European Suinae (Artiodactyla) from the Late Miocene onwards

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ABSTRACT — European Suidae that have a time distribution near the Mio-Pliocene boundary have been studied. They belong to two tribes: Dicoryphochoerini (Korynochoerus, Microstonyx and Eumaiochoerus) and Suini (only the genus Sus). The first tribe was well represented in the Late Miocene and the other tribe was represented from the Early Pliocene onwards. The immigrants K. palaeochoerus, Microstonyx and K. provincialis entered in the latest Middle Miocene and Late Miocene. Microstonyx is a lineage of three forms, the endemic island form Eumaiochoerus is an offshoot of this line. In the Pliocene Sus arvernensis and S. strozzii immigrated. Sus scrofa entered late in the Early Pleistocene. The endemic Sardinian Sus nanus is believed to be a descendant of S. arvernensis. A range chart for the Suinae is given.

European Microstonyx was a lineage characterized by a size decrease of the dentition and loss of premolars: M. antiquus, M. major major and M. major erymanthius. "Propotamochoerus" provincialis is found to be related to Korynochoerus palaeochoerus and is included in this genus. These two species are not related to Propotamochoerus. Fossils described as subgenus Postpotamochoerus are found to be related to Sus and not to Potamochoerus. Cladograms of the Dicoryphochoerini and the Suini are given.

RIASSUNTO — [Suinae (Artiodactyla) europei a partire dal Miocene superiore] — Sono stati studiati i suidi europei che hanno una distribuzione temporale vicina al limite Mio-Pliocene. Essi appartengono a due tribù: Dicoryphochoerini (Korynochoerus, Microstonyx e Eumaiochoerus) e Suini (il solo genere Sus). La prima tribù era ben rappresentata alla fine del Miocene mentre la seconda compare a partire dal primo Pliocene. Korynochoerus palaeochoerus, K. provincialis e Microstonyx giunsero come immigranti alla fine del Miocene medio e nel Miocene superiore. Microstonyx costituisce una linea filetica di tre forme; la forma insulare endemica Eumaiochoerus trova la sua origine in questa linea. Nel Pliocene immigrarono Sus arvernensis e S. strozzii. S. scrofa giunse nel tardo Pleistocene inferiore. Si pensa che la forma endemica Sus nanus della Sardegna discenda da S. arvernensis. Viene stilata una carta di distribuzione dei Suinae.

La linea evolutiva europea di Microstonyx fu caratterizzata dalla diminuzione di taglia della dentizione e dalla perdita dei premolari: Microstonyx antiquus, M. major major e M. major erymanthius. Viene riconosciuto che "Propotamochoerus" provincialis è collegato a Korynochoerus palaeochoerus e pertanto incluso in quest'ultimo genere. Queste due specie non sono in relazione con Propotamochoerus. I resti fossili riferiti al sottogenere Postpotamochoerus vengono considerati vicini a Sus e non a Potamochoerus. Vengono forniti i cladogrammi delle tribù Dicoryphochoerini e Suini.

INTRODUCTION

The African Pliocene and Pleistocene Suidae are considered to be of great value in stratigraphy. White & Harris (1977) provided an alternative stratigraphy on the basis of suid evolution in cases where absolute methods were controversial.

It is doubtless under the influence of that and similar papers that interest in Eurasian Suidae is growing. The workshop on continental faunas at the Miocene/Pliocene boundary is a good opportunity for drawing up an inventory of the data available on the European Suidae of that time.

Apart from a suid from Samos little attention is paid to Asian suids in this paper. The Samos suid might also prove to occur in Europe.

THE TAXA AND THEIR CHARACTERISTICS

This section has two purposes. One purpose is to give the characters of the teeth that are frequently found, so that a taxon can be recognized in a collection. Another purpose is to give characters that can be used in phylogeny; these characters are usually only seen in rare fossils such as complete skulls.

Dicoryphochoerini Schmidt-Kittler, 1971

The Dicoryphochoerini share several characters, such as the morphology of P_4 and the morphology of the upper incisors.

The P_4 has a main cusp positioned labially to the

midline. From this cusp an antero-lingually directed ridge descends to the anterior cingulum ending somewhat lingually of the middle of the tooth. This ridge is not smooth, but may have swellings, which look like cusps. A second main cusp is placed a little behind the other and much more lingually. Posteriorly these two cusps are connected by a ridge or cusp to the much lower posterior cusp of the talonid. On both sides a cingulum runs up to this cusp and fuses with it. The anterior and posterior ends of the tooth are about the same height and clearly lower than the maincusps.

A detailed study of the incisors of the Suoidea is being prepared by one of us (J. v. d. M.); it is sufficient to deal only with the I^2 and I^3 in this paper. The second upper incisors are long and narrow. They have a postero-lingual cingulum.

All Dicoryphochoerini have more elongated molars than primitive Suidae. The males of *K. palaeochoerus*, *"P." provincialis* and *Microstonyx* and probably also *Eumaiochoerus* have well-developed alveolar crests above the canines. The alveolar crests of *"P." provincialis* are more slender. The females of *K. palaeochoerus*, *"P." provincialis* and probably also of *Microstonyx* and *Eumaiochoerus* lack such crests. (This is also the case in modern suids such as *Potamochoerus*, *S. verrucosus*, *S. barbatus* and *S. celebensis*).

Korynochoerus palaeochoerus (Kaup, 1833)

K. palaeochoerus is about the size of a recent wild boar. The males have much inflated zygomatic arches that depart nearly at right angles from the snout. In the females this angle is less acute, it is not known if their zygomatic arches are also inflated. The occiput was elevated in the males, whereas in the females this is not known. The anterior end of the orbit is behind the M$_3$. The I^3 is large but not elongated; it does not always have a postero-lingual cingulum.
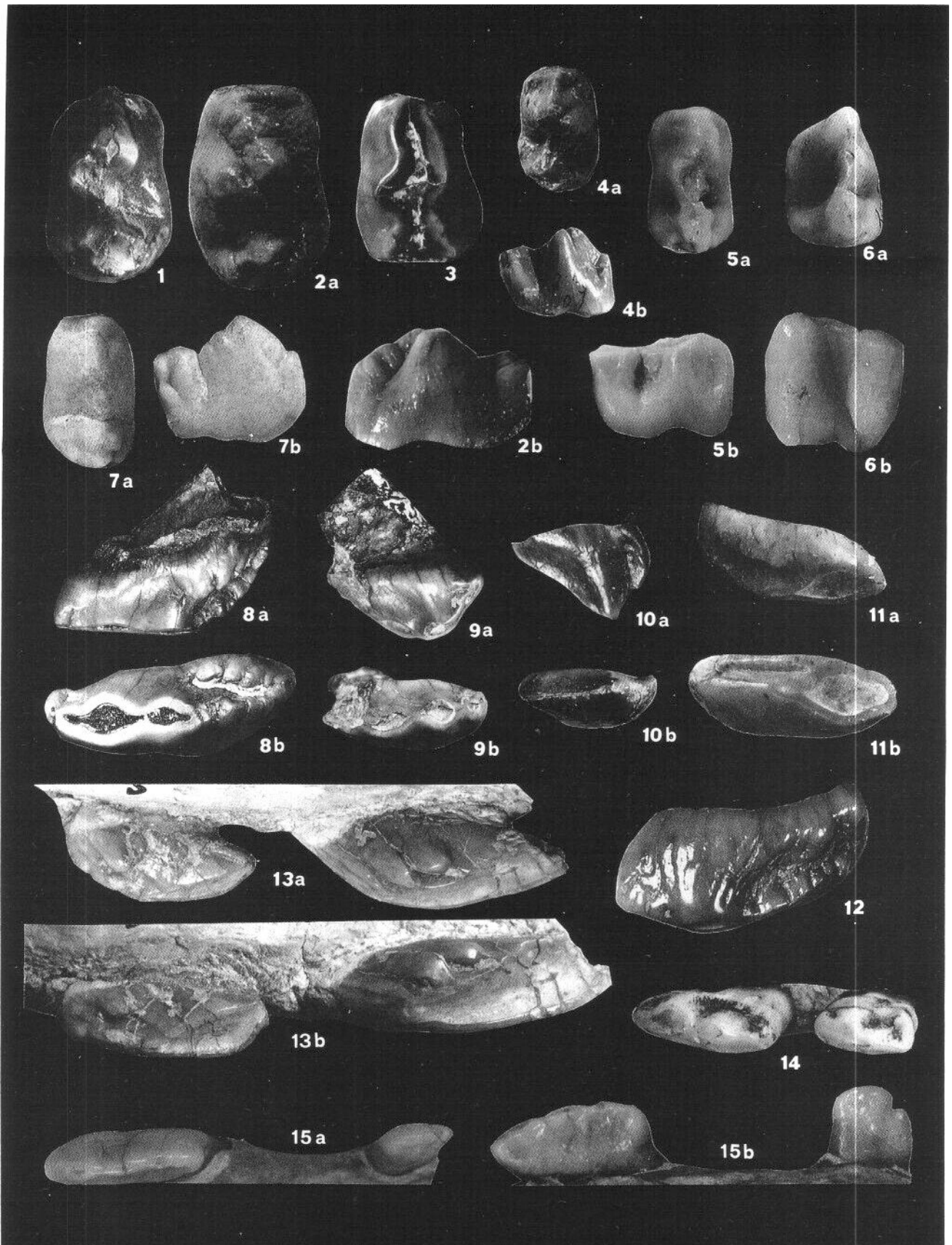
"Propotamochoerus" provincialis (Gervais, 1859)

"P." provincialis has dentition that is a little larger than in *K. palaeochoerus*. The size range of the teeth is not well known but it is known that the two species overlap in size. The molars have somewhat more pronounced accessory cusps and the labial wall of the labial cusps of the upper molars is more convex. The I^3 resembles that of *K. palaeochoerus*.

In a female skull from Ptolemais Kardia the occiput is not elevated as it is in the male *K. palaeochoerus* skull from Johnsdorf (see Mottl, 1966 and Thenius, 1972). In *Sus barbatus* and *Metridiochoerus andrewsi* both males and females have elevated occiputs. Although the skull structure is different, this indicates that the difference in the shape of the occiput of the male *K. palaeochoerus* and of the female *"P." provincialis* skulls is not due to sex but to specific characters. The Johnsdorf skull has inflated zygomatic arches, whereas in the skull from Ptolemais these arches are not inflated. This is a feature that is related to mastication; in *Potamochoerus* the shape of the zygomatic arches in females and males does not differ much, although their zygomatic arches differ greatly from those of a primitive type such as those of *S. scrofa*. In *Metridiochoerus* however the degree of inflation is surprisingly related to sex.

We expect that *"P." provincialis* does not have the zygomatic arches inflated nor the occiput elevated. In the crushed Ptolemais skull the anterior rim of the orbit seems to be somewhere above the M^3. The individual is fully adult. It should be borne in mind that this character is age dependant. The *"P." provincialis* from Montpellier has lost its I^3. The skull from Ptolemais Kardia has lost both I^2, the alveoli are still open but were in the process of closing when the animal died. The loss of I^2 and I^3 during life seems to have been common.

EXPLANATION OF PLATE 1

Microstonyx Pilgrim, 1926

Microstonyx is a large suid with an elevated occiput, lengthened snout, relatively small canines, relatively shallow mandibles, I³ that are greatly elongated and that have postero-lingual cingula, inflated zygomatic arches; the parietal ridges are wide apart (at least in the male skulls that we know). The anterior rim of the orbit is well behind the M³.

A lower Vallesian form has a very large dentition and retains its P¹ and P₁. An upper Vallesian to middle Turolian form has a smaller dentition and also retains its first premolars (the P₁ is probably lost early in life). There is also an upper middle Turolian form from Pikermi and Kerasia that has a still smaller dentition, but the skull is just as long as it is in upper Vallesian and middle Turolian forms, it has no P₁ and often lacks its P¹ (which is probably lost during the life of the individual). Gaudry (1862-1867) reports alveoli for the P¹ on two of six skulls from Pikermi. He did not find any indication of the existence of a P₁. It seems that the size of the canine and the depth of the mandible decrease from the first to the last form (these characters are probably related).

Other differences between forms of Microstonyx that have been mentioned (for instance by Thenius, 1972, pp. 555-557) are:

1) The degree of complication of P₄. We failed to find significant differences: this apparent difference was probably an artefact of individual variation or of wear.

2) The lenght of the snout (indicated by the distance C_x — P_3 and by the lenght and position of the symphysis). It should be realized that both characters are related to sex and probably to ontogenetic age.

3) The length of the part of the skull anterior to the orbit relative to the lenght of the posterior part of the skull. This ratio is influenced by the different rates of development of the different parts of the skull; these developments are ontogenetic age related.

4) The structure of the M₃. In both lower Vallesian and the middle Turolian forms the third lobe generally consists of a small cusp on the axis of the tooth and two larger cusps behind this small cusp; the morphology of the M₃ is probably not of much utility.

Trofimov (1954) gives measurements for Russian Microstonyx. Measurements from Eldar, Berislave and Grossulovo (MN 11) and Grebeniki and Taraklia (MN 12) are similar to those of contemporary Microstonyx from western Europe. The Microstonyx from Tudurovo is comparable in size to Microstonyx from Pikermi. Its mean size is greater than that of Microstonyx from Kerassia, indicating a greater age (?). Tudurovo is dated MN 13 (Mein, 1975). Kerassia still has Deinotherium and Dorcatherium: Kerassia probably should be

placed in MN 12. Maybe Tudurovo should be correlated to MN 12 if this is not contradictory to evidence from other taxa.

Since the smallest form has not been found in western Europe one of us (S. M.) thinks that it is a geographical subspecies. But as the size decrease seems to occur in many places, the smaller form may also be a younger subspecies. The large form has been found in France, Germany and Turkey; the intermediate form in Spain, France, Russia etc. and the small form in Greece and Russia.

Eumaiochoerus etruscus (Michelotti, 1861)

Eumaiochoerus Hürzeler, 1982 is an endemic island form. It has relatively small canines like Microstonyx and greatly elongated I³, but is smaller. Its dentition is of about the same size as in K. palaeochoerus. The anterior edge of the orbit is above the anterior end of the M³ (in one adult animal) and the orbit was probably higher than in most other Suidae. These characters are probably related. The talon and talonid of the M³ and M₃ tend to be wider than in K. palaeochoerus and in "P." provincialis (although overlap occurs). The talonid of the M₃ has two larger posterior cusps, as occur frequently in Microstonyx, to a lesser degree in "P." provincialis and not at all in K. palaeochoerus. Compared to K. palaeochoerus the mandible of Eumaiochoerus is relatively shallow in view of the size of the dentition. The depth measured lingually in a mandible from Can Llobateres is about 49 mm below M₁ and M₂; in a mandible with only slightly smaller teeth the depth is about 32 mm in E. etruscus. Eumaiochoerus may have a P₁, but this tooth may also be lacking. We do not know whether Eumaiochoerus had a P¹, but it is likely since a P₁ usually disappears first during dental reduction.

Suini

The Suini share the shape of the P₄, and probably the shape of their incisors.

The P₄ is one high meso-distally directed ridge. There is one main cusp; a second equally large cusp may be placed immediately postero-lingually to it. After only a little wear the two cusps can no longer be differentiated. From the main cusp a ridge is directed anterolingually. This is a homologous ridge to the one seen in the Dicoryphochoerini, but it does not slope downwards.

What is called the anterior cingulum in that group is either absent or is directed nearly vertically and forms lingual and labial stylids. The cusp of the talonid is nearly as high as the main cusp. What is homologous to the posterior cingulum is absent in Suini or it has

been converted into a lingual and a labial, nearly vertical stylid.

The I² is very low and elongated, a postero-lingual cingulum is lacking (this may be due to reduction). We do not know this tooth in *S. arvernensis* but suppose that it has the same morphology as in the other species. The I³ is small and short in *S. scrofa*; we suppose it to be like the I³ in the other species, since short I³ are primitive and common in Suidae.

The genus *Sus* is currently divided into two groups: the species with a "verrucosic" male lower canine and those with the "scrofic" male lower canine. The section of the lower canine is verrucosic if the length of the lingual side is about the same as the length of the antero-labial side (measured horizontally). If the lingual side is much wider than the antero-labial side the canine is scrofic. Since female lower canines have a verrucosic section this is often thought to be the primitive state. But primitive pigs like *Conohyus*, *Hyotherium*, peccaries like *Barberahyus*, *Albanohyus*, *Taucanamo* have scrofic canines. This indicates the contrary. In *Listriodon splendens* both types of canines occur. The character is not sufficiently understood for great phylogenetic or taxonomic weight to be attached to it.

The verrucosic group (species with a canine like that of *S. verrucosus*, which for this reason are thought to be related to this species) is characterized by several other features. There are well developed alveolar crests above the canines in the males. These are higher and more slender than in *K. palaeochoerus* and *Microstonyx*. In most forms the zygomatic arches depart abruptly from the skull. In all verrucosic species the styles and stylids of the premolars, especially of the P4, are more pronounced and the bases of the premolars are much lower than the bases of the molars compared with *S. scrofa*. The last character is not a constant one, being dependent on age and being difficult to measure. However it seems to be useful within certain limits. The skull structure and canine shape could not be checked in *S. nanus*. In the scrofic group the zygomatic arches are more slender, the alveolar crests above the canines in the males are less developed and the base of the premolars is higher.

Sus arvernensis Croizet & Jobert, 1828

Sus arvernensis is the smallest *Sus* known from the mainland of Europe. The M₃'s have a simple talonid with one terminal cusp. The talon of the M³ is also simple. The anterior and posterior ends of the P₄ are much lower than in *S. strozzii* and *S. scrofa*. The length of premolar row of *S. arvernensis* relative to the molar row is large for *Sus*; the relative length is probably the same as in the Dicoryphochoerini.

Sus nanus van der Made, 1988

Sus nanus is a dwarf form from Sardinia. It is 75-80% of the size of *Sus arvernensis*. Its P4 and molars are slightly more hypsodont than the same teeth in most species of *Sus*. The enamel surface of the molars looks very smooth and simple. The talon of the M³ consists of one cusp and in the M₃ only a small cusp and a larger cusp behind it follow the second pair of cusps. Its P₂ and P₃ are reduced in size and a P₁ is absent. The diastema between P₂ and the canine is short; the snout is shortened.

Sus strozzii Meneghini

Very large species. The premolar row is shortened compared to the state in *S. arvernensis*. Usually the last molar has a simple talon(id). The M₃ from Valdeganga II and Tegelen are much more elongated; other teeth from Tegelen seem to be large as well. These differences cannot be explained by evolution towards more elongated molars since these localities are among oldest at which *S. strozzii* has been found. It is not impossible that this material represents yet another species of suid. The wider molars of the regular type can be differentiated from those of *S. scrofa* by their relatively great width. Azzaroli (1954) reports that one cranium from Senèze still had its I³ and that the younger crania of Valdarno had lost the I³.

Sus scrofa Linnaeus, 1758

The premolar row is shorter than in *S. arvernensis*. In the European forms the talon and talonid of the last molars always seem to be complicated: a third pair of cusps and a terminal cusp are common in the M₃ in the oldest populations (Mosbach). These teeth are more elongated than those of the Dicoryphochoerini. *S. arvernensis* and *S. nanus*.

PHYLOGENY AND TAXONOMY

Suinae Von Zittel, 1893

In recent literature all taxa described here are included in the Suinae. *Microstonyx* has traditionally been considered to belong to the Suinae (Many Suidae were first described as a species of *Sus*. Later some authors attached more importance to the differences and made new genera; others created a tribe or subfamily. For some reason, in the minds of paleontologists *Microstonyx* remained connected with *Sus*.) Only Thenius (1972) placed this genus in the Hyotheriinae. He did this because he recognized the relantionship between "*Hyotherium*" *palaeochoerus* and *Microstonyx*. "*Hyotherium*" *palaeochoerus* was thought to be

descendant of *Hyotherium soemmeringi* until Schmidt-Kittler (1971) proved this idea to be false; he created the genus *Korynochoerus* for the species *"H." palaeochoerus* and created the tribe Dicoryphochoerini for *Dicoryphochoerus* (including only *D. titan* with certainty), *Microstonyx* and *Korynochoerus*. This tribe was characterized by the morphology of the P_4 and placed in the Suinae. Schmidt-Kittler probably placed the Dicoryphochoerini in the Suinae because *Sus* is traditionally thought to be derived from *Dicoryphochoerus* (in this case *Dicoryphochoerus* includes all species that were included by Pilgrim, 1926). He derived the *Sus*-type P_4 from the *Dicoryphochoerus* type by supposing that the position of the lingual cusp had changed and that the anterior part of the tooth had been raised. However the *Sus*-type P_4 can be derived also from the *Potamochoerus* P_4 by supposing that the anterior end of this tooth has been raised. Biologists believe that *Potamochoerus* and *Sus* are closely related; they may have shared a long part of their history. The Suinae are a group with many more different forms than other subfamilies of the Suidae and we were unable to find any synapomorphy uniting all Suinae. Consequently we do not know if this group is really monophyletic; however we follow current taxonomy, since at the moment we cannot offer a better alternative.

The relationship between *Potamochoerus* and *"Propotamochoerus" provincialis*

Several authors consider explicitly or implicitly that *"P." provincialis* is closely related to *Potamochoerus*, or even to be its immediate ancestor (for instance Guérin & Faure, 1985). This is unlikely for several reasons. Stehlin (1899-1900) derived *Potamochoerus* from *K. palaeochoerus*. This is also not likely to be correct for almost the same reasons.

Stehlin (1899-1900) already noted the trend in Suiformes to acquire more elongated molars. This happened parallel in many branches, even within the Suidae. *Potamochoerus* is more conservative in this respect than several other Suidae. We take the M_2 as an example.

M.	DTmax/DAP		
	n	mean	min.	max.
Potamochoerus (specimen in RMNHL)	8	0.77	0.70	0.81
K. palaeochoerus (Deinotheriensande, data from Hünermann, 1968)	39	0.74	0.66	0.79
"P." provincialis (div. loc.)	6	0.72	0.69	0.76
Microstonyx (from Pikermi, data from Pearson, 1928)	15	0.73	0.64	0.80

Potamochoerus has a P_4 with one main cusp. A P_4 with only one main cusp is probably primitive in Suoidea. The Dicoryphochoerini P_4 is farther from the supposed ancestral form than the *Potamochoerus* P_4.

The M_3 of *Potamochoerus* does not have a third pair of cusps. The talonid consists of several smaller cusps and one larger cusp. The latter may be divided by a cleft. In several M_3 of *"P." provincialis* this cusp can already be seen to be divided. The M_3 of this species is also more elongated (lower DT/DAP ratio). If this is an evolving feature it seems strange that the specimens from Montpellier are equally progressive or even more progressive than recent *Potamochoerus* M_3.

"P." provincialis possibly starts to lose its I^2 and I^3 early in life, there is no size reduction of these teeth. *Potamochoerus* retains its (small) I^2 into old age. Only one *Potamochoerus* in the collection of the Rijksmuseum v. Natuurlijke Historie in Leyden-(RMNHL) had not replaced its DI^2. It is unlikely that *Potamochoerus* or its forerunners ever had an elongated I^2, since short I^2 are primitive.

The relationship between *Korynochoerus palaeochoerus* and *"P." provincialis*

It has been suggested that *K. palaeochoerus* might be the ancestor of *"P." provincialis* (for instance Ginsburg 1980). Both species resemble each other very much in the morphology of their dentition. *K. palaeochoerus* has an elevated occiput. In this respect it resembles *Microstonyx*. Probably *"P." provincialis* and *K. palaeochoerus* are closely related, but are not an evolutionary lineage. Moreover their ranges overlap.

Propotamochoerus

The type species of *Propotamochoerus* Pilgrim, 1926 is *P. salinus* Pilgrim, 1926. The morphology of the P_4 was considered important by Pilgrim (1926, p. 22): "The fact that the height of the main cusp of P_4 much exceeds that of the anterior and posterior cusps distinguishes it from the *Sus* — *Hippohyus* series. The cone -like character of the main cusp of P_4 distinguishes it from the corresponding tooth of the *Dicoryphochoerus* branch, ...". The morphology of the P_4 of the holotype of *P. salinus* corresponds well to this description (pl. 7, fig. 1). *"Propotamochoerus" provincialis* was included in this genus by Pilgrim (pl. 1), although the structure of its P_4 is more like that of *Dicoryphochoerus*. From the definition of *Dicoryphochoerus* (Pilgrim, 1926, p. 37): "The main cusp of the last lower premolar, instead of being single as in the *Conohyus* and *Potamochoerus* lines, is divided into two of approximately equal value, which may be known as the principal cusp and the inner cusp. The latter stands generally a

little behind the other; in some species it is almost on a level with it, but it never stands directly behind it, as in many species of *Sus.*". *"P." provincialis* has a P$_4$ with two main cusps arranged in the same way as in the P$_4$ of *Dicoryphochoerus titan*, the type species of this genus. However in other characters it differs from *D. titan*. *"P." provincialis* resembles *Korynochoerus palaeochoerus* in many features, as we have seen above. The most important differences are the shape of the occiput and a slight size difference of the dentition. The differences are like those between *Sus scrofa vittatus* and *Sus barbatus*, which are sympatric. It would be better to place *"P." provincialis* in *Korynochoerus* Schmidt-Kittler, 1971.
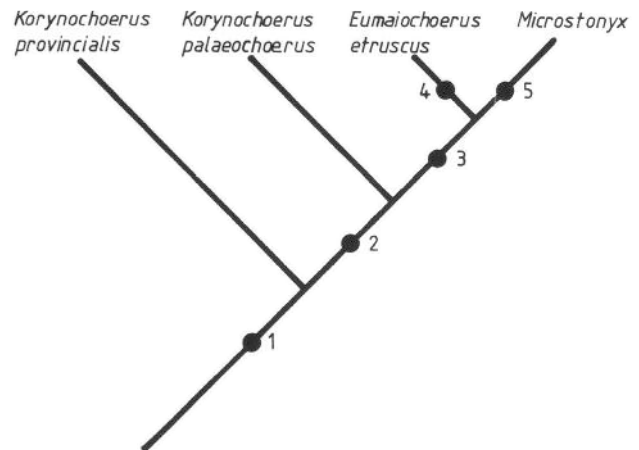
Microstonyx

Currently two species are recognized: *Microstonyx antiquus* Kaup, 1833 (holotype from Eppelsheim) and *M. major* Gervais, 1848/1852 (holotype from Cucuron). *M. erymanthius* Roth & Wagner, 1854 (from Pikermi) is thought to be a synonym of *M. major*. According to Thenius 1972 the two species are contemporaneus but lived in different habitats. Ginsburg 1980 thinks they form one lineage: *M. antiquus* in MN 9 and 10 and *M. major* in MN 11 and 12. As we have seen, three forms can be recognized. We failed to find any reliable indication that two forms existed at the same moment and we think that the three form are a lineage.

Pearson (1928) gives measurements from Pikermi, the M^3 range in length from 38.1 to 43.2 mm (n = 12). The holotype of *M. major* is an M^3 which is 45 mm long (Gervais, 1848-1852). The M^3 of the Eppelsheim form is not known. Judging from the M$_3$, a mean length of 50 to 52 mm can be expected. The form of Kerassia is even smaller than that of Pikermi. The size of the type of *M. major* does not indicate that this animal is identical to one of the two other "species", but there is certainly a size overlap between the *major* and *erymanthius* forms. The differences between the three forms are very small: presence or absence of a premolar and small size differences of the dentition. Differences between recent subspecies are larger. In order not to change the accepted nomenclature too much and in order to reflect in taxonomy the differences we see, we recognize *M. antiquus*, *M. major major* and *M. major erymanthius*.

The Dicoryphochoerini cladogram

Node 1 — All share the "Dicoryphochoerini-type P$_4$", the elongated I^2 with postero-lingual cingulum, molars that are somewhat elongated and some type of alveolar crest above the male canines.

Node 2 — Elevated occiput and inflated zygomatic

Text-fig. 1 - The Dicoryphochoerini cladogram

arches are shared by *K. palaeochoerus* and *Microstonyx* and probably also by *Eumaiochoerus* but probably not by *K. provincialis*. In *K. palaechoerus* and *Microstonyx* the anterior rim of the orbit is placed behind M^3. In the Ptolemais-Kardia skull it is difficult to see whether this was already the case in *K. provincialis*, but the molars were probably in a less forward position. In *Eumaiochoerus* the orbit is placed further forward, but this is related to other changes in the skull.

Node 3 — Elongated I^3, canines of reduced size and, related to these, shallow mandibles are shared by *Microstonyx* and *Eumaiochoerus*. A wide occipital and parietal zone are probably also shared, but evidence concerning *Eumaiochoerus* is lacking. This is the beginning of the *Microstonyx* lineage: *Microstonyx antiquus*.

Node 4 — In *Eumaiochoerus* the anterior rim of the orbit lies above the anterior end of M^3. This is probably due to size reduction of the part of the skull that is used for mastication. The orbit lies relatively high above the dentition; this may be related to the relatively high position of the glenoid combined with a backward shift of the dentition. (The eyes, brain-case, glenoid and occipital condyles are considered to be stationary, but the dentition is considered to move relative to this group of elements.) In *K. palaeochoerus* and *Microstonyx* the anterior rim of the orbit was behind the M^3 but in *K. provincialis* it is not quite clear.

Node 5 — Further size decrease of dentition, complete loss of P$_1$ and loss of P^1 early in life.

The Suini cladogram

Node 1 — All share: "*Sus*-type P$_4$" and probably also elongated I^2 without postero-lingual cingulum, although this is not known for *Sus arvernensis* and *S.*
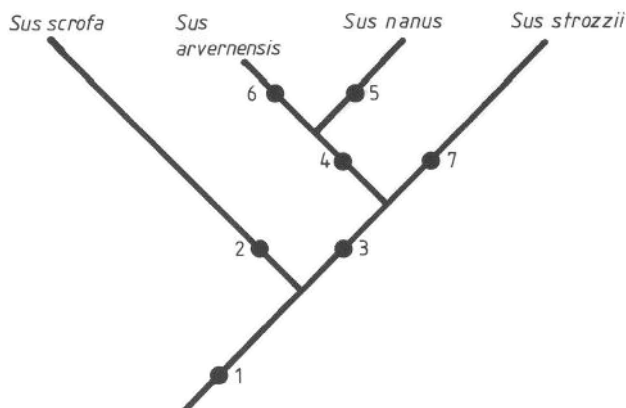
Text-fig. 2 - The Suini cladogram.

nanus. Recent Sus species such as S. verrucosus and others have such an I² and are considered to be closely related to S. arvernensis and S. strozzii.

Node 2 — Elevation of anterior and posterior end of P3 and P2, reduction in the length of premolar row compared to molar row and, at least in the European forms, a strong elongation of M3. All these characters have developed parallel in at least some species of the verrucosus-group.

Node 3 — Strong alveolar crests above Cˢ of the males, Cₓ of the males "verrucosic", stronger styles and stylids in P¹ and probably wider zygomatic arches in both sexes. (This is the "verrucosus-group".) Primitive pigs lack alveolar crests. This character is given more weight here than the canines.

Node 4 — The known common characters of these species are all primitive or difficult to interpret (like the morphology of P₄, which is in course of reduction in S. nanus but resembles the morphology of P₃ in S. arvernensis). S. nanus must derive from a European Sus. The primitive morphology of its last molars make the decrescent of S. nanus from S. arvernensis most probable; that is why the two are placed together in the cladogram.

Node 5 — Increase of hypsodonty, loss of P₁, reduction of function of P₂ and P₃ (neither of the two occludes, P₂ has only one root), shortening of the snout and 20-25% reduction of absolute linear size.

Node 6 — No typical specializations of this species are known. It differs from the other species of verrucosus- group by having characters that are all primitive.

Node 7 — Elevation of the anterior and posterior ends of P3 and P2 and reduction of the length of premolar row compared to molar row. This last character has a parallel in S. scrofa; in this character S. arvernensis is like the Dicoryphochoerini.

"Postpotamochoerus" from Samos

Thenius (1950) described a suid from Samos as Potamochoerus (Postpotamochoerus nov. subgen.) hyotherioides. But its P₄ has the typical morphology of a Sus P₄. The talonid and the anterior part of the tooth are high. The anterior part of the P₄ of Potamochoerus is low. The anterior and posterior ends of the P₄ are higher relative to the main cusp than in Potamochoerus (and S. arvernensis). In addition the molars are elongated. Potamochoerus molars are conservative in this respect.

The animal from Samos resembles Sus strozzii in the morphology of its individual teeth. Apart from this the base of its P4 is much lower than the M1 (in both the upper and lower dentition). However the molars are smaller than in S. strozzii from Sénèze and the premolars are larger. Sus arvernensis has a premolar row that is relatively longer than that of Sus strozzii. The premolar row of S. strozzii is probably reduced in length. In Suidae a long premolar row is generally primitive. It is possible that the animal from Samos is an ancestral form of Sus strozzii. The description of the skull given by Thenius does not exclude this possibility.

The figures and data presented by Thenius indicate that the Samos animal is Sus and not Potamochoerus. The sub-genus is based on the species created by Schlosser, 1903: Sus hyotherioides. It was Pearson (1928) who related this species to Potamochoerus. The syntypes of S. hyotherioides do not include a P₄. We do not wish to speculate here about the specific identity of the Samos material, nor about the generic identity of Sus? hyotherioides.

THE STRATIGRAPHIC RANGES OF THE TAXA

Text-fig. 3 gives the stratigraphic ranges of the taxa. The first and last localities where a species has been found are given. The biozonations of Mein (1975) and Augusti et al. (1987) have been used in this diagram.

Information on the temporal ranges of Sus strozzii, Sus arvernensis and Korynochoerus provincialis has been taken and adapted from Guérin & Faure (1985) and Faure & Guérin (1984). Something should be said here about the stratigraphic position of the Tegelen fauna. Guérin (1981) places the macro-mammal fauna from Tegelen much higher than the micro-mammal fauna. The small mammals were collected from a channel which had cut into clay and it was in this clay that the macro-mammals were found. The channel is immediately overlain by another formation. For these reasons the macro-mammals cannot be younger than the

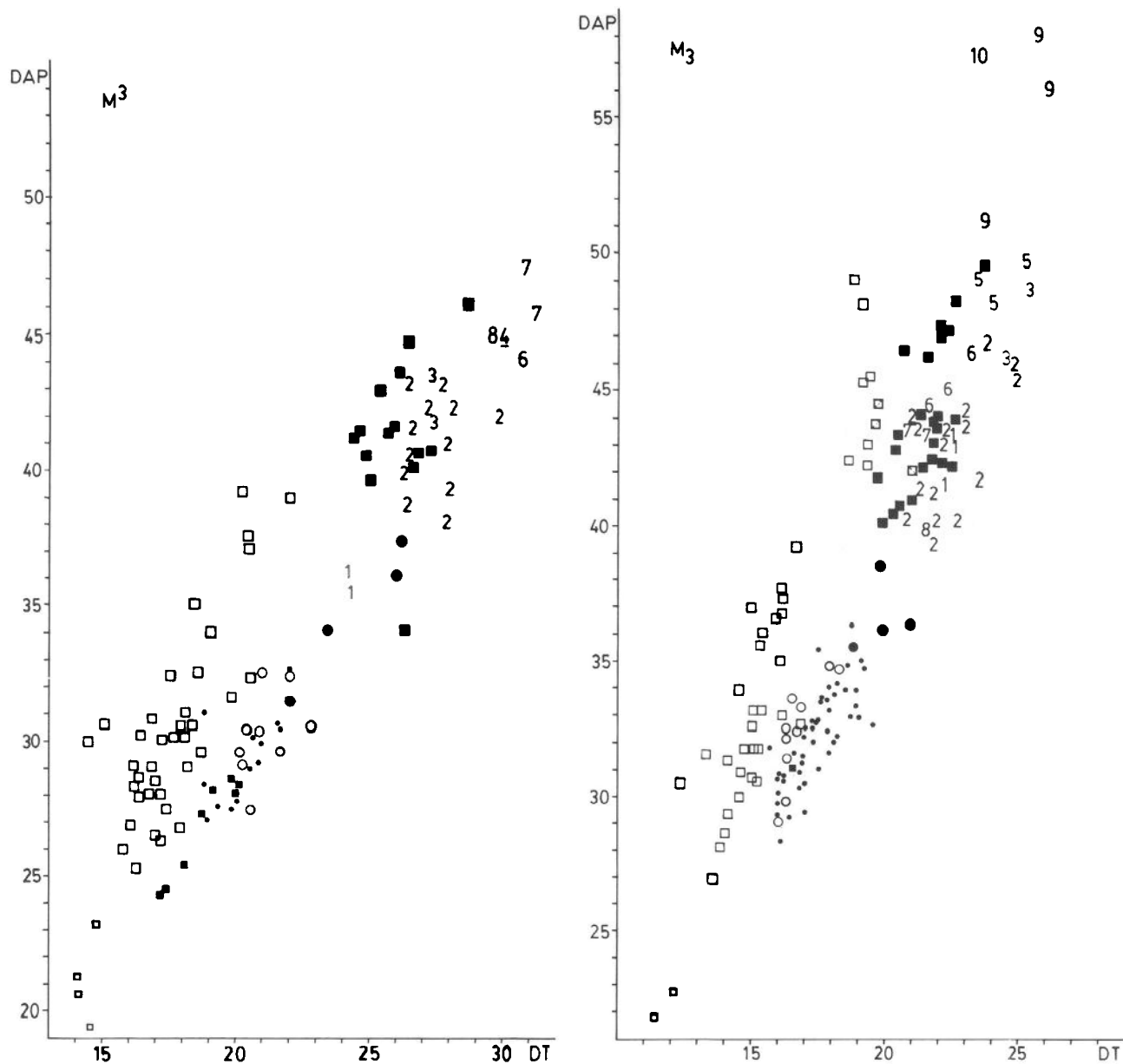micro-mammals; they must be slightly older (V. d. Meulen pers. com.).

K. palaeochoerus has been cited from the Baccinello V3 level (Hünermann, 1969; Hürzeler & Engesser, 1976) which the last authors placed in MN 13 or 14. Some first upper incisors from this level lack a distal cusplet which is normally present in *K. palaeochoerus.* Some molars of this level are closer in morphology to *K. provincialis.* Measurements of the dentition of the two species overlap. A more detailed study might prove that the Baccinello V3 suid is *K. provincialis.*

Eumaiochoerus can be derived from *Microstonyx* if in this genus the first premolars were not yet completely reduced. It cannot be derived from *M. major erymanthius,* since this subspecies had already lost its P_1. The Baccinello V2 level is correlated to MN 13 because of the presence of *Apodemus* and the V1 level

(without *Eumaiochoerus*) is correlated to MN 11 or MN 12. Sediments in the V2 level have been dated radiometrically at 8 MY (Hürzeler & Engesser, 1976). The MN 12 Samos and Maragheh faunas have also been dated radiometrically (Weidmann *et al.,* 1984; Campbell *et al.,* 1980). Their ages are 7.35 MY (mean age for the Main Bone Beds) and 7.6 MY (mean for the highest level with *Microstonyx*) respectively. Berggren *et al.* (1985) dated Crevillente VI (MN 13; with the oldest Spanish *Apodemus*) 6.5 MY and they dated Tudurovo 6.8 MY. Tudurovo is the youngest or one fo the youngest localities with *Microstonyx.* It seems probable that the Baccinello V2 level comprises a longer period, ranging from the earlier part of MN 12 to MN 13. This conclusion is based on the early radiometric date and the fact that *Eumaiochoerus* is derived from *M. major major,* combined with the presence of *Apodemus* in

	Korynochoerus palaeochoerus	K. provincialis	Microstonyx antiquus	M. major major	M. major erymanthius	Eumaiochoerus etruscus	Sus arvernensis	Sus nanus	Sus strozzii	Sus scrofa
Holocene										*
L. & M. Pleistocene										* *
M_nQ 3										Bovila Ordis Mosbach
M_nQ 2										
M_nQ 1								C. Figari I? * ?	Il Tasso Olivola	
MN 17							SÜtß	C. Figari I?	*	
MN 16b							* * * *	C. Figari I? * * *	Damatria Red Crag Nodule Bed Valdeganga	
MN 16a							*	*		
MN 15		Citadelle de Perpignan Serrat d'En Vaquer St. Estève quarries of Millas & Cavaillé					* * * * * * *	* * * * * * *		
MN 14		* *					Gorafe IV Dinar Akçaköy	Mandriola		
MN 13	Alcoy * * * * *	Baccinello V3 ? Venta del Moro Arenas del Rey				Baccinello V2 Monte Bamboli				
MN 12 late?	* * *				Kerassia Tudurovo Pikermi	Baccinello V2 * ? * ?				
MN 12 early?	* * * *			Concud Cucuron Taraklia Grebeniki		Baccinello V2?				
MN 11	*			*						
MN 10	* *			Terrasa Stratzing						
MN 9	* * *		Montrigaud Eppelsheim Esme Açaköy							
MN 8	Castell de Barberà San Quirze St. Gaudens									
MN 7										

Text-fig. 3 - Stratigrafic range of the Suinae.

Text-fig. 4 - Greatest length (DAP) versus greatest width (DT) of M^3 and M_3.

    ● *Korynochoerus palaeochoerus* from Gau Weinheim (data from Hünermann 1968, excl. no. 1933/833 which might be *Conohyus*). ● *Korynochoerus provincialis* from various localities.

    Microstonyx antiquus. 10) Montrigaud, 9) Eppelsheim (data from Hünermann 1968). *Microstonyx major major.* 8) Stratzing (measurements taken from figures given by Thenius 1972; comparison of different views indicate that the drawings are not exactly to scale), 7) Terrasa, 6) Montredon, 5) Piera, 4) Cucuron (holotype; data from Gervais 1848/52), 3) Concud. *Microstonyx major erymanthius.* 2) Pikermi (holotype; data from Roth & Wagner 1854), 2) Pikermi (data from Pearson 1928), 1) Kerassia. ○ *Eumaiochoerus etruscus* from various localities. ■ *Sus arvernensis* from various localities. ■ *Sus strozzii* from various localities. □ *Sus nanus* from Capo Figari. ⊡ *Sus scrofa*, recent and fossil from various localities, including fossil domestic pigs.

the level. Even *M. major erymanthius* and *Apodemus* did not coexist in Europe.

Janòssy (1986) reported *S. arvernensis* from Sütö, which is correlated to MN 17. The animal is certainly present in Etouaires and Hajnačka (MN 16b).

It should be noted that *Sus scrofa* arrived in North Africa at about the same time that it arrived in Europe (Cooke & Wilkinson, 1978).

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