoi (Cooke & Ewer 1972); and *S. australis* from Langebaanweg (Cooke & Hendey 1992). *Conohyus giganteus* is the type specimen. *Propotamochoerus*, *Kolpochoerus*, *Hippo/hyus* & *Sivahyus*, *Hippopotamodon* and *Sus* are those specimens that are associated with M². In the case of literature cited, generally the width of the first and second lobes is not given separately and 'width' is used.

contradict myself. This is misleading. I placed *Conohyus giganteus* in the Nyanzachoerini in the Tetraconodontinae, and this is consistent with its skull morphology.

Pickford (2001, section 4) cited Azzaroli (1989), for a suine morphology of the lectotype skull of '*giganteus*'. However, Azzaroli (1989, figure 1), made a 'restoration' of the skull of '*Propotamochoerus giganteus*' on the basis of skulls 15385 and 16166 (both present as casts in the IGF), and based his discussion on both specimens, particularly on the latter in the morphology of the P³ and the anterior part of the snout. Skull 16166 has a P³ with suine morphology as indicated by Azzaroli, a P⁴ with well-developed sagittal cusp and metacone, more massive and more backward placed zygomatic arches than skull 15385, and probably belongs to '*Microstonyx*' *major*, a form close to *Propotamochoerus*, which might explain Azzaroli's assignment of '*giganteus*' to the latter genus. Material from Pakistan has been assigned to '*Microstonyx*' *major* (Van der Made & Hussain 1989).

2.4. The hypodigm of *Conohyus giganteus*

Pickford (2001, section 6), did not agree with the inclusion of *Conohyus ebroensis* and *Nyanzachoerus devauxi* in *Conohyus giganteus*, and gave as his sole argument that the former two species are tetraconodontine and the latter suine. He failed, in my opinion (sections 2.1–2.3), to demonstrate that the type of *C. giganteus* is a suine.

Pickford (2001, section 8) cited Barry *et al.* (1982) for giving the date for the appearance of *Conohyus giganteus* as being

1.6 Ma later than indicated by Van der Made (1999). However, these authors did not mention this species, nor any of its synonyms.

Pickford (2001) himself assigned an Indian specimen of the *Conohyus giganteus* hypodigm (*sensu* Van der Made 1999) to the Tetraconodontinae. The holotype of *Propotamochoerus ingens* was tentatively assigned by Pickford (1988) to the early Late Miocene *Conohyus indicus*, though he suggested that part of the *C. indicus* hypodigm might belong to *Sivachoerus ingens*. This is a mandible from Hasnot with a canine with a very scrofic section (as may occur in *Conohyus*) and a P₃ and P₄ with a tetraconodontine morphology. Metrically, the specimen does not group with *Sivachoerus prior*, nor with *Sivachoerus indicus* (Fig. 5). The first molar and P₄ of the latter species indicate that it is relatively small, though it has a very large P₃ (Pickford & Gupta 2001). The *Conohyus giganteus* hypodigm thus includes a specimen that is accepted by Pickford as tetraconodontine and that is not *S. prior*, nor *S. indicus*.

Elsewhere (2001, section 7), Pickford gave what might be an additional argument against the inclusion of the African and European material in *C. giganteus*: '... *Nyanzachoerus devauxi*, which despite its allocation to *Conohyus giganteus* by Van der Made (1999), is a relatively small species.' Table 1 shows the size of the principal specimens assigned to *Conohyus giganteus*. It can be seen that Pickford's claim that *C. giganteus* is much larger is not true. Instead, all specimens are close in size, and in particular, the size of types of *C. giganteus* and '*P. ingens*' is close to that of the European and African material.

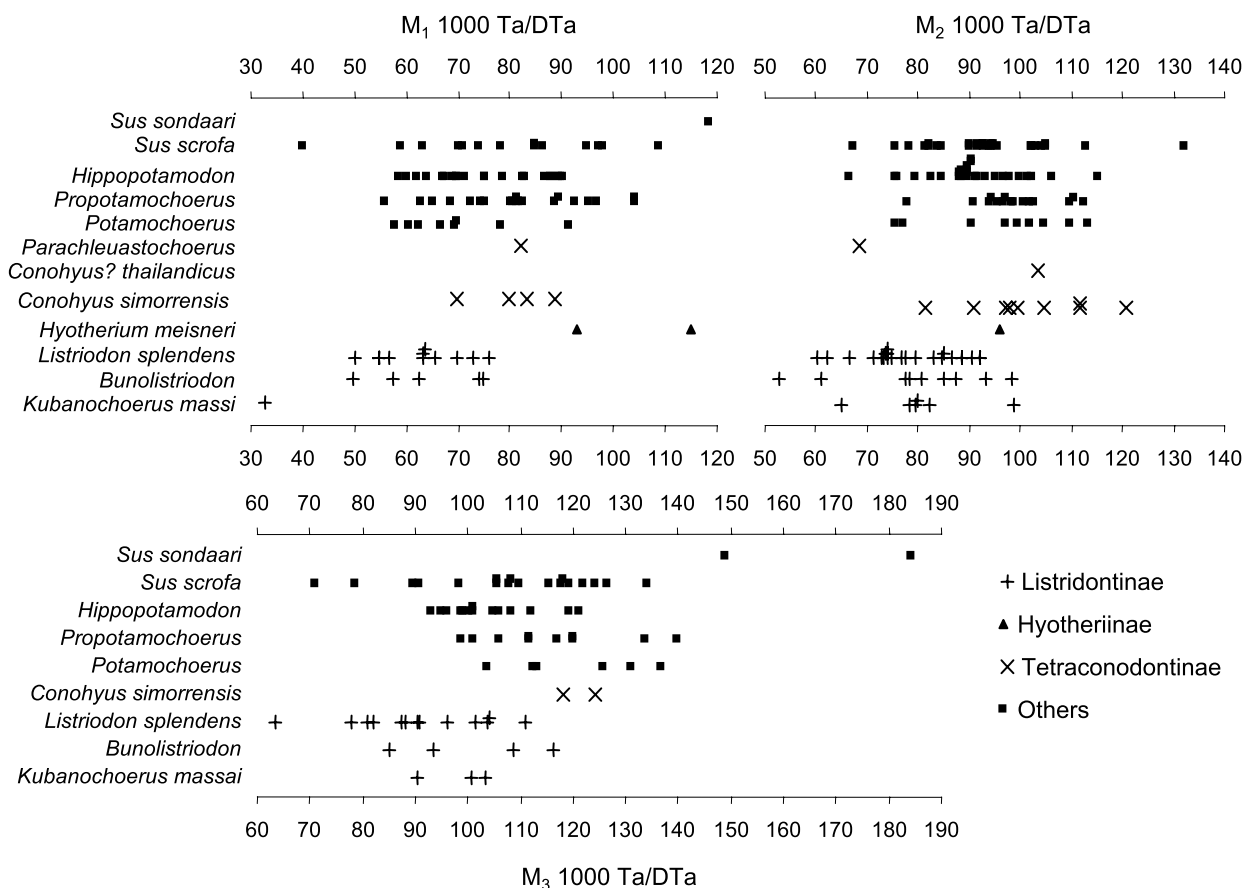


Figure 4 Enamel thickness (expressed as the index 1000 Ta/DTa) in *Kubanochoerus massai* and *Bunolistriodon* spp. (Van der Made 1996, table 19); *Listriodon splendens* (Van der Made 1996, table 19; data on Çandir: MTA; PDTFAU); *Hyotherium meisneri* from Cetina de Aragón (MNCN); *Conohyus simorrensis* (SLJG, NMW, IPUW, IGGML); *Conohyus? thailandicus* from Ban San Klang (LPUMM); *Parachleuastochoerus steinheimensis* from Przeworno (ISEAK); Recent *Potamochoerus* (ZMA, EBD); *Propotamochoerus* from various localities (NMW, IPUW, NMNHK, MNHN, HGSB); *Hippopotamodon major* and *H. erymanthius* from various localities (NMW, VMM, NHM, HGSB, IPUW, MSNO); Recent *Sus scrofa vittatus* from Deli (Sumatra, Indonesia; ZMA); and *Sus sondaari* from Capo Figari (Sardinia, Italy; NMB).

The assignment of the European and African material to *C. giganteus* is a result of a careful consideration of the possibilities. As indicated (Van der Made 1999, p. 212), the material is similar in morphology and size, but is scarce, and we have to choose between: (a) recognising different species on no morphological or metrical basis (which is clearly wrong), or (b) applying a single name to all material (running the risk that that is wrong). In the present case, even if the material assigned to *C. giganteus* belongs to more than one species, these species are similar in many important characters, and will very probably be closely related, and, contrary to Pickford's (2001, abstract) suggestion, this does not 'radically modify' tetraconodont systematics.

2.5. Diagnosis

Pickford (2001, section 5) stated that: 'Apart from size, no evidence from the Indian Subcontinent figures in the diagnosis of the species.' (meaning *C. giganteus*).

However, the diagnosis of *C. giganteus* was given as: 'Large species of *Conohyus*, DAP M₁ about 20 mm. DAP' M₃ about 165–200.' The diagnosis of the species refers to the diagnosis of the genus, and thus to the diagnoses of the tribe and subfamily; and in this way, characters are used that are observed in the types of all three Indian taxa that I included in *Conohyus giganteus*.

2.6. Origin of the *Nyanzachoerus–Notochoerus* lineage
Conohyus simorrensis evolved in Europe into a larger species ('*C. ebroensis*'), which at present is inseparable from *C. gigan-*

teus, and which spread to the Indian Subcontinent, where it continued (type *C. giganteus*), and to Africa, where it gave rise to a lineage *C. giganteus* (= *N. devauxi*)–*Nyanzachoerus–Notochoerus* (Van der Made 1999).

Pickford (2001, section 7) stated that, because *Conohyus giganteus* is a suine, the derivation of the *Nyanzachoerus–Notochoerus* lineage, described above, needs revision. However, in the same section, he admits the possibility that *Nyanzachoerus* evolved from *Conohyus simorrensis*, and in section 6 he admits that *Nyanzachoerus devauxi* and *Conohyus ebroensis* might be synonyms. Accepting in addition a close relationship between *Conohyus simorrensis* and *C. ebroensis* (Pickford 1989), this amounts to accepting that the *Nyanzachoerus–Notochoerus* lineage evolved from tetraconodontines that initially lived in Europe and spread into Africa during the Vallesian, which is essentially the model described above.

Apparently, Pickford argues mainly for the exclusion of the later Indian material, thereby reducing the 'need of revision' of the model of the origin of the *Nyanzachoerus–Notochoerus* lineage largely to the nomenclatorial problem of whether the name *C. giganteus* or *N. devauxi* should be applied.

2.7. Origin of *Sivachoerus prior*

Pickford (2001, section 8) states that there are no fossils from the Indian Subcontinent with an age between of 9 and 4.5 Ma that can be assigned to *Sivachoerus*, and therefore *Sivachoerus prior* is more likely to have originated in Africa and dispersed into the Indian Subcontinent. He cited Barry *et al.*

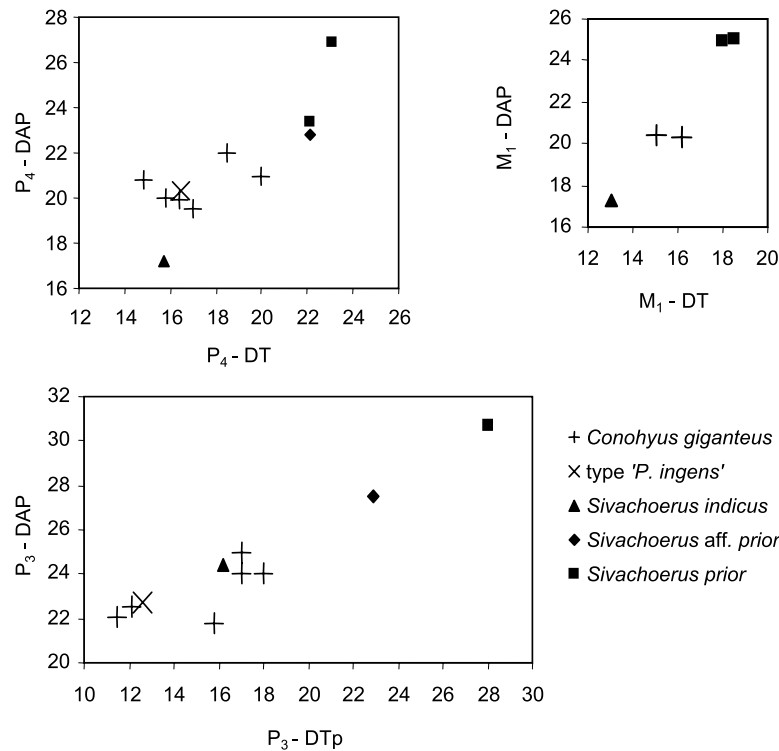


Figure 5 Bivariate plots of the P_{3-4} and M_1 of *Conohyus giganteus*, including the type of '*P. ingens*', (measurements from Table 1); *Sivachoerus indicus* (data from Pickford & Gupta 2001); *Sivachoerus aff. prior* Chaingzauk (Burma; IM); and *S. prior* from Hatar and Tatrot (IM, NHM).

(1982), who indicate that recently collected material from the Tatrot beds is not older than 2.9 Ma (which in fact is where Van der Made (1999, fig. 20) puts *S. prior* from Tatrot). If Pickford means to say that 2.9 Ma really is the first appearance datum of *Sivachoerus* in the Indian Subcontinent, then this is an important change from his earlier opinion that the species appeared 5 Ma ago (Pickford 1988, p. 51), in the late Miocene (Pickford 1993, p. 247), or 6 Ma ago (Pickford 1989, fig. 4).

Pickford (2001, section 8) stated that: 'The Late Miocene is one of the best-represented fossiliferous successions in the Indian Subcontinent (Pickford 1988) from which many hundreds of fossil suids have been collected.' However, the Indian Subcontinent is a large area, whilst the Mio-Pliocene suid fossils mostly come from a much smaller area, which may thus not be representative. Moreover, Barry *et al.* (2002, fig. 7a) indicated that the number of catalogued large mammal fossils from this area decreases markedly after 8 Ma and Barry *et al.* (1982) indicated just three fossiliferous localities with *S. prior*. Pickford (1988) described *S. prior* and listed six specimens from Tatrot, at least part of them from the old collections. Some other specimens described by Pickford (1988) are from the old collections from Hasnot and other localities. Pickford (1988) considered that *Tetraconodon magnus*, present at Hasnot, is around 9 Ma old (p. 20) and *Hippohyus lydekkeri* and *Sivahus*, also present at Hasnot, about 4–5 Ma (pp. 80 and 20, respectively). The suids from Hasnot, including *S. prior*, fit well an age of 3–5 Ma. It is obvious that *S. prior* is rare, and the complete range of this species cannot be inferred from just three new records in a restricted area.

Pickford (2001, section 8) admits the possibility that the Burmese material is late Miocene in age. Ages of around some 9–10 Ma and 7–8 Ma are suggested by the stage of evolution of primitive *Sivachoerus aff. prior* and a primitive *Tetraconodon* (Van der Made 1999, section 4.4). Because of these *Sivachoerus* specimens, which are intermediate between *S. indicus* and *S. prior*, there is no need to derive *Sivachoerus* from Africa, and, as explained earlier (Van der Made 1999), *Sivachoerus*

from the Indian subcontinent is more primitive than the African forms, which is an argument against a derivation from Africa.

2.8. Biogeography

Pickford (2001, section 8) stated that a model with a single dispersal of Tetraconodontinae into Africa (*Nyanzachoerus devauxi*) and one from Africa into the Indian Subcontinent (*Sivachoerus prior*) is more parsimonious than the model with four dispersals into Africa (*Conohyus giganteus* twice and *Sivachoerus* twice). However, the most parsimonious biogeographical model should not only count the number of dispersal events, but also involve a study of phylogeny. Alternative phylogenetic and biogeographic scenarios were discussed, but considered to be less likely on the basis of morphological evidence (eg. Van der Made 1999, section 3.1).

3. Points of convergence

The previous sections (2.1–2.8) treat the points of divergence between Pickford and myself. However, it should not go unnoticed that there is also some convergence of our opinions.

3.1. Origin of the *Nyanzachoerus*–*Notochoerus* lineage

Pickford (1989, 1993) presented a model in which: (1) *Conohyus ebroensis* and *C. simorrensis* form part of a clade that became extinct in Europe and that did not give rise to any Indian or African form; (2) *Nyanzachoerus* is derived from an African form, indicated as *Conohyus* sp. and present in the early Middle Miocene of Maboko.

Van der Made (1999) presented a different model in which *Conohyus simorrensis* evolved into a large species ('*C. ebroensis*') inseparable from *C. giganteus*, and spread during the Vallesian into Africa (where it is known as '*N. devauxi*'), giving rise to the *Nyanzachoerus*–*Notochoerus* lineage.

Table 1 Measurements of the principal specimens assigned here to *Conohyus giganteus*. Provenance of data: '*Conohyus ebroensis*' holotype (MPZ) and Fonte do Pinheiro (GML); '*P. devauxi*' type (Arambourg, 1968) and material from the Beglia Formation (casts sent by Dr P. Robinson), type of *Conohyus giganteus* (cast in IGF); type of '*P. ingens*' (IM); type of '*Potamochoerus prasadi*' (Verma, Gupta & Tewari, 1981).

			P ²	P ³	P ⁴	M ¹	M ²	M ³
<i>Conohyus giganteus</i> , lectotype	s	DAP			17.2	>16.1	23.4	39.9
		DTa			23.1	--	26.9	28.8
IGF 1470v (=NHM M 15385)	d	DTp				--	24.7	24.0
		DTpp						15.9
		DAP					23.4	~38.9
		DTa					--	--
' <i>Propotamochoerus devauxi</i> ' cast	s	DTp					--	--
		DTpp						--
		DAP	~17	19.8	15.4	21.1	27.9	39.4
		DTa	7.3	15.8	20.3	19.2	25.8	26.5
' <i>Propotamochoerus devauxi</i> ' casts	d	DTp	≥8.7	19.0		18.3	23.3	20.8
		DTpp						13.8
		DAP		17.6	13.7	17.6	24.0	
		DTa		14.2	≥19.1	17.2	22.2	
		DTp		17.6		17.0	21.9	
			P ₂	P ₃	P ₄	M ₁	M ₂	M ₃
holotype of ' <i>Propotamochoerus ingens</i> ' IM B10	s	DAP		22.7	20.3			
		DTa		11.9	13.7			
		DTp		12.6	16.5			
holotype of ' <i>Potamochoerus prasadi</i> ' Verma, Gupta & Tewari (1981)	s	DAP	13	24	19.5	17	24	42
		DTa	23
		DTp	7	17	17	16	21	..
		DTpp						..
Holotype of ' <i>Conohyus ebroensis</i> ' DPZ 2001	s	DAP			20.8	20.3	23.1	
		DTa			..	16.2	18.7	
		DTp			~14.8	15.5	17.6	
' <i>Conohyus ebroensis</i> ' GML	s	DAP	~19	22.1	20.0	20.4	23.7	34.4
		DTa	--	14.6	17.9	18.5
		DTp	--	11.8	15.8	15.0	17.0	16.4
	d	DTpp						12.2
		DAP		22.5			23.0	34.6
		DTa		..			18.2	19.9
Holotype of ' <i>Propotamochoerus devauxi</i> ' Arambourg (1968)	s	DTp		12.1		18.2	16.5	11.6
		DTpp						11.6
		DAP	18	24	21	>17	26	>32
	d	DTa	20?
		DTp	8	18	20	17	20	..
		DTpp						..
' <i>Propotamochoerus devauxi</i> ' cast	s	DAP	15	25	22	≥19	23	38
		DTa	21
		DTp	9	17	18.5	18	19	..
		DTpp						..
' <i>Propotamochoerus devauxi</i> ' cast	s	DAP		21.8	19.9	21.1	25.7	
		DTa		13.4	14.4	--	19.4	
		DTp		15.8	16.4	--	18.6	

As we have seen above (section 2.6), Pickford (2001) admits that *Nyanzachoerus* may have evolved from *Conohyus simorensis*, and accepts that *Nyanzachoerus devauxi* and *Conohyus ebroensis* might be synonyms, which is a shift from his earlier opinion (Pickford 1989), and a move towards the model presented by Van der Made (1999).

3.2. Origin of *Sivachoerus prior*

Pickford (1989) indicated that the '*C. sindiense-indicus*' lineage became extinct and that *Sivachoerus prior* arrived in the Indian Subcontinent by dispersal, possibly originating from a group

of African tetraconodontines with particularly large premolars. Contradicting earlier authors (Pilgrim 1926; Colbert 1935), Pickford (1988) claimed that *Tetraconodon magnus* is an early Late Miocene form, and (1989) proposed that the small *Tetraconodon minor* evolved from the large *Tetraconodon magnus*. In this model, *T. minor* becomes intermediate in age and size between *T. magnus* and the African tetraconodontines with large premolars. Pickford (1989) gave two possible origins for these tetraconodontines: (1) evolution *in situ* from *N. devauxi*, and (2) evolution from *Tetraconodon* after dispersal from the Indian Subcontinent. *Sivachoerus prior* is thus

not derived from the *S. sindiense-indicus* lineage, whilst the possibility of an evolution from a *Tetraconodon* lineage of decreasing size is considered possible.

It was pointed out that Pilgrim (1926) and Colbert (1935) considered the large *Tetraconodon magnus* a much younger species, evolving from the smaller and older *T. minor*, and that Pickford (1988, 1989) presented an inverse phylogenetic and stratigraphic model without having any new data that justified this (Van der Made 1999). Colbert (1935) believed *Sivachoerus* prior to be a descendant of the '*C. sindiense-indicus*' lineage and Van der Made (1999) put forward arguments for such a relationship.

Pickford (2001, section 8) states: '... the only Indian suid likely to have given rise to *Sivachoerus* is *Conohyus indicus*, known from late Chinji to Nagri levels (c. 11.5–11.9 Ma); the other tetraconodonts from the period being either very small (*Lophochoerus* species) or very large and specialised (*Tetraconodon*) species.' This statement implies a change of opinion, that is a shift towards a model supported by Van der Made (1999) and earlier authors.

3.3. Origin of *Tetraconodon*

Pickford (1989) indicated that the '*C. sindiense-indicus*' lineage became extinct and that the large *Tetraconodon magnus* arrived by dispersal and evolved into the smaller *T. minor*.

Pilgrim (1926), Colbert (1935) and Van der Made (1999, section 3.3, figure 19) believed the *Sivachoerus sindiense-indicus* lineage to have given rise to the *Tetraconodon minor-magnus* lineage, which increased in size.

Pickford & Gupta (2001) discussed *Conohyus thailandicus* Ducrocq *et al.* 1997, concluding that it is a synonym of *Conohyus indicus* and suggesting that it may have given rise to *Tetraconodon*. This is a break with earlier views held by Pickford (1989), and an approximation to the model of Pilgrim (1926), Colbert (1935) and Van der Made (1999).

Though I am not completely convinced that '*C. thailandicus*' is a synonym of *Sivachoerus indicus*, it may well be ancestral to *Tetraconodon*.

Pickford & Gupta (2001) referred to a remark by Van der Made (1999, p. 206) that *S. indicus* might prove to be a *nomen dubium* and maintained that the new material described by them 'clears up the matter'. There is little doubt about the existence of a large form close to *S. sindiense* in the upper Chinji and Nagri Formations, or time-equivalent strata, and Van der Made (1999, p. 206) followed earlier authors in applying the name '*indicus*' to that form. However, the holotype is an isolated tooth of unknown exact stratigraphic provenance. Pickford & Gupta (2001) measured its length on Lydekker's figure (23 mm), which suggests that they have not seen the original, and thus do not know its occlusal view, nor its width. The morphology, as indicated by Lydekker's figure, is not very different from other early tetraconodontines, and a length of 23 mm is given by Pickford (1988) for '*Conohyus sindiense*', which coincides with my observations, and is within the ranges for *Conohyus giganteus* and *C. simorrensis*. Possibly, the holotype belongs to the taxon that is indicated with the name '*indicus*', but this is not certain, and the interesting specimens described by Pickford & Gupta do not change this situation; but I agree they do add to our knowledge of the taxon that is tentatively indicated by that name.

4. Conclusions

Pickford (2001) made eight major objections to a model of evolution and biogeography of the Tetraconodontinae presented recently (Van der Made 1999). However, his points of

criticism: (a) contradict morphology, metrics and presence/absence of taxa as observed in the fossil record (points 1, 2, 4, 7); (b) contradict his own published opinions (points 4, 7); (c) give a wrong impression of what Van der Made (1999) wrote (points 3, 5); (d) ignore the discussion that led to certain conclusions and (e) present an alternative view that either has been discarded already, or that is not supported by data (points 6, 8). Pickford's (2001) paper fails conclusively to demonstrate any of the eight objections. Having been allowed a right of reply by the editors, this author thinks it is fair also to note that Pickford's opinions seem to have changed through time in favour of the model presented by Van der Made (1995, 1997a, 2001).

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