

Phylogeny of the genus *Stephanorhinus* in the Plio-Pleistocene of Europe

Phylogenie der Gattung *Stephanorhinus* im Plio-Pleistozän Europas

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Five species of the genus *Stephanorhinus* occur in the Plio-Pleistocene of Europe: *S. jeanvireti*, *S. etruscus*, *S. hundsheimensis*, *S. hemitoechus*, *S. kirchbergensis*. Other species occur in the same period: *Coelodonta antiquitatis*, the well known woolly rhino; *Lartetotherium megarhinus* previously assigned to the genus *Stephanorhinus* and the poorly known '*S.*' *miguelcrusafonti* which possesses an uncertain taxonomic attribution. Several phylogenetic analyses investigated the relation of *Stephanorhinus* to the other genera of the Rhinocerotidae. Among the latest ones, GUÉRIN (1980, 1982), who does not use the name *Stephanorhinus* for the European Plio-Pleistocene fossil rhinoceroses, places all the species in the recent genus *Dicerorhinus*. In a more factual study, GROVES (1983) introduce *Stephanorhinus* and *Coelodonta* as sister-groups derived from the archaic *Dicerorhinus*. This hypothesis, slightly modified, is accepted latter by PROTHERO et al. (1986) and CERDEÑO (1995).

Stephanorhinus jeanvireti is only known, so far, from the Early Villafranchian (MN16, Middle Pliocene) of Europe. It is a slender, medium- to large-sized rhinoceros, showing brachyodont teeth without cementum. The two first premolars are developed. The internal folds of the upper premolars present both crochet and crista. Upper molars also possess this features but the crista is less frequently observed. The protocone is isolated on the upper P2 and a slight protocone constriction can be observed on the upper molars. The posterior valleys of the lower teeth are broad V-shaped. The anterior valley is mainly V-shaped. Limb bones and metapodia are long and slender suggesting cursorial proportions. The morphology and the proportions of this species are highly similar to those of *S. hundsheimensis* (FORTELIUS et al. 1993, LACOMBAT 2005), which could be a close relative. However, for GUÉRIN (1980), *S. jeanvireti* has no progeny.

The earliest occurrence of *Stephanorhinus etruscus* in Europe is in the Early Villafranchian (Middle Pliocene) together with *S. jeanvireti*. The teeth are brachyodont. Upper teeth show a single crochet and an infrequent crista. The protocone constriction is observed on the two first molars. The paracone fold is not prominent. The anterior valley of the lower premolars is V or broad V-shaped while the posterior valley is always observed V-shaped. The anterior and posterior valleys of the lower molars are broad V-shaped to U-shaped. Post-cranial bones are relatively less slender than the previous species. According to GUÉRIN (1980) *S. etruscus* is the common ancestor of *S. hundsheimensis* (syn. *D. etruscus brachycephalus*) and of *S. hemitoechus* but the relation between *S. jeanvireti*, *S. etruscus* and *S. hundsheimensis* appears to FORTELIUS et al. (1993) to be a non-resolvable question. Another reasonable hypothesis is to include, in the phylogenetic story of this species, a possible migration from Asia. Indeed, *S. etruscus* is, according to MAZZA (1988), related to *Stephanorhinus yunchuchenensis* from China. The revision of the Asian specimens is essential to solve this question.

The first appearance of *Stephanorhinus hundsheimensis*, in Europe, is established at the beginning of the Early Pleistocene. This rhinoceros is characterized by elongated nasal and frontal bones of the skull. Teeth are brachyodont. The crista is frequently present on upper teeth and an antecrochet can be observed. The protocone constriction is rare on upper molars and absent on upper premolars. The paracone fold is more developed than that of *S. etruscus*. The valleys of the lower premolars are mainly V-shaped; the posterior valley can eventually be broad V-shaped. Lower molars posses an anterior valley V to broad V-shaped and a posterior valley broad V- to U-shaped. Limb bones are longer and more slender than those of *S. etruscus*. MADE (2000) sees *S. hundsheimensis* as an Asian migrant, but the strong similarity with *S. jeanvireti* cannot be ignored. Both hypotheses should be explored.

Stephanorhinus hemitoechus probably occurs for the first time in Europe in Mosbach. This rhinoceros is characterized by a low head and pseudo-hypsodont teeth. The premolar row is reduced. Upper teeth show a very prominent paracone fold. Crista, antecrochet and protocone constriction are rare but can be observed. The valleys of the lower teeth are V-shaped in the majority of the specimens (a broad V-shaped posterior valley is present on some lower molars). Shallow limb joints, short and broad limb bones, metapodials, tarsal and carpals bones suggest a more graviportal locomotion adapted to open habitats than *S. jeanvireti*, *S. etruscus* and *S.*

hundsheimensis. A direct lineage *S. etruscus*/*S. hemitoechus* is proposed by GUÉRIN (1980) and MADE (2000). A migration from Asia cannot be excluded (CERDEÑO 1997).

The earliest occurrence of *Stephanorhinus kirchbergensis* in Europe, the largest species of the *Stephanorhinus* genus, is dated to the early Middle Pleistocene. Premolars are much more hypsodont than the molars. A frequently multiple crochet, a protocone constriction and a very slight paracone fold characterized the upper premolars. Crochet and crista are often observed on the upper molars and the antecrochet can occur on the upper M2 and M3. The protocone constriction is absent and the wavy ectoloph does not possess a clear paracone fold. The anterior valley of the lower teeth is U-shaped and the posterior valley is broad V- to U-shaped. The long limb bones and the strongly concave limb joints suggest a closed habitat. This species is directly connected to *L. megarhinus* by WÜST (1922), STAESCHE (1941) and GUÉRIN (1980). They form a sister-group to the *S. jeanvireti* – *S. etruscus* – *S. hundsheimensis* – *S. hemitoechus* group in the analysis of FORTELIUS et al. (1993). In addition, the occurrence of *S. kirchbergensis* (e.g. syn. *S. choukoutiensis*) in Asia, and especially in China where its origin may lay, is well known. If a different lineage from the *S. jeanvireti* – *S. etruscus* – *S. hundsheimensis* – *S. hemitoechus* group is established, the connection with *L. megarhinus* (and some Miocene species e.g. *L. schleiermacheri*) and *S. kirchbergensis* (and the Asian forms) could correspond to a clade (HEISSIG 1973) or to a strong convergence of the characters.

The phylogenetic analysis of the European *Stephanorhinus* does not appear to be a resolvable question without the revision of the material of the Early Pliocene of Europe and of the specimens from Asia. Some Miocene species have also to be included in interpretation to clarify the existence or not of two (or more?) different lineages, and migrations from eastern Eurasia should be taken into account.

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