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Anschriften der Verfasser: Prof. Dr. Jochen Niethammer, Zoologisches Institut der Universität, D - 53 Bonn, Poppelsdorfer Schloß; Prof. Dr. Jochen Martens, Instiut für Zoologie der Johannes Gutenberg-Universität, D - 65 Mainz, Saarstraße 21

Remarks on the Pliocene Suidae of Europe

By A. Azzaroli

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Stratigraphical notes

The continental stages equivalent to the Pliocene are the Ruscinian (Tobien 1970; = "zone de Perpignan" of Thaler 1966) and the Early Villifranchian (Azzaroli 1970; Azzaroli and Vialli 1971). Tobien inserted a "Csarnotian" between the Ruscinian and the Early Villafranchian, but it is doubtful that this stage is really distinct from the Ruscinian, although the latter may be subdivided into smaller faunal zones.

The continental equivalent of the late Middle Miocene (Tortonian *pro parte)* is the Vallesian of Crusafont Pairò 1951 (Marks 1971); the equivalent of the late Miocene (Messinian, Andalusian) is the Pikermian of Crusafont Pairò 1950 (De Bruijn 1971), a name that was later changed into Turolian (Crusafont Pairò 1965; Marks 1971).

In the past the Vallesian and Turolian were often united under the name of Pontian (Barbot de Marny 1869), but this name was proposed for the brackish and freshwater Odessa limestone and its use for continental mammalian faunas is incorrect. There has also been a great deal of confusion as to the correlation of continental and marine stages, and several authors referred the "Pontian" mammalian faunas to the Early Pliocene. Investigations on several localities of Eastern and Southern Spain (Librilla, La Alberca, several sites near Arenas del Rey) gave however conclusive evidence that the Turolian is the time equivalent of the Andalusian (Aguirre et al. 1974; Aguirre 1974), while a reevaluation of the fauna of Gravitelli, Sicily, showed that this also is of Turolian age and equivalent to the Messinian (Azzaroli, in press).

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Historical

Few species of suids have been recorded from the Pliocene (Ruscinian and Early Villafranchian) of Europe and Western Asia, nevertheless their taxonomy is still confused.

"*Aper*" *arvernensis* was described by Croizet and Jobert in 1828. It was based on a fragment of a juvenile skull and mandible with some milk and some permanent teeth. This fossil comes from the Perrier Hills of the French Central Massif and was subsequently dated as Early Villafranchian (Etouaires horizon, see Kurtén 1963).

In 1859 Gervais described another species, *Sus provincialis,* from the Pliocene basin of Hérault, Southern France. This species was based on seven molars and a premolar, all isolated except a second and third lower molar found in connection. These fossils seem to be of Ruscinian age.

In 1885 Depéret described under the name *Sus arvernensis* a row of upper cheek teeth from the Roussillon basin, Southern France, also of Ruscinian age. In 1890 Depéret changed his mind. He described and figured a third lower molar from the Roussillon basin, which he referred to *Sus provincialis;* at the same time he referred the tooth row figured in 1885 to a new subspecies, *Sus provincialis* race *minor,* to which Depéret attributed also some other teeth found in the meanwhile.

All these fossils were reexamined by Stehlin (1900). According to this author *Sus provincialis* should perhaps be transferred to the genus *Potamochoerus;* the same would apply to *Sus provincialis* race *minor,* which Stehlin recognized as valid. *Sus arvernensis* was also considered valid and distinct from both former taxa. Distinguishing criteria were considered the size of the (mostly isolated) teeth, the thickness of the enamel, the degree and depth of folding.

In 1926 Pilgrim created the new genus *Propotamochoerus* for some fossils from the Siwalik Hills, with *P. salinus* Pilgrim as type species for the genus, and at the same time referred to it "*Propotamochoerus provincialis major*" (sic) and "*Propotamochoerus provincialis minor*". The reason for this generic attribution was not stated. Pilgrim considered *Propotamochoerus* a more primitive forerunner of *Potamochoerus,* and possibly for this simple reason transferred to his new genus the Pliocene species of Southern France.

Pilgrim's generic attribution was accepted by Mottl (1939: *Propotamochoerus provincialis* race *minor).* Some years later however Schaub (1943), while keeping to Stehlin's idea that "*Sus*" *provincialis* is a *Potamochoerus,* restored the smaller suid from the Roussillon to the genus *Sus* and gave it the rank of a full species, *Sus minor,* disctinct from both *P. provincialis* and *Sus arvernensis.* In this paper Schaub made reference to an unpublished skull from the Roussillon and expressed the idea that *Sus minor* is the direct ancestor of the (late) Villafranchian *Sus strozzii.*

The essence of Schaub's views was accepted by Azzaroli (1954), who expressed however the doubt that *Sus minor* might be identical with "*Aper*" *arvernensis.* Azzaroli described and figured the almost complete skull of *Sus minor* in the Museum of Basle (Rss. 70) and part of a mandible, also from the Roussillon, and concluded that *Sus minor,* as Schaub had supposed, is actually an ancestor of *Sus strozzii,* and that both are close relatives of the living Indonesian species *Sus verrucosus* and *Sus celebensis.*

It should be pointed out that for the first time Azzaroli's paper contained the description of a nearly complete skull. All previous identifications had been based on teeth only.

Fejfar (1964) reverted to Pilgrim's conception and referred the suids from Hajnačka to *Propotamochoerus provincialis* and *Propotamochoerus provincialis minor.*

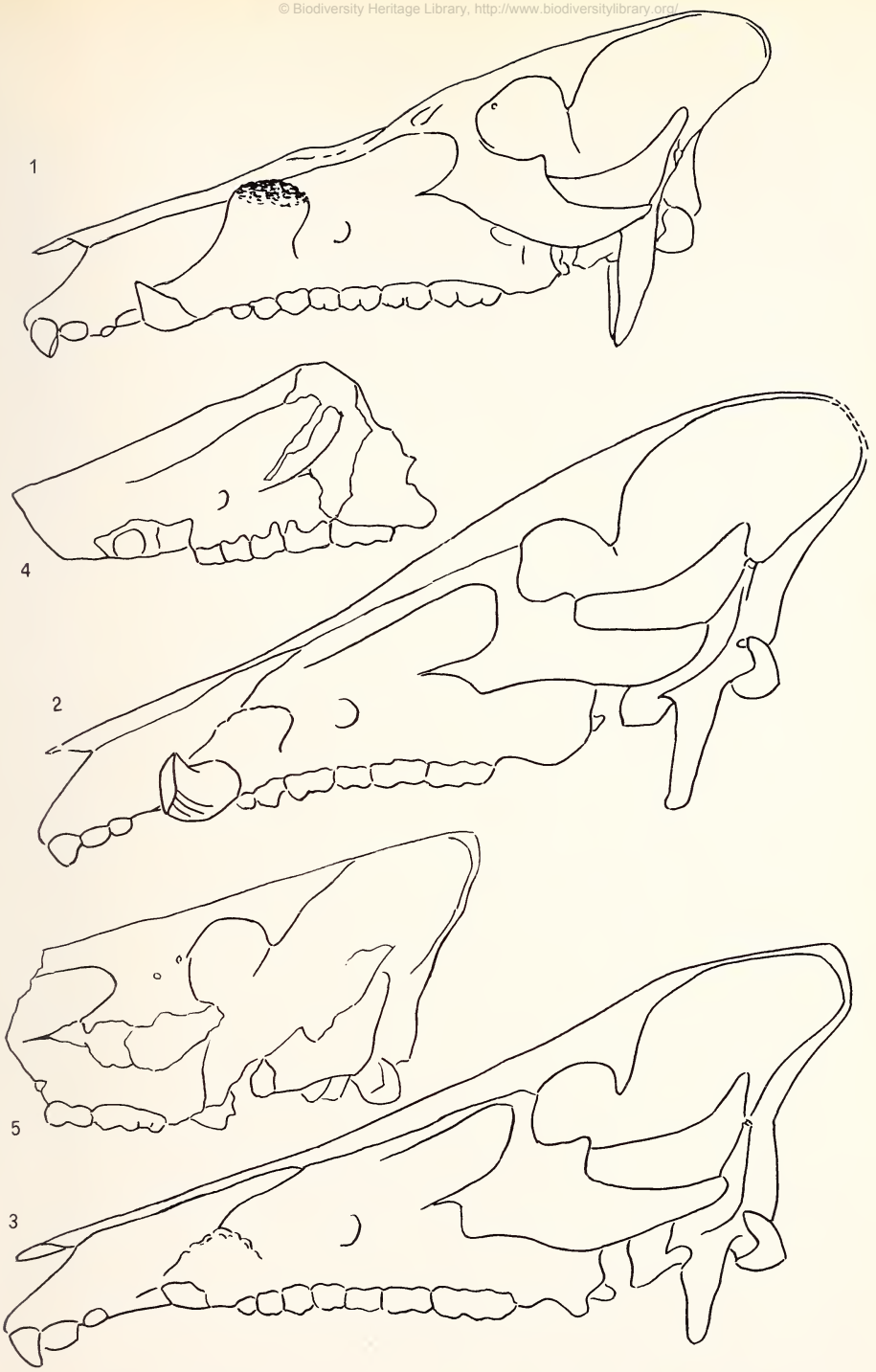

Plate I. Fig. 1. Potamochoerus larvatus — recent. Torda, Lower Juba, Somalia. Florence, Zoological Museum, M 4804, skull, side view. — *Fig. 2. Sus minor* — Pliocene (Ruscinian). Perpignan, S. France (after Azzaroli 1954), Basel, Natural History Museum, Rss 70, skull, side view, restored. — *Fig. 3. Sus verrucosus* — recent. Java. Basel, Natural History Museum, C 1174, skull, side view. — *Fig. 4. Propotamochoerus hysudricus* — Dhok Patan horizon (Early Pliocene?). Hasnot, Siwalik Hills (after Pilgrim 1926), Calcutta, Indian Museum, B 689, fragment of skull, side view. — *Fig. 5. Propotamochoerus hysudricus* — Early Pliocene? Punjab, Siwalik Hills (after Pilgrim 1926), Calcutta, Indian Museum, B 28, fragment of skull, side view. (All figures 1/3 natural size.)

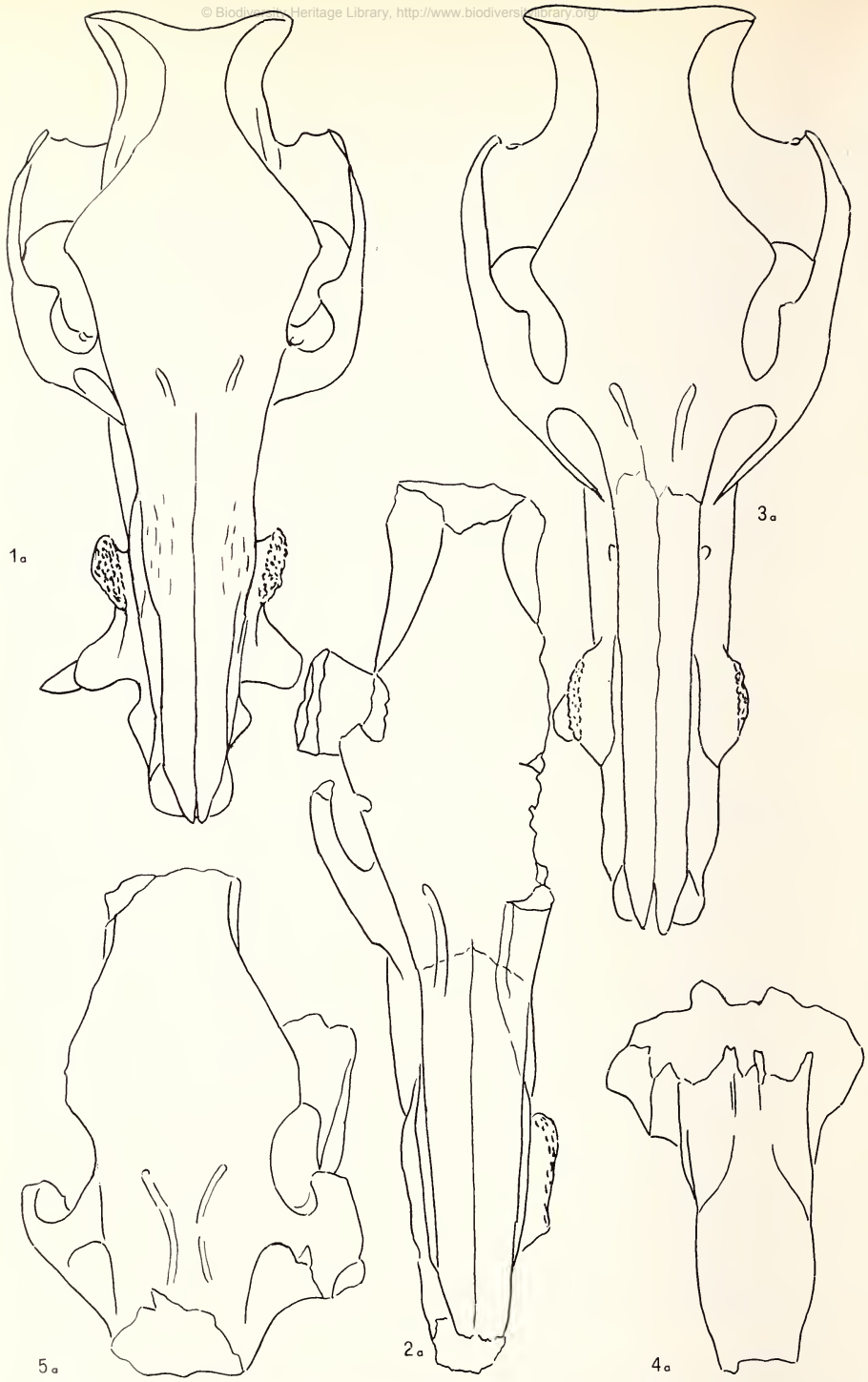

Plate II. Fig. 1a. Potamochoerus larvatus — same specimen as pl. I, fig. 1. Skull, upper view. — *Fig. 2a. Sus minor* — same specimen as pl. I, fig. 2, not restored (after AZZAROLI 1954). Skull, upper view. — *Fig. 3a. Sus verrucosus* — same specimen as pl. I, fig. 3. Skull, upper view. — *Fig. 4a. Propotamochoerus hysudricus* — same specimen as pl. I, fig. 4. Fragment of skull, upper view. — *Fig. 5a. Propotamochoerus hysudricus* — same specimen as pl. I, fig. 5. Fragment of skull, upper view. (All figures 1/3 natural size.)

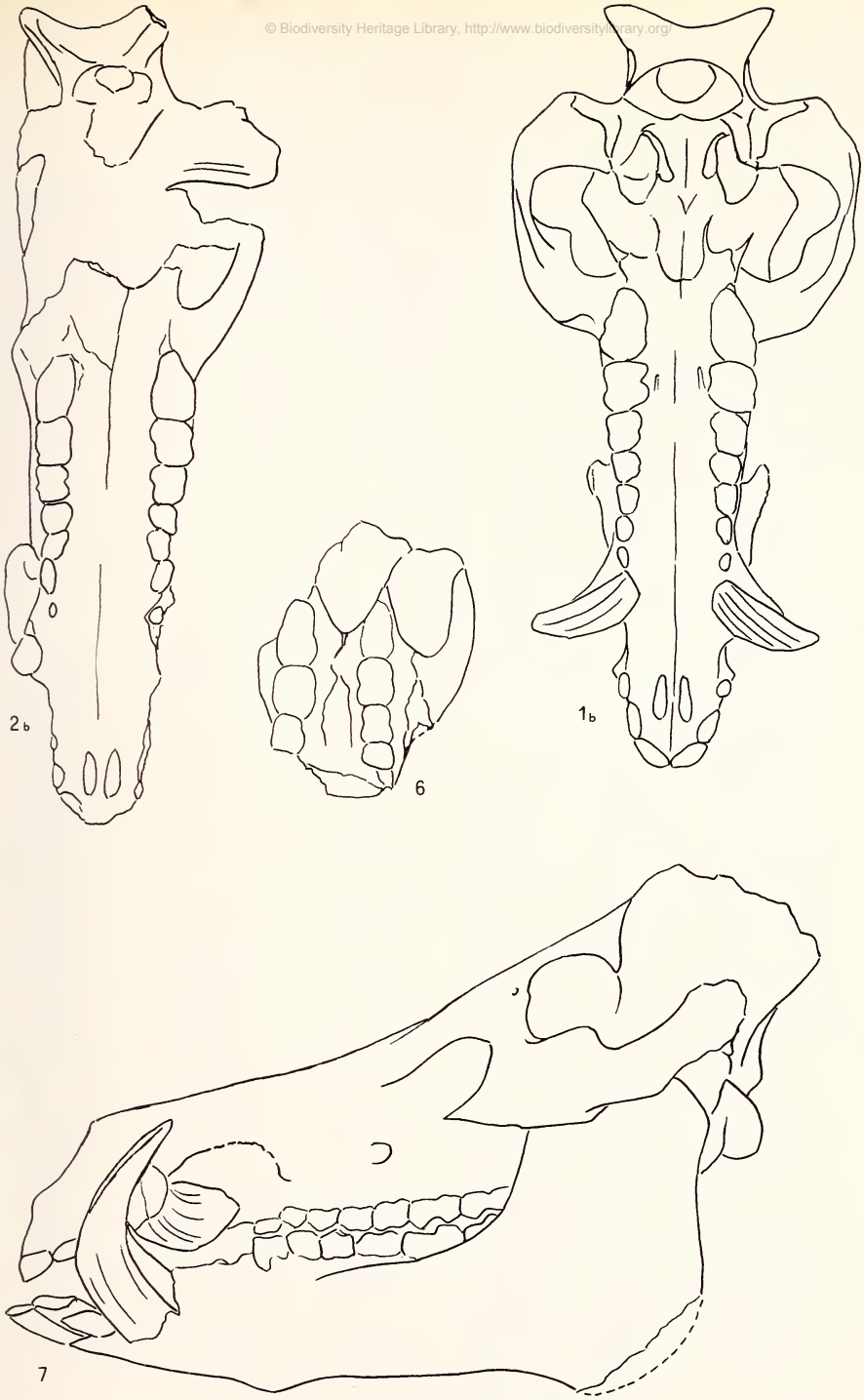

Plate III. Fig. 1b. Potamochoerus larvatus — same specimen as pl. I, fig. 1. Skull, basal view. — *Fig. 2b. Sus minor* — same specimen as pl. I, fig. 1. Skull, basal view (not restored), (after Azzaroli 1954). — *Fig. 6. Propotamochoerus salinus* — Chinji Stage (Late Miocene). Chinji, Salt Range (after Pilgrim 1926), Calcutta, Indian Museum, B 681, fragment of skull, basal view. — *Fig. 7. Sus minor* — Pliocene (Ruscinian?). Kvabebi, Georgia SSR (after Vekua 1972), Tbilisi, Acad. of Sciences, Inst. of Paleobiol., K-15, skull, side view. (All figures 1/3 natural size.)

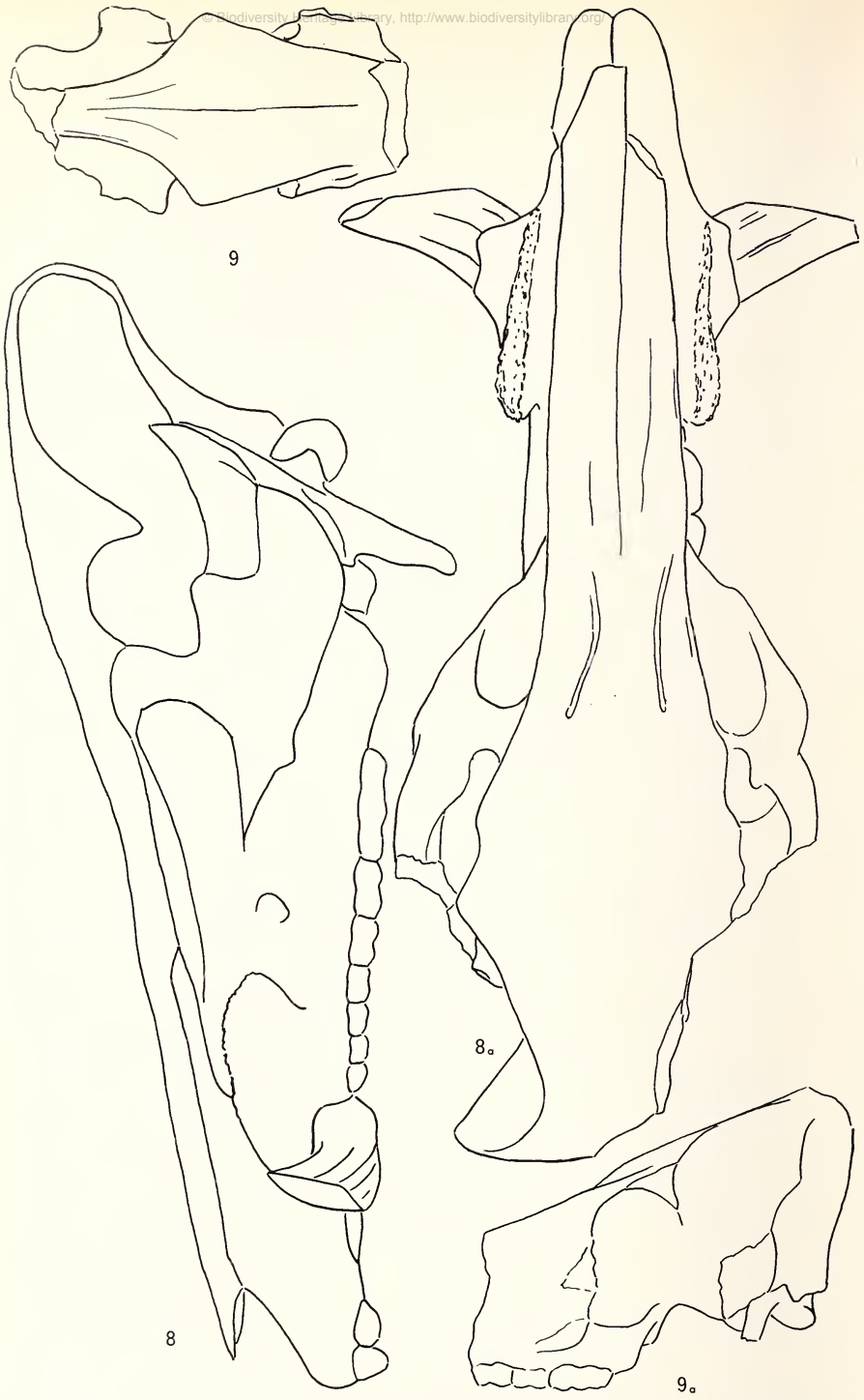

Plate IV. Fig. 8. Sus strozzii — Late Villafranchian (Early Pleistocene). Upper Valdarno, Central Italy (after AZZAROLI 1954), Lectotype, Florence, Palaeontological Museum, Igf 414, skull (restored), side view. — *Fig. 8a.* Id., skull, partly restored, upper view (after AZZAROLI 1954). — *Fig. 9. Propotamochoerus uliginosus* — Dhok Patan horizon (Early Pliocene?). Punjab (after PILGRIM 1926), fragment of skull, upper view. — *Fig. 9a.* Id., fragment of skull, side view. (All figures 1/3 natural size.)

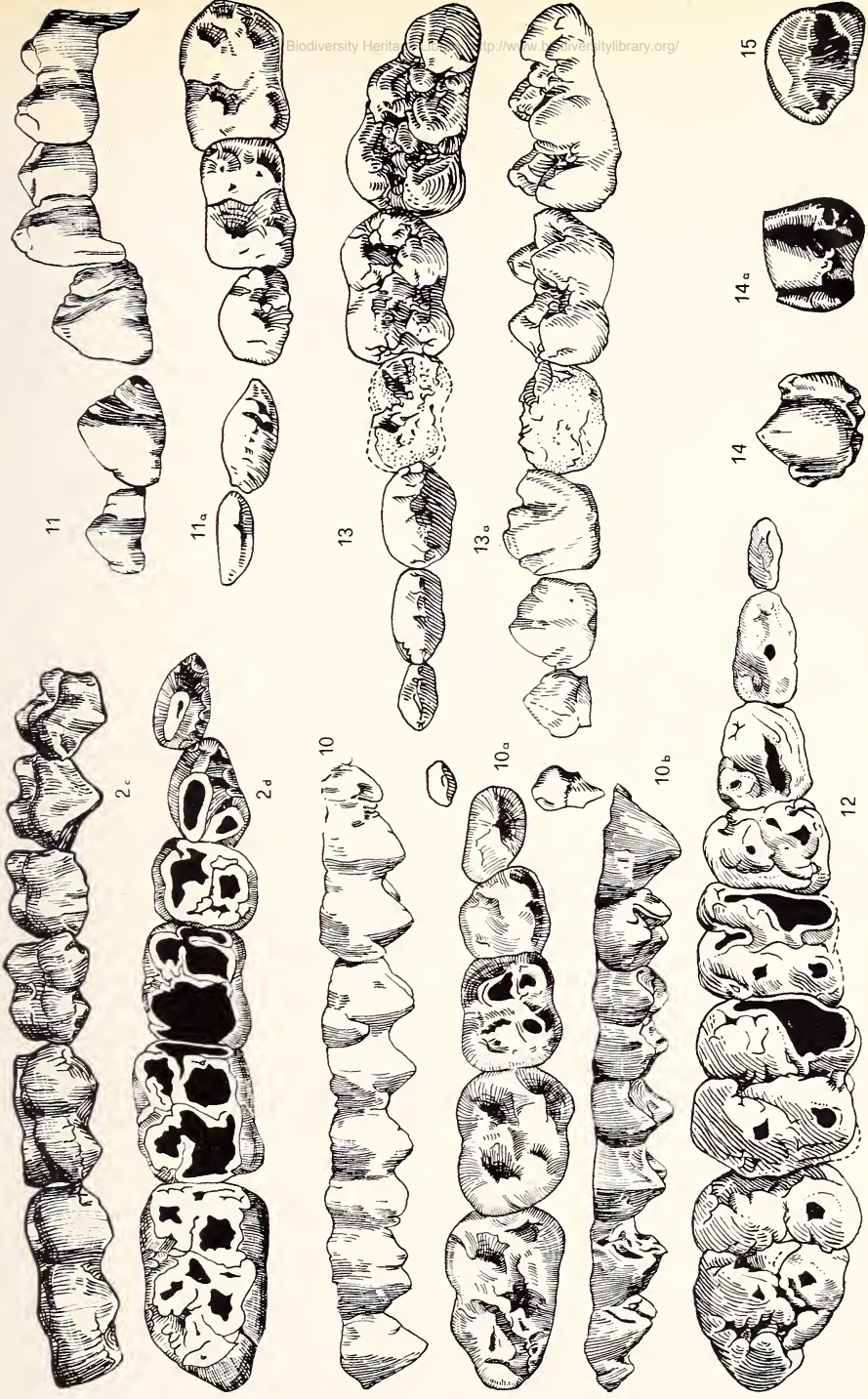

Plate V. Fig. 2c, 2d. Sus minor — same specimen as pl. I, fig. 2. Right upper tooth row. — *Fig. 10, 10a, 10b. Sus minor* — Pliocene (Ruscinian). Roussillon basin, S. France. Specimen figured under the name of *Sus arvernensis* by Depéret 1885, pl. V, fig. 1. Left upper tooth row (after Azzaroli 1954, from a cast in the Natural History Museum of Basle). — *Fig. 11, 11a. Sus minor* — Pliocene (Ruscinian). Roussillon basin, S. France. Specimen figured by Depéret 1890, Pl. V, fig. 13. Left lower tooth row (after Azzaroli 1954, from a cast in the Natural History Museum of Basle). — *Fig. 12. Sus minor* — Pliocene (Ruscinian?) Kvabebi, Georgia SSR (after Vekua 1972), Tbilisi, Acad. of Sciences, Inst. of Paleobiology, left upper tooth row. — *Fig. 13, 13a. Sus minor* — Pliocene (Ruscinian?). Kvabebi, Georgia SSR (after Vekua 1972), Tbilisi, Acad. of Sciences, Inst. of Paleobiology, left lower tooth ropw. — *Fig. 14, 14a. Propotamochoerus uliginosus* — Pliocene? Pohta, Jhelum District, Siwalik Hills (after Pilgrim 1926), Calcutta, Indian Museum, B 683, left fourth upper premolar, medial and upper views. —*Fig. 15. Propotamochoerus salinus* — Dhok Patan stage (Early Pliocene?). Siwalik Hills (after Pilgrim 1926), Calcutta, Indian Museum, B 682, left third upper premolar, grinding surface. (All figures natural size.)

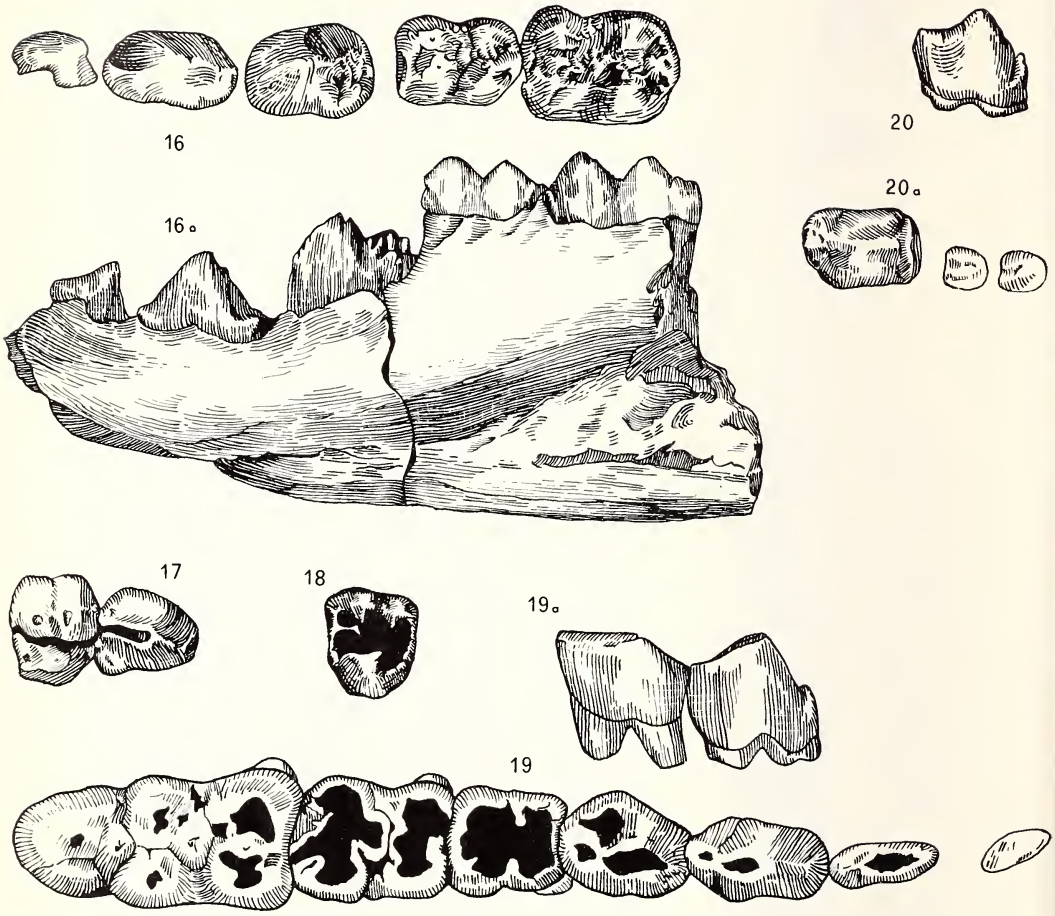

Plate VI. Fig. 16, 16a. Propotamochoerus salinus — Nagri zone (Early Pliocene?), Nagri, Salt Range (after Pilgrim 1926), Calcutta, Indian Museum, B 680, left lower tooth row. — *Fig. 17. Propotamochoerus uliginosus* — Chinji stage (Late Miocene). Chinji, Salt Range after Pilgrim 1926), Calcutta, Indian Museum, B 686, third fourth right upper premolars, grinding surface. — *Fig. 18. Propotamochoerus uliginosus?* — Nagri zone (Early Pliocene?). Haritalyangar, Simla Hills (after Pilgrim 1926), Calcutta, Indian Museum, B 684, right fourth upper premolar. — *Fig. 19, 19a. Propotamochoerus hysudricus* — Tatrot stage (Late Pliocene?). Kotalkund, Siwalik Hills (after Pilgrim 1926), Calcutta, Indian Museum, B 687, right lower tooth row, and detail of the third and fourth premolars. — *Fig. 20. Propotamochoerus uliginosus* — Chinji stage (Late Miocene). Chinji, Salt Range (after Pilgrim 1926), Calcutta, Indian Museum, B 685, thrid right lower premolar, lateral and upper views. (All figures natural size.)

Hünermann (1971) accepted the term *Sus minor* proposed by Schaub and by Azzaroli and considered *Sus arvernensis* as a non valid synonym of *Sus minor*.

Vekua (1972) was even more fortunate than Azzaroli, in that he had a nearly complete and two fragmentary skulls at his disposal, and in addition jaws, isolated teeth, limb bones. His fossils came from Kvabebi in Georgia, USSR, a site that has been somewhat doubtfully referred to the Early Villafranchian, but could possibly be of Ruscinian age. Vekua expressed an entirely different idea from Schaub, Azzaroli and Hünermann: "*Sus*" *provincialis* belongs to *Propotamochoerus;* "*Sus*" *minor* is a synonym of the former; *Sus strozzii* is not closely related to it.

Discussion

It is indeed strange that Pilgrim's idea persisted so long, in spite of the rich documentation for a different interpretation presented by Azzaroli. Fejfar's and Vekua's views are the result of the great confusion still present in the paleontological literature, and are obviously based on a misunderstanding of the genus *Propotamochoerus* as originally defined by Pilgrim. It is fair to state, however, that Pilgrim also had his own share in making things unnecessarily complicated. The genus *Propotamochoerus* in his original definition included four species: *P. salinus* Pilgrim, *P. uliginosus* Pilgrim, *P. hysudricus* (Lydekker) and *P. ingens* Pilgrim. *P. salinus* was chosen as the type of the genus, although *P. uliginosus* and *P. hysudricus* are represented by better material. In fact, from a skull of *P. uliginosus* „are largely taken the characters of the genus" (Pilgrim 1926, p. 25); so that one is left to wonder why the type species of the genus should not be the latter instead of the poorly represented *P. salinus*. Be this as it may, the genus *Propotamochoerus,* in Pilgrim's original definition, is similar to *Potamochoerus* in dentition but differs in some features of the skull that Pilgrim considered more primitive. The cheek teeth are massive, of a relatively simple pattern, and the last lower premolar is characterised by a massive conical cusp ending in a single point. The lower canines, partly preserved only in *P. ingens,* seem to be intermediate in shape between those of *Sus scrofa* and those of *Sus verrucosus*. The jugal processes of the maxillaries spring out suddenly, almost at a right angle, from the side of the cheek; the root of the jugal process is placed as far forward as P^4, while in *Potamochoerus* it reaches only to M^2. The surface of the nose is flat, broad and rugose, and projects laterally over the maxillaries. The orbit is placed high and the front is flat. The bony palate extends very little behind M^3 in *P. hysudricus,* and it appears from Pilgrim's figure that is does not extend at all behind this tooth in *P. salinus*. In proportion to the face, the cranial region of the skull is longer in *Propotamochoerus* than in *Potamochoerus*. "It will thus be seen that the general shape of the skull is much more primitive than in the recent genus and more like *Hyotherium* and *Hippohyus*" (Pilgrim 1926, p. 23).

It is doubtful however that the features described as distinctive for *Propotamochoerus* are really primitive. If the zygomatic arches were really like those of *Hyotherium* and *Hippohyus,* as the fragmentary fossils seem to indicate, then this would appear to be rather a highly specialised feature and such as to rule out *Propotamochoerus* from the possible ancestry of *Potamochoerus*.

Nomenclature

As pointed out above, three distinct taxa were described from the Pliocene of Europe. The first of these in order of time, "*Aper*" *arvernensis* Croizet and Jobert 1828, or

better *Sus arvernensis,* is considered by HÜNERMANN an early synonym of *Sus minor.* Its name is not valid: „Die Bezeichnung *‚arvernensis'* muß als älteres, unbenutztes Synonym angesehen werden, da sie nach 1900 nur noch in Synonymie- und Faunenlisten Anwendung fand."

Though admitting that *arvernensis* and *minor* may be practically undistinguishable on dental features alone, I cannot fully agree with HÜNERMANN: *arvernensis* is geologically younger than *minor* and might possibly prove to be distinct, though it is certainly closely related to it. Since the type is not sufficient to define the species and no better material has been described from the type locality, I consider *Sus arvernensis* a "nomen dubium". The same can be said of *Sus provincialis* Gervais, which is also based on very scanty material. It seems to be markedly larger than its contemporary *Sus minor* (the greatest lengths of the third lower molars of the two species are 44 and 33 mm., respectively) and therefore VEKUA's idea that the two are synonyms appears unlikely. In any case *Sus provincialis* is also a "nomen dubium".

Sus minor is represented by a fine skull from the type locality, Perpignan. This specimen, now in the Museum of Natural History of Basle (Rss. 70), was mentioned by SCHAUB in 1943 and fully described and figured by AZZAROLI in 1954.

What can be said of the suid from Kvabebi? Its skull is of about the same size as *Sus minor:* the male skull K-15 described by VEKUA has a basilar length of 320 mm; the same length in the slightly damaged skull Rss. 70 may be evaluated around 330 mm. The dentitions are practically identical but the skulls are not so. K-15 has a dished profile, while in Rss. 70 the frontal and parietal regions are gently convex. In the published figures the orbit seems to be placed higher in K-15 than in Rss. 70, but this may be due to deformation. The significance of these differences is not easy to asses. They may perhaps be only individual variations; or perhaps the Georgian and the French suid may represent two distinct subspecies, but I am inclined to think that both may be included in the same species *Sus minor* Depéret.

Taxonomic position

Now to the question of the affinities and taxonomic position of *Sus minor,* the only well-defined species of suid in the Pliocene of Europe.

The dentition of this species does not bear out its supposed relationship to *Propotamochoerus* or *Potamochoerus.* In this lineage — if it is really a single lineage — the teeth are low crowned, covered by a thick enamel and relatively poorly folded. The most distinctive tooth is P_4, in which the main cusp is massive, nearly conical. In the various species of *Sus* the shape of this tooth varies to some extent and individual variation is rather broad in some species, though the typical form of *Potamochoerus* is never reached (AZZAROLI 1954); the main cusp is typically trenchant, but may be more or less bicuspidate in primitive species. This applies also to *Sus minor:* a P_4 from Roussillon (the lectotype, figured by AZZAROLI, pl. V, fig. 11, 11a) has a trenchant crown, while its homologue from Kvabebi figured by VEKUA (pl. V, fig. 13, 13a) is bicuspidate. VEKUA made also reference to some supposed differences in the shape of P^4 of *Sus minor* (his *P. provincialis* from Kvabebi) and of *Sus strozzii,* but I fail to find any significant difference in these teeth. Perhaps P^3 in the upper tooth row from the Roussillon basin described by DEPÉRET (AZZAROLI, pl. V, fig. 10, 10a), with its massive conical cusp, is more "potamochoerine", though not nearly as massive as in *Potamochoerus;* but in *Sus minor* this tooth is subject to individual variaton, and may be described as fully "suine" in the Roussillon skull Rss. 70 and in the tooth row from Kvabebi figured by VEKUA (pl. V, fig. 2c, 2d, 12).

In conclusion the features of the dentition do not support the attribution of the Pliocene suid from Europe and the Caucasus region to *Propotamochoerus*, or for that matter to *Potamochoerus*. Even less so do the features of the skull. The root of the zygomatic arch extends forward only as far as M^3 or M^2 and the arch does not project squarely from the side of the cheek but widens backwards with an outward slope. This distinguishes sharply *Sus* from *Potamochoerus* and even more from *Propotamochoerus*. The upper surface of the nose is broad and rugose, but is convex, not flat as in *Potamochoerus;* the front is also transversely convex, the bony palate extends backwards well beyond the last molars, and these features also distinguish *Sus minor* from *Potamochoerus* and *Propotamochoerus*. The bony crests over the alveoles of the canines in male skulls are of a totally different shape in *Potamochoerus* and in *Sus minor,* while in the latter species they are similar to *Sus strozzii* and *Sus verrucosus*.

A comparison of figures may help to point out affinities and differences better than any lengthy description. *Potamochoerus* differs from *Sus scrofa* by the stronger lateral projection of the jugal arches, the broad, rugose surface of the nasals, the flat forehead. *Sus minor* also differs from *Sus scrofa* in the shape of the jugal arches, the expanded nasals, the supralveolar crests, but these features are differently developed than in *Potamochoerus* and altogether its skull is decidedley "suine" and not "potamochoerine". As a matter of fact *Sus minor* is a slightly modified and reduced copy of the living *Sus verrucosus,* just as *Sus strozzii* is almost exactly an enlarged copy of *Sus minor* and differs very slightly from *Sus verrucosus* in general proportions. *Propotamochoerus* differs from *Sus minor* even more than *Potamochoerus* and has no relationship to it.

In conclusion, the present writer cannot but substantiate his conclusions of twenty years ago: that *Sus minor* is closely related to the living Indonesian *Sus verrucosus* and *Sus celebensis,* and even more closely to the late Villafranchian *Sus strozzii,* of which it is a direct forerunner.

Geographical distribution

Suids of the size of *Sus minor* and possibly identical to it have been recorded from several Pliocene localities of Europe, Western Asia and North Africa. Hünermann (1971) gave the following list:

Spain: Alcoy (prov. Alicante)
France: Perpignan (Roussillon); Etouaires (Puy de Dôme)
Italy: Villafranca d'Asti (Piedmont)
Csechoslovakia: Ivanovice, Hajnačka
Hungary: Gödöllö (Pest)
Rumania: Baraolt (Trei Scane)
Turkey: Akça (Anatolia)
Egypt: Garet el Muluk (Natron Valley)

To this list should be added Kvabebi (Georgia) and four Italian localities:

Bra (Piedmont); (Dal Piaz 1930)
La Quercia (lacustrine basin of Barga, Tuscany): a first lower molar, unpublished
Pieve Fosciana (Tuscany): a second upper incisor, unpublished
Unknown locality, presumably from the Siena area (Tuscany): a skull, in the palaeontological museum of Siena.

The skull from Siena was mentioned by Stehlin (1900) and later by Azzaroli

(1954) in his synonymy of *Sus minor*, but was never described. It is a fine fossil. It is not deformed and the base of the skull is well preserved, but all the teeth except the right second molar have been broken off at the root. The anterior part of the muzzle is lacking and the skull roof has been largely destroyed, laying bare the natural endocasts of the brain cavity, of the frontal sinuses and of the cavity of the nose. Only the posterior root of the right zygomatic arch is preserved. The length of the upper molars (61 mm) agrees well with Rss. 70 (60 mm) and with K—15 (66 mm) and K—30 (64 mm). The root of the zygomatic arch, the bony palate and the muscular fossettes on the face agree in shape with those of *Sus minor* but the skull is shorter. The distance from the occipital condyles to the anterior margin of M^1 is 160 mm, while in Rss. 70 it is 185 mm. The anterior root of the zygomatic arch lies over M^3 and extends with a crest until M^2. The animal is fully grown and fairly old (M^2 is rather worn) but its sex is unknown. It is impossible therefore to tell whether the small size as compared to the male skulls of Perpignan and of Kvabebi is due to sex or to some other cause.

The geological age of the Siena skull is obviously unknown, but continental vertebrates with a similar fossilisation are not uncommon in the Pliocene sands and sandy clays around Siena.

Faunal relationships

As stated above, *Sus minor* is closely related to some living suids from Indonesia. On the other hand it has no relationship with the suidae that preceded it in Europe in the Miocene. Typical Vallesian suids are "*Hyotherium*" *palaeochoerus* (Kaup) and *Microstonyx antiquus* (Kaup); the Turolian is characterised by *Microstonyx major* (Gervais). These are all highly specialised suids, with very prominent jugals; the canines are rooted in both sexes and in *Microstonyx major* are secondarily reduced.

Sus minor appeared therefore in the Pliocene of Europe as an immigrant, and its relationship with the Indonesian suids makes it likely that it came from some area in Southern Asia.

Acknowledgements

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Summary

Three species of Suidae were described from the European Pliocene (= Ruscinian + Early Villafranchian): *Sus arvernensis*, *Sus provincialis* and *Sus minor*. Only *Sus minor* is well defined, being represented by some skulls. Former attributions of this species to the genera *Potamochoerus* and *Propotamochoerus* are rejected: the species belongs to *Sus* and is a close relative of the living Indonesian *Sus verrucosus* and *Sus celebensis*. *Sus arvernensis* is a "nomen dubium" and could possibly be a synonym of *Sus minor*. *Sus provincialis* is distinguished by its larger size but is also considered a "nomen dubium". *Sus minor* is an immigrant from Asia and is a forerunner of the Late Villafranchian *Sus strozzii*. Its range extends from Spain over France, Italy, Hungary Czechoslovakia, Rumania and outside Europe to Georgia and possibly to Northern Egypt.

Zusammenfassung

Bemerkungen über die pliozänen Suiden Europas

Drei Arten Suiden wurden aus dem Europäischen Pliozän (Ruscinium + Früh-Villafranchium) beschrieben: *Sus arvernensis*, *Sus provincialis* und *Sus minor*. Nur *Sus minor* ist klar definiert und ist durch einige Schädel vertreten. Früher angenommene Beziehungen dieser Art zu den Gattungen *Potamochoerus* und *Propotamochoerus* bestehen nicht: die Art gehört zu *Sus* und

ist mit den lebenden *Sus verrucosus* und *Sus celebensis* nahe verwandt. *Sus arvernensis* ist ein „nomen dubium" und ist möglicherweise ein Synonym von *Sus minor*. *Sus provincialis* unterscheidet sich durch eine größere Gestalt, ist jedoch auch als „nomen dubium" anzusehen. *Sus minor* ist ein Einwanderer aus Asien und ist ein Vorläufer der Spät-Villafrankischen Art *Sus strozzii*. Sein Lebensraum erstreckte sich von Spanien über Frankreich, Italien, Ungarn, Tschechoslowakei und Rumänien sowie außerhalb Europa bis Georgien und möglicherweise bis Nord-Ägypten.

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Author's address: Prof. Dr. A. Azzaroli, Istituto di Geologia e Paleontologia dell' Università di Firenze, Via Lamarmora 4, I—50121 Firenze, Italia