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Stephanorhinus (Mammalia: Rhinocerotidae) of the western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868)

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KEY WORDS - Rhinocerotidae, Perissodactyla, Mammalia, Middle Pleistocene, Western Europe.

ABSTRACT - The rhinoceroses of the European Plio-Pleistocene that have traditionally been placed in Dicerorhinus *Gloger (1841) are provisionally assigned to* Stephanorhinus *Kretzoi (1942).*

Stephanorhinus hundsheimensis *(Toula) (1902) is recognized as a separate species from* S. etruscus *(Falconer) (1868).* S. etruscus *is confined to the Late Pliocene and Early Pleistocene, while* S. hundsheimensis *occurs in the Middle Pleistocene, especially its lower part. These taxa are compared with each other and with* S. hemitoechus *(Falconer) (1868) and* S. kirchbergensis *(Jäeger) (1839), using both metric and non-metric characters of the skull, dentition and limb bones. There is evidence of a trend towards increasing size through time in* S. hemitoechus *and* S. kirchbergensis. S. kirchbergensis *is a hypsodont modification of the Pliocene* S. megarhinus *(de Christol) (1834), while* S. hemitoechus *is a hypsodont modification of the* etruscus*-like rhinoceroses. An ontogenetic model involving incisor loss is proposed to explain the correlation observed between relative development of the muzzle and the premolars.* S. etruscus *and* S. hundsheimensis *are lightly built, cursorial species,* S. kirchbergensis *is very large, but relatively cursorial, with joint surfaces of the limbs suggesting a forest or woodland environment. The compactly built* S. hemitoechus *is the most distinct species in the skeleton, being apparently convergent with* Coelodonta antiquitatis *(Blumenbach, 1799) in many features. The phylogenetic relationships of the taxa are discussed in the context of related Miocene to Pleistocene species.* S. kirchbergensis *is seen as the sister taxon of the other three, and* S. hemitoechus *as the most derived of these.* S. kirchbergensis *is probably part of a clade that also includes the Early Pliocene* S. megarhinus, *while* S. hunsheimensis *may be closely related to the Middle-Late Pliocene* S. jeanvireti *Guérin (1973). Small rhinoceroses, intermediate in age and morphology between* S. etruscus *and* S. hundsheimensis, *are known from Italy, Germany and The Netherlands. The precise relationship between* S. jeanvireti, S. etruscus *and* S. hundsheimensis *is left unresolved.*

RIASSUNTO - Si propone di assegnare al genere Stephanorhinus *Kretzoi (1942) i rinoceronti del Plio-Pleistocene europeo usualmente attribuiti al genere* Dicerorhinus *Gloger (1841).*

Stephanorhinus hundsheimensis *(Toula, 1902) è considerata una specie separata da* S. etruscus *(Falconer, 1868).* S. etruscus *è caratteristico delle faune del Pliocene superiore e del Pleistocene inferiore, mentre* S. hundsheimensis *è un elemento del Pleistocene medio, particolarmente della parte inferiore. Questi taxa sono confrontati sia fra loro che con* S. hemitoechus *(Falconer, 1868) e* S. kirchbergensis *(Jäger, 1839), usando caratteri morfologici e dimensionali del cranio, la dentizione e lo scheletro degli arti.*

E' stato osservato che in S. hemitoechus *e* S. kirchbergensis *vi è una tendenza alla crescita della taglia nel tempo.* S. kirchbergensis *è considerato un discendente ipsodonte di* S. megarhinus *(de Christol, 1834) del Pliocene inferiore e* S. hemitoechus *dei rinoceronti vicini a* S. etruscus. *E' proposto un modello ontogenetico che implica la perdita degli incisivi per giustificare la correlazione osservata fra le dimensioni della regione facciale e dei premolari.* S. etruscus *e* S. hundsheimensis *sono specie snelle e cursoriali,* S. kirchbergensis *è molto grande, ma anch'esso relativamente cursoriale, con superfici articolari degli arti modellate in modo simile a quelle che si riscontrano negli ungulati forestali. Il robusto* S. hemitoechus *è il rinoceronte che meglio si distingue, poichè presenta un'apparente somiglianza con* Coelodonta antiquitatis *(Blumenbach, 1799). Sono discussi i rapporti filogenetici di questi taxa, nel contesto di specie mio-pleistoceniche imparentate.* S. kirchbergensis *è considerato un sister taxon delle altre tre specie e* S. hemitoechus *come il più derivato di tutti.* S. kirchbergensis *può far parte di una linea che include* S. megarhinus *del Pliocene inferiore, mentre* S. hundsheimensis *potrebbe essere vicino a* S. jeanvireti *(Guérin, 1973) del Pliocene medio-superiore. Vengono considerati rinoceronti di piccola taglia, intermedi come età e caratteri tra* S. etruscus *e* S. hundsheimensis, *noti in Italia, Germania e Olanda. Non sono risolti i rapporti filetici fra* S. jeanvireti, S. etruscus *e* S. hundsheimensis.

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Cranial and dental material have been studied by M. Fortelius. P. Mazza devoted himself mostly to the postcranial material of *S. etruscus* and *S. hemitoechus*; B. Sala to that of *S. hundsheimensis* and *S. kirchbergensis*. General observations and conclusions are jointly by the three authors.

INTRODUCTION

The Rhinocerotidae have been the subject of several systematic studies during the past decade (Guérin, 1980, 1982; Heissig, 1981, 1989; Groves, 1983; Prothero *et al.*, 1986, 1989), and a certain degree of consensus appears to emerge on their overall relationships. There is still virtually no agreement on details, however. A major reason for this is undoubtedly that the rhinoceroses are a highly stereotyped group with little morphological divergence (Heissig, 1981).

The relationships of the European Plio-Pleistocene rhinoceroses are still controversial, and indeed do not appear much clearer now than they did over a century ago. With the exception of *Elasmotherium*, which we shall not discuss here, these rhinoceroses are morphologically highly uniform, and probably belong to one close-knit clade (Groves, 1983). The practical difficulties involved in the identification of isolated or fragmentary fossils of this group are formidable, and misidentifications abound in the literature as well as in museum collections. Some of the most prominent palaeontologists of the early nineteenth century, including Cuvier and Owen, were involved in the first modern work on this group, but very little material was available and stratigraphic knowledge was sketchy in the extreme. In 1863 Hermann von Meyer complained: "Wenn man bedenkt, wieviel schon über die fossilen Reste von Rhinozeros geschrieben ist, und welche Kräfte sich an deren Untersuchung geübt haben, so muss man sich mit Recht wundern, das es noch immer nicht gelingen wollte, die Mehrzahl der fossilen Spezies auf befriedigende Weise festzustellen" (quoted in Wurm, 1912). Franz Toula (1902:92) expressed his frustration with feeling: "Dieses Beispiel lässt erkennen, dass es mit der Deutung der verschiedenen Arten in der That 'ein wahres Elend' ist".

Although there is still ample cause for frustration, some progress has been made during this century. The literature is too voluminous to review here, but a string of contributions running from Wüst (1922) to Zeuner (1934), Staesche (1941), Loose (1975) and Guérin (1980,1982) have gradually brought about approximate agreement on the number and identity of the species, at least. Apart from the woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach, 1799), three species of rhinoceros are now commonly recognised in the European Pleistocene fossil record. All have been assigned to the Recent genus *Dicerorhinus*, although they have little in common with the highly plesiomorphic *Dicerorhinus sumatrensis*, and may indeed be closer to *Rhinoceros* than to *Dicerorhinus* (Groves, 1983). Following Groves (1983), we place these taxa in the genus *Stephanorhinus* Kretzoi, 1942, which we provisionally extend to include all the Plio-Pleistocene "dicerorhines" (whatever their true affinity) except *Coelodonta*. By keeping *Coelodonta* intact we are simply following current practise, rather than making a taxonomic statement.

The species usually recognised in the Pleistocene are *Stephanorhinus etruscus* (Falconer, 1868), *S. hemitoechus* (Falconer, 1868) and *S. kirchbergensis* (Jäger, 1839). Remains morphologically indistinguishable from those of *"Dicerorhinus" megarhinus* (de Christol, 1834), a species otherwise known from the Pliocene, are also known in the Late Pleistocene (Koenigswald, 1988), but the species must have been quite rare by that time, and is not included here. *S. jeanvireti* Guérin, 1972, another Pliocene species, is also excluded here. Both are briefly discussed in the context of phylogeny.

This study was motivated in part by the fact that we had quantitative material available that has not previously been published and which has bearing on some of the central problems involved. In preparing these data for publication we made a number of discoveries which prompted us to expand the original scope of the paper somewhat. Nevertheless, we still deal primarily with three common and well known Pleistocene "non-woolly" rhinoceros taxa, *S. etruscus* (*sensu lato*), *S. hemitoechus* and *S. kirchbergensis*. Our focus is especially on *S. etruscus*, which has been the most poorly understood taxon since the difference between *S. hemitoechus* and *S. kirchbergensis* was clarified by Wüst (1922), Zeuner (1934), Staesche (1941) and Azzaroli (1962).

We have followed the recommendation of the Proceedings of the 2nd Symposium on the Neogene-Quaternary Boundary (Bologna-Crotone, 1975), placing the lower boundary of the Pleistocene, on which much debate is under way, at about 1.7 Ma. As to our subdivisions of the Pleistocene, the reader is referred to Table 1.

We do not, then, intend to undertake a full scale revision of the group, but to bring together extant unpublished data as a basis for further study. Several earlier studies have relied mainly on cranial data (Zeuner, 1934; Azzaroli, 1962; Loose, 1975; Cigala-Fulgosi, 1976), while Guérin (1980) included postcranial material in his monograph. Very little quantitative analysis has previously been attempted for this group, however, and even Guérin (1980), who measured large samples, did little more than tabulate summary statistics. Rather than dwell on skulls, which have been extensively discussed before, we have concentrated on the dental and postcranial material that is available from most localities. One main concern has been to analyse statistically representative samples of the different taxa, and to study problems that can be addressed by quantitative methods. The phylogeny of the group is still controversial, and we have not attempted much more than a discussion of possible interpretations of available data. A general revision of the European Neogene and Quaternary rhinoceroses would be highly desirable, but is well beyond the scope of this paper.

NOMENCLATURE AND TAXONOMY

The two common species, *S. hemitoechus* and *S. kirchbergensis*, are quite distinct, even though, in practice, isolated teeth and postcranials are frequently misidentified. There are also two nomenclatural problems. The first regards Azzaroli's (1962) division of *S. hemitoechus* into two subspecies, the Middle Pleistocene *S. hemitoechus falconeri* and the Late Pleistocene *S. hemitoechus aretinus*. If these taxa are to be used, the valid form of the first should obviously be *S. hemitoechus hemitoechus*. The second point concerns a commonly used junior synonym of *S. kirchbergensis* (Jäger, 1839), namely *S. merckii* (Kaup, 1841). While Kaup's name may be brief and fitting, it is no longer valid, after Hooijer (1947) resurrected *S. kirchbergensis*. It should therefore not be used.

The most intricate problems arise with the forms usually referred to *S. etruscus* (Falconer, 1868), which is based on a skull from the Upper Valdarno (Mazza, 1988). Although rhinoceros remains from the British Isles and Germany were referred to *S. etruscus* by several authors (Boyd Dawkins, 1868; Falconer, 1868; Busk, 1870; Schroeder, 1903), other German-speaking authors seem, by the turn of the century, to have become doubtful of the unity of the species as it was conceived (Wüst, 1900; Toula, 1902, 1906; Wurm, 1912). The problem was addressed by Zeuner (1934) and Loose (1975), among others, but only Guérin (1980) has attempted a general revision. Unfortunately, Guérin made several mistakes which detract somewhat from the value of his monumental work. To the extent that they concern our present task, it is necessary to discuss these problems here.

Guérin (1980) erected the new subgenus *Dicerorhinus* (*Brandtorhinus*), with the type species *D. etruscus etruscus* (p.443). He assigned *D. sansaniensis* (p. 201) and *D. megarhinus* (p. 443) to *Dicerorhinus* (*Dicerorhinus*), but did not assign other pre-Pliocene species to subgenera. He explicitly rejected Kretzoi's (1942) division of *Dicerorhinus* into the genera *Stephanorhinus* and *Procerorhinus*, on the grounds that "...ces noms car ils sont fondés sur un mélange de caractères spécifiques, génériques et subgénériques, il sont justifiés par un schéma phylogénétique qui me parait discutable, ils sont insuffisamment distincts l'un de l'autre et ne sont étayés par aucun travail original apportant quoi que ce soit de noveau;..." (Guérin, 1980: 444). Later, Guérin (1989) raised *Brandtorhinus* to genus rank.

Stephanorhinus Kretzoi was originally defined as encompassing the *S. etruscus*-group, the *S. megarhinus-leptorhinus*-group and the *S. kirchbergensis*-group (Kretzoi, 1942: 312). *Brandtorhinus* Guérin excludes *"D". megarhinus* and includes *"B". hemitoechus*, but is otherwise identical to *Stephanorhinus*. Both schemes implicitly assume that *S. etruscus* and *S. kirchbergensis* belong to a monophyletic group that excludes all known pre-Pliocene species. In this basic assumption both are probably at fault, but pending a revision of the entire clade, Kretzoi's name may be used. It is preferable to Guérin's because it has priority and has been used quite extensively in the literature (e.g., Heissig, 1973, 1981, 1989; Groves, 1983; Prothero *et al.*, 1986).

Procerorhinus Kretzoi was erected for *"P". hemitoechus* only (Kretzoi, 1942: 314), and is fundamentally a simple subdivision of either *Stephanorhinus* Kretzoi or *Brandtorhinus* Guérin. Like every other since Kretzoi (1942), we see no reason to separate *S. hemitoechus* at the generic level.

In his treatment of *"Dicerorhinus" etruscus*, Guérin (1980: 444, 622) divided the species into the subspecies *"D". etruscus etruscus*, distributed only in the Early Pleistocene and *"D". etruscus brachycephalus*, from the Middle Pleistocene. The type of the former is Falconer's (1868) type of *Rhinoceros etruscus*, and the subspecies is formally valid. The type of *D. etruscus brachycephalus*, however, is the famous type skull of *Rhinoceros merckii* var. *brachycephala* Schroeder, 1903 from Daxlanden (the name derives from Schroeder's mistaken belief that the skull is especially short for its species, explained by the fact that he unwittingly compared it with skulls of *S. hemitoechus*). The famous skull, now the Landessammlungen für Naturkunde in Karslruhe, specimen Qp/650, has been the subject of considerable controversy. Hermann von Meyer (1864) referred it to *Rhinoceros Merckii* (=*S. kirchbergensis*), while, according to Guérin (1980: 623), Lartet (1867: 180-181) referred it to *Rhinoceros etruscus*. Schroeder (1903) considered it intermediate between *R. etruscus* and *R. Merckii*, but referred it to the latter (*Rhinoceros Merckii* var *brachycephala*). Toula (1906) thought that it might belong to *S. hemitoechus*, but Wüst (1922) and Staesche (1941) both regarded it as *S. kirchbergensis*. Azzaroli (1962a) was undecided, but suggested it had an affinity with *S. kirchbergensis*. Loose (1975) referred the skull to *S. kirchbergensis*, and gave good illustrations. Guérin (1980) selected it as the type specimen of his subspecies *Dicerorhinus etruscus brachycephalus*, but Mazza (1988) followed the majority of previous authors in referring it to *S. kirchbergensis*.

The Daxlanden skull is deep and stocky, with all the typical features of *S. kirchbergensis* (see Loose, 1975, pls. 5: 1, 8: 3, 10: 5). It has a forward-leaning occiput, massive maxillaries and zygomatic arches, and the anterior rim of the orbit lies above M1/, rather than further back as in *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*. Similarly, the posterior margin of the nasal notch reaches only to P3/, not to P4/ or M1/ as in the other species. The teeth are relatively large, with characteristically inflated lingual cusps and smooth ectolophs and without pronounced styli. The upper premolars are lingually short and mesially broad, a characteristic feature of the species (fig. 7). A case might be made for the division of *S. kirchbergensis* into two species, in which case the valid name for the Middle Pleistocene, small form would be *S. brachycephalus* Schroeder, 1903.

Guérin (1980: 623) also incorretly attributes the name *Rhinoceros hundsheimensis* to "Toula (1905)". *R. hundsheimensis* was named by Toula in 1902, and thus has priority over Schroeder's (1903) name in any case [incidentally, Guérin's (1980) bibliography contains no reference to Toula (1905), and the original description is incorrectly listed as "Toula (1901)"].

R. hundsheimensis is in fact the oldest available name for the Middle Pleistocene form of *Stephanorhinus etruscus* (*sensu lato*), as was noted by Staesche (1941). It is remarkably fortunate that the type specimen is not only one of the most complete Pleistocene rhinoceros skeletons known, but one that has been painstakingly described and superbly illustrated (Toula, 1902, 1906).

For reasons given by Mazza (1988) and further discussed below, we agree with Guérin (1980, 1989) that the distinction between an Early Pleistocene "etruscoid" taxon (*S. etruscus*) and Middle Pleistocene one (*S. hundsheimensis*) is sound, and we shall adopt it here.

We propose the following provisional classification, restricted to taxa discussed in the present paper:

Genus *Coelodonta* Bronn,1831

Species - *Rhinoceros antiquitatis* Blumenbach, 1799
Synonym - *Rhinoceros tichorhinus* Cuvier, 1812

Genus *Stephanorhinus* Kretzoi, 1942

Type species - *Rhinoceros etruscus* Falconer, 1868
Synonyms - *Dicerorhinus (Brandtorhinus) etruscus etruscus* Guérin, 1980

Species *Rhinoceros megarhinus* de Cristol, 1834

Species - *Rhinoceros kirchbergensis* Jäger, 1839
Synonym - *Rhinoceros Merckii* Kaup, 1841

Species *Rhinoceros hemitoechus* Falconer, 1868

Species *Rhinoceros hundsheimensis* Toula, 1902
Synonyms - *Rhinoceros etruscus heidelbergensis* Freudenberg, 1914; *Dicerominus etruscus brachycephalus* Guérin, 1980 (in intent, but excluding type specimen); *Dicerorhinus hemitoechus intermedius* Cigala-Fulgosi, 1976

Species *Dicerorhinus jeanvireti* Guérin, 1972

MATERIAL AND METHODS

This paper is based on the study of large part of the material available in the paleontological collections of Western Europe. table 1 lists the localities studied, with collections and ages assigned in this study. We gratefully acknowledge personal communications regarding chronology and stratigraphic correlations with Drs. Andrew Currant, Philip Gibbard, Thijs van Kolfschoten, Federico Masini and Danilo Torre, but take full responsibility for the decisions made here.

Our original sample being mainly composed of dental and postcranial remains, data from Guérin (1980) were used for quantitative comparisons of crania.

We made use of isolated teeth as well as teeth attached to jaws. In most species of rhinoceros, distinction between P3 and P4 or M1 and M2 is difficult if the teeth are isolated, and errors of identification are almost impossible to detect afterwards. To avoid this uncertainty, only teeth in jaws or teeth unequivocally associated with others by matching wear facets between them were used in this study. For the terminal teeth (P2 and M3) this difficulty does not exist, and isolated specimens were included to increase the M3 sample size and allow more detailed comparisons. In the study of the relative proportions of the teeth, only those teeth still embedded in the mandibles were used. Deciduous teeth were not included in this study. For postcanine teeth, the basal maximum length and width, buccal length (BBL), lingual length (BLL), mesial width (MBB), and distal width (DBB) of the individual teeth were measured. Widths were measured parallel to and somewhat above the plane of the crown base (at the level giving highest reading). The lengths of the upper teeth were measured the same way, with the level of measurement of the buccal side chosen at the point where the sides of the ectolophe become subparallel. The lengths of the lower teeth were measured slightly obliquely, from the level of the mesial cingulum of the posterior basal bulge of the enamel immediately above the crown base (this somewhat peculiar measurement gives the most comparable results for isolated teeth and dentitions).

The state of a number of morphological characters was scored for the entire sample, but only the lower teeth were used for the present study (characters and states listed in table 3). The states were determined subjectively by MF over a period spanning nearly a decade; repeated scoring of the same specimens at different times indicates the values obtained are reasonably consistent (MF, unpublished data). Furthermore, data for all species were obtained throughout the period. Because of the nature of the material, statistical significance tests were not considered appropriate.

The postcranial fossils examined are listed in table 2. Comparative analyses were carried out mainly on the basipodials and metapodials, since they are usually far better represented in the fossil record than stylopodials and zeugopodials. The bones of the axial skeleton, the pelvis and the falanges were disregarded in the present study.

In addition, data of especially significant specimens were drawn from literature. Thoroughly described material (such as that figured by Staesche (1941) and Guérin (1980)) that could be easily compared with our material was selected for this purpose.

The postcranial bones were measured following standard methodology for ease of comparison with the literature. Certain new measurements capable of providing a clear picture of the proportions of the specimens were also introduced in some cases.

The measurements of the individual bones are given, in anatomical order, in table 8 - 35. All diameters of each bone are given together, in order to show variation in size and proportions. Sketches were also prepared to show the main morphological differences observed. Measurements of young individuals are reported at the bottom of the tables, separated by an unbroken line.

Ratio diagrams were constructed according to Simpson (1941). The significance of the differences was investigated using the one-way Model II analysis of variance (Sokal & Rohlf, 1981). For two groups this is mathematically equivalent to a t-test (Sokal & Rohlf, 1981: 208). For postcranial elements, actual t-tests were also used to investigate

TABLE 1 - Material included in this study

Age *Mammal Age* Locality	Collection	*Mammal Age* Locality	Collection
		Late Pliocene	
Lower Villafranchian			
Città della Pieve (Perugia)	Private		
Palaia (Pisa)	Mus. Paleont. Firenze		
		Early Pleistocene	
Upper Villafranchian 1		*Upper Villafranchian 3*	
Olivola	Mus. Paleont. Firenze	Mugello	Mus. Montevarchi
Upper Villafranchia 2		*Upper Villafranchian 4*	
Figline	Mus. Paleont. Firenze	Pirro (Foggia)	Mus. Paleont. Firenze
Piagge di Caposelvi	Mus. Montevarchi	Pietrafitta (Perugia)	Coll. Pietrafitta
Piagge di Pernina	Mus. Montevarchi	Westerhoven (Brabant)	Rijskmus. Geol. Min. Leiden
Piana dei Cavalieri	Mus. Paleont. Roma		
Rapale	Mus. Montevarchi	*Upper Villafranchian undifferentiated*	
Tasso [1]	N.h. Mus. Basel		
	Mus. Montevarchi	Ganghereto	N.h. Mus. Basel
	Mus. Paleont. Firenze	Renai (Vitereta)	Mus. Montevarchi
Val di Peccioli (Trigesimo)	Mus. Montevarchi	Senèze	M.N.H.N. Paris
			Dep. Sci. Terr. Lyon
		Vacchereccia	
		«Valdarno superiore»	Mus. Montevarchi
		Early and Middle Pleistocene (Galerian)	
Daxlanden	L.N. Karlsruhe	Voigtstedt bei Weimar	Inst. Quart. Pal. Weimar
Isernia «La Pineta»	Ist. geol. Ferrara	Mundesley	N.H. Mus. London
	Mus. Isernia	West Runton	N.H. Mus. London
Lexden	N.H. Mus. London	Trimingham	N.H. Mus. London
Mauer bei Heidelberg	Geol. Inst. Heidelberg	Pakefield	N.H. Mus. London
	Hess. Landesmus.	Malagrotta	Mus. Paleont. Roma
Mosbach bei Wiesbaden	N.h. Mus. Mainz	Monte Sacro	Mus. Paleont. Roma
	Hess. Landesmus.	Ponte Milvio	Mus. Paleont. Roma
	Senckenberg Mus.	Vitinia	Mus. Paleont. Roma
Süssenborn bei Weimar	Inst. Quart. Pal. Weimar	Visogliano (Trieste)	Mus. Paleont. Firenze
		Late Middle Pleistocene	
Torrente Conca (Riccione)	Museum of Riccione	Steinheim am Murr	N.h. Mus. Stuttgart
Clacton-on-Sea	N.H. Mus. London	Swanscombe	N.H. Mus. London
Essex	N.H. Mus. London	Maastricht-Belvédère	Inst. Aardwetensch. Utrecht
Heppenloch	N.h. Mus. Stuttgart		
		Middle Pleistocene undifferentiated	
Sabbie di Bucine	Mus. Paleont. Firenze	Pratantico	Mus. Montevarchi
	Mus. Montevarchi		
		Late Middle or Late Pleistocene	
Botrio Maspino	Mus. Paleont. Firenze	Crayford	N.H. Mus. London
Ehringsdorf bei Weimar	Inst. Quart. Pal. Weimar	Ilford	N.H. Mus. London
Fiume Maspino presso S.Seo	Mus. Paleont. Firenze	Ponte alla Nave	Mus. Paleont. Firenze
Grays	N.H. Mus. London		
		Late Pleistocene	
Barrington	Mus. Zol. Cambridge	Bruhl (Rhein)	N.h. Mus. Stuttgart
	Sedgwick Mus. Cambridge	Minchin Hole	N.H. Mus. London
	N.H. Mus. London	Selsey	N.H. Mus. London
	Geol. Mus. London	Taubach	Inst. Quart. Pal. Weimar
		Uncertain age	
Arezzo	Mus. Paleont. Firenze	Serravalle	Mus. Paleont. Firenze
Bacton (East Anglia)	N.H. Mus. London	Stockstadt	H. Landesmus. Darmstadt
Malpignano	Mus. Paleont. Firenze	«Valdarno superiore»	Mus. Montevarchi
Renai	Mus. Montevarchi		Hess. Landesmus
«Rheinschotter» [2]	N.h. Mus. Stuttgart		N.h. Mus. Mainz

1) Tasso, Santa Maria al Tasso, Tasso (Le Strette), Le Strette (Tasso), Scuragnolo, «Hintergrund von Leville, nahe dem Scuragnolo», Le Ville (Terranuova), Le Ville (Inferno), Inferno (Le Ville), Le Ville (Le Fossette), Casa Inferno, Casa Frata, La Cicogna. 2) Edinger-Ried, Eich bei Worms, Huttenheim, Koller, Neulussheim, Rheinhausen, «Rheinschotter». Speyer.

Table 2 — List of specimens

Stephanorhinus etruscus (FALCONER)
1et Upper Valdarno, IGF 2285 v, MGPF
2et Upper Valdarno, IGF 2207 v, MGPF
3et Figline, Upper Valdarno, IGF 727, MGPF
4et Figline, Upper Valdarno, IGF 726, MGPF
5et Olivola, Magra valley, IGF 183 v, MGPF
6et Olivola, Magra valley, IGF 183 v, MGPF
7et Upper Valdarno, IGF 2206 v, MGPF
8et Figline, Upper Valdarno, IGF 725, MGPF
9et Upper Valdarno, IGF 2208 v, MGPF
10et Figline, Upper Valdarno, IGF 718, MGPF
11et Poggio al Pero, Upper Valdarno, IGF 716, MGPF
12et Casa Inferno, Upper Valdarno, IGF 2209 v, MGPF
13et Upper Valdarno, IGF 2210 v, MGPF
14et Upper Valdarno, IGF 14840, MGPF
15et Upper Valdarno, IGF 712, MGPF
16et Montecarlo, Upper Valdarno, IGF 730, MGPF
17et Upper Valdarno, IGF 717, MGPF
18et Figline, Upper Valdarno, IGF 732, MGPF
19et Olivola, Magra Valley, IGF 160, MGPF
20et Olivola, Magra Valley, IGF 170, MGPF
21et Olivola, Magra Valley, IGF 172, MGPF
22et Olivola, Magra Valley, IGF 171, MGPF
23et Olivola, Magra Valley, IGF 1981, MGPF
24et Olivola, Magra Valley, IGF 1415, MGPF
25et Olivola, Magra Valley, IGF 4328, MGPF
26et Olivola, Magra Valley, IGF 4324, MGPF
27et Olivola, Magra Valley, IGF 4325, MGPF
28et Olivola, Magra Valley, IGF 4322, MGPF
29et Olivola, Magra Valley, IGF 4329, MGPF
30et Olivola, Magra Valley, IGF 4323, MGPF
31et Olivola, Magra Valley, IGF 4327, MGPF
32et Olivola, Magra Valley, IGF 1869, MGPF
33et Fontana Acetosa, Frosinone, no number, IPUR
34et Upper Valdarno, IGF 2212 v, MGPF
35et Upper Valdarno, IGF 2211 v, MGPF
36et Upper Valdarno, IGF 721, MGPF
37et Figline, Upper Valdarno, IGF 2213 v, MGPF
38et Upper Valdarno, IGF 2214 v, MGPF
39et Upper Valdarno, IGF 2236 v, MGPF
40et Upper Valdarno, N 196, MGPF
41et Upper Valdarno, N 198 10715, MGPF
42et Olivola, Magra Valley, IGF 166 v, MGPF
43et Olivola, Magra Valley, IGF 4667, MGPF
44et Olivola, Magra Valley, IGF 4309, MGPF
45et Olivola, Magra Valley, IGF 4321, MGPF
46et Olivola, Magra Valley, IGF 1907, MGPF
47et Olivola, Magra Valley, IGF 1901, MGPF
48et Olivola, Magra Valley, IGF 1903, MGPF
49et Olivola, Magra Valley, IGF 1900, MGPF
50et Olivola, Magra Valley, IGF 1899, MGPF
51et Olivola, Magra Valley, IGF 1904, MGPF
52et Olivola, Magra Valley, IGF 4318, MGPF
53et Olivola, Magra Valley, IGF 1865, MGPF
54et Olivola, Magra Valley, IGF 4337, MGPF
55et Olivola, Magra Valley, IGF 1864, MGPF
56et Olivola, Magra Valley, IGF 4313, MGPF
57et Olivola, Magra Valley, IGF 4302, MGPF
58et Olivola, Magra Valley, IGF 4320, MGPF
59et Olivola, Magra Valley, IGF 1978, MGPF
60et Olivola, Magra Valley, IGF 4304, MGPF
61et Olivola, Magra Valley, IGF 2216 v, MGPF
62et Olivola, Magra Valley, IGF 1866, MGPF
63et Olivola, Magra Valley, IGF 2215 v, MGPF
64et Olivola, Magra Valley, IGF 4312, MGPF
65et Olivola, Magra Valley, IGF 1806, MGPF
66et Olivola, Magra Valley, IGF 163 v, MGPF
67et Olivola, Magra Valley, IGF 164 v, MGPF
68et Olivola, Magra Valley, IGF 173 v, MGPF
69et Olivola, Magra Valley, IGF 165 v, MGPF
70et Olivola, Magra Valley, IGF 175 v, MGPF
71et Olivola, Magra Valley, IGF 169 v, MGPF
72et Olivola, Magra Valley, IGF 177 v, MGPF
73et Olivola, Magra Valley, IGF 4319, MGPF
74et Olivola, Magra Valley, IGF 4315, MGPF
75et Olivola, Magra Valley, IGF 1939, MGPF
76et Olivola, Magra Valley, IGF 2217 v, MGPF
77et Olivola, Magra Valley, IGF 4314, MGPF
78et Olivola, Magra Valley, IGF 2236 v, MGPF
79et Olivola, Magra Valley, IGF 4311, MGPF
80et Il Tasso, Upper Valdarno, IGF 2223 v, MGPF
81et Il Tasso, Upper Valdarno, IGF 2222 v, MGPF
82et Olivola, Magra Valley, IGF 1969, MGPF
83et Olivola, Magra Valley, IGF 1968, MGPF
84et Olivola, Magra Valley, IGF 1966, MGPF
85et Olivola, Magra Valley, IGF 1967, MGPF
86et Il Tasso, Upper Valdarno, IGF 2225 v, MGPF
87et Olivola, Magra Valley, IGF 1965, MGPF
88et Olivola, Magra Valley, IGF 1964, MGPF
89et Upper Valdarno, IGF 2228 v, MGPF
90et Olivola, Magra Valley, IGF 1962, MGPF
91et Olivola, Magra Valley, IGF 1961, MGPF
92et Olivola, Magra Valley, IGF 1963, MGPF
93et Le Strette, Upper Valdarno, IGF 2224 v, MGPF
94et Upper Valdarno, IGF 2226 v, MGPF
95et Il Tasso, Upper Valdarno, IGF 2218 v, MGPF
96et Olivola, Magra Valley, IGF 4345, MGPF
97et Upper Valdarno, IGF 2219 v, MGPF
98et Il Tasso, Upper Valdarno, IGF 2227 v, MGPF
99et Il Tasso, Upper Valdarno, IGF 2221 v, MGPF
100et et Olivola, Magra Valley, IGF 1953, MGPF
101et Olivola, Magra Valley, IGF 1954, MGPF
102et Il Tasso, Upper Valdarno, IGF 2230 v, MGPF
103et Figline, Upper Valdarno, IGF 1355 v, MGPF
104et Olivola, Magra Valley, IGF 1935, MGPF
105et Il Tasso, Upper Valdarno, IGF 2231 v, MGPF
106et Olivola, Magra Valley, IGF 1928, MGPF
107et Olivola, Magra Valley, IGF 1925, MGPF
108et Olivola, Magra Valley, IGF 1926, MGPF
109et Olivola, Magra Valley, IGF 1929, MGPF
110et et Upper Valdarno, IGF 2232 v, MGPF
111et Olivola, Magra Valley, IGF 1945, MGPF
112et Olivola, Magra Valley, IGF 1944, MGPF
113et Olivola, Magra Valley, IGF 1946, MGPF
114et Olivola, Magra Valley, IGF 1949, MGPF
115et Olivola, Magra Valley, IGF 1948, MGPF
116et Olivola, Magra Valley, IGF 1936, MGPF
117et Olivola, Magra Valley, IGF 1947, MGPF
118et Upper Valdarno, IGF 2234 v, MGPF
119et Upper Valdarno, IGF 2235 v, MGPF
120et Il Tasso, Upper Valdarno, IGF 722, MGPF
121et Figline, Upper Valdarno, IGF 710, MGPF
122et Olivola, Magra Valley, IGF 1868, MGPF
123et Olivola, Magra Valley, IGF 1872, MGPF
124et Olivola, Magra Valley, IGF 4326, MGPF
125et Olivola, Magra Valley, IGF 1878, MGPF
126et Olivola, Magra Valley, IGF 1879, MGPF
127et Olivola, Magra Valley, IGF 1875, MGPF
128et Olivola, Magra Valley, IGF 1870, MGPF
129et Olivola, Magra Valley, IGF 1873, MGPF
130et Olivola, Magra Valley, IGF 162 v, MGPF
131et Olivola, Magra Valley, IGF 176 v, MGPF
132et Olivola, Magra Valley, IGF 4341, MGPF
133et Olivola, Magra Valley, IGF 4343, MGPF
134et Olivola, Magra Valley, IGF 4342, MGPF
135et Upper Valdarno, IGF 2237 v, MGPF
136et Olivola, Magra Valley, IGF 1883, MGPF
137et Olivola, Magra Valley, IGF 1912, MGPF
138et Olivola, Magra Valley, IGF 1884, MGPF
139et Olivola, Magra Valley, IGF 1882, MGPF
140et Olivola, Magra Valley, IGF 1881, MGPF
141et Olivola, Magra Valley, IGF 4339, MGPF
142et Olivola, Magra Valley, IGF 168 v, MGPF
143et Olivola, Magra Valley, IGF 4340, MGPF
144et Olivola, Magra Valley, IGF 161 v, MGPF
145et Olivola, Magra Valley, IGF 181 v, MGPF
146et Olivola, Magra Valley, IGF 180 v, MGPF
147et Olivola, Magra Valley, IGF 167 v, MGPF
148et Figline, Upper Valdarno, IGF 731, MGPF
149et Casa Frata, Upper Valdarno, IGF 1807 v, MGPF
150et Upper Valdarno, IGF 2243 v, MGPF
151et Upper Valdarno, IGF 728, MGPF
152et Olivola, Magra Valley, IGF 1897, MGPF
153et Olivola, Magra Valley, IGF 1894, MGPF
154et Olivola, Magra Valley, IGF 1895, MGPF
155et Olivola, Magra Valley, IGF 1893, MGPF
156et Olivola, Magra Valley, IGF 1892, MGPF
157et Olivola, Magra Valley, N 1888, MGPF
158et Upper Valdarno, IGF 2238 v, MGPF
159et Il Tasso, Upper Valdarno, IGF 719, MGPF
160et Olivola, Magra Valley, IGF 1885, MGPF
161et Olivola, Magra Valley, IGF 1887, MGPF
162et Olivola, Magra Valley, IGF 1952, MGPF
163et Olivola, Magra Valley, IGF 1951, MGPF

164et Le Strette, Upper Valdarno, IGF 2220 v, MGPF
165et Il Tasso, Upper Valdarno, IGF 2229 v, MGPF
166et Olivola, Magra Valley, IGF 1960, MGPF
167et Olivola, Magra Valley, IGF 1958, MGPF
168et Olivola, Magra Valley, IGF 1959, MGPF
169et Piana dei Cavalieri, no number, IPUR
170et Figline, Upper Valdarno, IGF 715, MGPF
171et La Cicogna, Upper Valdarno, IGF 2239 v, MGPF
172et Il Tasso, Upper Valdarno, IGF 714, MGPF
173et Olivola, Magra Valley, IGF 1923, MGPF
174et Olivola, Magra Valley, IGF 1933, MGPF
175et Olivola, Magra Valley, IGF 1924, MGPF
176et Olivola, Magra Valley, IGF 1919, MGPF
177et Olivola, Magra Valley, IGF 1922, MGPF
178et Olivola, Magra Valley, IGF 1920, MGPF
179et Olivola, Magra Valley, IGF 1917, MGPF
180et Olivola, Magra Valley, IGF 1918, MGPF
181et Olivola, Magra Valley, IGF 1921, MGPF
182et Upper Valdarno, IGF 2233 v, MGPF
183et Olivola, Magra Valley, IGF 1931, MGPF
184et Olivola, Magra Valley, IGF 1937, MGPF
185et Olivola, Magra Valley, IGF 1934, MGPF
186et Olivola, Magra Valley, IGF 1936, MGPF
187et young ind., Casa Inferno, Upper Valdarno, IGF 488 v, MGPF
188et young ind., Olivola, Magra Valley, IGF 4338, MGPF
189et young ind., Casa Inferno, Upper Valdarno, IGF 487 v, MGPF

Stephanorhinus hundsheimensis (TOULA)
1hu Mosbach, Mb 456, HLD
2hu Mosbach, 1955/900, NMM
3hu Mauer, Mau 140, HLD
4hu Mauer, Mau 141, HLD
5hu Mauer, Mau 142, HLD
6hu Mosbach, 1975/264, NMM
7hu Mosbach, 1961/373, NMM
8hu Mosbach, 1955/1109, NMM
9hu Mosbach, 1957/206, NMM
10hu Trimingham, Norfolk, M 17843, MNHL
11hu Mundesley, Norfolk, M 17841, MNHL
12hu Isernia, IS F 307, MNI
13hu Mosbach, Mb 153, HLD
14hu Mosbach, Mb 935, HLD
15hu Mosbach, 1958/216, NMM
16hu Mosbach, 1963/573, NMM
17hu Mosbach, 1958/631, NMM
18hu Isernia, IS I 16, MNI
19hu Isernia, IS F 314, MNI
20hu Isernia, IS I 317, MNI
21hu Isernia, no number, MNI
22hu Westerhoven, Brabant, RGM 14198, RML
23hu Westerhoven, Brabant, RGM 14195, RML
24hu Westerhoven, Brabant, RGM 14193, RML
25hu Mosbach, 1956/285, NMM
26hu Mosbach, 1955/154, NMM
27hu Mosbach, 1955/1366, NMM
28hu Mosbach, 1953/265, NMM
29hu Mosbach, 1961/593, NMM
30hu Mosbach, 1955/518, NMM
31hu Mosbach, 1967/76, NMM
32hu Mosbach, 1966/173, NMM
33hu Isernia, IS I Q53-4, NMI
34hu Mosbach, 1955/789, NMM
35hu Mosbach, 1957/651, NMM
36hu Isernia, IS I 326, MNI
37hu Isernia, IS I 336, MNI
38hu Mauer, Mau 161, HLD
39hu Mauer, Mau 435, HLD
40hu Mosbach, 1961/235, NMM
41hu Isernia, IS I 333, MNI
42hu Isernia, IS I Q71-107, MNI
43hu Isernia, IS I 332, MNI
44hu Isernia, IS I 331, MNI
45hu Mosbach, 1959/742, NMM
46hu Mosbach, 1954/466, NMM
47hu Isernia, IS F 365, MNI
48hu Mosbach, 1958/277, NMM
49hu Mosbach, 1954/80, NMM
50hu Mosbach, 1956/314, NMM
51hu Mosbach, 1962/216, NMM
52hu Isernia, IS F 378, MNI
53hu Mosbach, 1961/119, NMM
54hu Mosbach, 1954/368, NMM
55hu Mauer, Mau 150, HLD
56hu Mosbach, 1956/28, NMM
57hu Mosbach, 1959/791, NMM
58hu Mosbach, 1963/518, NMM
59hu Mosbach, 1962/931, NMM
60hu Mosbach, 1958/322, NMM
61hu Mosbach, 1955/1226, NMM
62hu Mosbach, 1955/276, NMM
63hu Mosbach, 1955/73, NMM
64hu Essex, Clacton, 27846, MNHL
65hu Vitinia, Ponte Galeria, 2768, MPUR
66hu Mosbach, 1959/555, NMM
67hu Mosbach, 1955/1343, NMM
68hu Mosbach, 1958/644, NMM
69hu Mosbach, 1957/121, NMM
70hu Mosbach, 1959/195, NMM
71hu Mosbach, 1956/606, NMM
72hu Isernia, IS I 383, MNI
73hu Isernia, IS F 382, MNI
74hu Isernia, IS 28926, MNI
75hu Mauer, Mau 139, HLD
76hu Mosbach, 1954/ , NMM
77hu Ponte Milvio, no number, MPUR
78hu Isernia, 30318, MNI
79hu Isernia, 29996, MNI
80hu Mosbach, Mb 931, HLD
81hu Isernia, IS F 321, MNI
82hu Isernia, IS I Q51-71, MNI
83hu Trimingham, Norfolk, M 18486, MNHL
84hu Trimingham, Norfolk, 209, MNHL
85hu Mosbach, 1956/601, NMM
86hu Mosbach, 1956/648, NMM
87hu Mosbach, 1970/171, NMM
88hu Isernia, IS F 302, MNI
89hu Mosbach, 1955/693, NMM
90hu Mosbach, 1952/376, NMM
91hu Mosbach, 1957/980, NMM
92hu Mosbach, 1952/197, NMM
93hu Mosbach, 1955/167, NMM
94hu Mosbach, 1947/16, NMM
95hu Mosbach, 1962/1281, NMM
96hu Mosbach, 1962/1282, NMM
97hu Monte Sacro, 1510, MPUR
98hu Isernia, IS F 368, MNI
99hu Isernia, 29814, MNI
100hu Mosbach, Mb 156, HLD
101hu Mauer, Mau 151, HLD
102hu Mosbach, 1961/616, NMM
103hu Mosbach, 1959/197, NMM
104hu Mosbach, 1956/996, NMM
105hu Mosbach, 1960/199, NMM
106hu Mosbach, 1967/79, NMM
107hu Mosbach, 1965/270, NMM
108hu Mosbach, 1954/135, NMM
109hu Mosbach, 1961/544, NMM
110hu Malagrotta, M 38, MPUR
111hu Isernia, IS I 370, MNI
112hu Isernia, IS I 44, MNI
113hu Isernia, 31281, MNI
114hu Isernia, IS F 377, MNI
115hu Isernia, IS F 374, MNI
116hu Isernia, IS F 375, MNI
117hu Isernia, IS I 376, MNI
118hu Isernia, IS I 81, MNI
119hu Isernia, IS I 51-21, MNI
120hu Isernia, IS I 327, MNI
121hu Isernia, IS I 329, MNI
122hu Isernia, IS I 328, MNI
123hu Isernia, IS I 330, MNI
124hu Isernia, IS I 381, MNI
125hu Isernia, IS I 379, MNI
126hu Mosbach, 1955/1225, NMM
127hu Mosbach, 1957/394, NMM
128hu Mosbach, 1960/144, NMM
129hu Mosbach, 1955/832, NMM
130hu Mosbach, 1964/503, NMM
131hu Mosbach, 1954/197, NMM
132hu Isernia, IS I 378, MNI
133hu Mosbach, 1954/564, NMM
134hu Mosbach, 1953/488, NMM
135hu Mosbach, 1959/790, NMM
136hu Mosbach, 1958/84, NMM

137hu Isernia, IS I 380, MNI
138hu young ind., Isernia, IS I 366, MNI
136hu young ind., Mosbach, 1955/316, NMM
137hu young ind., Mosbach, 1955/692, NMM
138hu young ind., Mosbach, 1970/29, NMM
139hu young ind., Mosbach, 1959/792, NMM

Stephanorhinus kirchbergensis (JAGER)
1ki Mosbach, 1975/263, NMM
2ki Mosbach, 1955/600, NMM
3ki Mosbach, 1955/609, NMM
4ki Mauer, Mau 420, HLD
5ki Mauer, Mau 421, HLD
6ki Mosbach, 1953/326, NMM
7ki Mosbach, 1954/167, NMM
8ki Mosbach, 1959/501, NMM
9ki Mosbach, 1963/516, NMM
10ki Mosbach, 1961/795, NMM
11ki Stockstadt,Rhein, 1811, DMC
12ki Mosbach, Mb 956, HLD
13ki Mosbach, 1953/134, NMM
14ki Mosbach, 1957/565, NMM
15ki Grays (Thurrock), Essex, 22038, MNHL
16ki Mosbach, 1927/657, NMM
17ki Grays (Thurrock), Essex, 21310, MNHL
18ki Grays (Thurrock), Essex, 23149, MNHL
19ki Mosbach, 1967/77, NMM
20ki Grays (Thurrock), Essex, 36614, MNHL
21ki Mauer, Mau 149, HLD
22ki Mosbach, 1961/958, NMM
23ki Westerhoven, Brabant, RGM 172414, RML
24ki Mosbach, 1961/241, NMM
25ki Mosbach, 1955/520, NMM
26ki Mosbach, 1959/299, NMM
27ki Mosbach, 1961/71, NMM
28ki Clacton, Essex, M 19838, MNHL
29ki Clacton, Essex, 22024, MNHL
30ki Mosbach, 1956/928, NMM
31ki Mosbach, 1967/81, NMM
32ki Grays (Thurrock), Essex, 21618, MNHL
33ki Grays (Thurrock), Essex, 21278a, MNHL
34ki Grays (Thurrock), Essex, 21278b, MNHL
35ki Grays (Thurrock), Essex, 21617, MNHL
36ki Clacton, Essex, M 19836, MNHL
37ki Calcton, Essex, M 19837, MNHL
38ki Mosbach, Mb 162, HLD
39ki Mosbach, Mb 161, HLD
40ki Mosbach, Mb 940, HLD
41ki Mosbach, Mb 938, HLD
42ki Mosbach, 1937/184, NMM
43ki Mosbach, 1963/621, NMM
44ki Mosbach, 1954/195, NMM
45ki Mosbach, 1968/180, NMM
46ki Mosbach, 1962/1283, NMM
47ki Mosbach, 1962/930, NMM
48ki Mosbach, 1955/325, NMM
49ki Clacton, Essex, M 19833, MNHL
50ki Grays (Thurrock), Essex, 21279, MNHL
51ki Grays (Thurrock), Essex, 20814, MNHL
52ki Grays (Thurrock), Essex, 22019, MNHL
53ki Mosbach, 1962/1052, NMM
54ki Mosbach, 1957/312, NMM
55ki Mosbach, 1959/199, NMM
56ki Grays (Thurrock), Essex, 21318a, MNHL
57ki Grays (Thurrock), Essex, 21318b, MNHL
58ki Mosbach, 1953/95, NMM
59ki Grays (Thurrock), Essex, 20277, MNHL
60ki Grays (Thurrock), Essex, 21286b, MNHL
61ki Grays (Thurrock), Essex, 23761g, MNHL
62ki Grays (Thurrock), Essex, 23761, MNHL
63ki Mosbach, 1975/374, NMM
64ki Mosbach, 1961/955, NMM
65ki Mosbach, 1949/194, NMM
66ki Mosbach, 1956/393, NMM
67ki Mosbach, 1955/944, NMM
68ki Mosbach, 1957/242, NMM
69ki Mosbach, 1955/691, NMM
70ki Mosbach, 1956/927, NMM
71ki Mosbach, 1962/291, NMM
72ki Mosbach, 1967/812, NMM
73ki Mosbach, 1963/620, NMM
74ki Mosbach, 1948/23, NMM
75ki Mosbach, 1967/78, NMM
76ki young ind., Grays (Thurrock), Essex, 21679, MNHL
77ki young ind., Mosbach, 1955/949, NMM
78ki young ind., Grays (Thurrock), Essex, 21286c, MNHL
79ki young ind., Grays (Thurrock), Essex, 18754, MNHL
80ki young ind., Mosbach, Mb 937, HLD
81ki young ind., Mosbach, Mb 939, HLD
82ki young ind., Grays (Thurrock), Essex, 21294, MNHL
83ki young ind., Mauer, Mau 163, HLD
84ki young ind., Mauer, Mau 158, HLD
85ki young ind., Mosbach, 1956/603, NMM
86ki young ind., Mosbach, 1954/781, NMM
87ki young ind., Mosbach, 1955/317, NMM
88ki young ind., Melpignano, Lecce, M 3-104, MGPF
89ki young ind., Melpignano, Lecce, M 3-105, MGPF

Stephanorhinus hemitoechus (FALCONER)
1he Grays (Thurrock), Essex, M 5135, MNHL
2he Grays (Thurrock), Essex, 20811, MNHL
3he Illford, Essex, 45253, MNHL
4he Illford, Essex, 45249-45250, MNHL
5he Illford, Essex, 45255, MNHL
6he Illford, Essex, 45249, MNHL
7he Illford, Essex, 45252, MNHL
8he Illford, Essex, 45251, MNHL
9he Meestricht-Belvédère, Limburg, no number, IAU
10he Illford, Essex, 45257, MNHL
11he Illford, Essex, 45259, MNHL
12he Illford, Essex, 45258, MNHL
13he Illford, Essex, 45262, MNHL
14he Illford, Essex, 45261, MNHL
15he Illford, Essex, 45256, MNHL
16he Grays (Thurrock), Essex, 19834, MNHL
17he Illford, Essex, 45264, MNHL
18he Grays (Thurrock), Essex, no number, MNHL
19he Illford, Essex, 45265, MNHL
20he Ponte alla Nave, Arezzo, IGF 1422 v, MGPF
21he Mauer, Mau 139, HLD
22he Illford, Essex, 21284b, MNHL
23he Illford, Essex, 27976, MNHL
24he Illford, Essex, 45270, MNHL
25he Maspino, Arezzo, IGF 1101, MGPF
26he Illford, Essex, 21278c, MNHL
27he Illford, Essex, 22019a, MNHL
28he Rhenen, Utrech, RV 154, IAU
29he Illford, Essex, 45272, MNHL
30he Grays (Thurrock), Essex, 19834c, MNHL
31he Grays (Thurrock), Essex, 20816b, MNHL
32he Grays (Thurrock), Essex, 19834a, MNHL
33he Illford, Essex, 45274, MNHL
34he Illford, Essex, 45273, MNHL
35he Illford, Essex, 20245, MNHL
36he Grays (Thurrock), Essex, 20816, MNHL
37he Illford, Essex, 45275, MNHL
38he Grays (Thurrock), Essex, 21294x, MNHL
39he Illford, Essex, 45276, MNHL
40he Illford, Essex, 45277, MNHL
41he young ind., Illford, Essex, 45254, MNHL

DMC = Dick Mol Collection ('s-Heerenberg, The Netherlands)
HLD = Hessisches Landesmuseum, Darmstadt
IAU = Instituut voor Aardwetenschappen, Utrecht
IPUR = Istituto di Paleontologia Umana, Rome
MGPF = Museo di Geologia e Paleontologia, Florence
MNI = Museo Nazionale, Isernia
MPUR = Museo Paleontologia dell'Università, Rome
NMM = Naturhistorisches Museum, Mainz
RML = Rijskmuseum van Geologie en Mineralogie, Leiden

TABLE 3 - Non-metric characters and character states for lower cheek teeth used in this investigation

1. BUC	buccal cingulum	
	a. continuous	
	b. mesial rising (on protoconid)	
	c. mesial horizontal (on metalophid, between proto- and hypoconid)	
	d. distal horizontal (on hypolophid, non the distal cingulum)	
	e. absent	
2. LIC	lingual cingulum	
	a. continuous	
	b. mesial rising (on paraconid)	
	c. mesial horizontal (below mesial valley entrance)	
	d. distal horizontal (below distal valley entrance)	
	e. absent	
3. BVF	buccal vertical fold	
	a. simple continuous	
	b. double and/or discontinuous	
4. MWB	buccal wall of metalophid	
	a. flattened	
	b. rounded	
5. MEV	shape of mesial valley	
6. DIV	shape of distal valley	
	a. closed	
	b. narrow V	
	c. broad V	
	d. narrow U	
	e. broad U	

Note: For cingula (BUC, LIC), combinations were treated as separate states (b+c, c+d, b+d, b+c+d). All valley shapes (MEV, DIV) were determined regardless of lingual cingula.

selected pairs found to be most different by analysis of variance (tables 11 - 35). Bivariate analysis was carried out for log-transformed variables, using major axis regression (Sokal & Rohlf, 1981; see dicussion in Fortelius, 1985).

(1903), Zeuner (1934), Staesche (1941), Cantaluppi (1969), Ambrosetti (1972), Loose (1975), Cigala-Fulgosi (1976), Anfossi and Cantaluppi (1988), and Mazza (1988). A ratio diagram based on data in Guérin (1980) illustrates the differences in proportion (fig. 1).

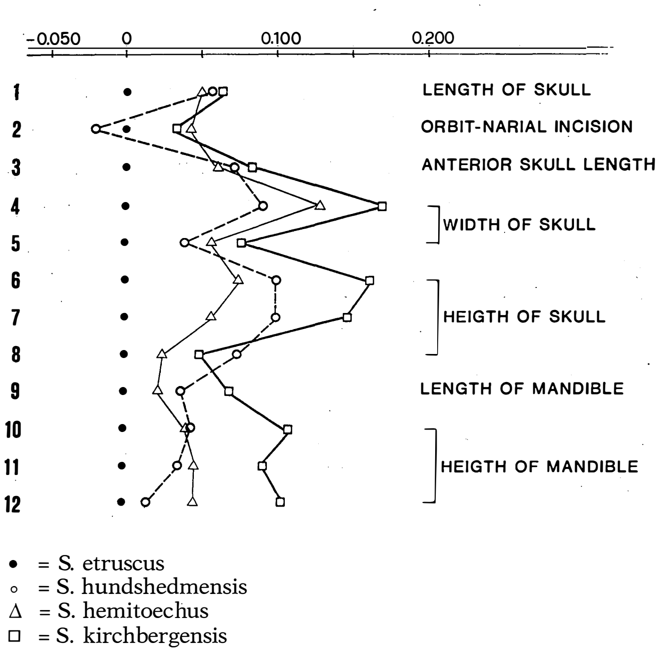


Fig. 1 - Ratio diagram of cranial and mandibular measurements in *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* against *S. etruscus* (standard). 1 = skull length from occipital condyle to tip of nasals, 2 = distance from anterior rim of orbit to posterior rim of narial incision, 3 = distance from anterior rim of orbit to tip of nasals, 4 = greatest skull width over orbits, 5 = greatest skull width over zygomatic arches, 6 = height of skull before P2, 7 = height of skull between P4 and M1, 8 = height of skull before M3, 9 = length of mandible from posterior border of angle to posterior border of symphysis, 10 = height of mandible between P2 and P3, 11 = height of mandible between M1 and M2, 12 = height of mandible behind M3. Based on means from Guérin (1980), his cranial measurements 2, 9, 4, 20, 21, 25, 26, 27 and mandibular measurements 1, 3, 6, 8.

RESULTS

Skull and mandible

The striking differences in the shapes of the skulls of *S. kirchbergensis* and *S. hemitoechus* have been dealt with by Zeuner (1934), Azzaroli (1962) and Loose (1975), among others, and we will not further discuss them here. The discussion in Staesche's (1941) otherwise excellent monograph is unfortunately based on a comparison of two skulls of *S. hemitoechus* from Steinheim an der Murr, and is thus misleading. Good illustrations can be found in Falconer (1868), Toula (1902, 1906), Schroeder (1903), Zeuner (1934), Staesche (1941), Cantaluppi (1969), Ambrosetti (1972), Loose (1975), Cigala-Fulgosi (1976), Anfossi and Cantaluppi (1988), and Mazza (1988).

The length of the skulls of all the species except *S. etruscus*, which has a shorter and generally smaller skull, are quite similar. The skull of *S. kirchbergensis*, which is usually larger than that of the other species, is massive and deep, especially in the facial region, has heavy maxillae and zygomatic arches, and robust nasals. The occipital plane is inclined forwards. The anterior rim of the orbit is situated above M1, and the narial incision is rela-0 tively shallow, reaching back to about P3 or P4.

The skull of *S. hemitoechus* is very low and dolichocephalic, broad across the zygoma and orbits, and its occipital plane is inclined backwards. The dentition is relatively shifted forward, with the anterior rim of the orbit above the contact between M2 and M3. The narial incision is deep, reaching back to M1, and the maxillae and zygomatic arches are relatively slender. The nasals are low and the horn bases weakly developed.

The skull of *S. etruscus* also has weakly developed nasals and horn bases, but a nearly vertical occipital plane. The narial incision generally extends above P4, while the anterior rim of the orbit lies above M3.

In contrast, *S. hundsheimensis* has much more strongly developed nasals and horn bases (Zeuner, 1934), and a longer skull that is deeper and generally has a more developed facial portion. These and other differences have been discussed in detail by Mazza (1988) and are discussed again below in the context of phylogeny. We note here that the upper dentition of *S. hundsheimensis* is more retracted, with M2 beneath the anterior rim of the orbit. Nevertheless, the deep narial incision frequently reaches back to the contact between P4 and M1, resulting in a very short distance between orbit and narial incision (fig. 1).

A similar pattern can be observed in the mandible (fig. 1). *S. kirchbergensis* has a very large, deep, massive mandible, with a strong, broad symphysis and an approximately right angle between the horizontal and the ascending ramus. In contrast, *S. hemitoechus* has a lighter mandible with a relatively slender and narrow symphysis. The horizontal ramus of *S. hemitoechus* tapers (becomes shallower) towards the symphysis, and the angle is more open, with a posteriorly inclined ascending branch. These differences are clearly related to the differences in cranial and dental proportions discussed above. The toothrow is located further back with respect to the symphysis in *S. kirchbergensis* than it is in *S. hemitoechus,* in which the molar battery and consequently the mandible are relatively protracted. This in turn is related to the reduction of the snout and the consequent emphasis of the molars in *S. hemitoechus* (see discussion of phylogeny below). In contrast, *S. kirchbergensis* has large, hypsodont premolars, which require a mandibular horizontal ramus (and maxilla) of considerable depth.

A similar, although less extreme difference can be observed between *S. etruscus* and *S. hundsheimensis*. The latter species is larger and heavier, with a more robust mandible, while the mandible of *S. etruscus* is more slender, with a horizontal ramus that tapers more to the front, and is similar in proportions to the mandible of *S. hemitoechus* (fig. 1). Unlike the mandible of *S. hemitoechus*, this difference is not, or at most is very weakly, reflected by the dental proportions of *S. etruscus* and *S. hunsheimensis*.

Teeth

Comparative description and discrete characters

In general, *S. etruscus* and *S. hundsheimensis* have a dentition of even proportions, brachydont teeth and enamel that is frequently quite rough. The upper premolars occasionally have metacone styli. Coronal cement is sometimes preserved, but never as a thick layer.

S. hemitoechus has not only enlarged posterior and reduced anterior teeth, but also quite hypsodont molars, especially M3. This tooth also has a very long ectoloph by comparison with the other species (Fortelius, 1982). The upper premolars frequently support a metacone style. The lower cheek teeth have very sharp and deep vertical folds buccally between the meta- and hypolophids. The enamel is rough and thick coronal cement is often present. However, worn premolars and molars other than the terminal ones may be difficult to distinguish from those of *S. etruscus* and *S. hundsheimensis*.

S. kirchbergensis is the most distinctive species, partly because of its larger size, but also because its teeth have smooth enamel surfaces, are rounded, and appear "molten", with shallow folds and styli. The premolars are quite hypsodont, while the molars are much less so. The upper premolars are very broad and their ectolophs curve strongly medially about the long axis of the toothrow. They never support a metacone style. The upper teeth are much higher buccally than lingually, and thus extremely ectolophodont (Fortelius 1982, 1985). The lingual sides of the upper teeth are bulbously inflated, and often polished. Coronal cement is usually absent and is never thick when present. Of the lower teeth, P2 is perhaps the most distinctive, with drastically reduced valleys and a simple, almost sectorial shape. Staesche (1941) gives a detailed comparison of the dental characteristics of *S. kirchbergensis* and *S. hemitoechus*.

Of the characters which were systematically scored for states of expression, several turned out to be invariant for the present selection of species, or showed only slight differences of limited interest and practical usefulness (tables 3-4). Several characters proved useful for separating the otherwise similar P3 and P4 or M1 and M2, (e.g., BVF, which has a very low frequency of state 'a' in M1 for all the species). Others, however, showed characteristic differences between the species; they are discussed below.

The most striking and consistent differences between *Stephanorhinus hemitoechus* on the one hand and *S. etruscus* plus *S. hundsheimensis* on the other lie in the distribution of the lingual cingula (LIC) and in the shape of the valleys (MEV, DIV). *S. hemitoechus* has a high percentage of a lingual cingulum below the entrance of the distal valley (LIC-d; fig. 2A). This is perhaps the most useful feature for making identifications, as it is also morphologically distinct, usually forming a very broad V or U with the center directly beneath the valley bottom and tapering symmetrically towards the mesial and distal ends. This feature practically never occurs in *S. kirchbergensis*, while this character state is present in very low percentage in *S. etruscus* and *S. hundsheimensis* (fig. 2A). *S. etruscus* and *S. hundsheimensis* also both have a markedly higher per-

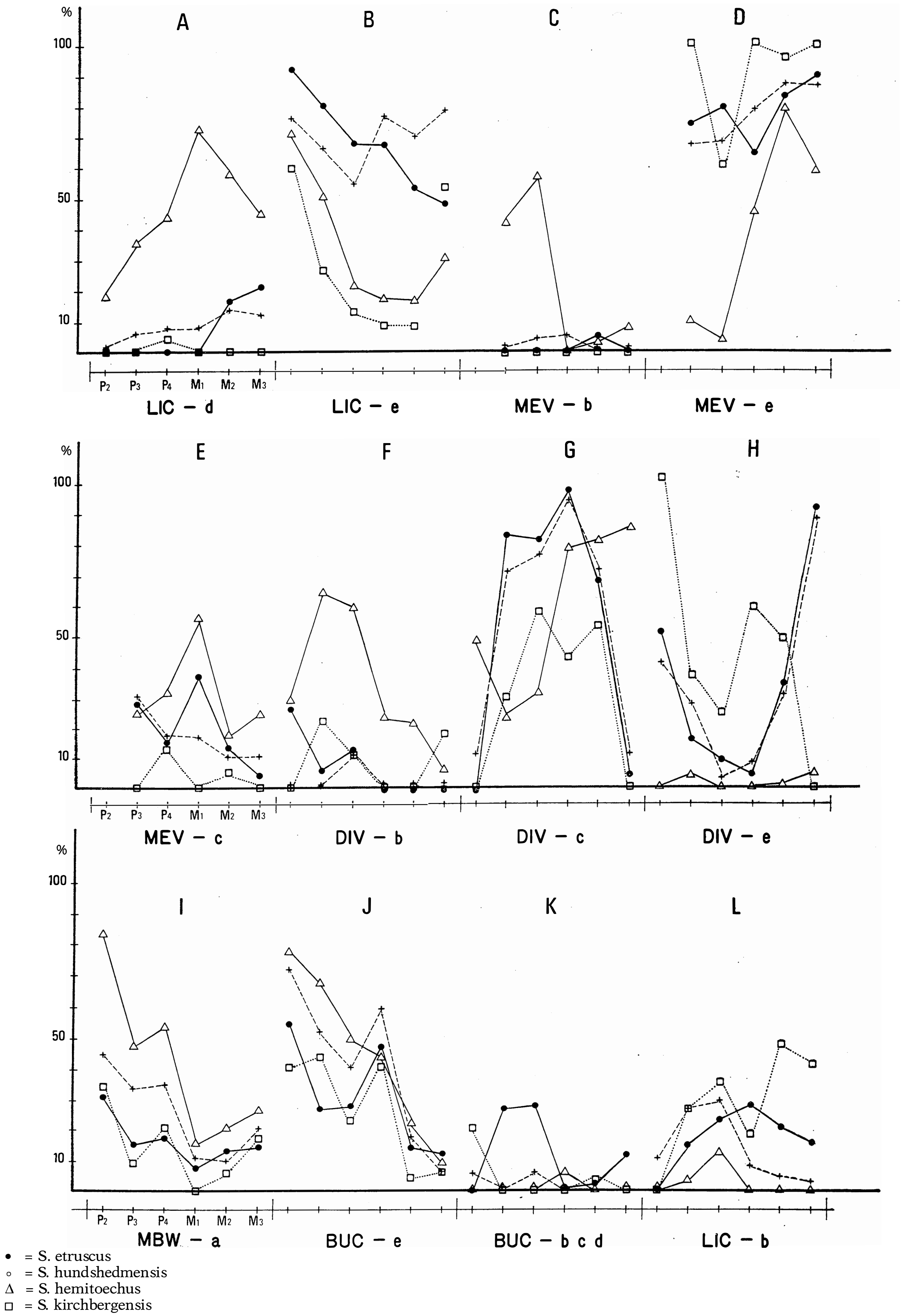


Fig. 2 - Percentage distributions of non-metric character states listed in table 3 for *S. etruscus*, *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis*. Data from table 4.

TABLE 4 - Percentage distribution of non-metric character states in the species studied. Specimen numbers approximately as for metric characters (Table 5)

	Character & state	spec.	P2	P3	P4	M1	M2	M3
BUC	a: continuous	etr	0	0	0	0	0	0
		hun	5	3	13	0	2	2
		hem	0	0	0	0	0	0
		kir	0	0	0	0	0	0
	b: mesial rising	etr	23	21	23	50	48	46
		hun	5	26	20	33	59	73
		hem	9	21	36	44	58	85
		kir	20	36	50	50	70	79
	c: Mesial horiz.	etr	8	0	4	0	0	11
		hun	0	0	3	0	0	0
		hem	0	0	0	0	0	0
		kir	0	0	0	0	0	0
	d: distal horiz.	etr	15	16	0	0	0	0
		hun	14	0	5	4	0	0
		hem	5	3	0	0	3	0
		kir	20	0	0	5	0	0
	e: absent	etr	54	26	27	46	13	11
		hun	71	51	40	59	14	5
		hem	77	66	48	44	21	7
		kir	40	43	23	41	4	5
	b+c	etr	0	0	0	0	32	21
		hun	0	3	2	0	18	17
		hem	0	0	3	0	6	0
		kir	0	21	18	4	22	16
	c+d	etr	0	5	15	0	0	0
		hum	0	7	3	0	0	0
		hem	0	0	0	0	0	0
		kir	0	0	0	0	0	0
	b+d	etr	0	5	4	4	3	0
		hum	0	11	10	4	6	2
		hem	10	3	3	0	6	0
		kir	0	0	9	0	0	0
	b+c+d	etr	0	26	27	0	3	11
		hun	5	0	5	0	0	0
		hem	0	0	0	4	0	0
		kir	20	0	0	0	4	0
	obscured by cement	etr	0	0	0	0	0	0
		hun	0	0	0	0	0	0
		hem	0	7	9	8	6	4
		kir	0	0	0	0	0	0
LIC	a: continuous	etr	0	0	0	0	0	0
		hun	0	0	0	0	0	0
		hem	0	0	0	0	0	0
		kir	0	0	0	0	0	0
	b: mesial rising	etr	0	15	23	28	20	15
		hun	10	26	29	8	4	3
		hem	0	3	12	0	0	0
		kir	0	27	36	18	48	41
	c: at mesial valley	etr	0	0	0	0	0	0
		hun	5	0	0	2	4	0
		hem	5	0	6	0	0	0
		kir	20	7	0	0	4	18
	d: at distal valley	etr	0	0	0	0	17	22
		hun	0	6	8	8	15	13
		hem	19	37	44	73	58	45
		kir	0	0	5	0	0	0
	e: absent	etr	92	80	68	68	53	48
		hun	76	67	55	77	70	79
		hem	71	50	21	18	17	31
		kir	60	27	14	9	9	53
	b+c	etr	0	5	9	4	7	11
		hun	5	3	5	0	2	0
		hem	5	0	3	3	6	0
		kir	20	40	45	73	26	0
	c+d	etr	0	0	0	0	0	0
		hun	0	0	0	0	2	5

		hem	0	0	0	0	8	3
		kir	0	0	0	0	0	0
	b+d	etr	0	0	0	0	0	0
		hun	5	0	3	2	0	0
		hem	0	3	12	0	0	0
		kir	0	0	0	0	4	0
	b+c+d	ert	43	0	0	0	3	4
		hun	0	0	0	2	2	0
		hem	0	0	0	0	8	7
		kir	0	0	0	0	9	0
	obscured by cement	etr	0	0	0	0	0	0
		hun	0	0	0	0	0	0
		hem	0	7	3	6	3	14
		kir	0	0	0	0	0	0
BVF	a: simple cont.	etr	17	95	100	33	100	100
		hun	26	100	100	45	98	100
		hem	81	76	91	32	89	87
		kir	0	79	100	67	96	100
MBW	a: flattened	etr	30	15	16	7	13	14
		hun	44	33	34	10	10	20
		hem	83	47	54	13	19	25
		kir	33	9	20	0	6	17
MEV	a: closed	etr	*	0	7	0	0	0
		hun	*	0	0	0	0	0
		hem	*	5	13	0	0	3
		kir	*	0	13	0	0	0
	b: narrow V	etr	*	0	0	0	4	0
		hun	*	0	4	5	0	0
		hem	*	42	57	0	4	7
		kir	*	0	0	0	0	0
	c: broad V	etr	*	27	14	36	13	3
		hun	*	29	16	16	10	10
		hem	*	26	31	55	16	24
		kir	*	0	13	0	5	0
	d: narrow U	etr	*	0	0	0	0	7
		hum	*	5	12	0	2	3
		hem	*	5	9	0	0	3
		kir	*	0	13	0	0	0
	e: broad U	etr	*	73	79	64	83	90
		hum	*	67	68	79	87	87
		hem	*	10	4	45	80	58
		kir	*	100	60	100	95	100
	obscured by cement	etr	*	0	0	0	0	0
		hun	*	0	0	0	0	0
		hem	*	11	4	0	0	3
		kir	*	0	0	0	0	0
DIV	a: closed	etr	25	0	0	0	0	0
		hun	40	0	8	0	0	0
		hem	0	7	9	0	0	0
		kir	0	7	0	0	0	0
	b: narrow V	etr	25	5	12	0	0	0
		hun	0	0	11	0	0	0
		hem	27	63	59	23	21	6
		kir	0	21	10	0	0	17
	c: broad V	etr	0	81	80	96	67	3
		hun	10	70	75	93	70	10
		hem	47	23	31	77	79	84
		kir	0	29	57	42	52	0
	d: narrow U	etr	0	0	0	0	0	7
		hun	10	3	3	0	0	3
		hem	20	0	0	0	0	0
		kir	0	7	9	0	0	83
	e: broad U	etr	50	15	8	4	33	90
		hun	40	27	3	7	30	87
		hem	0	3	0	0	0	3
		kir	100	36	24	58	48	0
	obscured by cement	etr	0	0	0	0	0	0
		hun	0	0	0	0	0	0
		hem	7	3	0	0	0	6
		kir	0	0	0	0	0	0

TABLE 5 - Descriptive statistics of dental measurements from dentitions. Isolated teeth excluded

1A. Stephanorhinus etruscus upper teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	15	31.29	2.550	27	36
	BLL	15	23.51	3.056	18	29
	MBB	16	36.16	2.486	32	40
	DBB	16	38.69	2.349	33	41
P3	BBL	16	36.12	2.365	31	40
	BLL	14	29.60	3.335	23	34
	MBB	14	49.69	3.043	45	55
	DBB	14	46.67	2.428	43	52
P4	BBL	16	39.34	2.997	34	44
	BLL	17	32.57	3.277	27	39
	MBB	16	55.46	4.260	48	64
	DBB	16	50.46	3.197	45	57
M1	BBL	14	44.94	3.535	41	53
	BLL	17	36.31	2.475	30	40
	MBB	16	55.81	3.830	48	62
	DBB	15	51.67	4.730	45	61
M2	BBL	16	48.59	2.678	46	54
	BLL	15	40.27	2.851	34	45
	MBB	15	58.08	2.825	54	63
	DBB	14	51.17	2.935	48	56
M3	BBL	14	55.09	3.928	50	60
	BLL	13	45.86	2.758	41	50
	MBB	13	52.95	2.568	48	56

1B. Stephanorhinus etruscus lower teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	12	29.43	1.502	27	32
	BLL	11	27.28	1.592	25	30
	MBB	15	17.22	1.202	15	20
	DBB	15	19.82	1.314	17	21
P3	BBL	24	34.61	1.949	31	38
	BLL	23	33.08	1.652	30	36
	MBB	24	22.84	1.324	20	25
	DBB	24	25.27	1.698	23	30
P4	BBL	28	37.88	2.368	34	43
	BLL	26	36.17	1.894	33	42
	MBB	28	26.38	1.324	24	30
	DBB	29	28.35	1.728	25	31
M1	BBL	30	42.02	2.337	38	49
	BLL	28	39.37	2.576	35	45
	MBB	33	28.29	1.497	25	31
	DBB	32	29.59	1.576	26	33
M2	BBL	36	44.24	1.919	40	49
	BLL	36	43.32	2.430	39	50
	MBB	36	30.21	1.647	27	34
	DBB	39	29.02	1.323	25	32
M3	BBL	33	43.90	1.898	39	48
	BLL	33	45.27	2.489	40	51
	MBB	35	29.03	1.589	26	33
	DBB	33	27.97	1.359	25	31

2A. Stephanorhinus hundsheimensis upper teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	30	32.10	1.995	27	35
	BLL	30	23.84	2.050	20	28
	MBB	29	36.66	2.464	32	42
	DBB	30	40.41	3.018	32	44
P3	BBL	33	36.31	2.483	32	41
	BLL	32	30.87	1.885	26	35
	MBB	33	50.92	2.337	45	54
	DBB	32	48.29	3.029	42	53
P4	BBL	34	40.03	2.345	35	46
	BLL	36	33.30	2.009	29	37
	MBB	35	55.69	2.571	51	62
	DBB	34	52.25	3.055	46	57
M1	BBL	31	46.16	2.723	42	56
	BLL	32	36.02	1.943	32	41
	MBB	30	57.80	2.539	52	65
	DBB	31	53.38	2.180	49	60
M2	BBL	30	49.98	2.206	46	55
	BLL	32	41.87	2.226	38	48
	MBB	32	59.72	3.176	54	68
	DBB	32	53.84	2.766	49	62
M3	BBL	25	55.11	3.080	48	61
	BLL	26	47.55	2.487	43	53
	MBB	25	54.10	3.194	48	61

2B. Stephanorhinus hundsheimensis lower teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	27	29.99	1.626	27	35
	BLL	24	28.28	1.704	25	32
	MBB	27	17.98	1.316	15	21
	DBB	29	21.28	1.627	19	26
P3	BBL	41	35.89	2.280	30	41
	BLL	40	34.23	1.942	30	39
	MBB	47	24.19	1.452	21	27
	DBB	49	26.49	1.792	23	31
P4	BBL	47	38.46	2.722	33	44
	BLL	50	36.35	2.548	32	42
	MBB	56	26.75	1.994	23	32
	DBB	56	28.92	2.228	23	34
M1	BBL	61	43.17	2.512	37	49
	BLL	56	41.53	2.238	37	46
	MBB	67	29.52	2.261	25	35
	DBB	69	30.64	1.945	27	36
M2	BBL	62	44.75	2.265	39	51
	BLL	60	45.26	2.596	40	52
	MBB	64	30.59	2.169	26	36
	DBB	64	30.39	1.691	26	34
M3	BBL	47	44.67	2.465	40	51
	BLL	45	47.30	2.741	43	53
	MBB	51	29.64	1.924	26	34
	DBB	46	28.53	1.773	25	33

3A. Stephanorhinus hemitoechus upper teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	13	31.11	1.499	28	34
	BLL	12	22.28	2.018	19	25
	MBB	13	33.33	1.373	31	36
	DBB	14	36.51	1.804	34	40
P3	BBL	15	37.74	1.862	34	41
	BLL	15	31.01	1.901	27	34
	MBB	14	49.19	2.300	44	53
	DBB	14	48.66	1.680	46	52
P4	BBL	16	41.12	2.054	38	46
	BLL	18	35.23	2.154	32	40
	MBB	17	56.54	2.958	50	62
	DBB	19	52.49	2.818	48	59
M1	BBL	15	47.80	2.967	42	53
	BLL	19	38.96	1.521	36	41
	MBB	18	61.48	3.005	55	68
	DBB	17	58.18	3.353	51	64
M2	BBL	18	54.91	1.963	52	59
	BLL	18	44.68	2.428	42	49
	MBB	18	64.06	2.673	60	68
	DBB	17	57.64	3.266	53	64
M3	BBL	15	66.34	4.590	59	77
	BLL	14	51.24	3.330	45	57
	MBB	16	59.48	3.336	52	64

3B. Stephanorhinus hemitoechus lower teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	30	26.54	1.790	23	31
	BLL	26	25.30	2.022	21	30
	MBB	28	15.71	1.429	13	20
	DBB	29	18.16	1.561	15	21
P3	BBL	40	32.19	1.710	28	36
	BLL	36	30.94	1.774	28	34
	MBB	40	21.65	1.450	19	24
	DBB	40	24.17	1.340	21	28
P4	BBL	40	37.04	2.145	34	43
	BLL	37	35.78	2.032	32	39
	MBB	43	25.49	1.534	21	28
	DBB	41	28.49	1.765	24	32
M1	BBL	38	42.33	2.253	38	47
	BLL	34	40.86	3.485	34	48
	MBB	38	28.79	1.912	26	33
	DBB	39	30.75	1.755	27	34
M2	BBL	41	46.12	2.909	40	52
	BLL	38	46.49	3.764	36	52
	MBB	43	30.46	1.511	27	34
	DBB	41	31.18	1.666	28	34
M3	BBL	30	49.16	3.223	42	54
	BLL	35	53.27	3.352	47	65
	MBB	36	30.91	1.865	26	35
	DBB	33	29.76	2.042	27	34

4. Stephanorhinus kirchbergensis upper teeth

Tooh	Dimension	N	Mean	stdev	Min	Max
P2	BBL	7	34.63	1.997	31	37
	BLL	5	22.90	2.480	20	26
	MBB	7	40.16	1.588	38	43
	DBB	7	43.81	2.056	41	47
P3	BBL	9	41.94	1.970	39	45
	BLL	11	33.57	2.326	30	37
	MBB	12	61.43	2.032	57	64
	DBB	12	54.59	2.198	51	58
P4	BBL	12	47.13	3.780	40	52
	BLL	12	38.57	2.392	34	43
	MBB	12	68.78	4.050	59	73
	DBB	12	61.38	4.210	53	70
M1	BBL	6	54.68	3.860	51	61
	BLL	12	42.70	1.792	39	46
	MBB	10	68.69	1.944	65	72
	DBB	12	64.48	2.968	59	69
M2	BBL	12	60.76	3.590	55	66
	BLL	12	50.72	3.520	45	57
	MBB	12	71.48	3.094	64	75
	DBB	12	63.52	2.774	58	68
M3	BBL	11	65.14	4.790	57	72
	BLL	11	55.91	4.980	48	65
	MBB	11	65.41	4.860	58	73

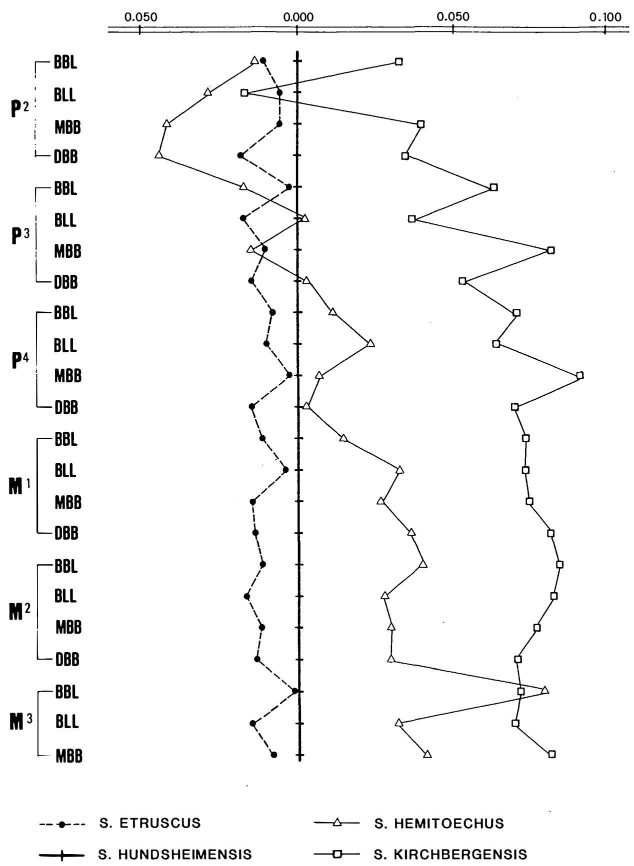


Fig. 3 - Ratio diagram of the upper dentitions of S. etruscus, *S. hemitoechus* and *S. kirchbergensis* versus *S. hundsheimensis* (standard). Data and abbreviations from table 5.

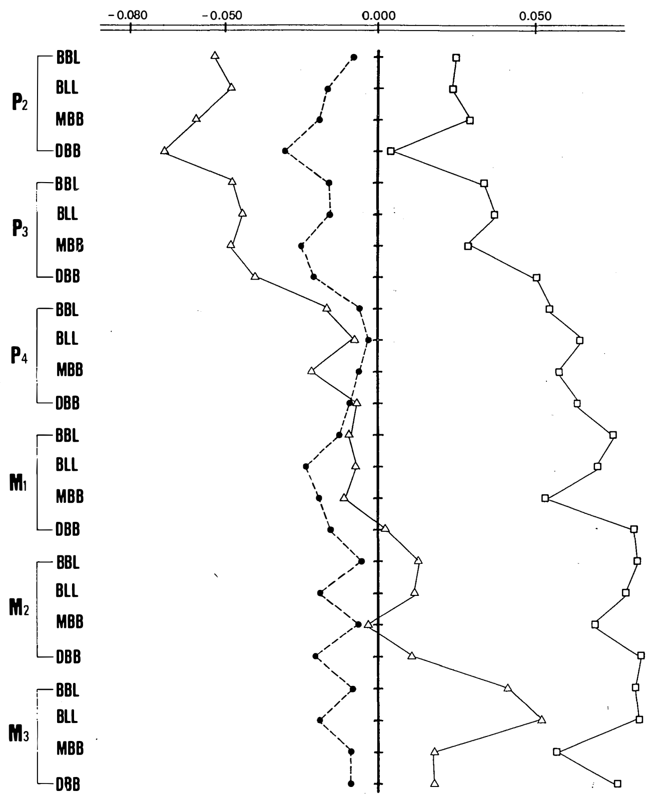


Fig. 4 - Ratio diagram of the lower dentitions of *S. etruscus*, *S. hemitoechus* and *S. kirchbergensis* versus *S. hundsheimensis* (standard). Data and abbreviations from table 5.

centages of teeth (especially P4-M2) lacking lingual cingula altogether (LIC-e; fig. 2B) than do *S. hemitoechus* or *S. kirchbergensis*.

The valleys are generally more V-shaped in *S. hemitoechus* than in the other species, in which a U-shape predominates (fig. 2C-G). A narrow V-shape is almost exclusively found in the premolars of *S. hemitoechus* (fig. 2C&F), while a broad V-shape characterizes a higher percentage of the molars of *S. hemitoechus* than of the other species (fig. 2E&H). For the molars, the mesial valleys (MEV) show the same tendency towards a narrower shape in *S. hemitoechus*, though the differences are quite moderate. The distal valleys (DIV) also follow the same pattern, but here the differences in the terminal teeth (P2, M2, M3) are striking, while they are minor for the central ones (P4, M1) (fig. 2H&G). Altogether, *S. kirchbergensis* has more open valleys than do the other species.

A classic distinguishing character of *S. hemitoechus* is the flattened buccal wall of the metalophid, especially in the premolars (Staesche, 1941). This was also noted in the present study (fig. 2I). The difference between *S. etruscus* and *S. hundsehimensis* on the one hand and *S. hemitoechus* on the other, is one of degree, and is marked only in P2, which is quite reduced, especially mesially, in *S. hemitoechus*.

The differences between *S. etruscus* and *S. hundsheimensis* are minor for most of the non-metric characters. Nevertheless, the differences are often consistent along the toothrows, or at least within tooth classes. There is perhaps a tendency for *S. hundsheimensis* to be intermediate between the other two taxa (e.g., fig. 2I&J), but there are exceptions to this. One of the few distinct differences is the relatively high percentage of separate buccal cingula along the teeth (BUC-b+c+d) observed in P3 and P4 of *S. hundsheimensis*, but not in the other species (fig. 2K). The presence of a mesially rising lingual cingulum on the paraconid (LIC-b) is also relatively more common in the molars of *S. etruscus*, while the situation is reversed for the premolars (fig. 2B&L).

None of the distributions of the non-metric characters studied allow absolute identifications, as all are more or less variable among species. There are, however, distinct patterns within the variation which allow comparisons between the species, and, presumably, between sufficiently large samples from different localities. There are major differences between *S. hemitoechus*, *S. kirchbergensis* and the *S. etruscus* - *S. hundsheimensis* group. The differences between *S. etruscus* and *S. hundsheimensis* are much less pronounced, and the separation of isolated teeth or even dentitions of the latter two species is probably impossible on dental data alone.

Quantitative analysis

Summary statistics of dental dimensions are given in table 5 and illustrated in figs. 3-4. The most obvious result is that *Stephanorhinus kirchbergensis* is larger than the other species. The difference is statistically highly significant for all but a few measurements (table 6A). *S. kirchbergensis* also has lingually short and mesially broad upper premolars (fig. 3). *Stephanorhinus hemitoechus* has very different dental proportions with respect to the other species,

TABLE 6 - Probability values from oneway analysis of variance (inter-group variance greater than intra-group variance) for dental measurements. See table 5 for sample sizes and descriptive statistics

A. Stephanorhinus etruscus, S. hundsheimensis, S. hemmitoechus and S. kirchbergensis

Tooth	BBL	BLL	MBB	DBB
P2	0.003	0.271	0.000	0.000
P3	0.000	0.000	0.000	0.000
P4	0.000	0.000	0.000	0.000
M1	0.000	0.000	0.000	0.000
M2	0.000	0.000	0.000	0.000
M3	0.000	0.000	0.000	—
P2	0.000	0.000	0.000	0.000
P3	0.000	0.000	0.000	0.000
P4	0.000	0.000	0.000	0.000
M1	0.000	0.000	0.000	0.000
M2	0.000	0.000	0.000	0.000
M3	0.000	0.000	0.000	0.000

B. Stephanorhinus etrüscus, S. hundsheimensis and S. hemitoechus

Tooth	BBL	BLL	MBB	DBB
P2	0.264	0.159	0.000	0.000
P3	0.099	0.176	0.072	0.099
P4	0.124	0.004	0.565	0.097
M1	0.036	0.000	0.000	0.000
M2	0.000	0.000	0.000	0.000
M3	0.000	0.000	0.000	—
P2	0.000	0.000	0.000	0.000
P3	0.000	0.000	0.000	0.000
P4	0.030	0.508	0.002	0.370
M1	0.065	0.004	0.012	0.013
M2	0.002	0.000	0.613	0.000
M3	0.000	0.000	0.000	0.000

C. Stephanorhinus etruscus and S. hundsheimensis

Tooth	BBL	BLL	MBB	DBB
P2	0.253	0.663	0.515	0.055
P3	0.800	0.108	0.141	0.084
P4	0.376	0.320	0.807	0.062
M1	0.213	0.650	0.041	0.099
M2	0.064	0.045	0.095	0.071
M3	0.985	0.062	0.270	—
P2	0.317	0.111	0.070	0.005
P3	0.025	0.020	0.000	0.007
P4	0.356	0.751	0.387	0.230
M1	0.039	0.000	0.006	0.009
M2	0.261	0.000	0.357	0.000
M3	0.136	0.001	0.127	0.134

having enlarged posterior and reduced anterior teeth. The third molar is clearly lengthened in both the upper and lower dentitions, and P2 is reduced, though the change involves all the teeth harmoniously (figs. 3-4). For the majority of the teeth the differences are statistically highly significant (table 6B).

The differences between *Stephanorhinus etruscus* and *S. hundsheimensis* are less clear cut, the main one being the somewhat larger size of *S. hundsheimensis*. Statistically significant differences can only be observed in the lower dentition, however (table 6C). In particular, P/3 and M/1 are broader in *S. hundsheimensis* and all the molars are longer lingually.

The samples are too small and their temporal distribution is too uncertainly known or too clumped to allow an analysis of possible evolutionary trends. Also an analysis of variance failed to reveal statistically significant differences between either ages or sites in any of the species. Nevertheless, there seems to be a trend of increasing size in both *S. hemitoechus* and *S. kirchbergensis*.

Adding the isolated M3 to the data produces sufficiently large samples to make these differences statistically significant. An ANOVA of a sample of 45 M3:s of *S. kirchbergensis*, grouped into early Middle Pleistocene (N=10), late Middle Pleistocene (N=3) and Late Pleistocene (N=32) teeth, gave the following P-values: BBL 0.000, BLL 0.015, MBB 0.004. The M3 of *S. hemitoechus* (N=74 [1, 14, 59] follow a similar trend, with P-values: BBL 0.000, BLL 0.009, MBB 0.000). An equivalent analysis of *S. etruscus* and *S. hundsheimensis* lumped together shows a significant difference only between the Early and the Middle Pleistocene subsamples, i.e., the two species as conceived here on the basis of cranial morphology (only for BLL: N=93 (13,80), P=0.021). A bivariate plot illustrates the differences and emphasises the increased buccal length (BBL) of *S. hemitoechus* (fig. 5). All the relationships are more or less isometric, and none is significantly allometric (table 7).

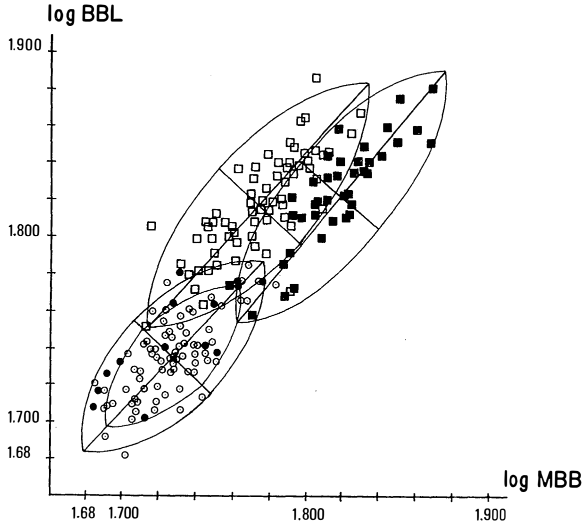


Fig 5 - Bivariate plot of buccal length (BBL) and mesial width (MBB) of M3 in *S. etruscus*, *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis*. Log-transformed variables, major and minor axes and 95% equiprobability ellipses indicated. Regression parameters given in table 7.

Postcranial data: comparative description

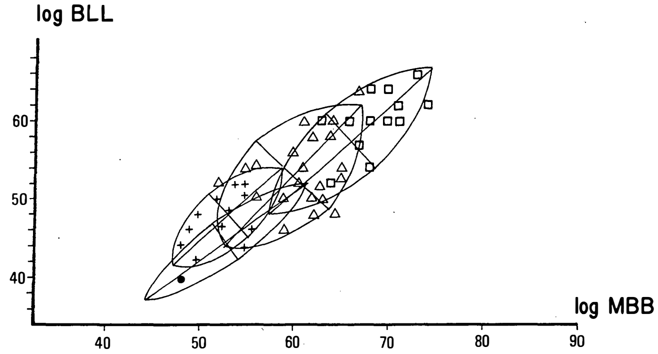
Most of the postcranial bones were fairly well represented in the samples available to us, although a few were either very scarce or highly variable. In the following section the postcranial bones of the four species are compared individually.

Very few atlases and axes were available to us, which makes comparison difficult. Measurements are given in tables 8 and 9, respectively.

Scapula - (table 10). Only the distal ends of few scapulae were available to us. In both *S. etruscus* and *S. hundsheimensis* the supraglenoidal tubercle is

TABLE 7 - Modell II (major axis) log-transformed regression statistics for M3 (see Figs. 5 and 6)

Species Variables	N	b	95%CL(b)	a	r2
S. etruscus + S. hundsheimensis					
BBL : MBB	90	1.047	0.48-1.30	– 0.072	0.491
BLL : MBB	93	1.206	0.99-1.48	– 0.412	0.531
S. etruscus					
BBL : MBB	13	1.105	0.45-3.01	– 0.161	0.445
BLL : MBB	13	1.056	0.81-1.39	– 0.162	0.863
S. hundsheimensis					
BBL : MBB	76	1.063	0.85-1.33	– 0.101	0.526
BLL : MBB	79	1.199	0.95-1.54	– 0.398	0.477
S. hemitoechus					
BBL : MBB	75	1.108	0.93-1.33	– 0.149	0.636
BLL : MBB	73	1.437	1.07-1.99	– 0.834	0.387
S. kirchbergensis					
BBL : MBB	44	1.196	0.97-1.49	– 0.354	0.674
BLL : MBB	43	1.287	0.99-1.70	– 0.585	0.596



• = S. etruscus
∘ = S. hundshedmensis
Δ = S. hemitoechus
□ = S. kirchbergensis

Fig 6 - Bivariate plot of buccal length (BLL) and mesial width (MBB) of M3 in *S. etruscus, S. hundsheimensis, S. hemitoechus* and *S. kirchbergensis*. Log-transformed variables, major and minor axes and 95% equiprobability ellipses indicated. Regression parameters given in table 7.

rather stretched cranially and the glenoid cavity appears more or less kidney-shaped. In the scapula of *S. kirchbergensis*, the glenoid cavity is more elliptical and the supraglenoid tubercle is powerful and sub-circular in ventral view. The coracoid process is extremely reduced in all the species and there is no trace of a glenoid incisure.

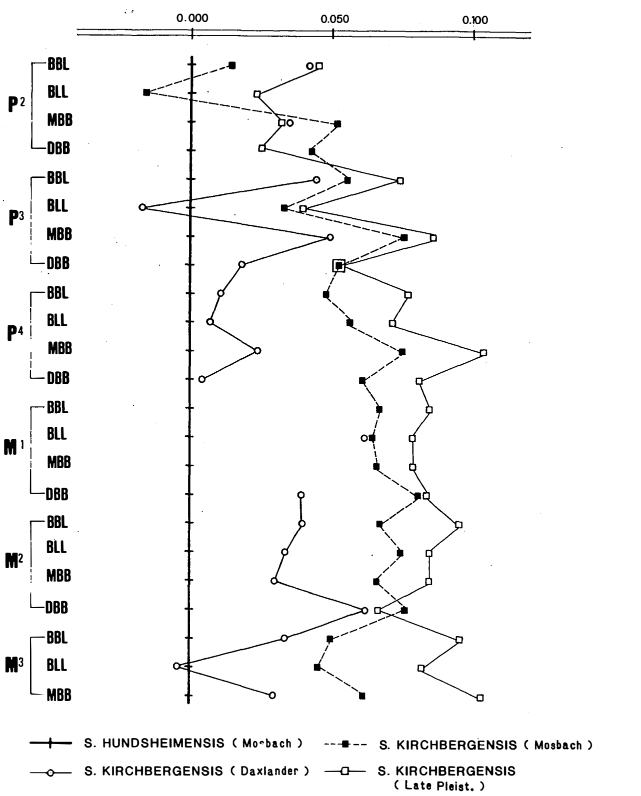


Fig 7 - Ratio diagram of the upper dentitions of *S. kirchbergensis* from Daxlanden, Mosbach and a sample from the late Pleistocene, versus means for *S. hundsheimensis* from Mosbach (standard).

Humerus - (table 11; fig. 11). The humeri of *S. etruscus* and *S. hundsheimensis* look rather alike, as is also evident in the ratio diagram (fig. 11). In the latter species the olecranic fossa is far wider than it is in *S. etruscus*. By comparison, the humerus of *S. kirchbergensis* shows, in proximal view, a proximal

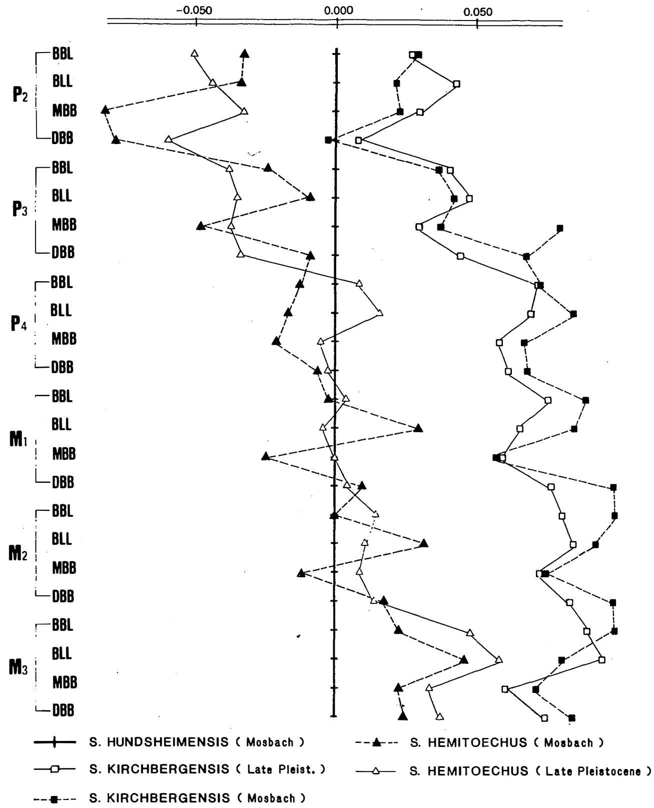


Fig. 8 - Ratio diagram of the lower dentitions of Middle and Late Pleistocene *S. hemitoechus* and *S. kirchbergensis* versus means for *S. hundsheimensis* from Mosbach (standard).

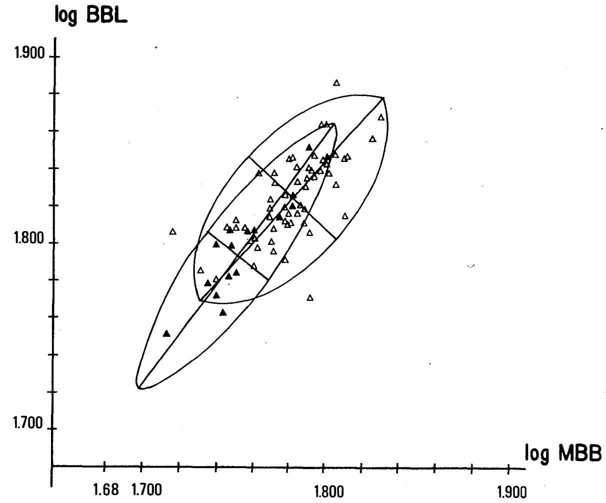


Fig. 9 - Bivariate plot of buccal length (BBL) and mesial width (MBB) of M3 in pre-late Middle Pleistocene and post-late Middle Pleistocene samples of *S. hemitoechus*. Log-transformed variables, major and minor axes and 95% equiprobability ellipses indicated. Difference highly significant (1-way ANOVA, P<0.005). Early localities: Arago, Bucine, Clacton, Heppenloch, Lexden, Swanscombe, Visogliano. Late localities: Barrington, Brühl, Ehringsdorf, Grays, Ilford, Minchin Hole, Selsey, Taubach, Tornewton Cave.

TABLE 8 - Atlas

Characters	L	La	Bw	Bcra	H	Bcaa
Specimens						
1et	114	(110)	(211)	143	118	152
2et	111	(108)	(178)	127	95	—
3et	114	(114)	(210)	143	94	135
4et	—	(107)	177	121	103	130
5et	(113)	—	(170)	(122)	—	—
6et	107	—	(175)	(131)	(89)	—

TABLE 9 - Axis

Characters	L	Bcra	Bcaa	Bc
7et	117	134	(69)	100
8et	112	129	47	(78)

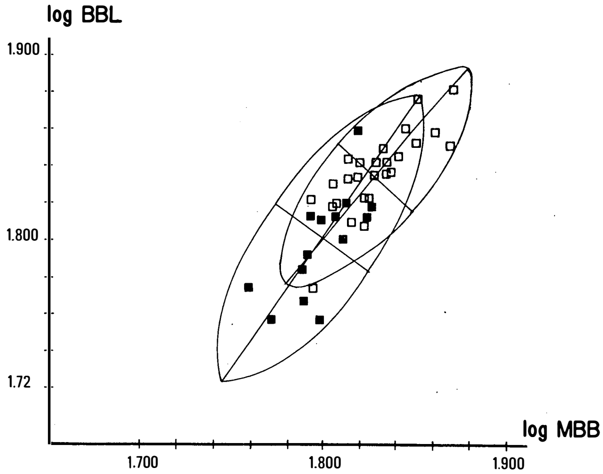


Fig. 10 - Bivariate plot of buccal length (BBL) and mesial width (MBB) of M3 in pre-late Middle Pleistocene and post-late Middle Pleistocene samples of *S. kirchbergensis*. Log-transformed variables, major and minor axes and 95% equiprobability ellipses indicated. Difference highly significant (1-way ANOVA, P<0.005). Early localities: Arago, Daxlanden, Mosbach. Late localities: Ehringsdorf, Grays, Taubach.

TABLE 10A - Scapula

Characters	AL	PL	PB	DB	CS	LG	BG
Specimens							
9et	—	—	—	—	—	72	58
10et	—	—	—	98	91	76	59
1hu	—	—	—	127	115	83	72.8
2hu	—	—	—	114	—	85	65
1ki	—	—	—	>143	—	—	—

epiphysis much more stretched laterally and a considerably broader bicipital fossa. Also, the distal epiphysis is more massive in *S. kirchbergensis* than in either *S. etruscus* or *S. hundsheimensis*; in particular the epicondyle is far more bulging. We could examine only two fragmentary humeri of *S. kirchbergensis* and none of *S. hemitoechus;* the analysis of variance was thus performed only on *S. etruscus* and *S. hundsheimensis*. The two species turned out to differ significantly in the dimensions of the distal trochlea (HTant, HT post, DT, Lml).

TABLE 10B - Scapula S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
AL	—	—	—	CS	1	(91.0000)	—
PL	—	—	—	LG	2	74.00000	2.82843
PD	—	—	—	BG	2	58.50000	0.70711
DB	1	(98.0000)	—				

Scapula S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
AL	—	—	—	CS	1	(115.0000)	—
PL	—	—	—	LG	2	84.00000	1.41421
PB	—	—	—	BG	2	68.90000	5.51543
DB	2	120.50000	9.19239				

Scapula S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
AL	—	—	—	CS	—	—	—
PL	—	—	—	LG	1	(99.0000)	—
PB	—	—	—	BG	1	(80.0000)	—
DB	1	(143.0000)	—				

TABLE 11A - Humerus

Charac-ters	L	LL	PL	BP	DP1	DP2	DP min	DAP CH	DT CH	Bd	BS	DS	BD	BT	Ht ant	Ht post	Dt	Lm1	Bo
Specimens																			
11et	—	392	360	138	158	128	145	75.3	(88.9)	115	56	53.8	128	87	43.2	42	45.8	81	38.9
12et	—	—	—	—	—	—	—	—	—	—	—	52.3	130	86	43.1	39.2	42.8	85	39.9
13et	—	(381)	(358)	—	—	—	—	—	—	119	55	51	116	77	41	39	43	80	41
14et	384	374	336	133	160	117	138	76	86	123	59	56.8	122	78	40	38	43	75	47.2
15et	—	379	353	136	158	117	(139)	77	82.5	111	58	52.2	126	86	44	44	46	81	(48)
16et	—	407	(398)	—	(169)	(141)	(159)	76	79.3	(116)	55	54	(153)	(86)	44.3	45.2	47	—	—
17et	—	—	—	—	—	—	—	—	—	—	53	51.3	125	79	38.8	37	40.8	77	41
18et	—	—	—	—	—	—	—	—	—	—	—	57.9	128	89	42	42	44	—	42
19et	387	384	355	143	—	110	112	—	91	—	59	54.8	134	89	41.5	38.3	43	84.6	46
20et	—	—	—	—	—	107	—	74.8	78	107	59	(50)	—	—	41	40	43	—	—
21et	—	—	—	—	—	—	—	—	—	—	60	53.2	114	81	46.2	42	47.1	77.9	32
22et	—	—	—	—	—	—	—	—	—	—	58	46	130	85	42.8	35	(33.3)	75	(51)
23et	—	—	—	—	—	—	—	—	—	123	—	—	—	—	—	—	—	—	—
24et	—	—	—	—	—	—	—	—	—	—	—	55	109	78	43.3	39.2	42.9	79.8	(33.3)
25et	—	—	—	—	—	—	—	—	—	—	50	44	—	—	—	—	—	—	—
26et	—	—	—	—	—	—	—	—	—	—	—	—	(99)	81	—	39.9	42	79.2	43.1
27et	—	—	—	—	—	—	—	—	—	—	58	51.3	—	—	—	—	—	—	—
28et	—	—	—	—	—	—	—	—	—	—	60	(53)	122	88	40.6	44	40.2	79	—
29et	—	—	—	—	—	—	—	—	—	—	52	46	—	—	—	—	—	—	—
30et	—	—	—	—	—	—	—	—	—	—	—	50	123	—	—	—	—	—	—
31et	—	—	—	—	—	—	—	—	—	—	56	(50)	—	—	—	—	—	—	—
32et	—	—	—	—	—	—	—	—	—	131	60	—	—	—	—	—	—	—	—
33et	—	—	—	—	—	—	—	—	—	—	—	—	125	—	—	—	—	—	—
3hu	—	—	—	—	—	—	—	—	—	—	67	56.2	—	95	51.5	—	—	83	—
4hu	—	—	—	—	—	—	—	—	—	—	66	56.5	147	97	46	—	—	83.5	—
5hu	—	—	—	—	—	—	—	—	—	—	62.2	54.5	—	—	48	—	—	88	—
6hu	—	—	—	—	181	—	143	83.5	93	—	—	—	—	—	—	—	—	—	—
7hu	—	—	—	—	172	—	140	90	90	—	—	—	—	—	—	—	—	—	—
8hu	—	—	—	—	188	163	137	95	93	—	—	—	—	—	—	—	—	—	—
9hu	—	—	—	—	—	—	—	—	—	—	—	—	138	—	—	—	—	—	—
10hu	—	—	—	—	—	—	—	—	—	—	58.5	52	—	>85	45	50	53	90	55
11hu	—	—	—	—	—	—	—	—	—	—	—	—	151	107	47	51	55.5	93.5	55.5
12hu	—	—	—	—	—	—	—	—	96	—	—	—	—	—	—	—	—	—	—
2ki	—	—	—	—	>225	—	172	120	112	—	—	—	—	—	—	—	—	—	—
3ki	—	—	—	—	—	—	—	—	—	—	—	—	157	121	—	—	—	—	—
187et	357	360	323	151	—	113	127	78	81	100	45	44.8	121	79	41	37	42	73	(46)

TABLE 11B

Humerus S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	385.50000	2.12132	BS	16	56.75000	3.06594
LL	6	386.16670	11.82230	DS	19	51.71579	3.59742
PL	6	358.50000	17.21337	BD	16	124.00000	11.75868
BP	4	137.50000	4.20317	BT	14	83.57143	4.38028
DP1	4	161.25000	5.25198	Ht ant	14	42.27143	1.94795
DP2	6	120.00000	12.58571	Ht post	15	40.32000	2.83705
DPmin	5	138.78000	17.33903	Dt	15	42.92667	3.36356
DAP CH	5	75.82000	0.83187	Lm1	12	79.54166	3.17274
DT CH	6	84.28333	5.23199	Bo	12	41.95000	5.66432
Bd	8	118.12500	7.58641				

Humerus S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev
L	—	—	—	BS	4	63.42500	3.88018
LL	—	—	—	DS	4	54.80000	2.06398
PL	—	—	—	BD	3	145.33330	6.65833
BP	—	—	—	BT	4	96.00000	9.01850
DP1	3	180.33330	8.02081	Ht ant	5	47.50000	2.50000
DP2	1	(163.0000)	—	Ht post	2	50.50000	0.70711
DPmin	3	140.00000	3.00000	Dt	2	54.25000	1.76777
DAP CH	3	89.50000	5.76628	Lm1	5	87.60000	4.43565
DT CH	4	93.00000	2.44949	Bo	2	55.25000	0.35355
Bd	—	—	—				

TABLE 11C - Humerus S. etruscus - S. hundsheimensis

	(F) Statistic	(P) (One-Tailed)
DP1	14.76463	<.05
DPmin	0.00137	>.20
DAP CH	30.39430	<.01
DT CH	9.41975	<.05
BS	13.78546	<.01
DS	2.68623	<.20
BD	9.03783	<.01
BT	15.58309	<.01
Ht ant	23.03582	<.001
Ht post	24.23674	<.001
Dt	21.01363	<.001
Lm1	18.14835	<.001
Bo	10.30684	<.01

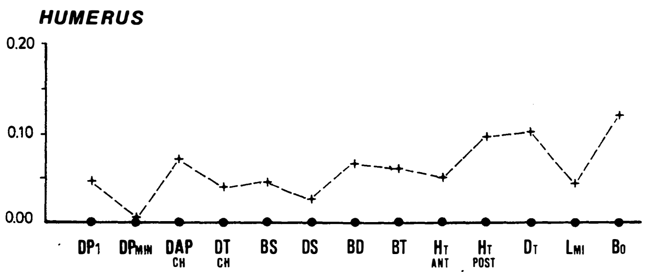


Fig. 11 - Ratio diagram of the humeri of *S. hundsheimensis*, versus means for *S. etruscus* from the Upper Valdarno (standard).

Radius - (table 12; fig. 12). By comparison with *S. etruscus*, the radial portion of the sigmoidal incisure in the radius of *S. hundsheimensis* is proportionally shorter, whereas the diaphysis is dorso-palmarly stronger. Compared with *S. etruscus* and *S. hundsheimensis*, the radius of *S. hemitoechus* appears stockier, with the radial portion of the sigmoidal incisure significantly thicker dorso-palmarly, the diaphysis shorter and more massive and the proximal articular surfaces less concave. The radius of *S. kirchbergensis* is larger than those of the other forms. Its diaphysis is narrower latero-medially and thicker dorso-palmarly. It has broader and stronger epiphyses and has a more concave proximal articular surface. In *S. kirchbergensis* there is less disproportion between the two sections of the proximal articular surface than there is in either *S. etruscus* or *S. hundsheimensis:* the medial portion of the articulation, in *S. kirchbergensis*, is wider, relative to the lateral portions, than it is in the other two species. In distal view, the palmar border of the medial portion of the distal articular surface is thicker in *S. hemitoechus* than in *S. kirchbergensis*. The analyses of variance revealed critical differences in both epiphyses among the four species; the ratio diagram shows that *S. kirchbergensis* and *S. hemitoechus* contribute most to the variance. It is worth noting that, according to the ratio diagram, the radii of *S. kirchbergensis* and *S. hundsheimensis* are proportionally similar, while that of *S. hemitoechus* differs to some extent in the dorso-palmar depth of the proximal epiphysis and in the breadth of the diaphysis.

Ulna - (table 12; fig. 12). The ulnae of *S. etruscus* and *S. hundsheimensis* look rather alike; in the latter species the olecranon is somewhat wider dorso-palmarly and the sigmoidal incisure has a relatively smaller bending radius. The diaphysis is triangular in cross section and its walls are rather flat. In lateral and medial view, the palmar profile of the diaphysis of the ulna of *S. etruscus* and *S. hundsheimensis* is less concave than is that of the ulna of *S. kirchbergensis* and more than is that of *S. hemitoechus*. In the ulna of *S. hemitoechus* the sigmoidal incisure is similar to that of *S. etruscus* and *S. hundsheimensis*. The cross section of the proximal part of its diaphysis is triangular; in the distal direction it turns poligonal or even roundish. The palmar border of the bone is blunted. By comparison with the other species, the ulna of *S. kirchbergensis* is large, with a rather wide open sigmoidal incisure. The cross section of its diaphysis is triangular with very flat walls. Its epiphyses are broad. The palmar border of the diaphysis is particularly sharp. The dorsal face of the diaphysis is wider than it is in the ulnae of the other species. Apart from size, the four species do not differ significantly in the proportions of their ulnae.

Scaphoid - (radial carpal) (table 13; fig. 13). By comparison with that of *S. etruscus*, the scaphoid of *S. hundsheimensis* is significantly longer, while that of *S. hemitoechus*, in proximal view, has a proximal articular surface that is more stretched latero-medially and narrower dorso-palmarly. In *S. kirchbergensis* the bone is much larger, with broad articular surfaces. The proximal articular facet is very concave, deep and stretched antero-posteriorly. The posterior portion of the distal articular surface is broad, without a clear posterior border to distinguish it from the wall of the corpus of the bone. The proximal border of the other two portions of the distal articular surface, in lateral view, is more widely undulated than it is in either *S. etruscus* or *S. hundsheimensis*. The ratio diagram for this bone shows that the four species are equipped with quite similar scaphoids; *S. hemitoechus* is represented here by only one specimen, which could explain its apparent disproportions. The analysis of variance

TABLE 12A - Radius/ulna

Characters	Lr	PL	BPr	BPar	DPr	DPar	DPsi	BDr	BDar	DDr	DDar	BSr	DSr	Lu	Lo	Do	DPa	Hsiu	BPau	BDu	BDau	DDau	BSu	Lru	BDru	BDaru
Specimens																										
11et	359	337	84	84	—	—	42	89	65	55	41	44	32	—	—	—	(95)	41	73	59	31	53.2	25	—	—	—
34et	—	—	88	—	56	—	(38)	—	—	—	—	44	34	—	—	—	—	—	—	—	—	—	—	—	—	—
35et	373	328	85	—	59	57	40	86	65	53	42	48	34.8	455	—	79	102	40.3	—	55	33	50.2	36	—	—	—
36et	—	—	—	—	—	—	—	—	—	—	—	—	—	458	—	77	101	51	77	63	34	57.2	33	—	—	—
37et	—	—	—	—	—	—	—	84	60	54	39.8	—	33	—	—	—	—	—	—	52	31	52	—	—	110	97
38et	—	—	85	85	55	—	39.8	—	—	—	—	46	31.9	—	—	—	—	—	—	—	—	—	—	—	—	—
39et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(40)	—	(70)	—	—	—	—	—	—
40et	386	338	89	89	—	—	42.6	88	70	59	38.3	48	32	—	—	—	—	41	76	—	34.6	60.2	34	—	118	100
41et	—	332	87	86	—	—	(40.2)	90	(70)	58	(39)	49	35	—	140	76	102	45.3	74	—	—	—	32	—	—	—
42et	384	352	82	81	—	—	39.5	(69)	53	60	42	43	33	468	126	79	101	44	71	—	32	58	31	478	111	92
43et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	—	—	—
44et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(73)	(85)	(40)	69	—	—	—	—	—	—	—
45et	—	—	84	—	51	(40.2)	—	—	—	—	—	43	30.8	—	—	—	—	—	—	—	—	—	—	—	—	—
46et	—	—	—	—	—	—	—	88	74	51	39	—	36	—	—	—	—	—	—	—	—	—	—	—	—	—
47et	—	—	—	—	—	—	—	—	—	—	—	48	34	—	—	—	—	—	—	—	—	—	—	—	—	—
48et	—	—	(81)	—	58	(57.8)	(45)	—	—	—	—	(43)	32.2	—	—	—	—	—	—	—	—	—	—	—	—	—
49et	—	—	—	—	—	—	—	—	—	—	—	55	40	—	—	—	—	—	—	—	—	—	—	—	—	—
50et	—	—	—	—	—	—	—	—	—	—	—	(53)	36.2	—	—	—	—	—	—	—	—	—	—	—	—	—
51et	—	—	(79)	—	(54)	(50)	(41)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
52et	—	—	(75)	—	(42)	(42)	(36)	—	—	—	—	(44)	27	—	—	—	—	—	—	—	—	—	—	—	—	—
53et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(47)	65	—	—	—	—	—	—	—
54et	—	—	—	—	—	—	—	85	—	51	41	41	37	—	—	—	—	—	—	—	—	—	—	—	—	—
55et	—	—	77	—	46	(47.2)	(37)	—	—	—	—	39	30	—	—	—	—	—	—	—	—	—	—	—	—	—
56et	—	—	83	—	49	(47.3)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
57et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(61)	(90)	37	74	—	—	—	—	—	—	—
58et	—	—	80	72	60	68.2	48.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
59et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57	39	57	—	—	—	—
60et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	63	—	—	—	—	—	—	—
61et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(70)	—	—	—	—	—	—	—
62et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	63	—	—	—	—	—	—	35	—	—	—
63et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	85	(41.3)	59	—	—	—	—	—	—	—
64et	—	—	79	—	57	(57.9)	(41)	—	—	—	—	—	(36)	—	—	—	—	—	—	—	—	—	—	—	—	—
65et	—	—	85	(85)	54	55	43	—	—	—	—	49	34.2	—	—	—	—	—	—	—	—	—	—	—	—	—
66et	—	—	81	—	—	—	(35)	—	—	—	—	—	34.8	—	—	—	—	—	(63)	—	—	—	35	—	—	—
67et	367	343	86	85	61	—	41	88	—	54	40.9	43	34	—	—	—	—	—	—	—	—	—	34	—	(96)	88
68et	354	335	84	85	51	(52)	34.8	90	(69)	46	37	45	32	—	—	—	—	—	—	—	—	—	—	—	—	—
69et	371	345	87	87	56	55	35	82	(71)	38	37.3	47	31.2	—	—	—	—	—	—	—	—	—	—	—	—	—
70et	378	351	80	80	(50)	—	35	84	(66)	47	39.8	49	30	—	121	69	92	44.7	—	—	—	—	—	486	—	—
71et	—	—	87	87	60	58.3	45.8	—	—	—	—	50	33.2	—	(98)	69	102	46	76	—	—	—	31	—	—	—
72et	—	—	(73)	(65)	—	—	—	—	—	—	—	—	36	—	124	81	106	45	67	—	—	—	(29)	—	—	—
73et	—	—	87	86	56	(58)	(40.2)	—	—	—	—	41	31.2	—	—	—	—	—	—	—	—	—	—	—	—	—
74et	—	—	83	—	49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
74et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	68	—	—	—	—	—	—	—
75et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(69)	—	—	—	—	—	—	—
77et	—	—	—	—	—	(56.3)	(39)	(71)	—	56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
78et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(70)	—	—	—	—	—	—	—
79et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(40)	—	—	—	—	—	—	—	—
13hu	384	369	88	—	62.5	—	—	92	—	>60	—	51.5	38	—	—	—	—	—	—	—	—	—	—	—	—	—
14hu	—	—	92	90	58.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15hu	373	348	91	91	63.5	57.5	—	96	77	60	47	49	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—
16hu	413	386	99	96	66	59	—	>83	77	54	45	53	39.5	—	—	—	—	—	—	—	—	—	—	—	—	—
17hu	—	—	—	—	—	—	—	91.5	78	57	43	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18hu	—	—	—	(98)	—	(54)	—	—	—	—	—	52	42	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 12A

Characters	Lr	PL	BPr	BPar	DPr	DPar	DPsi	BDr	BDar	DDr	DDar	BSr	DSr	Lu	Lo	Do	DPa	Hsiu	BPau	BDu	BDau	DDau	BSu	Lru	BDru	BDaru
Specimens																										
4ki	—	—	106	102	76.1	—	43	—	—	—	55.5	—	40	—	—	—	—	—	—	—	—	—	—	—	—	—
5ki	—	—	101	97	72.2	—	45.5	—	—	—	56.5	—	39.3	—	—	—	—	—	—	—	—	—	—	—	—	—
6ki	—	—	—	—	—	—	—	122	109	88	60	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7ki	—	—	—	—	—	—	—	—	99.5	—	53	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8ki	—	—	—	—	—	—	—	—	99	—	53	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9ki	—	—	—	—	—	—	—	106	80	61	48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10ki	—	—	113	111	83	73	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11ki	441	388	110	107	77	—	56.7	117	90.5	85	53.8	52	59	—	—	—	—	—	—	75.5	65	40	58	—	—	—
1he	371	336.5	99	96	60	—	58	100	85.5	66	46	51	35.5	—	—	—	—	—	—	—	—	—	—	—	—	—
2he	—	—	92	90.5	64	—	59	—	—	—	—	51.5	33	—	—	—	—	—	—	—	—	—	—	—	—	—
3he	386	349	100.5	97.5	67	—	62	112	93	70	44	58	37	—	—	—	—	—	—	—	—	—	—	—	—	—
4he	398	368	94.5	91	62.2	—	58.2	101	83	65	41	50	33.5	—	—	—	—	—	—	—	—	—	—	—	—	—
5he	369	341	95	92	60	—	57	107	86	66	46	52.5	36	—	—	—	—	—	—	—	—	—	—	—	—	—
6he	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(82)	(100)	—	83	36	33	53	37.5	—	—	—
7he	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	84	100	—	(74)	—	—	—	37	—	—	—
8he	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	78	107	—	(79)	—	—	—	39	—	—	—
9he	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	60	(37)	—	—	—
9he	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	42	—	—	—	—	—	—	—	—
187et	345	318	82	82	52	(38)	53.8	79	64	57	39.1	39	28	—	—	70	90	—	—	65	—	—	31	—	—	—
188et	—	—	—	—	—	—	—	87	(68)	50	(44)	—	(26)	—	—	—	—	—	—	—	—	—	—	—	(102)	—
76ki	424	386	113	112	69	66	—	108	88	63	(42)	58.5	35.5	—	—	—	—	—	—	—	—	—	—	—	—	—
41he	389	360	101.5	98	67	60	—	108	88	63	(42)	58.5	35.5	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 12B

Radius/Ulna S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
Lr	1	(441.0000)	—	Lu	—	—	—
PL	1	(338.0000)	—	Lo	—	—	—
BRr	4	107.50000	5.19615	Do	—	—	—
DPar	4	104.25000	6.07591	DPa	—	—	—
DPr	4	77.07500	4.46570	HSIU	—	—	—
DPar	1	(73.0000)	—	BPau	—	—	—
DPsi	3	48.40000	7.29589	BDu	1	(75.5000)	—
BDr	3	115.00000	8.18535	BDau	1	(65.0000)	—
BDar	5	95.60000	10.90528	DDau	1	(40.0000)	—
DDr	3	78.00000	14.79865	BSu	1	(58.0000)	—
DDar	7	54.40000	3.66106	Lru	—	—	—
BSr	1	(52.0000)	—	BDru	—	—	—
DSr	3	46.10000	11.17721	BDaru	—	—	—

Radius/Ulna S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev
Lr	4	381.00000	13.63818	Lu	—	—	—
PL	4	348.62500	13.91267	Lo	—	—	—
BPr	5	96.20000	3.47491	Do	3	81.33334	3.05505
BPar	5	93.40000	3.15040	DPa	3	102.33330	4.04145
DPr	5	62.64000	2.95770	Hsiu	1	(42.0000)	—
DPar	—	—	—	BPau	3	78.66666	4.50925
DPsi	5	58.84000	1.90473	BDu	1	(36.0000)	—
BDr	4	105.00000	5.59762	BDau	2	36.50000	4.94975
BDar	4	86.87500	4.28904	DDau	2	56.50000	4.94975
DDr	4	66.75000	2.21736	BSu	4	37.62500	0.94648
DDar	4	44.25000	2.36291	Lru	—	—	—
BSr	5	52.60000	3.15040	BDru	—	—	—
DSr	5	35.00000	1.69558	BDaru	—	—	—

Radius/Ulna S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
Lr	8	371.50000	11.30108	Lu	3	460.33340	6.80686
PL	9	340.11110	8.25295	Lo	5	121.80000	15.17234
BPr	25	82.84000	4.11987	Do	10	72.70000	6.96100
BPar	14	82.64286	6.55870	DPa	11	96.45454	7.42110
DPr	19	53.89474	5.14128	Hsiu	15	42.90667	3.61771
DPar	17	54.12942	5.86172	BPau	18	69.66666	4.97050
DPsi	23	39.96957	3.56465	BDu	5	57.20000	4.14729
BDr	14	84.15384	6.75581	BDau	7	33.51429	2.79012
BDar	11	66.30000	6.11101	DDau	7	55.40000	3.62951
DDr	14	52.46154	6.05001	BSu	12	32.91667	3.77692
DDar	13	39.75834	1.68871	Lru	2	482.00000	5.65685
BSr	22	46.00000	3.98808	BDru	4	108.75000	9.21502
DSr	29	33.37500	2.60649	BDaru	4	94.25000	5.31507

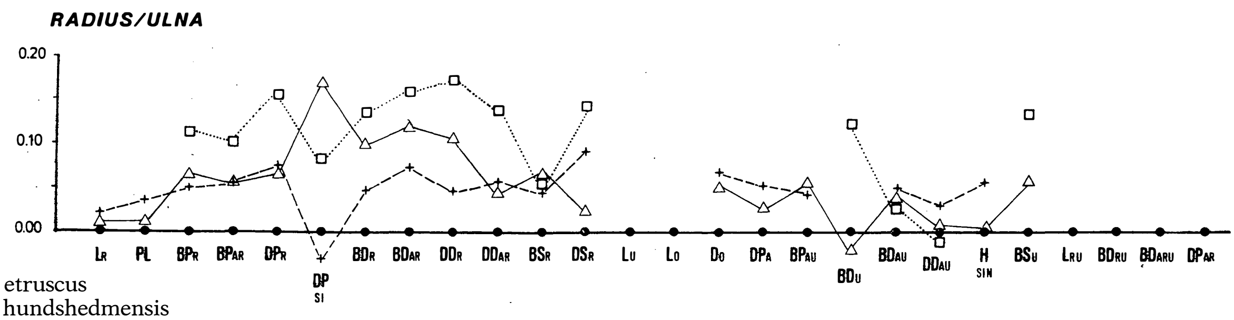
Table 12B

Radius/Ulna S. hunsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
Lr	4	391.75000	17.23127	Lu	—	—	—
PL	4	370.00000	16.22755	Lo	—	—	—
BPr	5	93.30000	4.41022	Do	—	—	—
BPar	5	94.00000	3.39117	DPa	3	108.33330	7.23418
DPr	5	63.70000	3.61594	Hsiu	2	48.75000	6.71751
DPar	2	56.83333	2.56580	BPau	2	76.75000	7.42462
DPsi	2	37.00000	0	BDu	—	—	—
BDr	5	94.10000	9.09945	BDau	1	(37.5000)	—
BDar	4	78.50000	2.38048	DDau	1	(59.0000)	—
DDr	5	58.30000	2.77489	BSu	—	—	—
DDar	4	45.37500	1.79699	Lru	—	—	—
BSr	5	51.70000	1.64317	BDru	—	—	—
DSr	5	41.20000	4.69840	BDaru	—	—	—

indicates that the scaphoid differs significantly among the species, that of *S. kirchbergensis* being more elongate and higher, and having a distal articular surface more stretched antero-posteriorly than is the case in *S. etruscus* and *S. hundsheimensis*.

Semilunar - (intermediate carpal) (table 14; fig. 14). By comparison with *S. etruscus*, the semilunar in *S. hundsheimensis* is slighlty higher proximo-distally. The medial portion of the distal articular surface, relative to the magnum, is more stretched as well, while the lateral portion, which articulates with the uncinate, appears proportionally broader and shorter in its dorsal section. In *S. hemitoechus*, by comparison with both *S. etruscus* and *S. hundsheimensis*, the bone is more compressed latero-medially and raised proximo-distally. Furthermore, the medial part of the distal articular surface is enlar



• = S. etruscus
∘ = S. hundshedmensis
Δ = S. hemitoechus
□ = S. kirchbergensis

Fig. 12 - Ratio diagram of the radii/ulnae of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

Table 12C

Radius-Ulna S. etruscus - S. hundsheimensis S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BRr	50.43498	<.001
BRar	18.04974	<.001
DPr	30.57120	<.001
DPsi	39.08804	<.001
BDr	19.29170	<.001
BDar	23.14580	<.001
DDr	14.27131	<.001
DDar	52.74452	<.001
DSr	14.50933	<.001

Radius-Ulna S. etruscus - S. hundsheimensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
Lr	3.09688	0.0857
PL	9.04539	0.0092
BSr	9.88242	<.001
Do	5.28126	0.0272
DPa	3.66305	0.0588
BPau	5.22817	0.0211

Radius-Ulna S. etruscus - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BDau	1.36316	>.20
DDau	0.12725	>.20
BSu	5.83363	<.05

Radius-Ulna S. etruscus - S. hundsheimensis

	(F) Statistic	(P) (One-Tailed)
HSiu	3.95799	<.20
DPar	0.59614	>.20

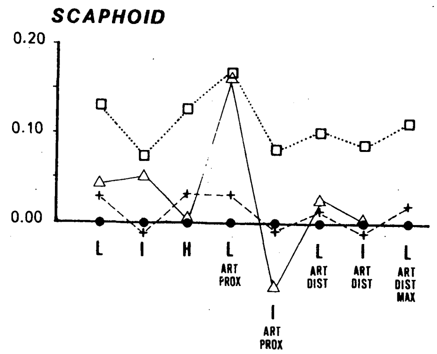


Fig. 13 - Ratio diagram of the scaphoids of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

Table 13A - Scaphoid

Characters	L	1	H	L art prox	1 art prox	L art dist	1 art dist	L art dist max
Specimens								
11et	79	52	62	34	48	55	27	60.2
80et	75	50	55	35	44	49	27	55
81et	73	50	53	31	47	54	28	60
82et	72	43	53	35	43	(47)	26	(56.2)
83et	73	51	65	34	50	53	28	59.8
84et	72	44	54	33	36	49	25	58
85et	73	51	54	33	47	53	28	59.3
25hu	79	51.2	62.1	39.5	48.4	53.2	27	62.5
26hu	79	47	62	35	45.3	55	24	61
27hu	78.4	45	60.5	34	41	51.5	26	61
28hu	80.8	45.5	60.2	36	41.2	52	28.1	60.7
12ki	102.8	(66)	80.5	62.5	(61.5)	67	38	—
13ki	101.5	56.8	75	42	53	65.5	32.7	80
14ki	95.3	51	72	44.3	49.5	62.8	29	72
10he	81.5	55	56.5	49	38	54.5	27	—
187et	—	—	59	32	43	—	(28)	—

TABLE 13B

Scaphoid S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	7	73.85714	2.47848	1 art prox	7	45.00000	4.61880
1	7	48.71429	3.63842	L art dist	7	51.42857	3.04725
H	7	56.57143	4.85994	1 art dist	7	27.00000	1.15470
L art prox	7	33.57143	1.39728	L art dist max	7	58.35715	2.04602

Scaphoid S. hundsheimensis

	N	Mean	St. Dev		N	Mean	St. Dev.
L	4	79.30000	1.03923	1 art prox	4	43.97500	3.55375
1	4	47.17500	2.81469	L art dist	4	52.92500	1.55644
H	4	61.20000	0.98995	1art dist	4	26.27500	1.74236
L art post	4	36.12500	2.39357	L art dist max	4	61.30000	0.81240

Scaphoid S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	99.86667	4.00791	1 art prox	3	54.66667	6.17117
1	3	57.93334	7.56395	L art dist	3	65.10000	2.12838
H	3	75.83334	4.31084	1 art dist	3	33.23333	4.52364
L art prox	3	49.60000	11.23078	L art dist max	2	76.00000	5.65685

TABLE 13C - Scaphoid S. etruscus - S. hundsheimensis - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
L	109.39670	<.001
1	5.84901	0.0284
H	23.68305	<.001
L art prox	10.83816	0.0087
1 art prox	5.45899	0.0288
L art dist	31.44598	<.001
1 art dist	9.55625	0.0102
L art dist max	41.19031	<.001

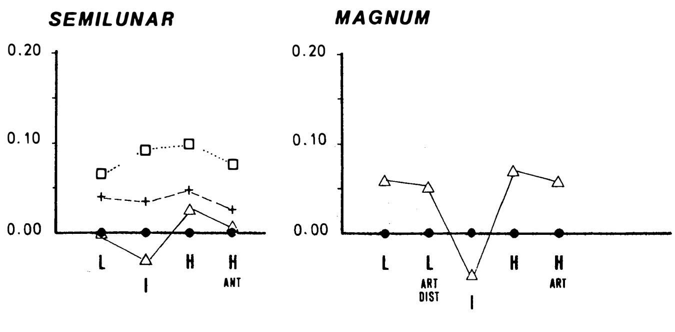


Fig. 14 - Ratio diagram of the semilunars of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 14A - Semilunar

Characters	L	1	H	H ant
11et	70	51	49	50
86et	61	45	45	47
87et	61	47	45	48
88et	60	47	43	46
29hu	68.5	50	49	50
30hu	68.2	53	50.5	50.2
31hu	68.9	52	50	50
32hu	—	—	51.7	51.3
33hu	72.5	52	54	53
15ki	74	58.5	56	55.5
16ki	73	58.5	58.5	59
11he	67	48.5	48	50.5
12he	60.5	45	48.5	51
9he	63	39	48	47
187et	61	43	47	49

ged latero-medially, especially in the middle, while the lateral portion is narrower in the middle. In *S. kirchbergensis* the bone appears morphologically similar to that of *S. etruscus*, though larger latero-medially and significantly higher proximo-distally. The curvature of the lateral portion of the distal articular surface differs among these species: in *S. etruscus* and *S. hundsheimensis* it is uniformly concave, while in both *S. hemitoechus* and *S. kirchber-*

TABLE 14B - Semilunar

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	63.00000	4.69042	H	4	45.50000	2.51661
1	4	47.50000	2.51661	H ant	4	47.75000	1.70785

Semilunar S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev
L	4	69.52500	2.00395	H	5	51.04000	1.91911
1	4	51.75000	1.25831	H ant	5	50.90000	1.29228

Semilunar S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	73.50000	0.70711	H	2	57.25000	1.76777
1	2	58.50000	0.00000	H ant	2	57.25000	2.47487

Semilunar S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	63.50000	3.27872	H	3	48.16667	0.28868
1	3	44.16667	4.80451	H ant	3	49.50000	2.17945

TABLE 14C - Semilunar S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	6.29290	0.0147
1	12.13835	0.0026
H	18.05916	<.001
H ant	13.41859	0.0018

gensis it forms a marked angle that is stressed by rather deep folds. The articular surface for the pyramidal is placed so as to form an obtuse angle with respect to the articular surface for the uncinate in *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis;* it is therefore visible in distal view. On the contrary, in *S. hemitoechus* the facet for the pyramidal is at right angles and therefore cannot be observed in distal view.

Pyramidal - (ulnar carpal) (table 15; fig. 15). By comparison with *S. etruscus*, the pyramidal of *S. hundsheimensis* is usually more stretched latero-medially and more compressed proximo-distally, though there are remarkable individual differences. The pyramidal of *S. hemitoechus*, in addition to having a wider proximal articular surface and being somewhat more stretched proximo-distally, resembles those of both *S. etruscus* and *S. hundesheimensis*. In *S. kirchbergensis*, instead, the bone is far more elongated proximo-distally, proportionally narrower latero-medially and somewhat flatter dorso-palmarly than in either *S. etruscus* or *S.*

TABLE 15A - Pyramidal

Characters	L	1	H max	H phys	H face ant
Specimens					
11et	34	44	48	41	48
89et	35	48	49	38	49
90et	36	44	47	38	48.2
91et	34	46	48	38	47
92et	31	49	50	35.2	49.2
34hu	35.2	54	46	37.3	—
35hu	36.2	55	48.5	38.6	—
36hu	39.5	62.5	49	—	—
16ki	—	—	(64)	56	—
17ki	44	56	62	—	52
18ki	42	53.4	59	—	51
13he	37	49	56	—	46.2
9he	41	49.5	55	42	50

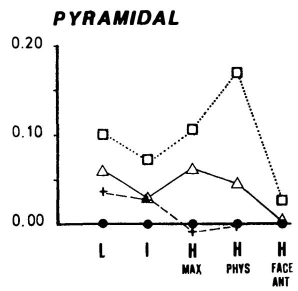


Fig. 15 - Ratio diagram of the pyramidals of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 15B

Pyramidal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	5	34.00000	1.87083	H phys	5	37.84000	2.10428
1	5	46.20000	2.28035	H face ant	5	48.28000	0.87864
H max	5	48.40000	1.14018				

Pyramidal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev
L	3	36.96667	2.25019	H phys	2	37.95000	0.91924
1	3	57.16667	4.64579	H face ant	—	—	—
H max	3	47.83333	1.60728				

Pyramidal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	43.00000	1.41442	H phys	1	(56.0000)	
1	2	54.70000	1.83848	H face ant	2	51.50000	0.70711
H max	3	61.66667	2.51661				

Pyramidal S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	39.00000	2.82843	H phys	1	(42.0000)	—
1	2	49.25000	0.35355	H face ant	2	48.10000	2.68701
H max	2	55.50000	0.70711				

TABLE 15C

Pyramidal S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	9.76252	0.0058
1	10.37769	0.0049
H max	53.46329	<.001

Pyramidal S. etruscus - S kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
H face ant	4.63385	0.0669

Pyramidal S. etruscus - S. hundsheimensis

	(F) Statistic	(P) (One-Tailed)
H phys	0.00466	>.20

hundsheimensis; the proximal and distal articular surfaces are consequently more stretched.

Pisiform - (accessory carpal) (table 16). We could examine one pisiform from Isernia (IS I 336) and two from Pietrafitta (n° 526 and 527), the latter belonging to rather small-sized individuals. The pisiform from Isernia has a pear-shaped, mediolaterally compressed corpus, while the two from Pietrafitta are compressed in the same manner but have more circular outlines.

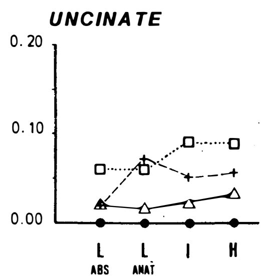


Fig. 16 - Ratio diagram of the uncinates of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 16 - Pisiform

Characters	L	l	H
Specimens			
37hu	68.8	42.5	30

TABLE 17A - Trapezoid

Characters	L	l	H
Specimens			
38hu	43	32	33.7
39hu	46.3	27.2	34.8
40hu	37.5	24.2	33.2
41hu	42.5	26	36
42hu	43.6	31.5	33.5
43hu	42	29.5	35.5
44hu	40.5	31	36
187et	36	26	32

TABLE 17B - Trapezoid S. hundsheimensis

	N	Mean	St. Dev.
L	7	42.20000	2.72397
l	7	28.77143	3.01149
H	7	34.67143	1.20515

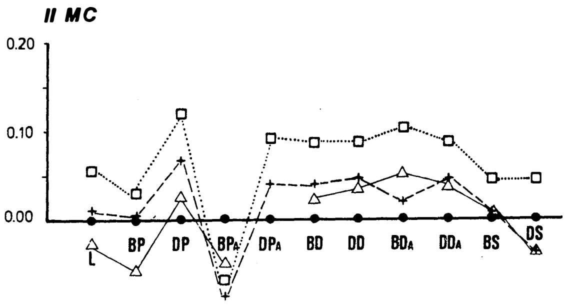


Fig. 17 - Ratio diagram of the second metacarpals of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 18A - Magnum

Characters	L	L art dist	l	H	H art
Specimens					
11et	82	43.9	49	58	58
93et	79	41	38	55	52
94et	—	48.8	45	—	58
95et	80	41.6	46	55	54
96et	83	41.7	44	60	57
45hu	95	—	50	—	65.8
46hu	93.2	—	43	—	62.2
47hu	(93)	—	(43)	—	63
14he	91.5	—	40	66	62.4
9he	94	49	38.6	67.7	65
187et	—	43	45	—	—
138hu	90	—	41	60	58
77ki	91.5	54	47	—	65

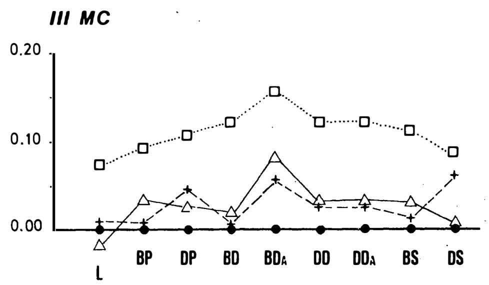


Fig. 18 - Ratio diagram of the third metacarpals of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

Trapezium - (first carpal). The trapezium was always absent from the collections we studied. We suppose that the collectors overlooked it because of its reduced dimensions.

Trapezoid - (second carpal) (table 17). Because of the considerable variability in dimensions and proportions exhibited by the trapezoid, we have not examined the differences among these bones.

Magnum - (third carpal) (table 18). The magnum of *S. hundsheimensis* is similar to that of *S. etruscus*, but is somewhat more stretched proximo-distally and more elongated antero-posteriorly. On the whole, it appears more slender than that of *S. etruscus*, with a narrower proximal articular surface. In *S. hemitoechus* the magnum looks like that of *S. hundsheimensis* except that the distal articular surface is narrower; the proximal articular face is too in some cases. Compared with the magnum of *S. etruscus*, that of *S. hemitoechus* is significantly narrower latero-medially. In *S. kirchbergensis* the magnum is flatter latero-medially and more stretched proximo-distally than it is in the other species. Both proximal and distal articular surfaces are stretched posteriorly, the latter more extensively than the former. The bone is, on the whole, quite high and elongated antero-posteriorly.

Uncinate - (fourth carpal) (table 19; fig. 16). The uncinate of *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* are similar. In the latter species, however, the proximal articular surface, which articulates with the pyramidal, is sometimes narrower dorso-palmarly. Allometrical differences have been observed in the uncinate of *S. hundsheimensis;* as it increases in size it gets proportionally wider latero-medially and lower proximo-distally. In *S. kirchbergensis* the dorsal articular surface of the uncinate is significantly broader latero-medially than it is in the other species.

II Metacarpal - (table 20; fig. 17). By comparison with *S. etruscus*, *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* have thicker proximal epiphy

TABLE 18B

Magnum S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	81.00000	1.82574	H	4	37.00000	2.44949
L art dist	5	43.40000	3.21325	H art	5	55.80000	2.68328
1	5	44.40000	4.03733				

Magnum S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev
L	3	93.73333	1.10151	H	—	—	—
L art dist	—	—	—	H art	3	63.66667	1.89033
1	3	45.33333	4.04145				

Magnum S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	92.75000	1.76777	H	2	66.85000	1.20208
L art dist	1	(49.00000)	0.98995	H art	2	63.70000	1.83848
1	2	39.30000	0.98995				

TABLE 18C

Magnum S. etruscus - S. hundsheimensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	65.50112	<.001
1	1.74058	0.2497
H art	13.81583	0.0099

Magnum S. etruscus - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
H	26.61113	<.001

ses and, instead, proportionally narrower proximal articular surfaces. In *S. hundsheimensis* the proximal articular surface of the second metacarpal is broader but about as deep as that of *S. etruscus*. In *S. kirchbergensis* the proximal articular surface is more concave and more stretched dorso-palmarly than it is in either *S. etruscus*, *S. hundsheimensis* or *S. hemitoechus*. In lateral view, the articular surface for the third metacarpal is concave in *S. hundsheimensis*, *S. etruscus* and *S. kirchbergensis*, while it is flat in *S. hemitoechus*. The dorsal surface of the diaphysis is slightly convex in *S. etruscus* and in the large-size specimens of *S. hundheimensis*, while it is flat in the small-size individuals of the latter species. In *S. kirchbergensis* the diaphysis is somewhat arched in dorsal direction, whereas it is straighter in both *S. etruscus* and *S. hundsheimensis*. In *S. hemitoechus* there is a very marked crest at the center of the palmar face of the diaphysis. In *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus* the diaphysis, in lateral and medial view, is slightly flatter dorso-palmarly than it is in *S. etruscus*. In *S. hundsheimensis* a rather sharp edge separates the proximal articular surface from the lateral facet for the third metacarpal; in *S. etruscus* this edge is blunt. In *S. hemitoechus* the distal articular surface is proportionally wider than it is in *S.*

TABLE 19A - Uncinate

Characters	L abs	L anat	1	H
Specimens				
11et	87	71	65	51
97et	85	64	58	45
98et	81	53	61	44
100et	82	61	61	45
101et	83	(65)	62	45
48hu	87	80	71	54
49hu	—	—	71	56
50hu	79	66	61	45
51hu	91	76	71	57
52hu	88.5	72	68	52.5
19ki	>103	78	82	61
20ki	94	72	73	—
15ki	89	66	71	52.5
9he	89	64	65	51.3
187et	—	—	62	48
136hu	85	65	63	53

TABLE 19B

Uncinate S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L abs	6	82.50000	3.44964	1	6	60.83333	2.63944
L anat	6	62.16667	6.08002	H	6	46.33333	2.65832

Uncinate S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev
L abs	4	86.37500	5.18612	1	5	68.40000	4.33590
L anat	4	73.50000	5.97216	H	5	52.90000	4.74868

Ulcinate S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L abs	3	95.33334	7.09460	1	3	75.33334	5.85947
L anat	3	72.00000	6.00000	H	2	56.75000	6.01041

Uncinate S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L abs	2	86.00000	4.24264	1	2	64.00000	1.41421
L anat	2	64.50000	0.70711	H	2	49.90000	1.97990

TABLE 19C - Uncinate S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L abs	4.68265	0.0252
L anat	3.95919	0.0397
1	10.1104	0.0023
H	4.68622	0.0251

hundsheimensis and even more than it is in *S. etruscus* more symmetrical than it is in *S. etruscus*. The analysis of variance performed on this bone did not reveal significant differences among the four species, and the ratio diagram shows a general similarity of proportions.

III Metacarpal (table 21; fig. 18). In *S. kirchbergensis* this bone is particularly larger than in the other species. By comparison with *S. etruscus* the proximal articular surface of the third metacarpal appears more concave in *S. kirchbergensis* and *S. hemitoechus*, and sometimes even in *S. hundsheimensis*. The edge separating the proximal articular surface from the articular facet for the uncinate is particularly salient in both *S. kirchbergensis* and *S. hemitoechus;* in the latter species it is distinctly acute. In proximal view, by comparison with the other species, the proximal articular surface in *S. kirchbergensis* is more stretched dorso-palmarly than latero-medially. In *S. hundsheimensis,* and to an even greater degree in *S. hemitoechus*, the proximo-lateral facet for the uncinate is broader than it is in *S. etruscus*. In *S. hemitoechus,* in lateral view, the anterior articular facet for the IV metacarpal is wide and stretched dorso-palmarly, while the posterior face is wide and rectangular or triangular-shaped. On the other hand, the two surfaces are both narrow and roundish in *S. etruscus*. In *S. hemitoechus,* the diaphysis appears considerably wider latero-medially, flatter dorso-palmarly and proportionally shorter than it does in *S. etruscus* and *S. hundsheimensis*. In *S. hundsheimensis* the lateral border of the diaphysis, at the transition to the proximal epiphysis, is more robust and slightly more swollen than it is in *S. etruscus*. In *S. kirchbergensis* the diaphysis, in dorsal view, is slightly asymmetrical and widens rapidly distally; its medial border bulges markedly just under the proximal epiphysis. This character is shared, in part, by *S. hemitoechus*. In lateral and medial view the diaphysis of *S. kirchbergensis* appears remarkably flat. In *S. hemitoechus* the lateral border of the diaphysis is thicker and somewhat more bulging than it is in *S. etruscus*. In *S. hundsheimensis, S. kirchbergensis* and *S. hemitoechus* the distal articular surface is broader than it is in *S. etruscus*. The analysis of variance revealed significant differences in all the dimensions except DS, which reflects the fact that diaphyses of the third metacarpals of the four species are all flattened. Apart from this similarity, the third metacarpal is one of the elements that most clearly discriminates among the species.

TABLE 20A - II Metacarpal

Characters	L	BP	DP	BPa	DPa	BS	DS	BD	DD	BDa
Specimens										
11et	166	44	32	39	32.4	31	19	39	37	31
102et	—	46	40	—	39.3	—	—	—	—	—
103et	173	43	39	39	37.8	33	37	40	37	33
104et	—	41	37	(37)	33.5	(36)	(15)	—	—	—
53hu	174	43.4	42	31	38.5	34.2	23.7	43.5	41.2	33.6
54hu	—	43.5	44.6	31.4	40.5	34	19.8	—	—	—
21ki	204	48.3	43	35	—	39.7	24.2	53.3	44.5	42.5
22ki	—	54	55	36	49.3	38.6	26.3	—	—	—
23ki	182	37.8	49	26	39	33.2	28.3	43.4	46	38.8
16he	157	33.5	39	29	—	29.7	22	41.5	39	34.5
17he	—	43	41.5	39.5	—	34	19	—	—	—
18he	153.5	—	(38)	—	—	37.7	22	40	40	36
9he	167	37.3	—	33.5	—	33.3	23	43.2	41.7	38
187et	—	—	—	—	—	—	—	41	37	33

TABLE 20B

II Metacarpal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	169.50000	4.94975	BS	3	33.33333	2.51661
BP	4	43.50000	2.08167	DS	3	23.66667	11.71893
DP	4	37.00000	3.55903	BD	2	39.50000	0.70711
BPa	3	38.33333	1.15470	DD	2	37.00000	0
DPa	4	35.75000	3.32114	BDa	2	32.00000	1.41421

II Metacarpal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(174.0000)	—	BS	2	34.100000	0.14142
BP	2	43.45000	0.07071	DS	2	21.75000	2.75772
DP	2	43.30000	1.83848	BD	1	(43.5000)	—
BPa	2	31.20000	0.28284	DD	1	(41.2000)	—
DPa	2	39.50000	1.41421	BDa	1	(33.6000)	—

II Metacarpal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	193.00000	15.55635	BS	3	37.16667	3.47898
BP	3	46.70000	8.21766	DS	3	26.26667	2.05020
DP	3	49.00000	6.00000	BD	2	48.35000	7.00036
BPa	3	32.33333	5.50757	DD	2	45.25000	1.06066
DPa	2	44.15000	7.28320	BDa	2	40.65000	2.61630

II Metacarpal S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	159.16670	7.00595	BS	4	33.67500	3.27859
BP	3	37.93334	4.78156	DS	4	21.50000	1.73205
DP	3	39.50000	1.80278	BD	3	41.56667	1.60104
BPa	3	34.00000	5.26783	DD	3	40.23333	1.36504
DPa	—	—	—	BDa	3	36.16667	1.75594

TABLE 20C - II Metacarpal S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BP	1.64256	0.2563
DP	5.95845	0.0205
BPa	1.56629	0.2918
BS	1.09712	0.4059
DS	0.39655	0.7602

II Metacarpal S. etruscus - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	7.61387	0.0495
BD	3.21633	0.1532
DD	28.61923	0.0105
BDa	9.97430	0.0341

II Metacarpal S. etruscus - S. hundsheimensis - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
DPa	2.70703	0.1660

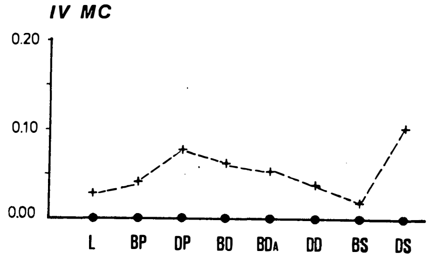


Fig. 19 - Ratio diagram of the fourth metacarpals of *S. hundsheimensis*, versus means for *S. etruscus* from the Upper Valdarno (standard).

IV Metacarpal - (table 22; fig. 19). By comparison with *S. etruscus*, the proximal articular surface of the fourth metacarpal of *S. hundheimensis*, in proximal view, has a relatively shorter dorsal border and, in turn, a longer medial border. In *S. kirchbergensis* the proximal articular surface is more concave latero-medially and much more convex dorso-palmarly than it is in *S. hundsheimensis* and *S. etruscus*. In *S. hundsheimensis* the proximal articular surface and the diaphysis are thicker dorso-palmarly than they are in *S. etruscus*. In the only one fragmentary specimen of *S. kirchbergensis* the diaphysis appears flatter than it does in both *S. etruscus* and *S. hundsheimensis*. Unfortunately, we did not find any fourth metacarpals of *S. hemitoe-*

TABLE 21A - III Metacarpal

Characters	L	PB	BP	BS	DS	BD	DD	BDa
Specimens								
11et	200	53	—	48	20	58	42	42.3
103et	200	53	45	45	19	54	41	41
105et	—	53	39	(47)	(18)	—	—	—
106et	—	52	43	—	(20)	—	—	—
107et	197	—	—	—	—	—	—	—
108et	—	58	42	—	(17)	—	—	40
108et	194	51	45	49	20	54	39	—
109et	—	—	—	48	—	(58)	—	—
55hu	201	(52)	47.5	50.8	23.7	56.8	43.8	45.5
56hu	201	52.8	47	51.8	26.4	>62	45	50
57hu	—	54.5	46	48.6	23	—	—	—
58hu	214	51.3	48.1	46	23.1	53.7	42.1	44.1
59hu	—	(56)	45.2	—	—	—	—	—
60hu	—	(57)	(47)	53	20	—	—	—
61hu	—	57	50.3	—	—	—	—	—
62hu	—	(59)	48.2	—	—	—	—	—
63hu	—	(50.5)	(49.7)	—	—	—	—	—
64hu	198	52	48	48	21	55	43	—
65hu	196	51	46.2	45.3	19	>55	42	47.7
24ki	—	>60	51.2	60	23.2	—	—	—
25ki	252	69	57.5	61.2	26.1	78	57.7	62.1
26ki	—	71.3	60.6	66	23.2	—	—	—
27ki	—	>73	53	62	24	—	—	—
28ki	—	66	56	—	24	—	—	—
29ki	223	60	51.2	59.5	21.2	72	51	57
29ki	227	63	53	59	21.5	73	53	(58)
19he	189	58.3	48.5	51	19	58.5	44	49.5
9he	—	57	43	—	19.7	—	—	—
187et	189	49	—	44	17	59	39	38.2
78ki	—	62	50	48.5	21	—	—	—

TABLE 21B

III Metacarpal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	197.75000	2.87228	DS	6	19.00000	1.26491
BP	6	53.33333	2.42212	BD	4	56.00000	2.30940
DP	5	42.80000	2.48998	DD	3	40.66667	1.52753
BS	5	47.40000	1.51658	BDa	3	41.10000	1.15326

III Metacarpal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	5	202.00000	7.03562	DS	7	22.05714	2.07514
BP	11	53.91818	2.91816	BD	5	56.50000	3.26650
DP	11	47.53637	1.53576	DD	5	43.18000	1.25379
BS	7	49.07143	2.91245	BDa	4	46.82500	2.58376

III Metacarpal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	234.00000	15.71623	DS	7	23.31429	1.65774
BP	7	66.04286	5.27695	BD	3	74.33334	3.21455
DP	7	54.64286	3.52603	DD	3	53.90000	3.43948
BS	6	61.28334	2.56158	BDa	3	59.03334	2.70247

III Metacarpal S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(189.0000)	—	DS	2	19.35000	0.49497
BP	2	57.65000	0.91924	BD	1	(58.5000)	—
DP	2	45.75000	3.88909	DD	1	(44.0000)	—
BS	1	(51.0000)	—	BDa	1	(49.5000)	—

TABLE 21C

III Metacarpal S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BP	19.61758	<.001
DP	22.90106	<.001
BS	54.46417	<.001
DS	8.49835	0.0020

III Metacarpal S. etruscus - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	16.47541	<.001
BD	41.631	<.001
DD	35.66138	<.001
BDa	47.64	<.001

chus in the collections we examined. The analysis of variance shows that the fourth metacarpal of *S. etruscus* is flatter in all the dorso-palmar diameters than that of *S. hundsheimensis*.

Femur - (table 23; fig. 20). As compared with the particularly slender femur of *S. etruscus* that of *S. hundsheimensis* has a stronger trochanter major, a much broader femoral head and a more powerful junction of the comparatively weak third trochanter. In addition its diaphysis becomes stockier distally from the third trochanter. The femur of *S. hemitoechus* is more massive than that of either *S. etruscus* or *S. hundsheimensis*, and its femoral head and third trochanter are more powerful than those of the latter species. With regards to the femur of *S. kirchbergensis*, we were only able to examine one distal epiphysis. In addition to its far larger overall dimensions, the axis of the trochlear trough, in distal view, is more inclined laterally than it is in the femurs of the other species. Neither the analysis of variance nor the ratio diagram revealed significant differences.

TABLE 22A - IV Metacarpal

Characters	L	BP	DP	BS	DS	BD	DD	BDa
Specimens								
11et	165	37	37	32	17	42	39	33
110et	169	43	38	39	20	46	39	(35)
111et	176	40	41	36	19	42	36	36
112et	157	(37)	40	35	17	40	36	32
113et	—	—	—	34	19	37	35	34
114et	—	—	—	(39)	—	—	—	—
115et	—	(36)	(29)	(37)	(12)	—	—	—
116et	(149)	(38)	32	32	21	33	34	(32)
117et	—	39	(31)	(36)	(17)	—	—	—
66hu	164	—	41	36	23	—	40.4	—
67hu	176	43	38.5	34.6	20	42.1	39.6	34
68hu	181.3	>41	>42	37.2	22	47.1	39.6	38
69hu	172	>41	43	35	23.1	45.5	37.2	41
70hu	177.3	42.8	>41.5	39	23	50.2	41.2	39.1
71hu	—	44	44	39.8	23.1	—	—	—
72hu	—	42	44	—	—	—	—	—
73hu	—	41.8	44.3	—	—	—	—	—
74hu	167	45.5	44.5	33.7	22	42.2	42	37
30ki	—	53.5	53	44.2	24	—	—	—
187et	161	38	37	30	16	42	37	33

TABLE 22B

IV Metacarpal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	5	163.20000	10.49762	DS	8	17.75000	2.76457
BP	7	38.57143	2.37047	BD	6	40.00000	4.51664
DP	7	35.42857	4.72077	DD	6	36.50000	2.07364
BS	9	35.55556	2.60342	BDa	6	33.66667	1.63299

IV Metacarpal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	6	172.95000	6.52035	DS	7	22.31429	1.13494
BP	8	42.63750	1.45359	BD	5	45.42000	3.43031
DP	9	42.53334	1.98368	DD	6	40.00000	1.65892
BS	7	36.47143	2.29399	BDa	5	37.82000	2.60038

IV Metacarpal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	—	—	—	DS	1	(24.0000)	—
BP	1	(53.5000)	—	BD	—	—	—
DP	1	(53.0000)	—	DD	—	—	—
BS	1	(44.2000)	—	BDa	—	—	—

Patella - (table 24). The patella of *S. hundsheimensis* is wider latero-medially and somewhat more flattened dorso-plantarly than that of *S. etruscus*.

Tibia - (table 25; fig. 21). The tibiae of *S. hundsheimensis* and *S. hemitoechus* are very similar; they differ from that of *S. etruscus* by having much

TABLE 22C - IV Metacarpal S. etruscus - S. hundsheimensis

	(F) Statistic	(P) (One-Tailed)
L	3.57123	<.20
BP	15.92281	<.01
DP	16.84429	<.01
BS	0.53895	<.20
DS	16.51322	<.01
BD	4.83710	<.20
DD	10.42258	<.01
BDa	10.48538	<.05

wider epiphyses and diaphyses more compressed dorso-plantarly. In the tibia of *S. hemitoechus*, the distal epiphysis appears to be rotated, with its lateral side more advanced dorsally than it is in the tibiae of *S. etruscus* and *S. hundsheimensis*. The ratio diagram illustrates the strict proportional agreement between *S. hundsheimensis* and *S. hemitoechus* and their differences from *S. etruscus*.

Astragalus - (talus) (table 26; fig. 22). The astragali of *S. etruscus* and *S. hundsheimensis* look very much alike. However, with increasing size, the dorsal articular surface of the astragalus of *S. hundsheimensis* becomes proportionally broader medio-

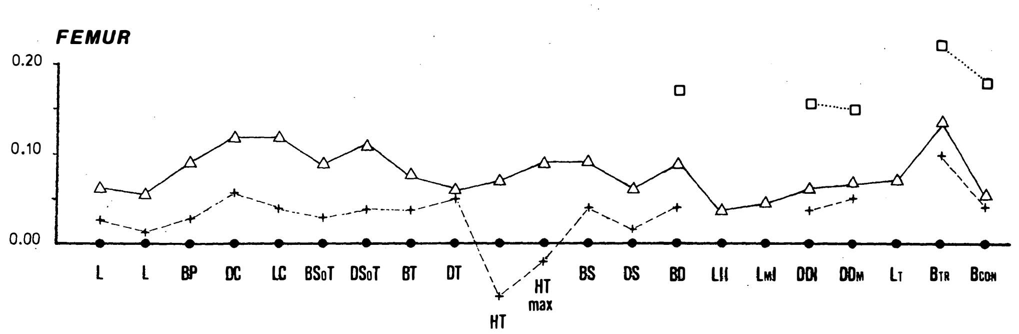


Fig. 20 - Ratio diagram of the femurs of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 23A - Femur

Characters	L	PL	BP	DC	LC	BSoT	DSoT	BT	DT	HT	HT	BS	DS	BD	L11	Lm1	DD1	DDm	Lt	Btr	Bcon
Specimens																					
11et	440	450	161	74	75.3	77.6	39.2	120	49	70	70.9	61	48	122	79.9	109	121	143.8	62	67	103
118et	—	—	155	66	72	80	36	(120)	41	—	—	56	47.2	—	—	—	—	—	—	—	—
119et	—	—	—	70	73.6	73.8	42	—	43	—	—	(59)	47.2	—	—	—	—	—	—	—	—
120et	407	442	150	66	71	66	38.1	109	43.9	59	(59)	51	45	115	76	95.2	111	138	60	62	95
121et	—	—	169	82	84	82.6	42	136	45.5	71	72	63	51	—	—	—	—	—	—	—	—
122et	—	—	—	—	—	78	41	—	—	—	—	(70)	53	—	—	—	—	—	—	—	—
123et	—	—	—	—	—	69.3	41	—	44	52	—	60	47.2	—	—	—	—	—	—	—	—
124et	—	—	—	—	—	—	—	—	42.5	—	—	58	47.3	—	—	—	—	—	—	—	—
125et	—	—	—	—	—	—	—	—	—	—	—	(71)	—	—	—	—	—	—	—	—	—
126et	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(58)	—	—
127et	—	—	—	—	—	72	(35)	—	43	—	—	57	46	—	—	—	—	—	—	—	—
128et	—	—	—	—	—	—	(32.5)	—	40	—	—	50	42.2	—	—	—	—	—	—	—	—
129et	—	—	—	—	—	77	41	—	44.2	(50)	—	61	47.2	—	—	—	—	—	—	—	—
130et	—	—	161	72	75.7	79	39	—	43	—	—	60	47	—	—	—	—	—	—	—	—
131et	—	—	—	—	(71.8)	(81)	—	—	—	60	—	(68)	—	—	—	—	—	—	—	—	—
132et	—	—	—	71	82.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
133et	—	—	—	(63)	69	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
134et	—	—	—	(67)	74	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
75hu	464	464	182	79	90.5	—	—	—	49.5	—	—	68	48.2	131	—	—	125.5	164	—	82	110.5
76hu	457	457	167	90	80.5	85	—	138	48.5	53	—	65	50.5	130	—	—	128	155	—	80	108
77hu	—	—	165	71.5	75	78	42.5	126	—	52	(64)	—	—	—	—	—	—	—	—	—	—
78hu	—	—	—	—	—	—	—	—	—	—	—	73.3	47	129.5	—	—	126	143	64	—	—
79hu	—	—	—	—	—	97.5	42.5	>137	—	>60	—	67	52.5	—	—	—	—	—	—	—	—
31ki	—	—	—	—	—	—	—	—	—	—	—	—	—	175	—	—	166	201	—	107	150
20he	483	502.5	187	91.3	94	97	48.2	148	50	74.5	81	73	54	142	83	112.5	128	161	69	80	117
21he	512	512	204	93	102.5	84.5	51	140.5	52	69.2	84.5	70	58	145	91.5	124	140	176.5	73	96	—
9he	—	—	—	—	—	98	—	—	47.5	68.5	—	79.5	52	148	79	104	133	158	—	89	108
189et	442	447	160	71	75.7	81.9	40.8	—	43	—	—	58	47.2	121	79.2	92.5	116.5	142	60	70	97.5

Table 23B

Femur S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	423.50000	23.33453	BS	14	60.35715	6.23399
PL	2	446.00000	5.65685	DS	12	47.35834	2.69257
BP	5	159.20000	7.15542	BD	2	118.50000	4.94975
DC	9	70.11111	5.64456	L11	2	77.95000	2.75772
LC	10	74.86000	4.80074	Lm1	2	102.10000	9.75807
BSoT	11	76.02728	5.16567	DD1	2	116.10000	6.92965
DSoT	11	38.80000	3.12506	DDm	2	141.00000	3.95980
BT	4	121.25000	11.11680	Lt	3	60.00000	2.00000
DT	11	43.55455	2.35303	Btr	2	64.50000	3.53553
HT	6	60.33333	8.77876	Bcon	2	99.00000	5.65685
HT max	3	67.30000	7.20902				

Femur S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	460.50000	4.94975	BS	4	68.32500	3.54342
PL	2	460.50000	4.94975	DS	4	49.55000	2.44472
BP	3	171.33330	9.29157	BD	3	130.16670	0.76376
DC	3	80.16666	9.30502	L11	—	—	—
BSoT	3	82.00000	7.85812	Lm1	—	—	—
DSoT	3	86.83334	9.87843	DD1	3	126.50000	1.32288
BT	2	42.50000	0	DDm	3	154.00000	10.53565
DT	3	133.66670	6.65833	Lt	1	(64.0000)	—
HT	3	49.00000	0.70711	Btr	2	81.00000	1.41421
HT	2	55.00000	4.35890	Bcon	2	109.25000	1.76777
HT max	1	(64.0000)	—				

Femur S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	—	—	—	BS	—	—	—
PL	—	—	—	DS	—	—	—
BP	—	—	—	BD	1	(175.0000)	—
DC	—	—	—	L11	—	—	—
LC	—	—	—	Lm1	—	—	—
BSoT	—	—	—	DD1	1	(166.0000)	—
DSoT	—	—	—	DDm	1	(201.0000)	—
BT	—	—	—	Lt	—	—	—
DT	—	—	—	Btr	1	(107.0000)	—
HT	—	—	—	Bcon	1	(150.0000)	—
HT max	—	—	—				

Femur hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	497.50000	20.50610	BS	3	74.16666	4.85627
PL	2	507.25000	6.71751	DS	3	54.66667	3.05505
BP	2	195.50000	12.02082	BD	3	145.00000	3.00000
DC	2	92.15000	1.20208	L11	3	85.26667	6.25007
LC	2	98.25000	6.10141	Lm1	3	113.50000	10.03743
BSoT	3	93.16666	7.52219	DD1	3	133.93330	5.65803
DSoT	2	49.60000	1.97990	DDm	3	165.16670	9.92891
BT	2	144.25000	5.30330	Lt	2	71.00000	2.82843
DT	3	49.83333	2.25462	Btr	3	88.33334	8.02081
HT	3	70.73333	3.28075	Bcon	2	112.50000	6.36396
HT max	2	82.75000	2.47487				

TABLE 23C

Femur S. etruscus - S. hundsheimensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	8.30116	0.0661
PL	60.49078	0.0100
BP	12.66607	0.0110
DC	11.28218	0.0084
LC	15.31742	<.001
BSoT	9.95700	0.0083
DSoT	12.08466	0.0076
BT	4.61781	0.0673
DT	12.04279	0.0073
HT	3.95072	0.0649
BS	8.69731	0.0085
DS	8.92999	0.0087
BD	50.16997	<.001
DD1	8.26077	0.0322
DDm	4.05345	0.0961
Btr	9.61882	0.0359
Bcon	3.93884	0.1511

Femur S. etruscus - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
HT max	7.80747	<.20
L11	2.24795	>.20
Lm1	1.57676	>.20
Lt	27.225	<.05

laterally and more compressed proximo-distally than that of *S. etruscus*. In the astragalus of *S. hemitoechus* the distal articular surface may come very close to the distal border of the trochlea. The distal articular surface is proportionally narrower dorso-plantarly and wider latero-medially than that of *S. etruscus*. In dorsal view the trochlea of the astragalus of *S. hemitoechus* is significantly broader latero-medially than it is in the other species and the lateral lip of the trochlea seems somewhat less steep. In *S. kirchbergensis* the astragalus is a very large bone. It is enlarged latero-medially, even in the juvenile forms, though it is never flattened dorso-plantarly, despite its large size. The trochlea is far wider and more asymmetrical than it is in the other species. For the differences between the astragali of *S. hemitoechus* and *S. kirchbergensis* the reader is also referred to Staesche (1941). The differences described above between the astragali of the four species are clearly depicted by the ratio diagram and the differences were shown to be significant by the analysis of variance. This bone therefo-

TABLE 24A - Patella

Characters	L	L art face	DT	DAP
Specimens				
11et	99	61	83	48
80hu	>91	—	(94.5)	52.5
81hu	—	68	—	(43)
82hu	108	63	84	43
9he	—	67	95	50
9he	106	—	94	50

TABLE 24B

Patella S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(99.0000)	—	DT	1	(83.0000)	—
L art face	1	(61.0000)	—	DAP	1	(48.0000)	—

Patella S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	99.50000	12.02081	DT	2	89.25000	7.42462
L art face	2	65.50000	3.53553	DAP	3	46.16667	5.48483

Patella hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(106.0000)	—	DT	2	94.50000	0.70711
L art face	1	(67.0000)	—	DAP	2	50.00000	0

re seems to be particularly useful for discriminating between the species.

Calcaneum - (table 27; fig. 23). The calcanei of both *S. etruscus* and *S. hundsheimensis* are rather similar. However, due to its more extended summital tuberosity, the plantar profile is more bulging in *S. hundsheimensis* than it is in the calcaneum of *S. etruscus*. The sustentaculum tali appears shorter and stronger in *S. hundsheimensis* than it does in *S. etruscus*. The corpus of the bone is somewhat stockier in *S. hundsheimensis* than it is in *S. etruscus*. As compared with the forms of the *etruscus* forms the calcaneum of *S. hemitoechus* has a shorter, broader and more massive corpus, so that the sustentaculum tali appears proportionally less elongated medially. This seems to be a diagnostic character. *S. kirchbergensis* has a very large calcaneum. The corpus of the bone is stocky and considerably stretched posteriorly. The distance between the beak and the distal articular surface for the cuboid is markedly reduced with respect to *S. etruscus* and *S. hundsheimensis*. The sustentaculum tali is about as stretched as it is in *S. etruscus*. The ratio diagram confirms that *S. hundsheimensis* and *S. etruscus* are proportionally similar to one another, while the other two species differ. Analyses of variance indicates that the most marked differences among the four species are the statistically most significant.

Navicular - (central tarsal) (table 28). The bones look very much alike in *S. etruscus* and *S. hundsheimensis*. In the latter species with the increasing size, there is a reduction in the concavity of the navicular. *S. kirchbergensis* has a very large navicular. The proximal articular surface is more enlarged latero-medially than it is in either *S. etruscus* or *S. hundsheimensis*. The posterior tubercle is much more developed than it is in *S. hundsheimensis*. In

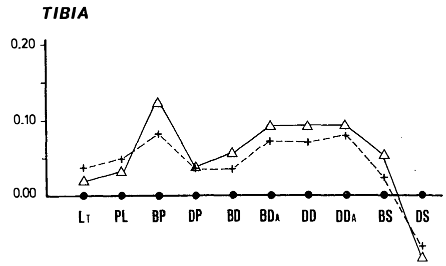


Fig. 21 - Ratio diagram of the tibiae of *S. hundsheimensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 25A - Tibia

Characters	Lt	PL	BP	DP	BS	DS	BD	DD	BDa	DDa	Lf
Specimens											
11et	354	(303)	11	107	54	67	100	67	68.3	51.2	311
120et	336	287	105	101	51	58	96	58	—	46	265
135et	—	—	110	115	50	—	—	—	—	—	—
136et	—	—	—	—	—	—	99	55	70	(51)	—
137et	—	—	—	—	49	—	—	—	—	—	—
138et	—	—	—	—	—	—	83	59	66.1	51	—
139et	—	—	—	—	—	—	(83)	(55)	—	—	—
140et	—	—	(97)	—	—	—	—	—	—	—	—
141et	—	—	—	—	54	—	—	—	—	—	—
142et	343	293	(104)	(113)	55	62	(85)	62	63.8	53	—
143et	—	—	—	—	55	61	91	61	69.8	54	—
144et	361	(317)	(79)	—	49	56	(75)	58	62	42	—
145et	338	(293)	(78)	—	—	60	(83)	59	55.2	51	—
146et	—	—	87	—	55	—	—	—	—	—	—
147et	—	—	94	—	46	—	—	—	—	—	—
83hu	399	353	118	116.2	56.5	50	99	66.4	75	58.5	—
84hu	—	—	117	144.5	57	—	—	—	—	—	—
85hu	365	321	119	—	52	56	97.5	70	80	60	—
86hu	367	332	111.5	—	53	49	91	72.5	76	60	—
87hu	—	—	118	124	—	—	—	—	—	—	—
88hu	—	—	—	—	—	—	—	—	—	67	—
22he	358	315	—	—	54	49	—	64	75	61	—
23he	348	303	—	—	58.5	49	99	73	74	65	—
24he	—	—	—	—	—	—	100	69	76	58	—
25he	(379)	340.2	(136.3)	—	66.8	58	107.3	82.7	95	55	—
9he	363	325	—	—	56.3	50	101	75	75	—	—
9he	365	325	(119)	119	56.3	50	95	75	87	68	—
189et	376	(331)	115	112	51	67	94	67	66	54.2	—

TABLE 25B

Tibia S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
Lt	5	346.40000	10.73778	BD	9	88.33334	8.58778
PL	5	298.60000	11.78134	DD	9	55.33333	3.70810
BP	9	96.11111	12.57423	BDa	7	65.02858	5.26963
DP	4	109.00000	6.32456	DDa	8	49.90000	3.95258
BS	10	51.80000	3.22490	Lf	2	288.00000	32.52691
DS	6	60.66667	3.77712				

Tibia S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
Lt	3	377.00000	19.07879	BD	3	95.83334	4.25245
PL	3	335.33340	16.25833	DD	3	69.63333	3.06649
BP	5	116.70000	2.99166	BDa	3	77.00000	2.64575
DP	3	118.23330	5.06590	DDa	4	61.37500	3.81608
BS	4	54.62500	2.49583	Lf	—	—	—
DS	3	51.66667	3.78594				

Patella hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
Lt	5	362.60000	11.28273	BD	5	100.46000	4.45062
PL	5	321.64000	13.77128	DD	6	73.11667	6.30886
BP	2	127.65000	12.23295	BDa	6	80.33334	8.66410
DP	1	(119.0000)	—	DDa	5	61.40000	5.22494
BS	5	58.38000	4.96860	Lf	—	—	—
DS	5	51.20000	3.83406				

TABLE 25C

Tibia S. etruscus - S. hundsheimensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
Lt	5.37085	0.0323
PL	7.58262	0.0161
BP	10.69431	0.0080
BS	5.51874	0.0213
DS	10.26624	0.0093
BD	4.93684	0.0301
DD	16.95795	<.001
BDa	9.53426	0.0091
DDa	14.92201	<.001

Tibia S. etruscus - S. hundsheimensis

	(F) Statistic	(P) (One-Tailed)
DP	4.26525	<.20

distal view the bone appears much more stretched dorso-plantarly than it does in *S. etruscus* or *S. hundsheimensis* and has a triangular-shaped distal articular surface. The navicular of *S. hemitoechus* is comparatively flatter than those of the other species. The distal articular facets for the second and third cuneiforms are indistinguishable one from another and the facet for the second metatarsal is not sub-vertical, but oblique.

Cuboid - (fourth tarsal) (table 29; fig. 24). In *S. etruscus* the bone appears shorter dorso-plantarly and stockier than it does in the other species and has proximo-distally stretched quadrate dorsal face. In *S. hemitoechus* the corpus of the bone is even more compressed dorso-plantarly than it is in *S. etruscus*. As compared with *S. etruscus*, the cuboid of *S. hundsheimensis* appears much more elongated dorso-plantarly, with the proximal articular surface more stretched latero-medially and a longer posterior tubercle. The dorsal face of the bone is narrow and high in *S. etruscus* and broader and lower in *S. hundsheimensis*. The distal articular surface is sub-rectangular in *S. etruscus* and sub-triangular in *S. hundsheimensis* and *S. hemitoechus*. *S.*

kirchbergensis has a very large cuboid. As compared with those of the other species the bone appears quite compressed proximo-distally, with the proximal articular facet enlarged medially; as also is the case in *S. hemitoechus*, the bone has a more developed posterior tubercle and a sub-triangular distal articulation. The dorsal face of the bone is broader latero-medially than it is in *S. hundsheimensis*. Perhaps because of the small sample sizes, the analysis of variance reveals only moderately significant differences, however.

III cuneiform - (third tarsal) (table 30). The third cuneiform of *S. hundsheimensis* is more compres-

TABLE 26A - Astragalus

Characters	LL	ML	B	BD	DD	BDa	Lmt	Dmt	L1t	Htt	DL
Specimens											
11et	73	—	86	72	44	—	61	50	64.2	41	54.8
148et	74	71	82	71	(45)	68	63	48	64.1	44	51.6
149et	70	65	75	64	38	63	57	47	—	—	—
150et	72	71	77	67	43	65	58	49	62	38.1	53
151et	74	74	(83)	70	40	(68)	62	50	61.7	41	57
152et	73	73	78	(63)	40	—	60	47	63	39.2	50
153et	(75)	70	(81)	—	(41)	—	61	(44)	—	43.5	56
154et	72	72	82	72	47	70	61	53	58	38	51.7
154et	73	67	79	(65)	41	(58)	(55)	47	59	37.5	50
155et	—	—	—	—	—	—	59	—	59.2	41.2	46.8
156et	69	58	—	(58)	41	(58)	54	44	62	37	56.6
89hu	81	78	85	74	41	72.5	63.5	51	65	—	58
90hu	82.2	72.6	80	76.6	55	74	61	49	61	—	56.5
91hu	85.3	77	91	76.5	45.5	72	67	54	69.3	—	62
92hu	83	73	85.5	73.5	42	70.5	62	50.5	64.3	—	57
93hu	79.2	74	88	78.3	45.5	73	64.7	54	66	—	56
94hu	87.5	77.5	92	81	44.7	79	64	55	67.8	—	66
95hu	90	78	95.8	82	42	78.5	64	51	72	—	67
96hu	82	75.5	88.3	73.5	44	72	63	52	67	—	57.5
97hu	–81	81.3	95	75	44.5	75	74	57.5	72	50.5	63
98hu	—	—	85	75	45	71.5	77.5	54	76	43.3	51
99hu	75	75	85	74	—	71	>59	50	—	—	—
100hu	92	77	88	80.6	45.8	80	64	51.8	67.2	—	72
32ki	94	85	93	82	52	(81)	71	61	—	52	71
33ki	—	81	105	91	54	90	73	61	—	57	71
34ki	(81)	80	97.5	84.5	53.5	79.5	73	63	—	54.5	72
35ki	83.5	81	98.5	90	51	86	72	63	—	56	79
36ki	84	84	100	82	53	79	70	61	74	—	72
37ki	—	87	101	86	—	(82)	70	58	—	—	—
38ki	84.5	76	95	81	49.2	(78)	62.5	49	69	—	65
39ki	86	80	93	81.2	(46)	(78)	64	52	68.8	—	66
40ki	100	92	107.8	96.5	57.2	95.5	79.7	72	80.5	—	84
41ki	99	(90)	>95	—	—	—	(77)	68	(75)	—	79
42ki	99.2	86.5	95	87	52	85	74	—	74	—	74
43ki	97	86.2	98	85.5	—	82	75	—	74	—	70.5
44ki	97	82	—	—	—	—	>72	—	77	—	72
45ki	105	95	107	92	58	87	79.4	67.5	82	—	77
46ki	97	85	98	88	55	83.8	>72	—	>70.5	—	73
47ki	92	91.5	103	89	60	86.5	83.5	71	79.5	—	78.5
26he	78	78	95	78	48	74.5	75.5	60	76.8	53	68
27he	(75)	75.5	85	73	45	67	68	55	69	47	61
9he	71	79.5	73.5	90	39.5	70	66.2	54.8	63	38.5	62
28he	76.5	78	95.5	79.7	43.6	73	70.5	60	68.5	46	66.5
189et	70	68	79	70	41	(69)	59	50	60	37.2	49
137hu	82	79	87	77	42	74.5	63.6	52	66	—	60
138hu	83	71.2	82	73	38	72.5	55.3	49	61.8	—	59
79ki	73	71.5	87.5	71	47	70	63.5	(53)	—	47	68
80ki	91	75	91	81.5	54	78	62	50.3	72.5	—	78
81ki	84	74.5	84	75.4	42	76	(66)	51.3	70	—	70

TABLE 26B

Astragalus S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
LL	10	72.50000	1.84089	Lmt	11	59.18182	2.89200
ML	9	69.00000	5.00000	Dmt	10	47.90000	2.76687
B	9	80.33334	3.39117	L1t	9	61.46667	2.25333
BD	9	66.88889	4.80740	Htt	10	40.50000	2.47577
DD	10	42.00000	2.70801	DL	10	52.75000	3.34440
BDa	7	64.28571	4.85504				

Astragalus S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
LL	11	83.47273	4.91082	Lmt	12	65.30833	5.31250
ML	11	76.26363	2.55706	Dmt	12	52.48334	2.44460
B	12	88.21667	4.58869	L1t	11	67.96364	4.18384
BD	12	76.66666	3.09291	Htt	2	46.90000	5.09117
DD	11	45.00000	3.69432	DL	11	60.54546	6.05993
BDa	12	74.08334	3.31548				

Astragalus kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
LL	14	92.80000	7.61264	Lmt	16	73.00625	5.37494
ML	16	85.13750	5.14223	Dmt	12	62.20833	6.98524
B	15	99.12000	4.80122	L1t	11	74.93636	4.48492
BD	14	86.83572	4.59106	Htt	4	54.87500	2.17466
DD	12	53.40834	3.86510	DL	15	73.60000	5.10672
BDa	14	83.80715	4.97895				

Astragalus hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
LL	4	75.12500	3.01040	Lmt	4	70.05000	4.03856
ML	4	77.75000	1.65831	Dmt	4	57.45000	2.94562
B	4	87.25000	10.36420	L1t	4	69.32500	5.67649
BD	4	80.17500	7.14067	Htt	4	46.12500	5.94944
DD	4	44.02500	3.53117	DL	4	64.37500	3.40037
BDa	4	71.12500	3.32603				

TABLE 26C - Astragalus S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
LL	29.89972	<.001
ML	28.16572	<.001
B	26.62995	<.001
BD	36.40181	<.001
DD	22.33869	<.001
BDa	34.66277	<.001
Lmt	19.59605	<.001
Dmt	19.93993	<.001
L1t	18.23464	<.001
Htt	17.13427	<.001
DL	38.43679	<.001

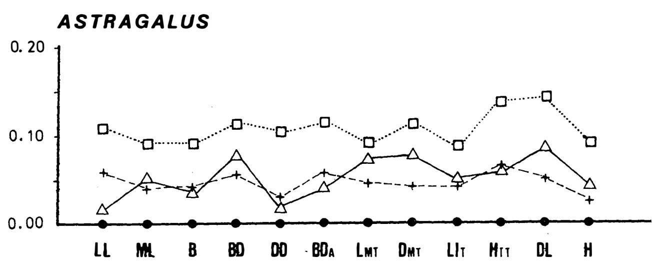


Fig. 22 - Ratio diagram of the astragali of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

sed proximo-distally than that of *S. etruscus*. The third cuneiform appears considerably compressed proximo-distally in *S. hemitoechus* too, though it also appears somewhat stretched dorso-plantarly when compared with that of *S. etruscus*. This bone is quite variable. The only thing that was constantly noted was that the small inner articular facet of the distal articulation is vertical or sub-vertical in *S. etruscus* and *S. hundsheimensis* and oblique in *S. hemitoechus*.

Second cuneiform - (second tarsal) (table 31). Very few second cuneiforms were available to us. They are quite variable in *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*.

I cuneiform - (first tarsal) (table 32). The sample available to us was too poor for any reliable comparison among the species to be made. Nevertheless, the bone appears to be strongly variable.

II Metatarsal - (table 33; fig. 25). The shapes of the proximal epiphysis and of the proximal articular surface are extremely variable. The articular surface appears to be proportionally narrower, but deeper dorso-plantarly, in *S. hundsheimensis* and *S. kirchbergensis* than it is in *S. etruscus*. In proximal view, the proximal epiphysis has a semicircular outline in *S. kirchbergensis* and, instead, a triangular outline in *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*. In *S. etruscus*, the lateral side of the epiphysis is more concave than it is in *S. hundsheimensis*. In *S. kirchbergensis* and *S. hundsheimensis* the posterior articular facet for the third cuneiform and the third metatarsal, in lateral view, is divided into two portions which are separated by a very weak, barely visible line. In *S. hemitoechus*, on the other hand, the posterior facet is small and varies markedly, from roundish to elongated proximo-distally in shape; in addition, it is divided into two parts by a distinct ridge. The diaphysis in *S. kirchbergensis* tends to be straighter and comparatively more slender, but thicker dorso-plantarly than it is in *S. etruscus*, while in *S. hemitoechus* it is again straighter than it is in both *S. etruscus* and *S. hundsheimensis*, but far stockier. The distal articular surface is more asymmetrical in *S. hundsheimensis* than it is in *S. etruscus*; in *S. kirchbergensis* it appears broader than it does in the former two species. In *S. hemitoechus* this articular surface appears rather thickset. The ratio diagram shows how similar are these bones in the four species, and illustrates the slight differences mentioned above.

III Metatarsal - (table 34; fig. 26). As compared with *S. etruscus*, the proximal articular surface appears more convex and deeper dorso-plantarly in both *S. hundsheimensis* and *S. hemitoechus*. In *S. kirchbergensis* this facet is convex and very broad. In *S. etruscus* the diaphysis, in dorsal view, appears parallel-flanked in that its width remains constant throughout its length. On the contrary in the other species the diaphysis widens distalwards, gradually in both *S. hemitoechus* and *S. hundsheimensis* and much more abruptly in *S. kirchbergensis*. In *S. kirchbergensis* the diaphysis is significantly flatter dorso-plantarly than it is in *S. etruscus*, *S. hundsheimensis* or *S. hemitoechus*. In *S. kirchbergensis* the dorsal face of the diaphysis is scored by a broad and rather marked groove that runs obliquely from the proximal border obliquely towards the medial side of the bone. As compared with *S. etruscus* the distal articular surface appears much broader in *S. kirchbergensis* and *S. hemitoechus*. Like in the third metacarpal, all the dimensional differences of the third metatarsal of the four species are statistically significant. Both central metapodials are thus among the most useful bones for discriminating between the species.

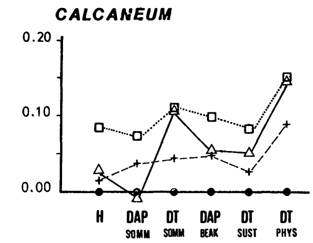


Fig. 23. Ratio diagram of the calcaneums of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 27A - Calcaneum

Characters	H	DAP somm	DT somm	DAP beak	DT sust	DT min post
Specimens						
11et	121	66	44	62	76	34
148et	122	70	44	64	—	31
157et	(120)	66	44	62	—	30
158et	—	64	45	—	—	(34)
159et	109	61	41	57	69.8	32
160et	—	52.5	41	54.6	74.8	31
161et	120	67	46	58	68	31.3
101hu	126	—	46	59	80	37
102hu	—	—	—	69	76	36
103hu	—	—	—	70	78.5	47
104hu	117.3	67	44.3	65.3	74.5	38
105hu	129.2	77	52	68	78	39
106hu	121.8	66	46.1	65	69	36
107hu	127	72	51	64	77.8	41.2
108hu	120.5	70.1	46.7	63.1	75	38
109hu	117	70	46.5	62	69.3	34.2
110hu	126	62	51.5	72	77	44.2
111hu	—	72	49.5	—	—	39.5
112hu	—	—	—	(73)	88	43
113hu	132	68.5	55	62	84.5	45
48ki	151	86	60	74.3	93.2	50
49ki	142	—	56	91	>96	45.5
50ki	—	71	54	65	82	49
51ki	142	70	52	73	83	41
52ki	139	75	57	70	84	44
29he	128	65	56	74	—	45
9he	125	60	55.5	61	81	45
189et	121	67	45.9	60	68.2	35
139hu	119	58	46	62	71.2	39

TABLE 27B

Calcaneum S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
H	5	118.40000	5.31977	DAP beak	6	59.60000	3.61109
DAP somm	7	63.78572	5.68519	DT sust	4	72.15000	3.85530
DT somm	7	43.57143	1.90283	DT min post	7	31.90000	1.55027

Calcaneum S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
H	9	124.08890	5.23150	DAP beak	12	66.03333	4.35772
DAP somm	9	69.40000	4.25764	DT sust	12	77.30000	5.42385
DT somm	10	48.86000	3.43744	DT min post	13	39.85385	3.93375

Calcaneum kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
H	4	143.50000	5.19615	DAP beak	5	74.66001	9.80959
DAP somm	4	75.50000	7.32575	DT sust	5	87.64000	6.46900
DT somm	5	55.80000	3.03315	DT min post	5	45.90000	3.68103

Calcaneum hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
H	2	126.50000	2.12132	DAP beak	2	67.50000	9.19239
DAP somm	2	62.50000	3.53553	DT sust	1	(81.0000)	—
DT somm	2	55.75000	0.35355	DT min post	2	45.00000	0

TABLE 27B

Calcaneum S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
H	19.59782	<.001
DAP somm	5.00258	0.0117
DT somm	21.25763	<.001
DAP beak	5.86076	0.0055
DT min post	20.20086	<.001

Calcaneum S. etruscus - S. hundsheimensis - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
DT sust	9.99192	0.0074

TABLE 28A - Navicular

Characters	L	1	H	H min phys
Specimens				
11et	59	47	30	21.5
148et	54	45	28	21
162et	56	46	27	19
163et	56	45	28	21.2
53ki	84	65.5	40	29.7
54ki	81	60	36	28.3
9he	56	46	29	19.8
189et	—	—	(30)	22
82ki	63	48	28	23.5
83ki	61.5	47.5	(28)	21
84ki	62.1	48.3	(29)	(24)

IV Metatarsal - (table 35; fig. 27). The proximal epiphysis and proximal articular surface are much deeper dorso-plantarly in *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* than they are in *S. etruscus*. In *S. hunsheimensis* and *S. kirchbergensis* the proximal articular surface is sub-circular, while in *S. etruscus* it is sub-triangular. The proximal facet is more concave in *S. kirchbergensis* than it is in the other species. In *S. hemitoechus* the proximal epiphysis is strengthened by the thicke-

TABLE 28B

Navicular S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	56.25000	2.06115	H	4	28.25000	1.25831
1	4	45.75000	0.95743	H min phys	4	20.67500	1.13541

Navicular S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	82.50000	2.12132	H	2	38.00000	2.82843
1	2	62.75000	3.88909	H min phys	2	29.00000	0.98995

Navicular hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(56.0000)	—	H	1	(29.0000)	—
1	1	(46.0000)	—	H min phys	1	(19.8000)	—

TABLE 28C - Navicular S. etruscus - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
L	213.0435	<.001
1	86.22844	<.001
H	39.76471	<.01
H min phys	76.25168	<.001

ning of its medio-plantar portion and swollen. In medial view, the articular facets for the III Metatarsal are more prominent in *S. hunsheimensis* and *S. hemitoechus* than they are in *S. etruscus*. In *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* the diaphysis and the distal epiphysis are always narrower latero-medially and thicker dorso-plantarly than they are in *S. etruscus*. The cross section of the diaphysis varies in the four species: it is elliptical in *S. etruscus*; elliptical, but much flatter, in *S. kirchbergensis*; elliptical to ovoidal in *S. hemitoechus*; sub-circular in *S. hundsheimensis*. The diaphysis is arched to essentially the same degree in *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*, while it is straighter in *S. kirchbergensis*. In *S. hundsheimensis* the lateral condyle of the distal articular surface is stronger and less concave than it is in either *S. etruscus* or *S. hemitoechus*. In *S. hundsheimensis* and especially in *S. hemitoechus* the distal epiphysis is broader than it is in *S. etruscus*. The analysis of variance shows that three dimensions are particularly discriminating, DP, DPa, and DS, which reflects the flattening of the fourth metatarsal of *S. etruscus*. The differences described above are well depicted by the ratio diagram.

In summary, the skeleton of *S. hundsheimensis* is slightly larger than that of *S. etruscus*, with bones that are in some cases more robust. The postcranial

TABLE 29A - Cuboid

Characters	L	1	H	DAP art prox	DT art prox	H face ant
Specimens						
11et	61	47	60	35	40	42
148et	—	43	—	36	39	42
164et	56	36	50	41	32	37
165et	56	42	51	37	38	37
166et	—	39	—	(41)	37	36
114hu	69	47	64	53	41	43
115hu	64.5	45.5	58	45	40.5	39.5
116hu	67	40.5	66	53	42	44.3
117hu	—	39.5	57	55	40.5	44
118hu	64	(40)	(57)	—	(39)	(40)
55ki	74	48.8	64	42	52	46
56ki	73.5	57	59.2	39	49	50
57ki	64	47.5	57	42	45	39
58ki	71	51	55	49	43	44
9he	63	43.3	58.5	33	42.3	45.5

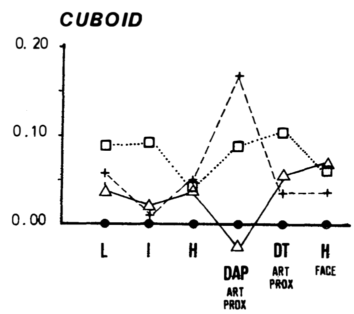


Fig. 24 - Ratio diagram of the cuboids of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

TABLE 29B

Cuboid S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	57.66667	2.88675	DAP art prox	5	38.00000	2.82843
1	5	41.40000	4.15933	DT art prox	5	37.20000	3.11448
H	3	53.66667	5.50757	H face ant	5	38.80000	2.94958

Cuboid S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	66.12500	2.32289	DAP art prox	4	51.50000	4.43471
1	5	42.50000	3.48210	DT art prox	5	40.60000	1.08397
H	5	60.40000	4.27785	H face ant	5	42.16000	2.25898

Cuboid S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	70.62500	4.60751	DAP art prox	4	43.00000	4.24264
1	4	51.07500	4.20585	DT art prox	4	47.25000	4.03113
H	4	58.80000	3.86782	H face ant	4	44.75000	4.57347

Cuboid S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(63.0000)	—	DAP art prox	1	(33.0000)	—
1	1	(43.3000)	—	DT art prox	1	(42.3000)	—
H	1	(58.5000)	—	H face ant	1	(45.5000)	—

TABLE 29C - Cuboid S. etruscus - S. hundsheimensis - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
L	12.04394	0.0101
1	7.75966	0.0141
H	2.19755	0.1733
DAP art prox	14.06101	0.0075
DT art prox	13.59988	0.0073
H face ant	3.74484	0.0637

skeletons of *S. etruscus* and *S. hundsheimensis* look rather alike. The main differences between the two species are that, in proportion, *S. hunsheimensis* has long bones with broader joints, especially evident in the distal epiphyses, while its metapodials are more developed dorso-palmarly (or -plantarly). The intervening basipodials individually contribute to form a transition between these two opposite conditions; thus, a correspondingly general, dominating feature of these bones is lacking.

The absolute sizes and proportions of the bones of *S. hemitoechus* are sometimes close to those of *S. hundsheimensis*, and more rarely to those of *S. etruscus*; but they usually are morphologically distinguishable.

In these rhinoceroses metapodials are the most indicative bones of the postcranial skeleton. *S. etruscus* and *S. hundsheimensis* have rather similar second and third metacarpals, whereas both these bones are usually shorter in *S. hemitoechus*. The

TABLE 30A - III Cuneiform

Characters	L	1	H	H min phys
Specimens				
11et	46	41	26	21
148et	42	39	23	20
167et	46	43	23	20
168et	45	38	25	20.2
169et	45.5	43.1	24.5	19
119hu	45	41	22	19
120hu	—	46	22	19.4
121hu	49.5	44.5	26	21.8
122hu	51.5	—	24	21
9he	46	45	27	19
189h	44	36	24	21.8

TABLE 30B

III Cuneiform S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	5	44.90000	1.67332	H	5	24.30000	1.30384
1	5	40.82000	2.30478	H min phys	5	20.40000	0.71274

III Cuneiform S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	48.66667	3.32916	H	4	23.50000	1.91485
1	3	43.83333	2.56580	H min phys	4	20.30000	1.32162

III Cuneiform S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(46.0000)	—	H	1	(27.0000)	—
1	1	(45.0000)	—	H min phys	1	(19.0000)	—

TABLE 30C - Cuboid S. etruscus - S. hundsheimensis - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
L	4.78359	<.20
1	2.96827	<.20
H	0.55930	>.20
H min phys	0.14460	>.20

TABLE 31 - II Cuneiform

Characters	L	1	H
Specimens			
11et	32	21	18
169et	25.6	24	17.2
123hu	32.5	29	16
9he	33.5	18.4	21

TABLE 32 - I Cuneiform

Characters	L	DT	DAP	DAP art	DT art
Specimens					
11et	46	29	19	26	16
59ki	69.2	38	26	—	—
9he	76	32	18	—	—

largest metapodials are those of *S. kirchbergensis*. In *S. hemitoechus* and, to a much greater degree, in *S. kirchbergensis*, the diaphysis of the third metacarpal enlarges distalwards and the bone has a distal epiphysis which is proportionally broader than those of both *S. etruscus* and *S. hundsheimensis*. This is readily shown by the ratio of the breadths of the diaphyses and the distal epiphyses by the total length of the bone.

The fourth metacarpal is the metapodial least represented in the collections we examined. That of *S. hundsheimensis* has thicker dorso-palmar diameters than that of *S. etruscus*.

As compared with the other species, the diaphysis of the second metatarsal of *S. hemitoechus* is enlarged distally and flattened dorso-palmarly.

The third metatarsal is indeed one of the most indicative metapodials. The ratio between the breadth of the distal epiphysis and the total length of the bone is highly discriminating. Whereas in *S. etruscus* and *S. hundsheimensis* this ratio ranges from 0.27 and 0.30, in *S. hemitoechus* it varies from 0.30 to 0.32 and in *S. kirchbergensis* it reaches even higher values. The ratio between the breadth of the diaphysis and the total length of the bone is also significant, though to a lesser degree.

On the other hand, the fourth metatarsals do not appear to be very indicative.

In all four species the metatarsals are always shorter than the metacarpals. In *S. kirchbergensis*

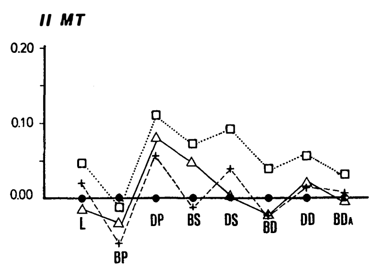


Fig. 25 - Ratio diagram of the second metatarsals of S. hundsheimensis, S. kirchbergensis and S. hemitoechus, versus means for S. etruscus from the Upper Valdarno (standard).

TABLE 33A - II Metatarsal

Characters	L	BP	DP	BS	DS	BD	DD	BDa
Specimens								
11et	162	34	34	29	24	37	37	32.3
148et	149	24	32	23	24	35	34	31
170et	179	42	39	30	29	44	44	35.3
171et	—	30	34	20	22	—	—	—
172et	145	34	36	25	23	34	33	31
173et	(131)	—	—	24	21	—	—	—
174et	—	—	—	28	21	—	—	—
175et	152	25	36	26	24	41	34	33
169et	—	30	34	(19.2)	(18.7)	—	—	—
33et	—	40.9	(30)	(22.3)	(21.5)	—	—	—
124hu	—	30	41.5	—	—	—	—	—
125hu	161	24	40	24	25	36	37.5	33
60ki	—	32	50	31	30	—	—	—
61ki	177	34.5	48	29	30	44	44	39.5
62ki	173.5	27	46	27.3	28.8	41.5	41	35
63ki	—	29.5	43.5	28	25	—	—	—
64ki	184.5	(>26)	45	30	(29.4)	42.9	42.5	34
65ki	158.1	29.1	42	27	26.4	39	38	32.5
66ki	175	33.5	48.5	32.5	28	44.1	41	36.3
67ki	161	31.2	45.8	29	27	39.3	41.8	33.2
30he	(148)	—	—	25	25	32.5	37.4	28.6
31he	150	30	45	31	24	39	45	36
32he	148.5	26.5	40	25	22	35	35.2	30
33he	144	28	42	27	22	36	35.3	31.5
34he	156	31	45	30	22.3	38.5	37	35
189et	—	—	—	(24)	(23)	34	36	31.8
85ki	158	—	—	22.5	22.5	35.5	36.2	31.8
86ki	178	—	—	27.8	27.7	(39)	43	35
87ki	155	27.3	40.5	25.3	21.2	36	35	30

TABLE 33B

II Metatarsal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	6	153.00000	16.26038	DS	10	22.82000	2.75713
BP	8	31.12500	5.69304	BD	5	38.20000	4.20714
DP	8	35.73750	2.93887	DD	5	36.40000	4.50555
BS	10	24.65000	3.66219	BDa	5	32.52000	1.77679

II Metatarsal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	1	(161.0000)	—	DS	1	(25.0000)	—
BP	2	27.00000	4.24264	BD	1	(36.0000)	—
DP	2	40.75000	1.06066	DD	1	(37.5000)	—
BS	1	(24.0000)	—	BDa	1	(33.0000)	—

II Metatarsal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	6	171.51670	10.05294	DS	8	28.07500	1.81718
BP	8	30.35000	3.00048	BD	6	41.80000	2.25920
DP	8	46.10000	2.65814	DD	6	41.38334	2.00042
BS	8	29.22500	1.87978	BDa	6	35.08333	2.54513

II Metatarsal S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	5	149.30000	4.35316	DS	5	23.06000	1.36675
BP	4	28.87500	2.01556	BD	5	36.20000	2.65989
DP	4	43.00000	2.44949	DD	5	37.98000	4.04623
BS	5	27.60000	2.79285	BDa	5	32.22000	3.18465

TABLE 33C
II Metatarsal S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BP	1.64256	0.2563
DP	5.95846	0.0205
BPa	1.56629	0.2818
BS	1.09711	0.4059
DS	0.39655	0.7602

II Metatarsal S. etruscus - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	7.61386	0.0495
BD	3.21633	0.1532
DD	28.61923	0.0105
BDa	9.97430	0.0341

and *S. hemitoechus* the difference between metatarsals and metacarpals is greater than it is in *S. etruscus* and *S. hundsheimensis*.

The overall dimensions of the astragali increase in the following order: *S. etruscus*, *S. hemitoechus*, *S. hundsheimensis* and *S. kirchbergensis*. However *S. hemitoechus* sometimes has an astragalus proportionally wider than that of *S. hundsheimensis*.

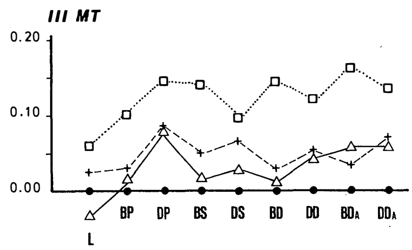


Fig. 26 - Ratio diagram of the third metatarsals of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus*
from the Upper Valdarno (standard).

TABLE 34A - III Metatarsal

Characters	L	BP	DP	BPa	DPa	BS	DS	BD	DD	BDa
Specimens										
11et	163	44	—	—	32	31	19	38	38	38
148et	—	41	35	36	31.5	—	—	—	—	—
182et	—	41	37	37	27	27	19	—	—	—
171et	—	35	34	32	30	26	18	—	—	—
183et	—	36	33	—	26	25	18	—	—	—
184et	150	36	35	—	30.5	28	20	32	33	33
185et	—	38	33	—	27	29	15	—	—	—
186et	149	38	32	(31)	(24.8)	32	21	33.5	34.2	33.8
133hu	—	35.5	38.2	32.9	33.5	—	—	—	—	—
134hu	—	43.5	40.1	37.5	34.8	—	—	—	—	—
135hu	—	40.3	40.1	35	36	22.1	30	—	—	—
136hu	155	39.5	40	32.8	33.4	18.5	31	31	38	29.9
137hu	161	43	41	35.7	40	29	26	35.5	41.3	35.5
73ki	—	46	53	43	41	22	36.3	—	—	—
74ki	—	46.3	56.2	38.5	46.2	—	—	—	—	—
75ki	—	—	55	—	46.8	—	—	—	—	—
40he	—	41	48	41	—	24	32	—	—	—
36he	—	46	46	46	—	26	31	—	—	—
9he	153.8	43.5	43	37.2	31.3	30	30	32.1	36	31.3
9he	151.5	47.1	43.2	36.2	32	30.5	24	34	38	33
189et	156	43	35	38	38	28	20	38	35	35.3
89ki	164	46	37	42	—	29	21	36	42	—

Table 34B

III Metatarsal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	181.00000	5.56776	DS	7	20.71429	2.87021
BP	8	48.00000	2.72554	BD	4	51.50000	4.43471
DP	5	35.25000	4.50000	DD	5	36.40000	4.50555
BS	5	39.84000	1.15239	BDa	2	41.00000	1.41421

III Metatarsal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	192.50000	7.59386	DS	6	24.11667	1.19066
BP	8	51.67500	4.10287	BD	4	55.25000	1.51987
DP	8	43.46250	3.04909	DD	4	41.25000	0.95743
BS	6	44.83333	0.87331	BDa	4	44.87500	2.24109

III Metatarsal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	4	208.00000	3.55903	DS	5	25.84000	1.97939
BP	5	61.06000	2.71717	BD	3	72.40000	1.44222
DP	5	49.48000	3.04335	DD	3	48.06667	3.90043
BS	5	55.36000	3.65349	BDa	4	59.67500	2.49449

III Metatarsal S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	7	167.64290	5.23382	DS	7	22.12857	1.53809
BP	7	49.85715	3.71612	BD	5	53.20000	1.30384
DP	7	42.47143	3.66366	DD	6	40.05000	2.83108
BS	7	41.67143	2.06939	BDa	6	46.73334	2.23398

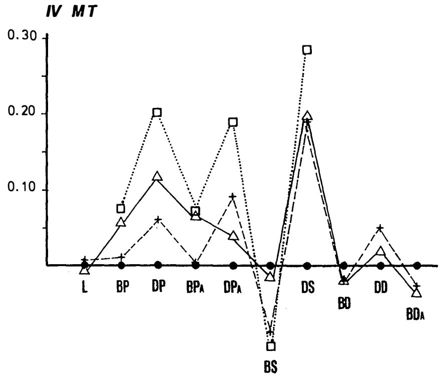


Fig. 27 - Ratio diagram of the fourth metatarsals of *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus*, versus means for *S. etruscus* from the Upper Valdarno (standard).

III Metatarsal S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BP	19.61758	<.001
DP	22.90106	<.001
BS	54.46417	<.001
DS	8.49835	0.0020

III Metatarsal S. etruscus - S. hundsheimensis - S. kirchbergensis

	(F) Statistic	(P) (One-Tailed)
L	16.47541	<.001
BD	41.631	<.001
BDa	47.64	<.001
DD	35.66138	<.001

TABLE 35A - IV Metatarsal

Characters	L	BP	DP	BS	DS	BD	DD	BDa
Specimens								
11et	182	52	—	41	24	55	37	42
148et	175	50	39	39	21	53	34	40
176et	—	49	35	—	21	—	44	—
177et	(186)	(43)	—	39	23	(53)	—	—
178et	—	47	—	—	20	—	33	—
179et	—	49	—	—	—	—	—	—
180et	—	—	—	—	—	(45)	—	—
181et	—	(46)	29	39	21	—	34	—
169et	—	48	38	(41.2)	(15)	—	—	—
100hu	197	53.3	45.7	45.7	25.2	56.3	42	44
126hu	199	55	42	44	25.2	55.7	40	42.2
127hu	192	50.3	41	44.3	24.5	53	42	47.3
128hu	—	(46)	43	45	23.8	—	—	—
129hu	—	55	46	—	—	—	—	—
130hu	—	55.2	48	44	24	—	—	—
131hu	—	45.1	38.5	—	—	—	—	—
132hu	182	53.5	43.5	46	22	56	41	46
68ki	206	58.1	45.1	54	24.5	—	44.2	58
69ki	211	65.2	53.3	56	25.9	72	52	62.5
70ki	211	—	—	54.8	27.5	71.2	48	61
71ki	—	62	51	61	28	—	—	—
72ki	—	59.5	49.5	—	—	—	—	—
61ki	204	60.5	48.5	51	23.3	74	—	57.2
35he	172	52	47	45	22	(54)	40.3	49.7
36he	169	48	40	43	22	52	38	45
37he	160	50	38	43	20.7	52	37	44
38he	(162.5)	(43)	40	39.5	20.5	—	—	—
39he	(165)	(51)	47.3	41	22.3	—	39	49
9he	171	50	41	40.8	22.2	53	41	46.7
9he	174	55	44	39.4	25.2	55	45	46
189et	183	49	—	43	22	54	36	40.5
88ki	181	50	42	44	21	61	42	49

TABLE 35B

IV Metatarsal S. etruscus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	3	154.00000	7.81025	BS	7	28.28572	2.56348
BP	8	38.62500	3.11391	DS	7	18.57143	1.90238
DP	7	34.14286	1.67616	BD	3	34.50000	3.12250
BPa	4	34.00000	2.94392	DD	3	35.06667	2.61024
DPa	8	28.60000	2.72187	BDa	3	34.93334	2.68576

IV Metatarsal S. hundsheimensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	158.00000	4.24264	BS	3	23.20000	5.33573
BP	5	40.36000	3.20905	DS	3	29.00000	2.64575
DP	5	39.88000	1.02323	BD	2	33.25000	3.18198
BPa	5	34.78000	1.98419	DD	2	39.65000	2.33345
DPa	5	35.54000	2.71072	BDa	2	32.70000	3.95980

IV Metatarsal S. kirchbergensis

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	—	—	—	BS	1	(22.0000)	—
BP	2	46.15000	0.21213	DS	1	(36.2000)	—
DP	3	54.73334	1.61658	BD	—	—	—
BPa	2	40.75000	3.18198	DD	—	—	—
DPa	3	44.66667	3.18957	BDa	—	—	—

IV Metatarsal S. hemitoechus

	N	Mean	St. Dev.		N	Mean	St. Dev.
L	2	152.65000	1.62635	BS	4	27.62500	3.14576
BP	4	44.40000	2.72152	DS	4	29.25000	3.59398
DP	4	45.05000	2.39653	BD	2	33.05000	1.34350
BPa	4	40.10000	4.44372	DD	2	37.00000	1.41421
DPa	2	31.65000	0.49497	BDa	2	32.15000	1.20208

TABLE 35C

IV Metatarsal S. etruscus - S. hundsheimensis - S. kirchbergensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
BP	5.57007	0.0100
DP	111.0389	<.001
BPa	4.17523	0.0345
DPa	27.20814	<.001

IV Metatarsal S. etruscus - S. hundsheimensis - S. hemitoechus

	(F) Statistic	(P) (One-Tailed)
L	0.44351	0.6762
BS	2.46313	0.1369
DS	28.98808	<.001
BD	0.20135	0.8317
DD	2.39398	0.2134
BDa	0.70286	0.5538

DISCUSSION

In this section we shall review the phylogeny, temporal distribution and evolution of the European Plio-Pleistocene *Stephanorhinus* in the light of the data presented in previous sections. We emphasise again that our main objective has been to make available data collected for various purposes over an extended period of time, and that our study is therefore arbitrarily limited to the Plio-Pleistocene of Western Europe. It is not our intention to review the entire clade to which our taxa belong, nor do we wish our conclusions to be extended beyond the limits of our material.

Phylogeny

Stephanorhinus, comprising dolichocephalic, two-horned rhinoceroses with strongly molarised premolars and without functional incisors, is apparently and by concensus either the paraphyletic stem group from which *Coelodonta* arose or the sister-group of *Coelodonta* (Guérin, 1980; Heissig, 1981; Groves, 1983). Its position within the Rhinocerotidae is controversial (Groves, 1983), but is of no consequence here.

Several phylogenetic schemes have been proposed for the taxa under discussion. The simplest and most extreme versions are probably those of Schroeder (1903), who derives *S. kirchbergensis* from *S. hundsheimensis*, and Cigala-Fulgosi (1976), who suggests a transformation series *S. etruscus* — *S. hundsheimensis* (*"D. hemitoechus intermedius"*) — *S. hemitoechus*. We shall show that neither of these heterodox schemes is tenable, but also that the present material is insufficient to resolve the phylogenetic relationships in detail.

Two assumptions underlie our interpretation of the phylogenetic relationships of the species considered in this study. First, that complex associations of characters are less subject to convergent evolution than are simple characters or proportions. Secondly, that changes in different organ systems can be related to underlying ontogenetic and functional scenarios.

Throughout the results discussed above, *S. kirchbergensis* emerges as the most distinctive species. This apparently reflects the fact that *S. kirchbergensis* belongs to a different clade within *Stephanorhinus* than the other species investigated. A complex of associated dental characters unites the Pliocene *S. megarhinus* with *S. kirchbergensis* (in which it is more strongly expressed): smooth enamel, "molten" overall shape with weak styli and folds, open valleys and inflated lingual cusps on the upper premolars and molars. Largely on the basis of this similarity, Wüst (1922) and Staesche (1941) derived *S. kirchbergensis* from *S. megarhinus*. The same complex is seen in East Asian species usually considered closely related to or synonymous with *S. kirchbergensis* (*S. choukoutiensis*, *S. nipponicus*), as well as in certain Miocene species such as *S.* (?) *schleiermacheri* and *S.* (?) *orientalis*. Heissig (1973) suggested that all these form one clade, which would have had to be independent at least since the later Miocene. Similarly, *S. hemitoechus* shows the strongest expression of a dental character complex also seen in *S. hundsheimensis*, *S. etruscus* and the Early Villafranchian *S. jeanvireti*: relatively rough enamel, distinct folds and styli, relatively narrow valley entrances and frequent occurrence (in each species) of a small lingual cingulum beneath the posterior valley entrance on lower molars. Polarity is not an issue here, since both complexes of associated dental characters, the one of *S. megarhinus* - *S. kirchbergensis* and that of *S. jeanvireti* - *S. etruscus* - *S. hundsheimensis* - *S. hemitoechus*, are mixtures of primitive and derived characters. As complexes they define a clade each, but are useless for further phylogenetic analysis. In the present limited context this is not a problem.

An ontogentic and functional evolutionary scenario emerges naturally from consideration of the morphology seen in the two groups defined by the dental character complexes described above. In the *S. kirchbergensis*-clade, mandibles are deep in their rostral portion, with deep symphyses, while in the *S. hemitoechus*-clade mandibles characteristically taper rostrally and the symphysis is shallow. Both *S. kirchbergensis* and *S. hemitoechus* are hypsodont, but their dentitions have very different proportions. *S. kirchbergensis* has high premolars and low last molars, while *S. hemitoechus* has the opposite: quite low premolars and very high molars, especially the last. High premolars can only grow in deep jaws, and could therefore not have evolved in *S. hemitoechus* without redesign of the mandible. Such did not take place, and the molars were emphasised instead.

Taking this one step further one may hypothesise that a general reduction of the rostral portion of the head and the jaws was related to incisor loss. The incisors were already completely lost in all the species of the *S. hemitoechus*-clade considered here, whereas *S. megarhinus* still retained vestigial, non-functional incisors. Consequently, incisor loss in *Stephanorhinus* must have happened at least twice, and was completed later in the *S. kirchbergensis* clade than in the *S. hemitoechus*-clade. Different timing of incisor loss might thus explain the different paths to hypsodonty seen in the two clades.

It is worth pointing out that the dentition of *Diceros bicornis* is quite similar to that of *S. kirchbergensis*, including the markedly ectolophodont morphology with hypsodont premolars and weak styli, and that *D. bicornis*, too, lost its incisors without a reduction of its rostral part of the head. Indeed, even *Ceratotherium simum*, with its highly hypsodont and plagiolophodont dentition, retained its rostrally deep head, significantly in association with hypsodont premolars. In contrast, *Coelodonta antiquitatis*, which had an equally plagiolophodont dentition but a rostrally shallow head, had increased molars and reduced premolars, just as *S. hemitoechus*. It is thus probable that incisor loss in *Coelodonta* occurred before the evolution of hypsodonty.

A summary of this discussion is presented in the form of a cladogram in fig. 28. We regard *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti* as the unresolved sister group of *S. hemitoechus*, and this whole complex as the sister group of the distinctive *S. megarhinus* — *S. kirchbergensis* clade. Note that this is not a complete suggested phylogeny, only a cladogram depicting the relationships between the taxa included in the present study. Other Pliocene and even Miocene species are certainly part of the phylogeny of the entire clade.

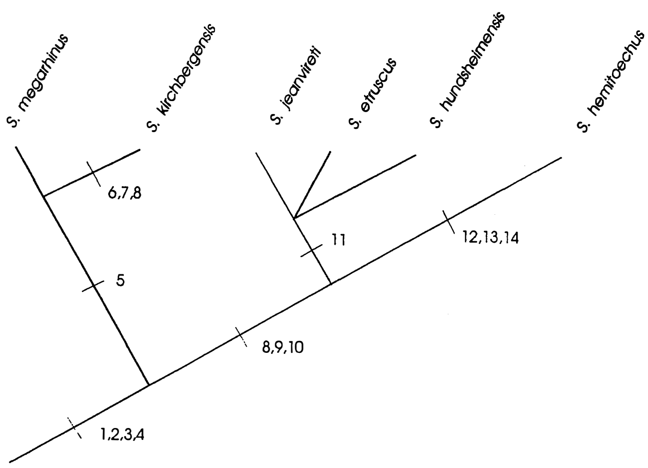


Fig. 28 - Cladogram of the taxa treated in this study, with *Stephanorhinus megarhinus* and *S. jeanvireti* added. Note that Miocene and other Pliocene taxa which form part of the full phylogeny of the clade are excluded.

A few points may be made with regard to the unresolved trichotomy of "etruscoid" species. It is certainly conceivable that *S. etruscus* is relatively close to the ancestral morphotype of the *S. hemitoechus*-clade, with *S. hundsheimensis* and *S. hemitoechus* representing divergently derived forms, as has been assumed on the basis of their stratigraphic position by most authors (e.g., Zeuner, 1934; Guérin, 1980, 1982; Mazza, 1988). Alternatively, *S. hundsheimensis* might represent the most primitive condition, with *S. etruscus* and *S. hemitoechus* showing different stages of a trend towards a reduction of the muzzle and, perhaps consequently, an increased importance of the posterior teeth. With regard to this possibility, it must be noted that the Early Villafranchian *S. jeanvireti* from Vialette (Guérin, 1972) is highly similar in most characters to *S. hundsheimensis*. The 8 characters that distinguish *S. hundsheimensis* from *S. etruscus* listed by Mazza (1988: 63) would seem to apply with equal force to *Stephanorhinus jeanvireti*, as far as the incomplete material allows one to determine. Both are larger, with a steeper parietal profile shifted more posteriorly in the skull, a characteristic bump over the frontals, relatively low orbits, more plunging and less diverging zygomatic arches, large narial incisions and trapezoidal occiputs. In addition, both lack incisors, have relatively large M1, long 'diastemata', a similar otic morphology and similar, laterally compressed distal humeri. It would thus be quite reasonable to regard the morphotype represented by *Stephanorhinus jeanvireti* and *S. hundsheimensis* as primitive relative to *S. etruscus* and *S. hemitoechus*. We do not believe that the matter is resolvable at present, nor do we wish to assign a role for the small sized etruscus-group rhinoceroses of Western Europe at the transition between Early and Middle Pleistocene discussed in the following section.

Stratigraphy

There are a number of stratigraphically problematic occurrences of rhinoceros fossils in the European Pleistocene. A number of specimens from Meyrargues in the Rhone Valley were identified as *Dicerorhinus merckii* by Bonifay (1961) and later as *D. megarhinus* by Guérin (1980), the latter identification being in accordance with the morphology of the specimens but not with the apparently Late Pleistocene age of the deposit. Skull and jaw fragments, partial dentitions and isolated teeth found at Gross-Rohrheim and a number of other localities in the Upper Rhine Valley are also undistinguishable from those of *S. megarhinus* (Koenigswald, 1988). These multiple occurrences make explanations based on stratigraphic misinterpretation or aberrant individuals improbable, but their significance is unclear.

The earliest occurrence of *S. etruscus* is in the Early Villafranchian site of Città della Pieve, Palaia, and the species persists throughout the Late Villafranchian assemblages, being replaced at its very end by small sized forms, currently unassigned to species (see below).

As *S. etruscus* and *S. hundsheimensis* cannot be separated on the basis of isolated teeth, and diagnostic material is therefore relatively rare, the stratigraphic relationship between the two species is unclear at the transition from the Early to the Middle Pleistocene. As far as can be determined, the early Middle Pleistocene (Galerian) "etruscoid" rhinoceros is referable to *S. hundsheimensis* throughout Europe (see also Guérin, 1980). The most notable anomaly with respect to the whole *S. etruscus—S.hundsheimensis* group is a good specimen from the late Middle Pleistocene at Torrente Conca, associated with unquestionable *S. hemitoechus* material (Conti *et al.*, 1982).

Remains of small rhinoceroses with *S. etruscus* - *S. hundsheimensis* affinities occur at Pietrafitta (Umbria, central Italy), Pirro (Gargano, southern Italy), Westerhoven (Brabant, Netherland), Colle Curti (Colfiorito Basin, Macerata, central Italy), Loreto (Venosa, southern Italy) and Wissel (Kalkar, Germany) (Mazza *et al.* in this volume).

The taxa appearing in these sites are characteristic elements of the latest Late Villafranchian faunas that are chronologically referrable to the latest Early Pleistocene - early Middle Pleistocene. Pirro is taken to be more recent than Pietrafitta on the basis of the first occurrence of *Eobison* and *Equus* cf. *altidens* (De Giuli *et al.*, 1987) (*E. stenonis* according to Azzaroli, pers. comm.). Westerhoven is the type locality of the Interglacial II of the "Cromerian" of the Dutch continental stages (Kolfschoten, 1989). However, the rhinoceros material and remains of *Archidiskodon meridionalis* from this locality, are of unknown stratigraphical provenance.

The scanty postcranial bones of the form from Pirro and Westerhoven, and the more abundant specimens from Pietrafitta have characters and proportions suggestive of *S. hundsheimensis*. Even though little is still known of these forms, the dental remains from Pietrafitta show some *S. etruscus*-like characters (Mazza *et al.* in this volume). The only common character shared by the Pirro, Pietrafitta and Westerhoven rhinoceroses appears to be their reduced body size. The small rhinoceroses might serve as a useful stratigraphic marker, as they are easily recognisable, seem to be widely dispersed throughout Europe and to have a restricted distribution in time.

The Pietrafitta, Pirro and Westerhoven rhinoceroses might be considered transitional forms showing various stages intermediate between *S. etruscus* and *S. hundsheimensis*, or they might be seen as small sized populations unrelated to a speciation event. Since they appeared concomitantly with the changing climatic conditions that characterized the end of the Early Pleistocene, one might hypothesise that the size reduction was due to environmental stress. If so, it could show up in other taxa as well.

A number of early occurrences of *S. hemitoechus* are also stratigraphically problematic. A partial mandible, referrable to this species, is known from Croce dei Cappuccini (Montevarchi MV 8/18). The site appears to be of Villafranchian age but the specimen is part of an old collection and its provenance is uncertain. A pair of mandibles of *S. hemitoechus* are also known from Bacton in East Anglia (London NHM M19425), but may be from Late Pleistocene deposits (Andrew P. Currant, personal communication 1983, 1990).

S. hemitoechus is rare at Mosbach, but definitely does occur there, along with *S. hundsheimensis* and *S. kirchbergensis*. From the long stratigraphic sequence Koenigswald & Tobien (1987) list *S. hundsheimensis* (*D. etruscus* in their nomenclature) from Mosbach-1 (older than 0.89 Ma), *S. hundsheimensis* and *S. kirchbergensis* from Mosbach-2 (younger than 0.7 Ma), and no rhinoceros remains from the still younger Mosbach-3. Guérin (1980: 917) listed *S. hundsheimensis* (*D. etruscus brachycephalus*) and *S. kirchbergensis* (*D. merckii*) from Mosbach I, and most other authors have also referred the Mosbach material to these taxa. However, Toula (1906), and especially Wüst (1922), identified several specimens from Mosbach as *S. hemitoechus*, including some figured by Schroeder (1903, Plate VII:1-2, Plate IX:2 and Plate XII:1).

In addition to the *S. hemitoechus* specimens correctly identified by Toula and Wüst, there are at least three mandibles and an upper molar from Mosbach that show the characteristics of *S. hemitoechus*. The mandibles (Mainz 1935/289, an unnumbered specimen at Mainz, and Darmstadt Mb130) have the characteristically slender symphysis of *S. hemitoechus*, and the toothrows show the mesio-distally increasing size gradient of this species (fig. 8). The molar (Darmstadt Mb137) is distincly more hypsodont than is common in *S. hundsheimensis* molars, with a very narrow medisinus entrance and rough enamel. The lingually long and mesially narrow molars appear to be characteristic of the Mosbach form (fig. 8). Other specimens are probably present as well, but no systematic inventory to locate them has yet been carried out. The three mandibles most probably are from Mosbach-2, which suggests that *S. hundsheimensis*, *S. kirchbergensis*, and *S. hemitoechus* lived there roughly contemporaneously.

S. hemitoechus also definitely occurs before the late Middle Pleistocene at Petralona (Fortelius & Poulianos, 1978), at Visogliano (Bartolomei *et al.* 1977) and at Caune de l'Arago (Guérin 1981). The species became common in the late Middle and Late Pleistocene.

Cerdeño & Sanchez (1988) reported *S. hemitoechus* from Atapuerca. The presence of *Canis lupus* cf. *mosbachensis*, *Panthera gombaszoegensis* and *Bison schoetensacki* among the faunal components reported in this paper indicates that the Atapuerca fauna is referrable to the early Middle Pleistocene (sensu Azzaroli, 1977 and Azzaroli *et al.*, 1988). The attribution of these remains to *S. hemitoechus* is probably mistaken, although the lower dentition figured shows some *S. hemitoechus*-like features, notably the strongly angled and buccally flat metalophids. The postcranial material figured by Cerdeño & Sanchez definitely suggests that the rhinoceros from Atapuerca should be attributed to *S. hundsheimensis*. This conclusion is supported in particular by the form of the astragalus, calcaneum and third metatarsal, which correspond closely to those of Toula's species (see description above and figures 22, 23, 26). As compared with *S. hemitoechus* the astragalus from Atapuerca is less expanded latero-medially and more stretched proximodistally, the corpus of the calcaneum is much more slender and more elongated proximally, with a more prominent sustentaculum tali and the third metatarsal has a comparatively more slender and stretched diaphysis. These features are all typical of *S. hundsheimensis*. The metric data given by Cerdeño & Sanchez, which also covers other bones not mentioned above, further support our conclusion.

S. kirchbergensis first occured in the early Middle Pleistocene (Mosbach and presumably Daxlanden), but, like *S. hemitoechus*, became common only in the late Middle Pleistocene.

It thus appears that *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* all occurred in the early Middle Pleistocene of Western Europe. Their remains are rarely found together, but all three occur at Mosbach, as noted.

Evolution and palaeoecology

Within the Early and early Middle Pleistocene, sample sizes are too small and/or the temporal resolution is too poor to allow recognition of evolutionary change within species. For both the species with ranges extending into the late Middle and Late Pleistocene, *S. hemitoechus* and *S. kirchbergensis*, a trend of increasing size is seen, as shown above, but the details remain obscure. The differences between species, on the other hand, have long been recognised as being of evolutionary interest, especially in terms of palaeoecology (Zeuner, 1934, Fortelius, 1982). We are now in a position to summarise and develop these arguments in the light of our findings.

The European Pleistocene species of *Stephanorhinus* fall conveniently into three functional and ecological classes. *S. etruscus* and *S. hundsheimensis* were long-limbed animals with a dentition and head posture suggestive of browsing on vegetation of intermediate height. The limb joints are relatively shallow, which together with cursorial limb proportions suggests locomotion in predominantly open habitats. *S. hundsheimensis* was the larger and less cursorial of the two, with a longer face and larger horn bases suggesting larger horns.

S. hemitoechus, although closely related to the former, was a rather different kind of animal, much more short-limbed, with hypsodont molars and a low-slung cranium with narrow nasals and weak horn bases (Late Pleistocene skulls appear more robust, and frequently have larger horn bases as well). The limb joints are similar to those of the "etruscoid" species, and may be taken as evidence for an open rather than closed habitat. *S. hemitoechus* shows remarkable convergence in many details with *Coelodonta antiquitatis*, notably in its compact build, low-slung cranium and hypsodont teeth. It differs from the woolly rhino in having ectolophodont rather than plagiolophodont molars, and was therefore most probably not a true grazer but more of an intermediate feeder on low growing vegetation (Fortelius, 1982).

S. kirchbergensis, finally, was a very large rhinoceros with long legs and a high head posture. The ectolophodont dentition with very high crowned premolars but moderately hypsodont molars in combination with the high head suggest a predominantly browsing mode of feeding, while the strongly concave limb joints suggest locomotion in a predominantly closed forest or woodland environment.

CONCLUSIONS

Whereas the status of *S. kirchbergensis* and *S. hemitoechus* has been more or less unequivocal at least since Azzaroli (1962), the status *S. etruscus* and *S. hundsheimensis* of the European Early and early Middle Pleistocene has long been muddled. We have followed the intent if not the form of Guérin's (1980) revision, recognizing two morphologically distinct taxa, *S. etruscus* (Falconer, 1868) in the Villafranchian and *S. hundsheimensis* (Toula, 1902) in the Galerian and earliest post-Galerian. The type specimen *Dicerorhinus etruscus brachycephalus* Guérin, 1980 (the Daxlanden skull) belongs to *S. kirchbergensis*, as concluded by the majority of previous authors.

The results presented here are not sufficiently clear to unequivocally resolve the phylogeny of the group, mainly because of homoplasy and unknown polarity of characters. Thus, *S. etruscus* shares several characters of its dentition and mandible with *S. hemitoechus*, while its postcranial skeleton is somewhat more similar to that of *S. hundsheimensis*. Furthermore, *S. hundsheimensis* shares a number of dental characters with the Pliocene *S. jeanvireti* that both *S. etruscus* and *S. hemitoechus* lack. The presence of small, possibly transitional specimens in the latest Early Pleistocene at several localities suggests that *S. hundsheimensis* might be a descendant of *S. etruscus*. On the other hand, the considerable similarity between *S. hundsheimensis* and *S. jeanvireti* suggests that *S. etruscus* might be a more derived morphotype, of which *S. hemitoechus* would perhaps be a more extreme expression. We have therefore left *S. jeanvireti*, *S. etruscus*, and *S. hundsheimensis* as an unresolved trichotomy (fig. 28).

The stratigraphic ranges of the taxa remain somewhat controversial, with repeated occurences of "young" (Pleistocene) *S. megarhinus* and "old" (Early to early Middle Pleistocene) *S. hemitoechus*. Co-occurrence of *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* at Mosbach suggests possible sympatry of these taxa during "Mosbach-2" time (Koenigswald & Tobien, 1987).

Both *S. hemitoechus* and *S. kirchbergensis* show size increase from their first occurrence in the early Middle Pleistocene to their extinction in the latest Pleistocene, but the tempo and mode of the change is unknown. Other evolutionary changes within species have not been discovered.

S. hundsheimensis was larger than *S. etruscus*, with a longer head and a more robust skeleton. Both species were lightly built and long limbed by rhinoceros standards, browsers or mixed feeders in open environments. *S. hemitoechus* was much more robust, with a very low-slung head and a hypsodont dentition with enlarged M3 and reduced anterior premolars. In its compact build, skull shape and dental proportions (though not morphology) it showed remarkable convergence with the much more graviportal woolly rhinoceros, *Coelodonta antiquitatis*. While the plagiolophodont *Coelodonta* was probably a specialised grazer, *S. hemitoechus* was more probably a mixed feeder on low-growing vegetation in open habitats. *S. kirchbergensis* was much larger and somewhat more graviportal, with relatively long limbs and with a large, deep skull and mandible, a markedly ectolophodont dentition with hypsodont premolars, a very large skeleton and a limb joint morphology suggestive of a closed woodland or forest environment. Its long limbs and high head posture taken together with the extremely ectolophodont, premolar-dominated dentition suggest a browsing mode of life.

We hypothesize that the differences in dental proportions may be related to the sequence in which the loss of incisors and the evolution of hypsodonty occurred. If incisor loss occurred while the animal still had a brachydont dentition, a reduction of the depth of the muzzle occurred. When hypsodonty evolved thereafter, the posterior part of the dentition was emphasised, as there was no room in the shallow maxilla and mandible for the development of hypsodont teeth. If, on the other hand, incisor loss occurred after the premolars had already become hypsodont, then no reduction of the rostral part of the mandible and maxilla resulted. This scenario can be extended to the Recent African species and the Late Pleistocene woolly rhinoceros, *Coelodonta antiquitatis*.

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Characters:

1. Dolichocephaly
2. Lack of functional incisors 3. Partial ossification of nasal septum
4. Locomotory character complex with long, relatively cursorially proportionated limbs and slender metapodials that are enlarged distally
5. Dental character complex, including smooth enamel, "mol ten" overall shape with weak styli and folds, open valleys and inflated lingual cusp of upper cheek teeth
6. Long limbs with relatively graviportal proportions
7. Hypsodont premolars
8. Complete lack of incisors
9. Dental character complex, including relatively rough enamel, distinct folds and styli, relatively narrow valley entrances and occurrence of a lingual cingulum beneath the posterior valley entrance
11. Very long limbs with cursorial proportions, long metapodials with parallel-sided shafts
12. Relatively short limbs with stocky metapodials, not very graviportal proportions
13. Low head posture
14. Enlarged, hypsodont distal molars, reduced mesial premolars

Postcranial characters

ATLAS

L - greatest length
La - length from the cranial to the caudal articulation
BW - breadth across the wings
Bcra - breadth of the cranial articular surface
H - height
Bcaa - breadth of the caudal articular surface

AXIS

L - greatest length
Bcra - breadth of the cranial articular surface
Bcaa - breadth of the caudal articular surface
Bc - breadth across the transverse processes

SCAPULA

AL - anterior (cranial) length
PL - posterior (caudal) length
PB - proximal breadth
DB - distal breadth
CS - breadth of the collum scapulae
LG - length of the glenoid cavity
BG - breadth of the glenoid cavity

HUMERUS

L - greatest length
LL - lateral length
PL - physiologic length
BP - proximal breadth
DP1 - proximal depth, from the caput humeri to the greaster tubercle
DP2 - proximal depth, from the caput humeri to the lesser tubercle
DPmin - smallest proximal depth in the intertuberal fossa
DAP CH - antero-posterior diameter of the caput humeri
DT CH - transverse diameter of the caput humeri
Bd - greatest breadth at the deltoid tuberosity
BS - smallest breadth of the shaft
DS - smallest depth of the depth
BD - distal breadth
BT - breadth of the trochlea
Ht ant - anterior height of the trochlear trough
Ht post - posterior height of the trochlear trough
Dt - depth of the trochlear trough
Lml - length of the medial lip of the trochlea
Bo - breadth of the olecranic fossa

RADIUS/ULNA

Lr - greatest length of the radius
PL - physiologic length of the radius
BPr - proximal breadth of the radius
BPar - breadth of the proximal articular surface
DPr - proximal depth of the radius
DPar - depth of the proximal articular surface
DPsi - depth of the proximal articular surface along the sigmoidal crest
BDr - distal breadth of the radius
BDar - breadth of the distal articular surface of the radius
DDr - distal depth of the radius
DDar - depth of the distal articular surface of the radius
BSr - smallest breadth of the shaft of the radius
DSr - smallest depth of the shaft of the radius
Lu - greatest length of the ulna
Lo - length of the olecranon
Do - depth of the olecranon
DPa - depth of the anconeal process
Hsiu - height of the sigmoidal incisure of the ulna
BPau - breadth of the proximal articular surface of the ulna
BDu - distal breadth of the ulna
BDau - breadth of the distal articular surface of the ulna
DDau - depth of the distal articular surface of the ulna
BSu - breadth of the shaft of the ulna
Lru - length of the radius + ulna
BDru - distal breadth of the radius + ulna
BDaru - breadth of the distal articular surfaces of radius + ulna

SCAPHOID

L - greatest length
l - greatest breadth
H - height
L art prox - length of the proximal articular surface
l art prox - breadth of the proximal articular surface
L art dist - length of the distal articular surface
l art dist - breadth of the distal articular surface
L art dist max - greatest length of the distal articular surface

SEMILUNAR

L - length
l - greatest breadth
H - height
H ant - anterior height

PYRAMIDAL

L - greatest length
l - greatest breadth
H max - greatest height
H phys - physiologic height
H face ant - height of the anterior face

PISIFORM

L - greatest length
l - greatest breadth
H - height

TRAPEZOID

L - greatest length
l - greatest breadth
H - height

MAGNUM

L - greatest length
L art dist - greatest length
l - greatest breadth
H - height
H art - physiologic height

UNCINATE

L abs - absolute length
L anat - anatomical length
l - greatest breadth
H - height

METACARPALS

L - greatest length
BP - proximal breadth
DP - proximal depth

BPa - breadth of the proximal articular surface
DPa - depth of the proximal articular surface
BS - smallest breadth of the shaft
DS - smallest depth of the shaft
BD - distal breadth
DD - distal depth
BDa - breadth of the distal articular surface

FEMUR

L - greatest length
PL - physiologic length
BP - proximal breadth
DC - depth of the caput femoris
LC - length of the caput femoris
BSoT - breadth of the shaft over the third trocanter
DSoT - depth of the shaft over the third trocanter
BT - breadth of the shaft at the third trocanter
DT - depth of the shaft at the third trocanter
HT - smallest height of the third trocanter
HT max - depth of the shaft at the third trocanter
BS - smallest breadth of the shaft
DS - smallest depth of the shaft
BD - distal breadth
Lll - length of the lateral lip of the trochlea
Lml - length of the medial lip of the trochlea
DDl - greatest depth of the lateral portion of the distal epiphysis
DDm - greatest depth of the medial portion of the distal epiphysis
Lt - length of the trochlear trough
Btr - breadth of the trochlea
Bcon - breadth across the condyles

PATELLA

L - greatest length
L art face - greatest length of the articular surface
DT - transversal diameter
DAP - antero-posterior diameter

TIBIA/FIBULA

Lt - greatest length of the tibia
PL - physiologic length of the tibia
BP - proximal breadth of the tibia
DP - proximal depth of the tibia
BS - smallest breadth of the tibia
DS - smallest depth of the trochlea
BD - distal breadth of the tibia
DD - distal depth of the tibia
BDa - breadth of the distal articular surface of the tibia
DDa - depth of the distal articular surface of the tibia
Lf - greatest length of the fibula

ASTRAGALUS

LL - lateral length
ML - medial length
B - greatest breadth
BD - distal breadth
DD - distal depth
BDa - breadth of the distal articular surface
Lmt - length of the medial lip of the trochlea
Dmt - depth of the medial lip of the trochlea
Llt - length of the lateral lip of the trochlea
Htt - height of the trochlear trough
DL - distance of the trochlear lips

CALCANEUM

H - height
DAP somm - antero-posterior diameter of the tuberosity summit
DT somm - transverse diameter of the tuberosity summit
DAP beak - antero-posterior diameter at the beak
DT sust - transverse diameter at the sustentaculum tali
DT min post - smallest plantar transverse diameter

NAVICULAR

L - greatest length
l - greatest breadth
H - height
H min phys - smallest physiologic height

CUBOID

L - greatest length
l - greatest breadth
H - height
DAP art prox - antero-posterior diameter of the proximal articular surface
DT art prox - transverse diameter of the proximal articular surface
H face ant - height of the dorsal face of the bone

THIRD CUNEIFORM

L - greatest length
l - greatest breadth
H - height
H min phys - smallest physiologic height

SECOND CUNEIFORM

L - greatest length
l - greatest breadth
H - height

FIRST CUNEIFORM

L - greatest length
DT - transverse diameter
DAP - antero-posterior diameter
DT art - transverse diameter of the proximal articulation
DAP art - antero-posterior diameter of the proximal articulation

METATARSALS

L - greatest length
BP - proximal breadth
DP - proximal depth
BPa - breadth of the proximal articular surface
DPa - depth of the proximal articular surface
BS - smallest breadth of the shaft
DS - smallest depth of the shaft
BD - distal breadth
DD - distal depth
BDa - breadth of the distal articular surface

PLATE 1

Scapula 1. - *S. etruscus* (Falconer) - Capitone (Terni) - Museum of Paleontology of the University of Rome:
a - lateral view
b - distal view
2. - *S. hundsheimensis* (Toula) - redrawn from Toula (1902):
a - lateral view
b - distal view
3. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1975/263:
- distal view

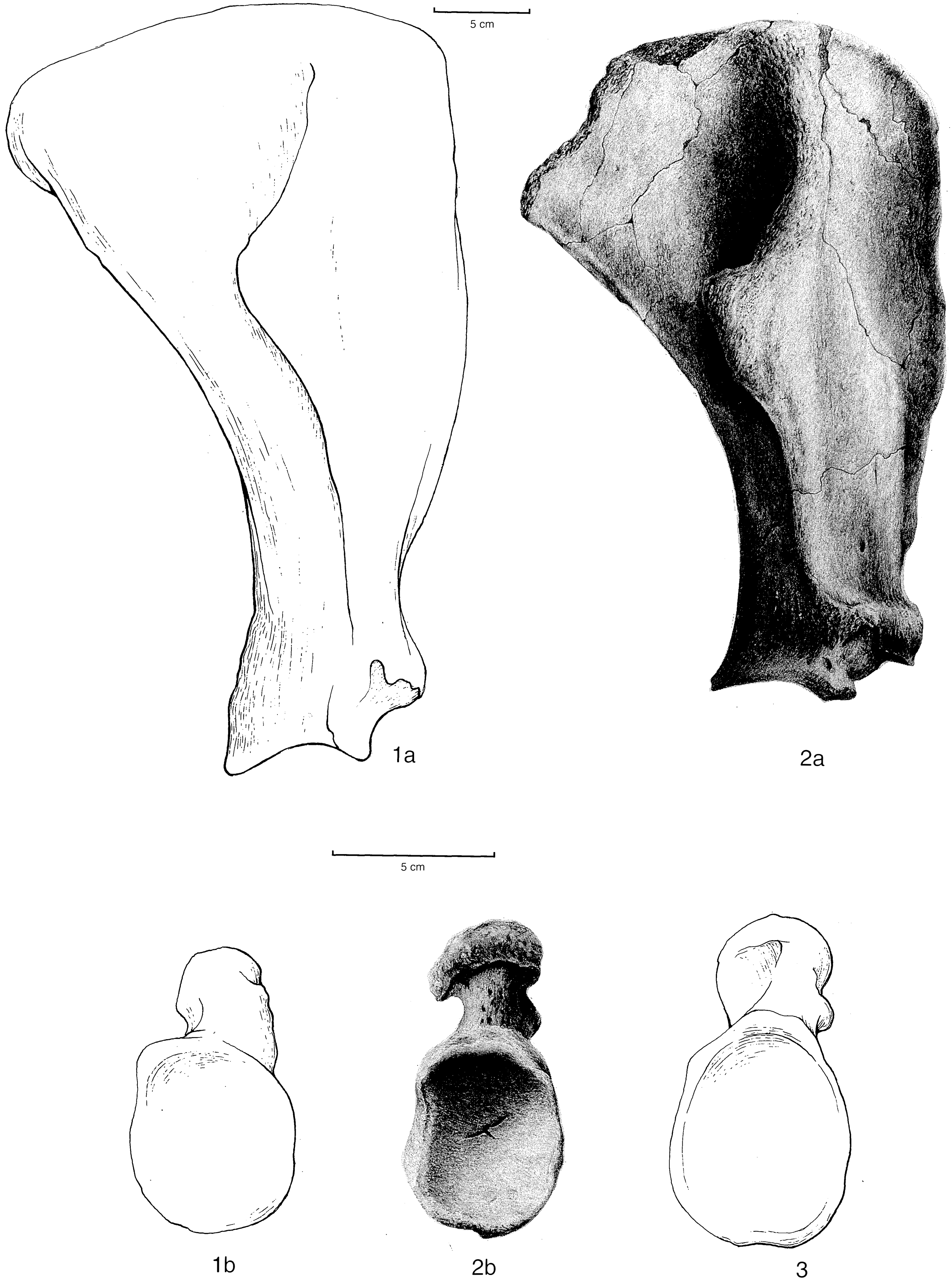


PLATE 1

PLATE 2

Humerus 1. - *S. etruscus* (Falconer) - Upper Valdarno - Museum of Geology and Paleontology of Florence - IGF 14840:
a - cranial view
b - caudal view
c - proximal view

2. - *S. hundsheimensis* (Toula) - redrawn from Toula (1902):
a - cranial view
b - caudal view

3. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1955/609:
a - cranial view
b - caudal view

- *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1955/600:
c - proximal view

PLATE 2

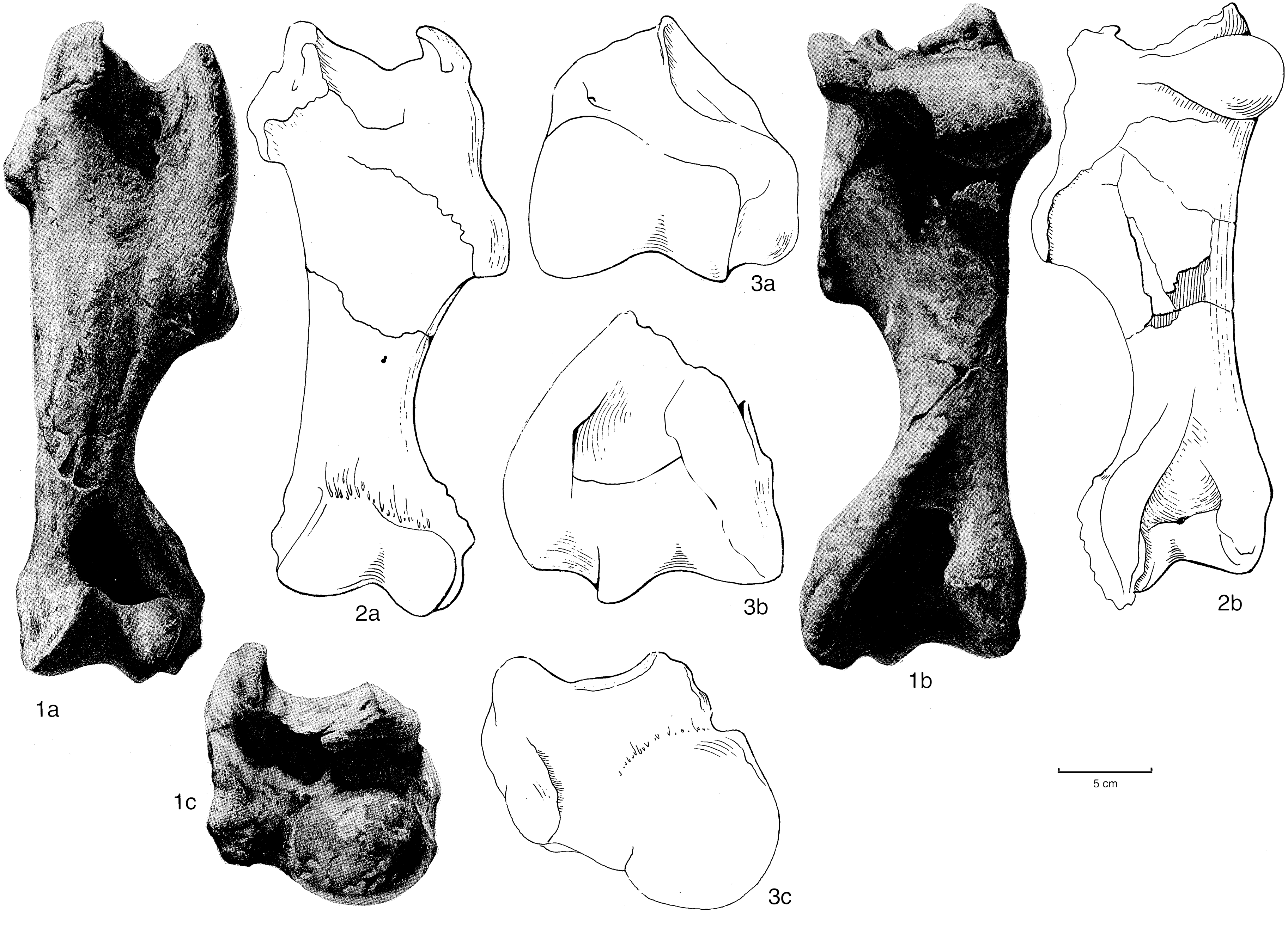


PLATE 3

Ulna 1. - *S. etruscus* (Falconer) - Upper Valdarno - Museum of Geology and Paleontology of Florence - IGF 2211V:
a - dorso-medial view
b - dorsal view
c - lateral view

2. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. F. 314:
a - dorsal view
b - lateral view

PLATE 3

PLATE 4

Radius 1. - *S. etruscus* (Falconer) - Upper Valdarno - Museum of Geology and Paleontology of Florence - IGF 2211V:
a - dorsal view
b - proximal view
2. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 45255:
a - dorsal view
3. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1963/573:
a - dorsal view
b - proximal view
4. - *S. kirchbergensis* (Jäeger) - Stockstadt (Rhein) - Dick Mol Collection (‘s-Heerenberg, The Netherlands) - 1811:
a - dorsal view
b - proximal view

PLATE 4

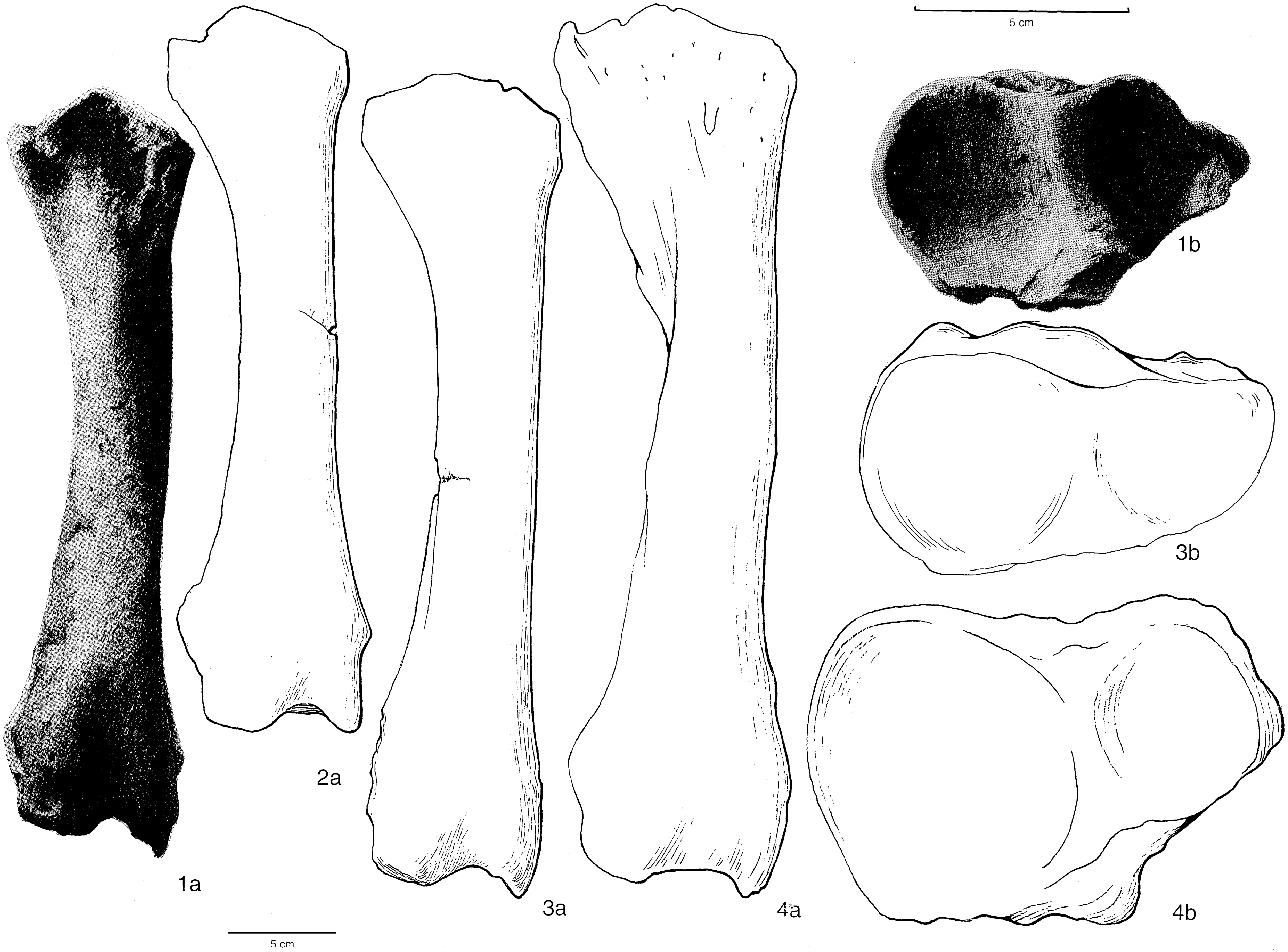


PLATE 5

Scaphoid 1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
a - dorsal view
b - proximal view
2. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 45257:
- dorsal view
3. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1957/565:
a - dorsal view
b - proximal view
Semilunar 4. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
a - dorsal view
b - distal view
5. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
a - dorsal view
b - distal view
6. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1967/76:
a - dorsal view
b - distal view
7. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1927/657:
- distal view

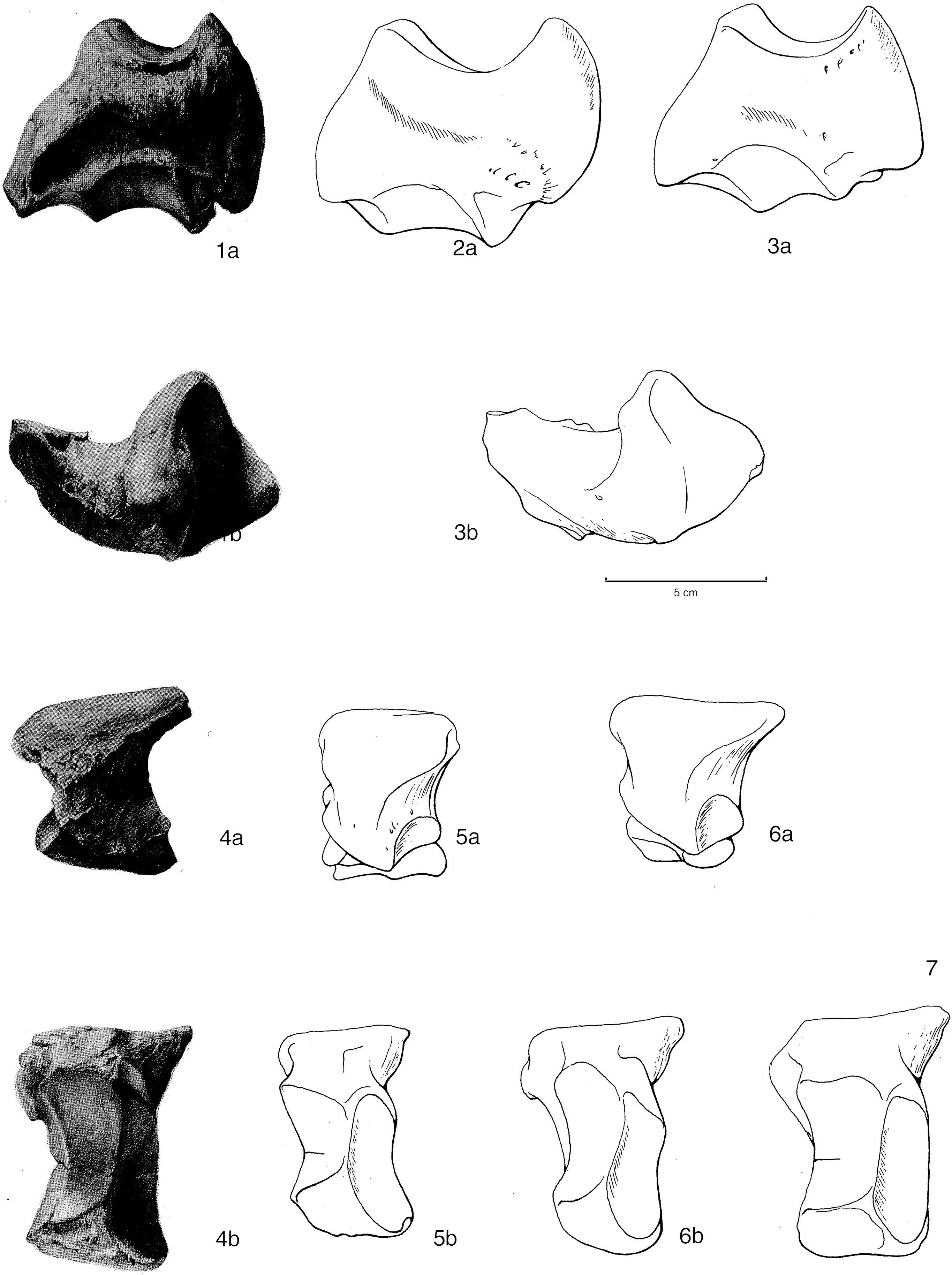


PLATE 5

PLATE 6

Pyramidal 1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716
a - dorsal view
b - proximal view
c - medial view

2. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
a - dorsal view
b - proximal view
c - medial view

3. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 326:
a - dorsal view
b - proximal view
c - medial view

Pisiform 4. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia- IS. I. 336:
a - dorsal view
b - proximal view

Trapezoidal 5. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia- IS. I. 333:
- dorsal view

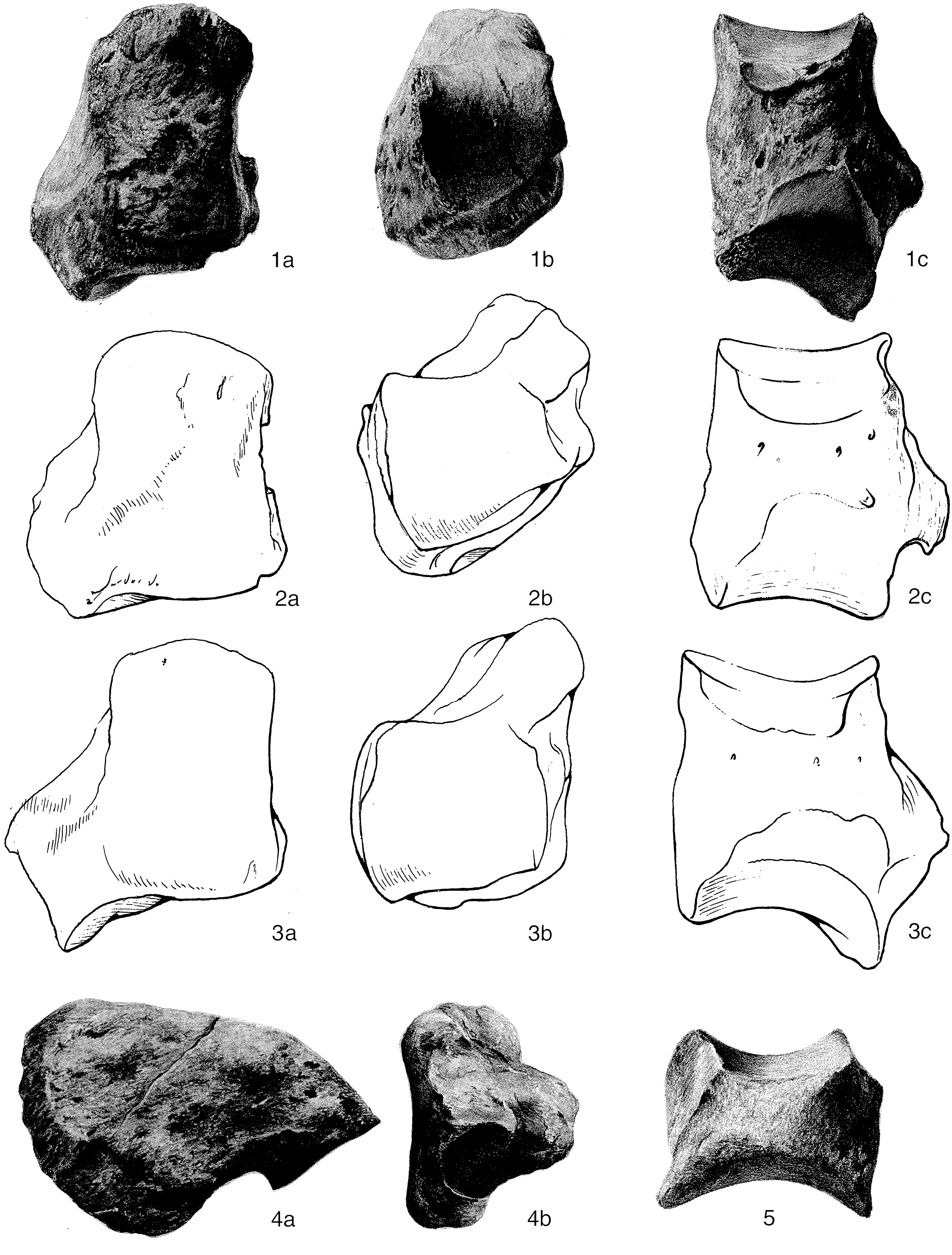


PLATE 6

5 cm

PLATE 7

Magnum 1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716 (the same scale as in Plate 5):
a - dorsal view
b - distal view

2. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
a - dorsal view
b - distal view

3. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1959/742:
a - dorsal view
b - distal view

Uncinate 4. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - I GF 716:
a - dorsal view
b - proximal view

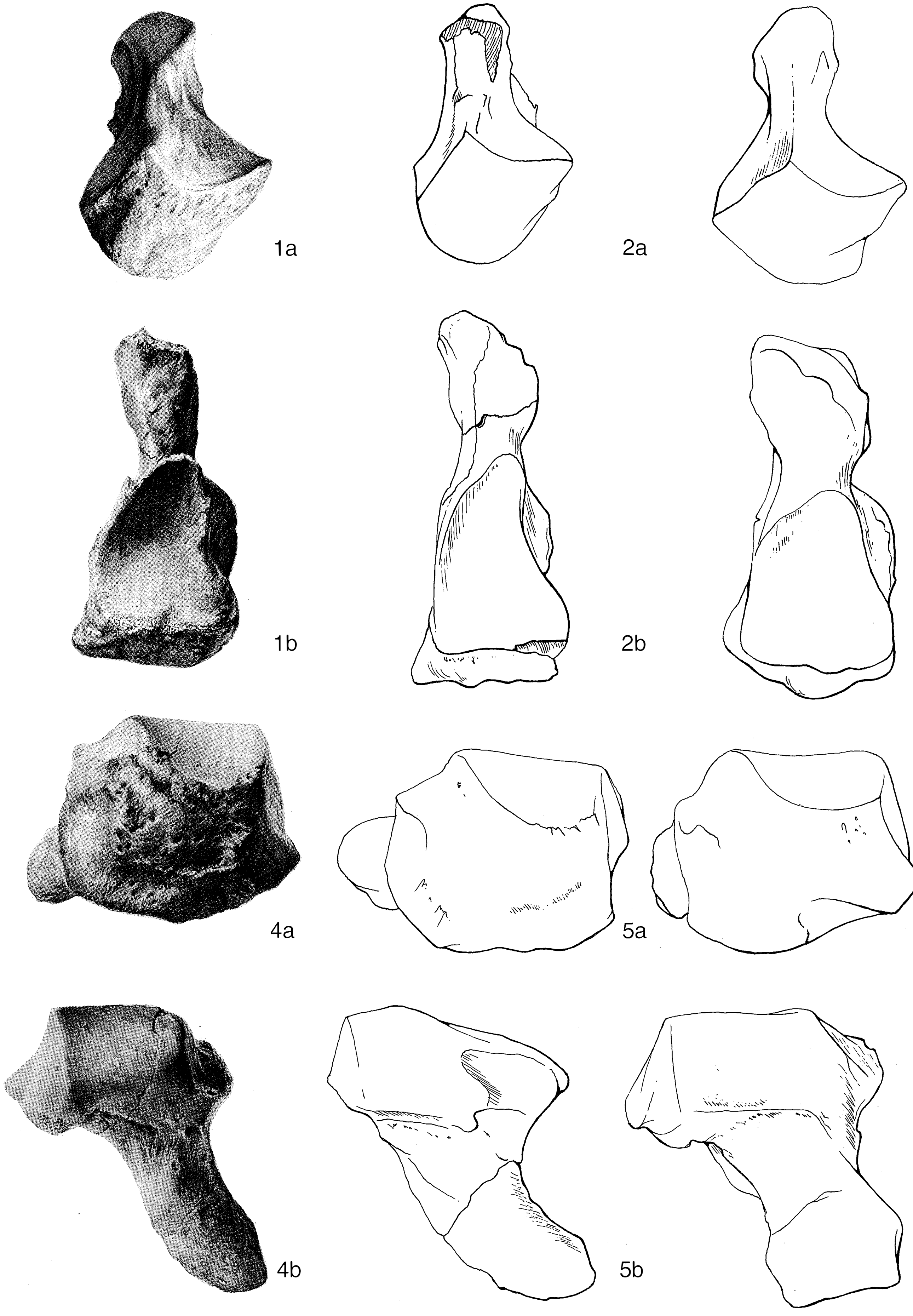


PLATE 7

PLATE 8

Second metacarpal 1. - *S. etruscus* (Falconer) - Figline (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 1355V:
- dorsal view

2. - *S. hemitoechus* (Falconer) - Grays (Thurrock, Essex) - Natural History Museum of London - uncatalogued:
- dorsal view

3. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1961/119:
- dorsal view

4. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1961/958:
- dorsal view

Third metacarpal 5. - *S. etruscus* (Falconer) - Figline (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 1355V:
- dorsal view

6. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 45265:
- dorsal view

7. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1956/28:
- dorsal view

8. - *S. kirchbergensis* - Mosbach - Naturhistorisches Museum of Mainz - 1955/520:
- dorsal view

Fourth metacarpal 9. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- dorsal view

10. - *S. hundsheimensis* - Mosbach - Naturhistorisches Museum of Mainz - 1955/1343:
- dorsal view

11. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1956/928:
- dorsal view

PLATE 8

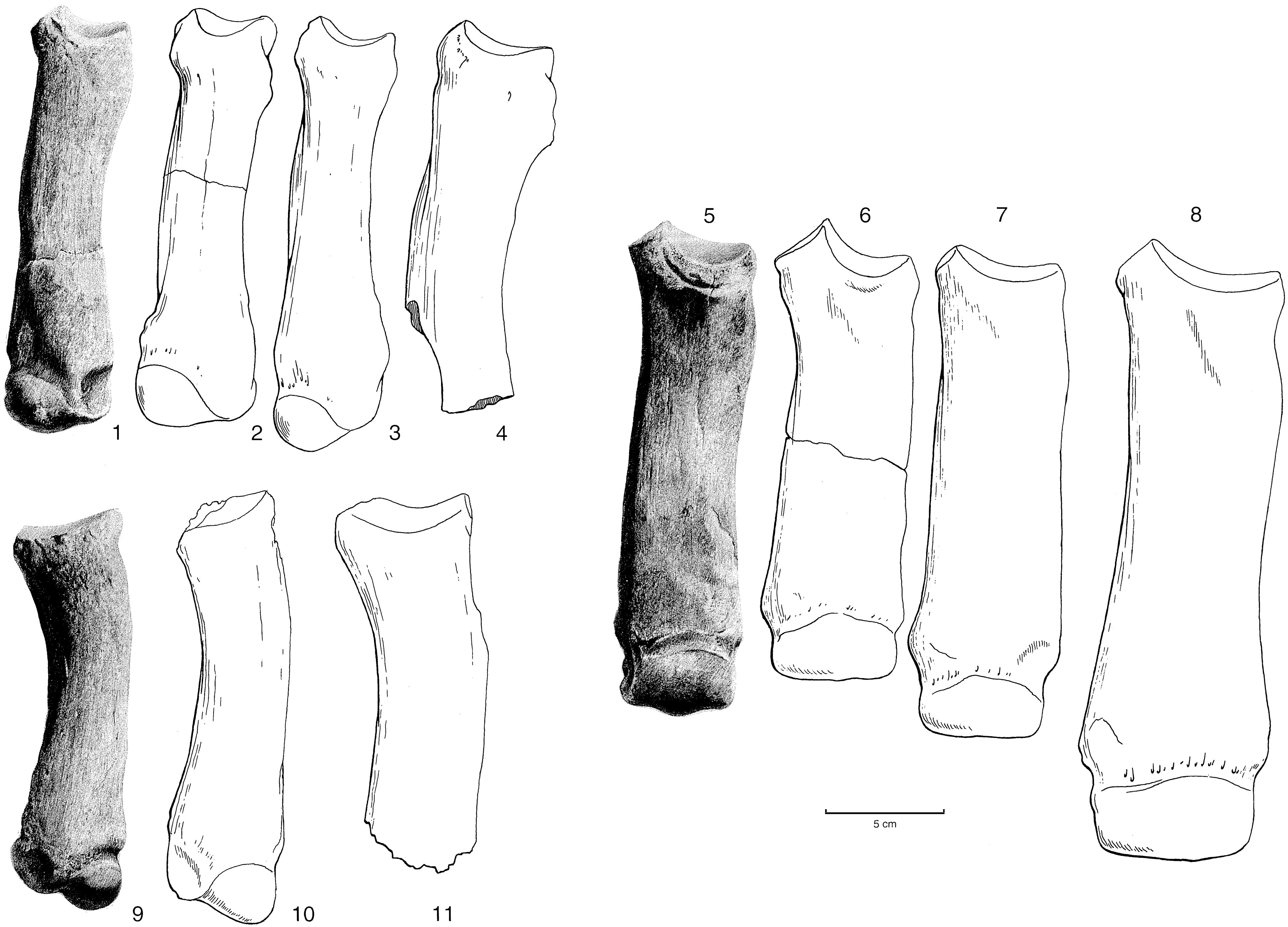


PLATE 9

Femur 1. - *S. etruscus* (Falconer) - Il Tasso (Upper Valdarno) Museum of Geology and Paleontology of Florence - IGF 722:
a - cranial view
b - proximal view
c - distal view

2. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
- distal view

3. - *S. hundsheimensis* (Toula) - Mauer - Hessisches Landesmuseum, Darmstadt - Mau 139:
a - cranial view
b - proximal view
c - distal view

4. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1967/81:
- distal view

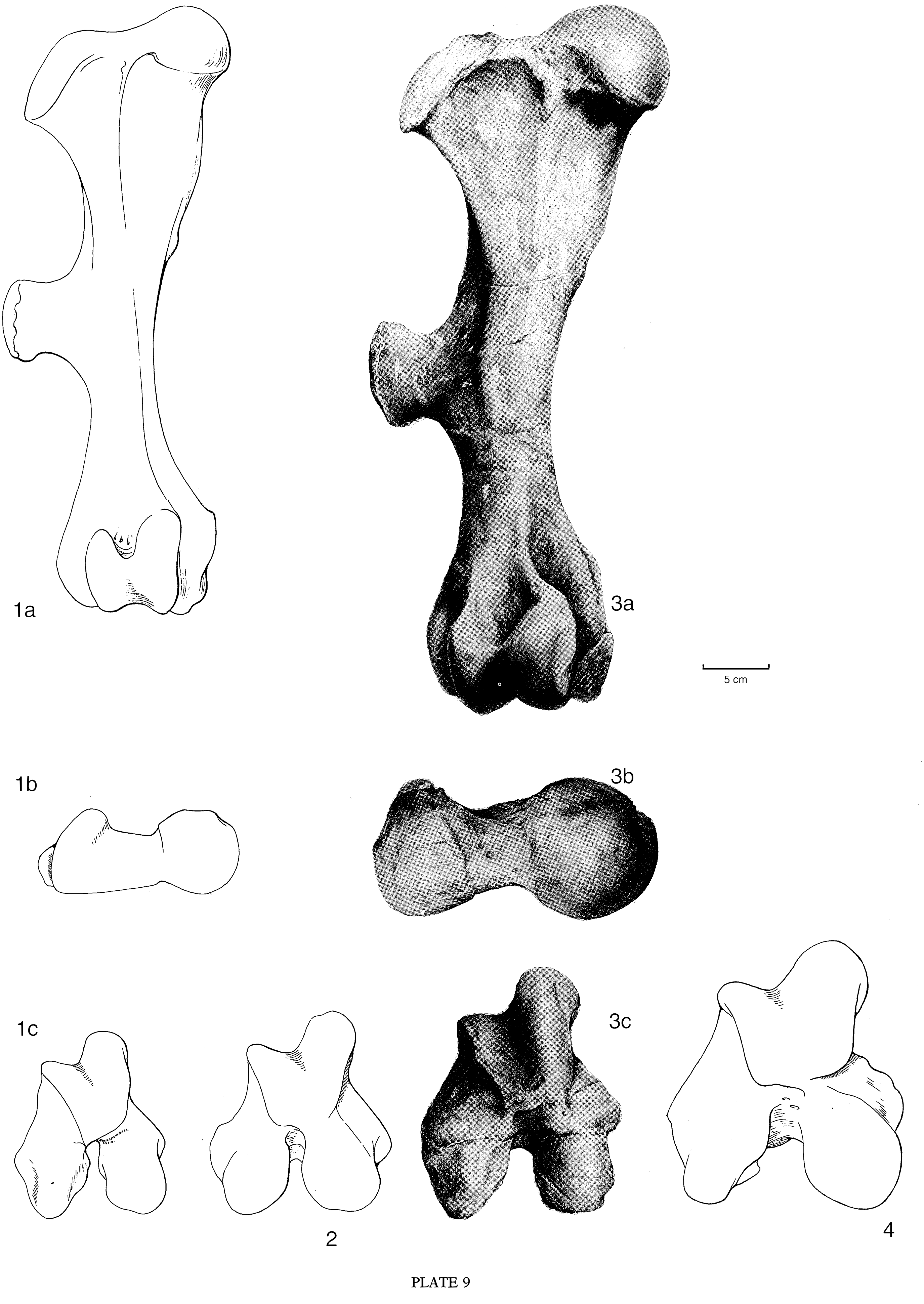


PLATE 9

PLATE 10

Tibia 1. - *S. etruscus* (Falconer) - Il Tasso (Upper Valdarno) Museum of Geology and Paleontology of Florence - IGF 722:
a - dorsal view
b - distal view

2. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 27976:
a - dorsal view
b - distal view

3. - *S. hundsheimensis* (Toula) - Trimmingham (Norfolk) Natural History Museum of London - M 18486:
a - dorsal view
b - distal view

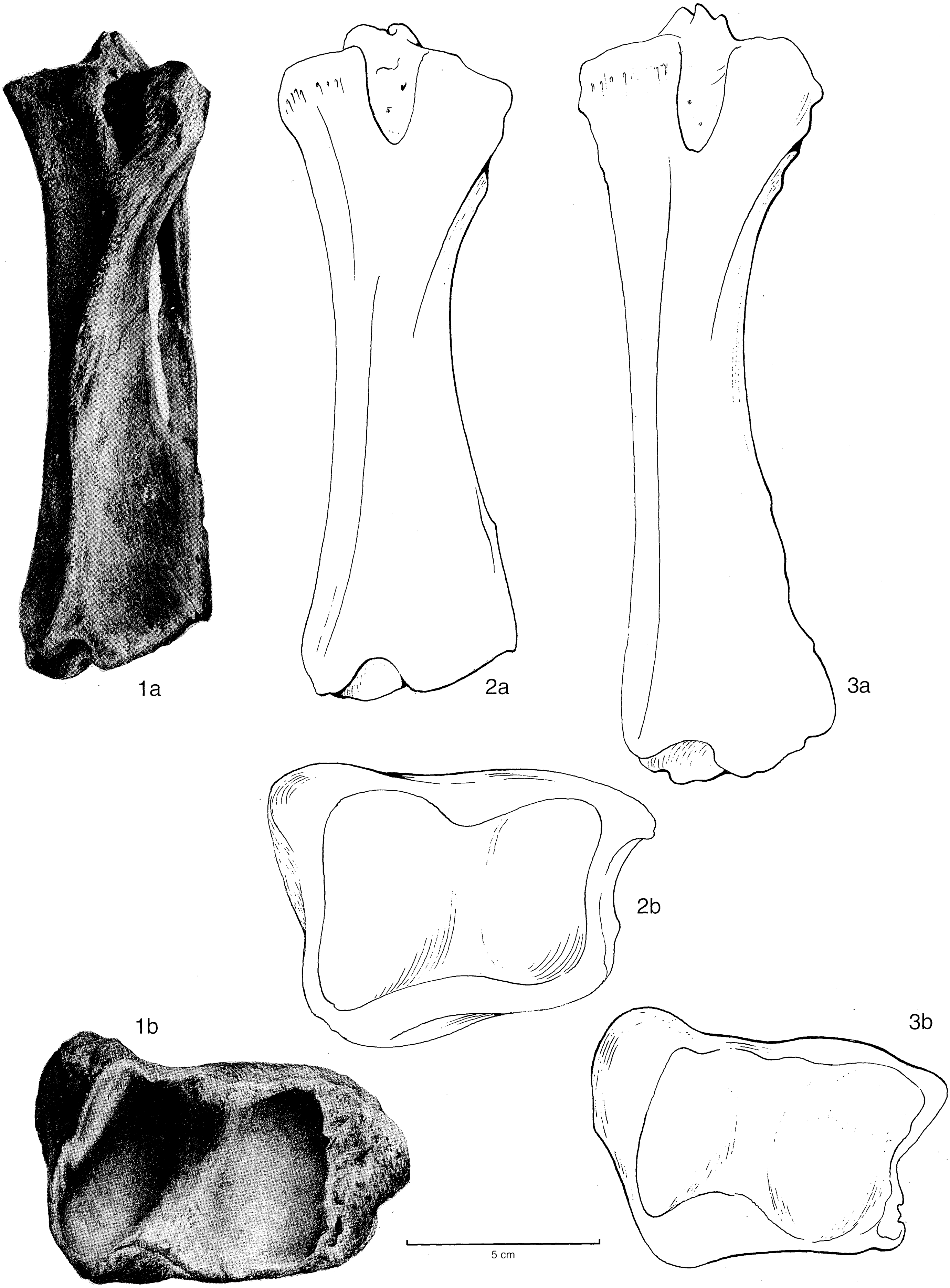


PLATE 10

PLATE 11

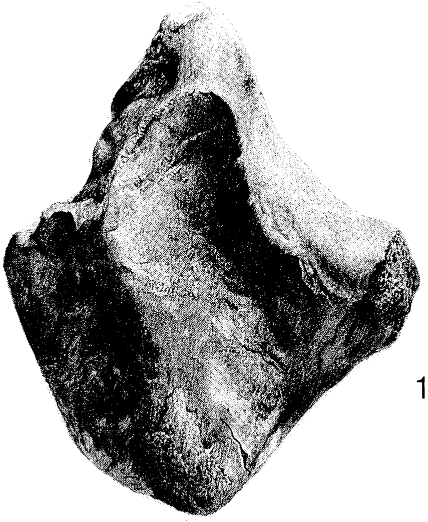
Patella 1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716
- articular view

2. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. Q51-71:
- articular view

Astragalus 3. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
a - dorsal view
b - distal view

4. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 22019a:
a - dorsal view
b - distal view

5. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1963/621:
- dorsal view



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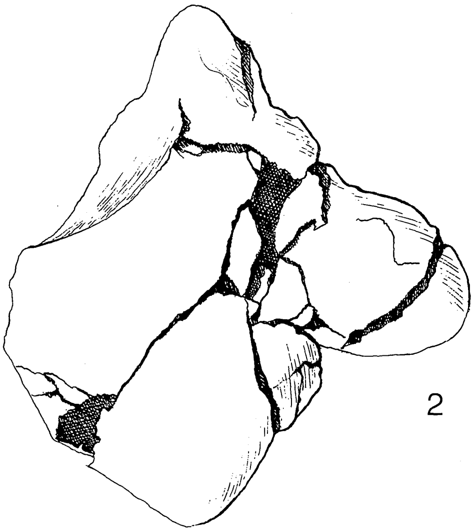

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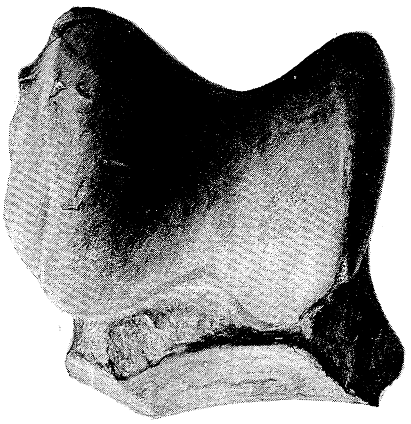

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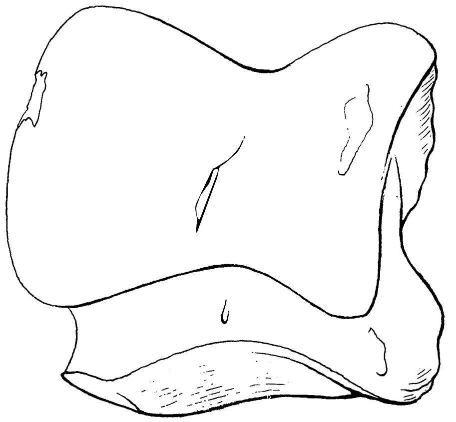
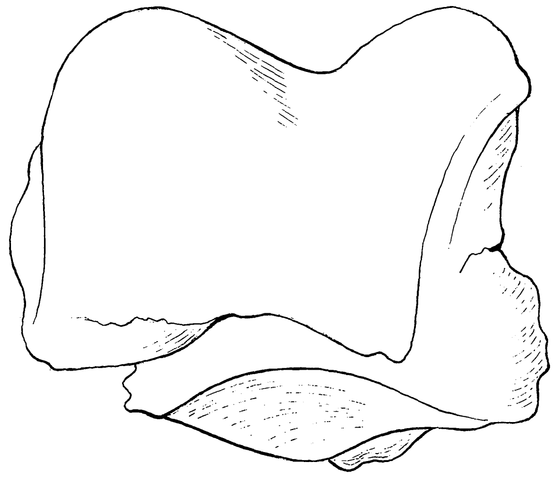


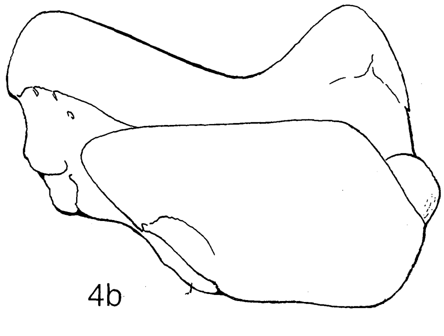
4a



5

5 cm

3b



4b

PLATE 11

PLATE 12

Calcaneum 1. - *S. etruscus* (Falconer) Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
a - dorsal view
b - medial view

2. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
a - dorsal view
b - medial view

3. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - 31281:
a - dorsal view
b - medial view

4. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1955/325:
a - dorsal view
b - medial view

PLATE 12

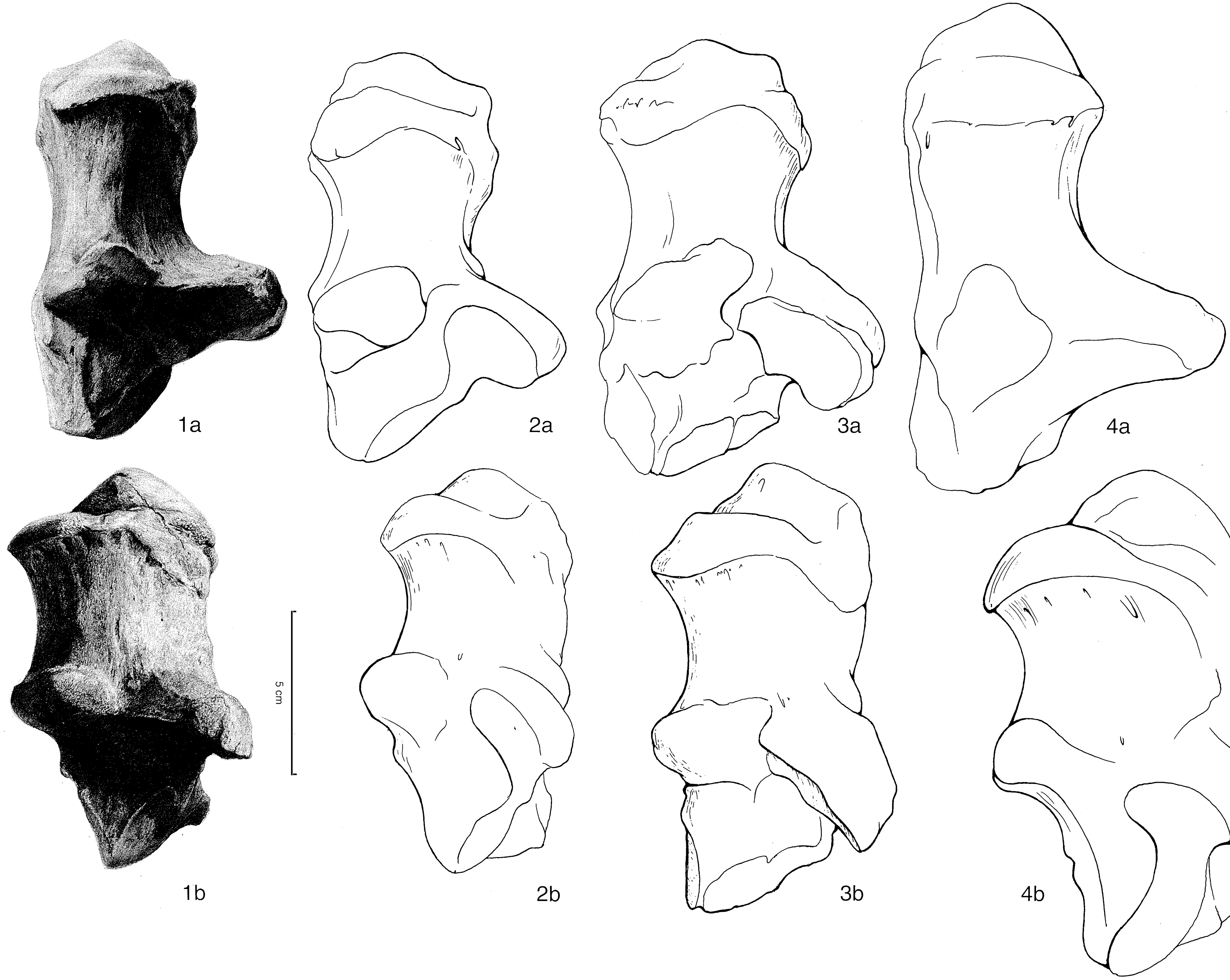


PLATE 13

Navicular 1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
a - proximal view
b - dorso-medial view

2. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
a - proximal view
b - dorso-medial view

3. - *S. cf. hundsheimensis* - Pietrafitta mine (Perugia) - n. 502 - (inverted):
a - proximal view
b - dorso-medial view

4. - *S. kirchbergensis* (Jäeger) - Grays (Thurrock, Essex) - Natural History Museum of London - 21294:
a - proximal view
b - dorso-medial view

Cuboid 5. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
a - proximal view
b - medial view

6. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
a - proximal view
b - medial view

7. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 81:
a - proximal view
b - medial view

PLATE 13

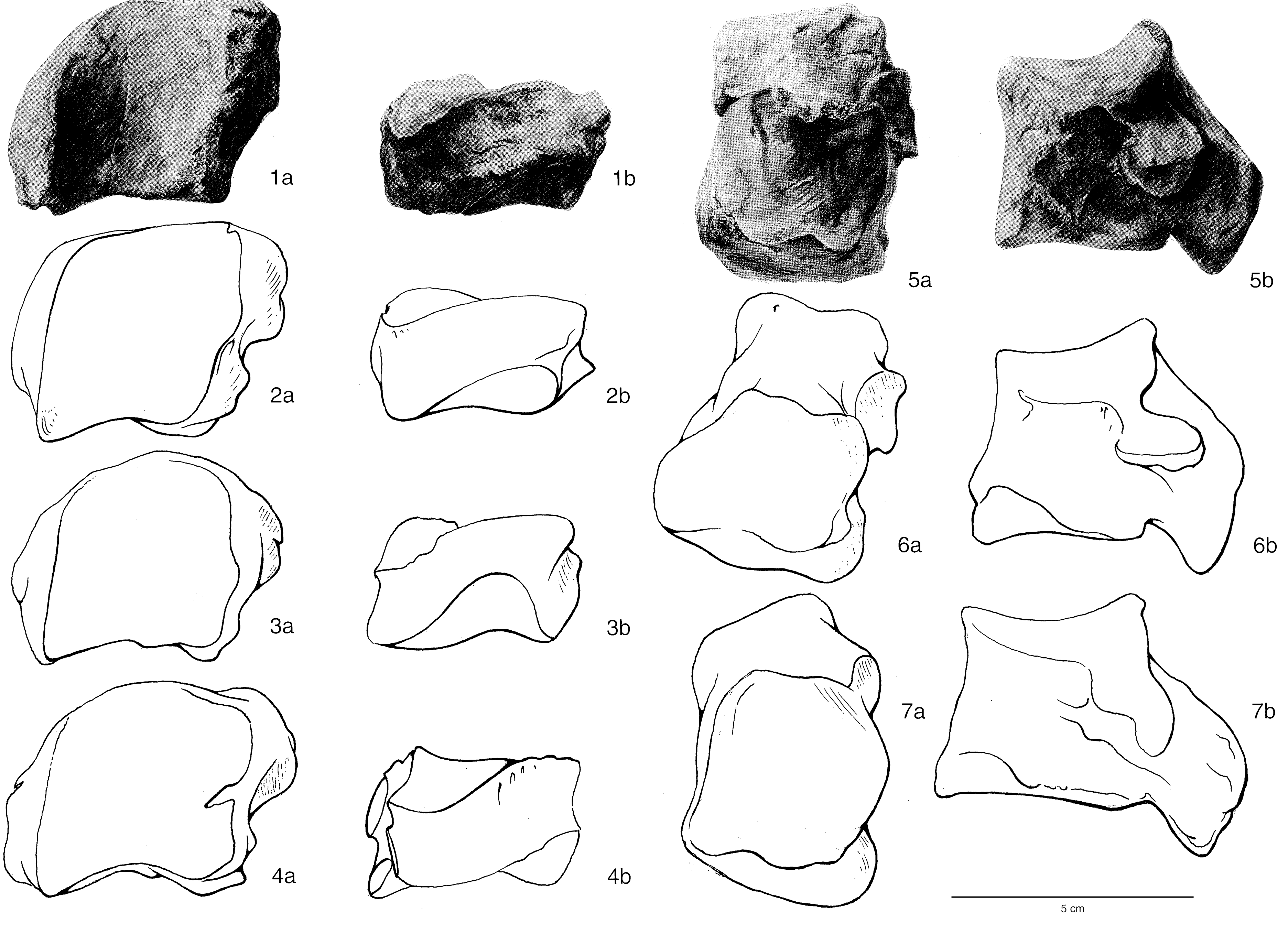


PLATE 14

First cuneiform
1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716
   - medial view
2. - *S. hemitoechu* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
   - medial view
3. - *S. cf. hundsheimensis* - Pietrafitta mine (Perugia) - n. 530:
   - medial view

Second cuneiform
4. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
   a - dorsal view
   b - proximal view
5. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
   a - dorsal view
   b - proximal view
6. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 330:
   a - dorsal view
   b - proximal view

Third cuneiform
7. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
   a - dorsal view
   b - proximal view
8. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
   a - dorsal view
   b - proximal view
9. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 328:
   a - dorsal view
   b - proximal view

PLATE 14

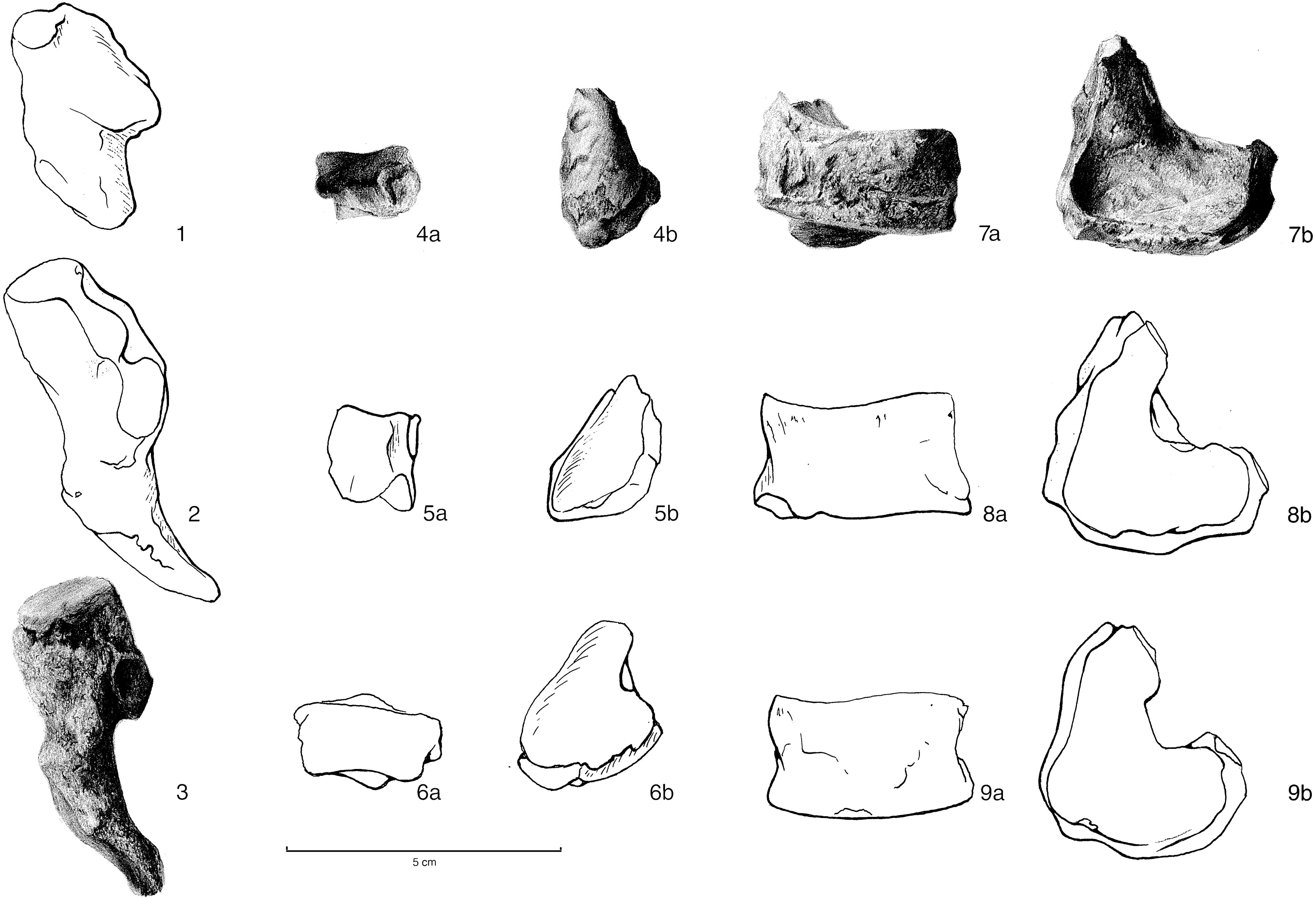


PLATE 15

Second metatarsal 1. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- dorsal view

2. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 45273:
- dorsal view

3. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 379:
- dorsal view

4. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1955/944:
- dorsal view

Third metatarsal 5. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- dorsal view

6. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
- dorsal view

7. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 378:
- dorsal view

8. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1957/242:
- dorsal view

Fourth metatarsal 9. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- dorsal view

10. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
- dorsal view

11. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1958/84:
- dorsal view

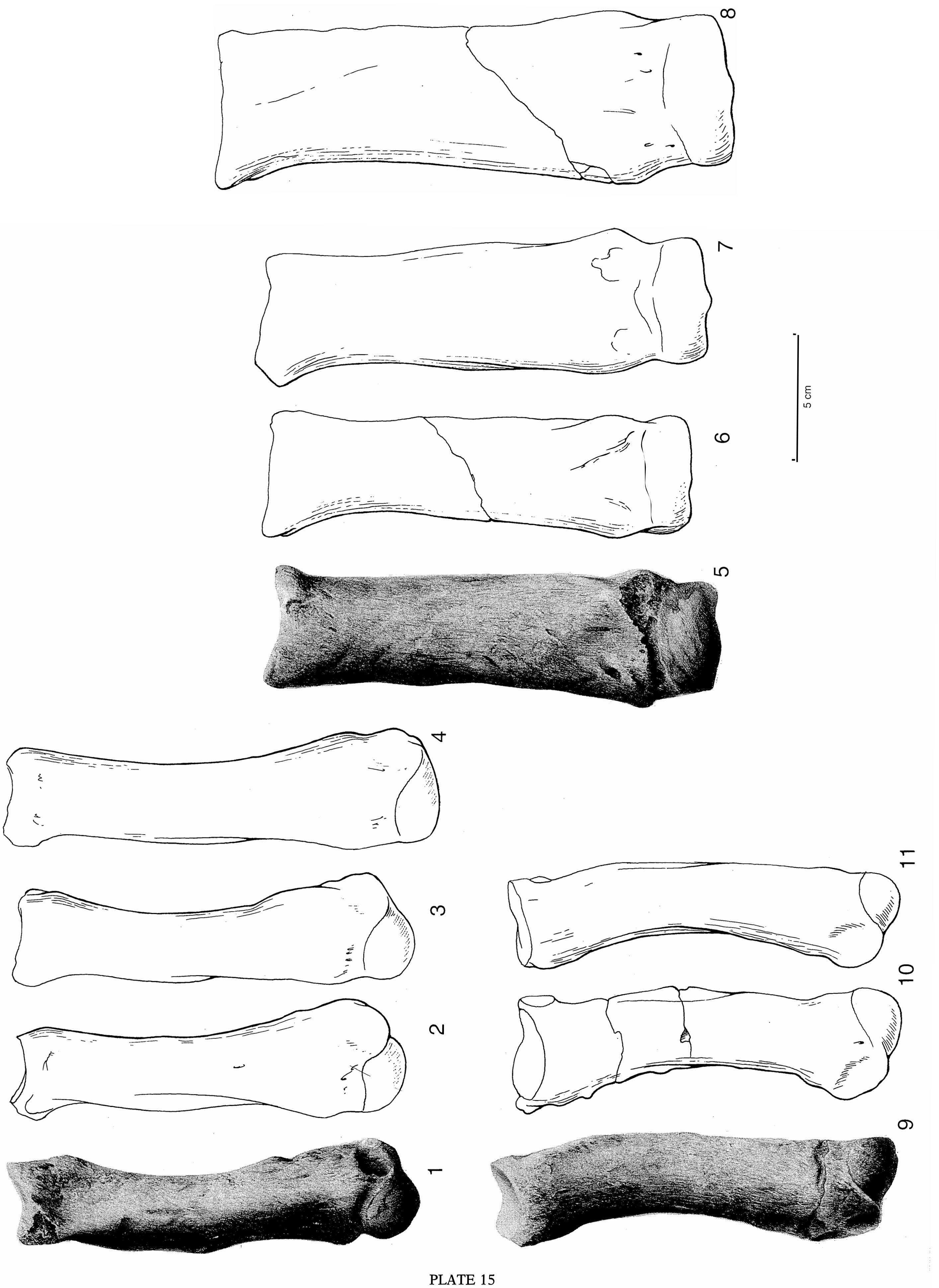


PLATE 15

PLATE 16

Second metacarpal 1. - *S. etruscus* (Falconer) - Figline (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 1355V:
- proximal view

2. - *S. hemitoechus* (Falconer) - Grays (Thurrock, Essex) - Natural History Museum of London - uncatalogued:
- proximal view

3. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1961/119:
- proximal view

4. - S. kirchbergensis (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1961/958:
- proximal view

Third metacarpal 5. - *S. etruscus* (Falconer) - Figline (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 1355V:
- proximal view

6. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 45265:
- proximal view

7. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1956/28:
- proximal view

8. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1955/520:
- proximal view

Fourth metacarpal 9. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716: (Falconer) (Toula) (Jäeger)
- proximal view

10. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1955/1343:
- proximal view

11. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1956/928:
- proximal view

Second metatarsal 12. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- proximal view

13. - *S. hemitoechus* (Falconer) - Ilford (Essex) - Natural History Museum of London - 45273:
- proximal view

14. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 379:
- proximal view

15. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1955/944:
- proximal view

Third metatarsal 16. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- proximal view

17. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued:
- proximal view

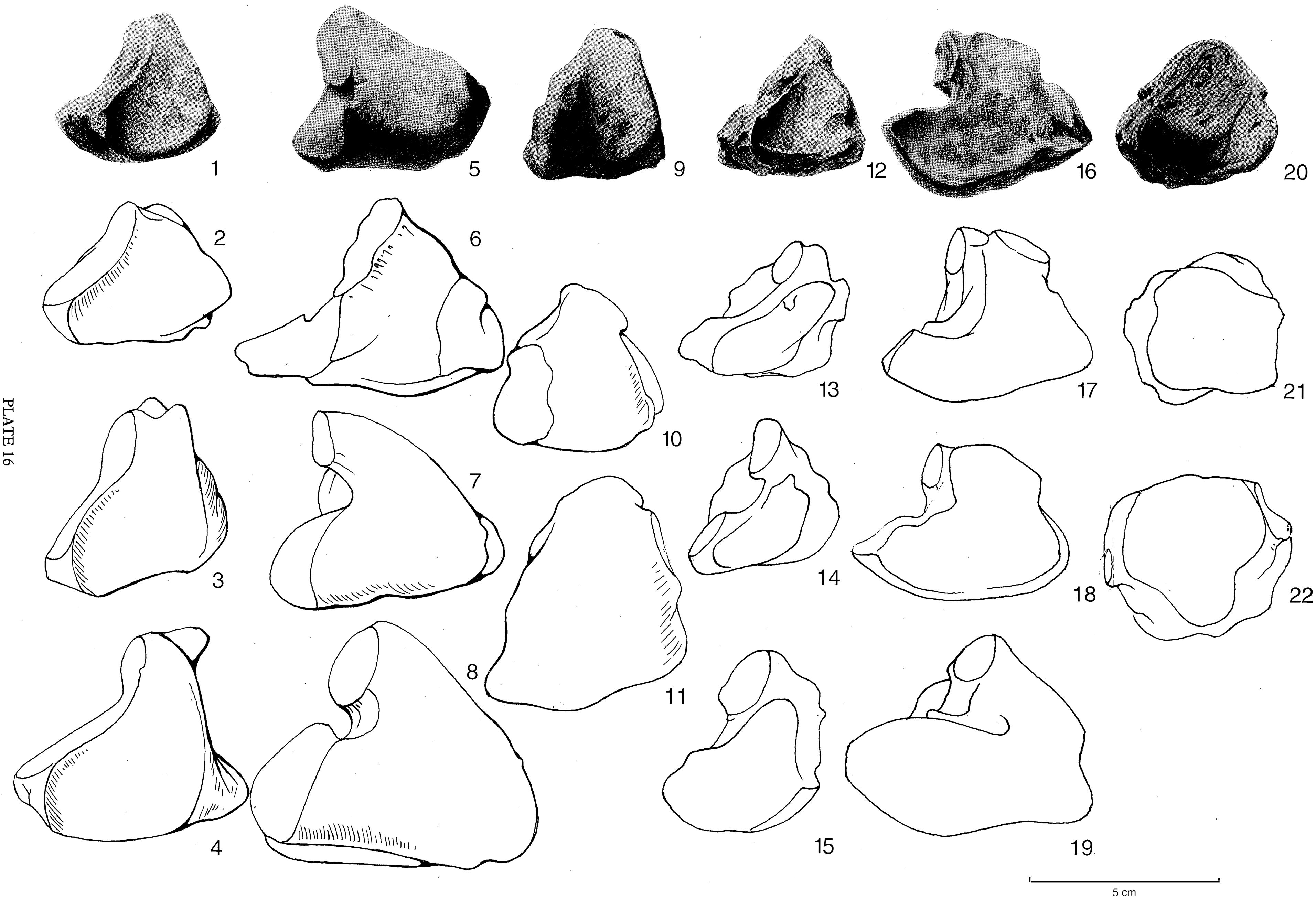
18. - *S. hundsheimensis* (Toula) - Isernia - Museo Nazionale di Isernia - IS. I. 378:
- proximal view

19. - *S. kirchbergensis* (Jäeger) - Mosbach - Naturhistorisches Museum of Mainz - 1957/242:
- proximal view

Fourth metatarsal 20. - *S. etruscus* (Falconer) - Poggio al Pero (Upper Valdarno) - Museum of Geology and Paleontology of Florence - IGF 716:
- proximal view

21. - *S. hemitoechus* (Falconer) - Maastricht-Belvédère (Limburg, The Netherlands) - Instituut voor Aardwetenschappen, Utrect - uncatalogued
- proximal view

22. - *S. hundsheimensis* (Toula) - Mosbach - Naturhistorisches Museum of Mainz - 1958/84:
- proximal view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