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## II. THE FIRST DESCRIBED LISTRIODONT REMAINS

JAN VAN DER MADE

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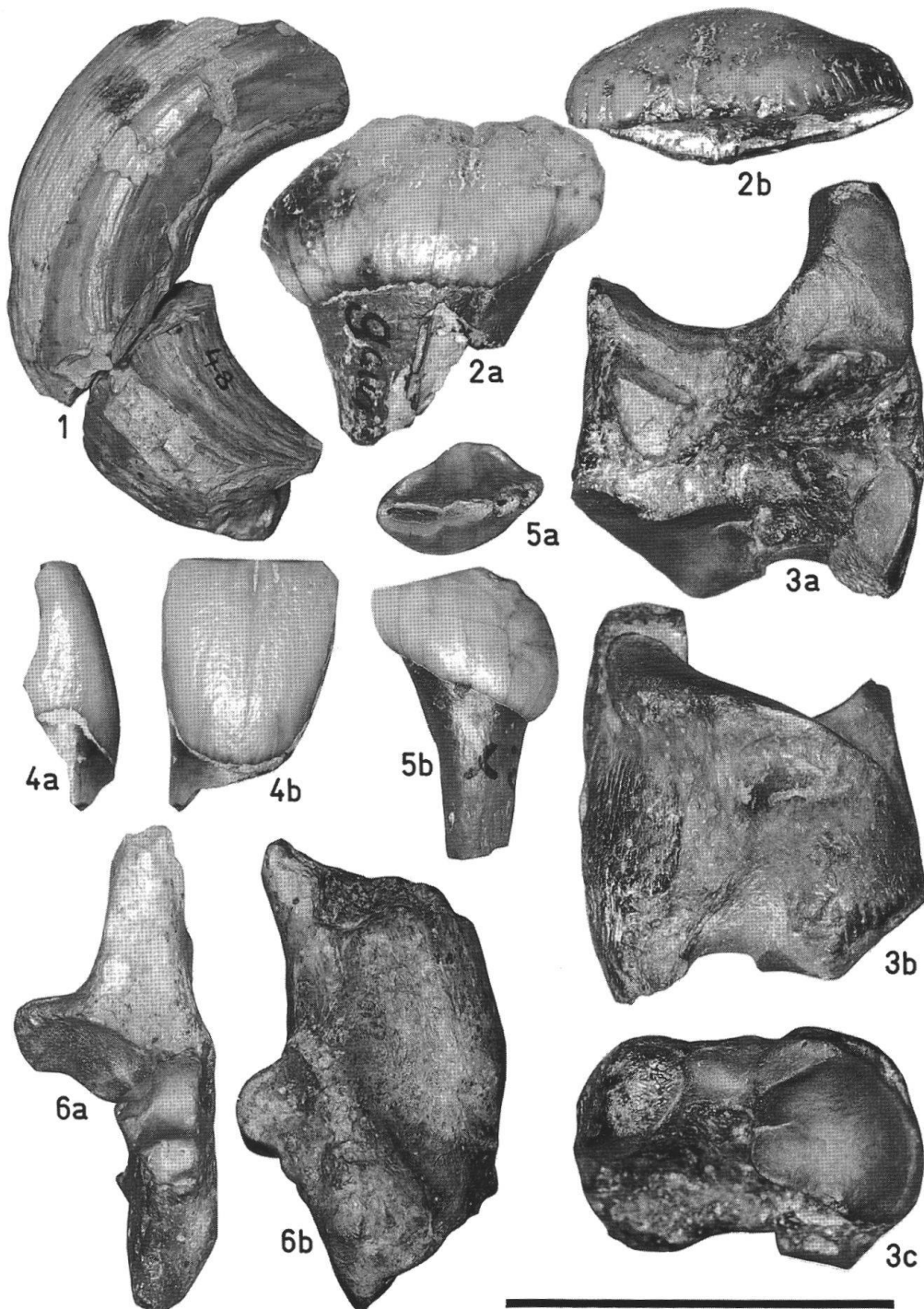
Listriodonts (Listriodontinae, Suidae) are a very characteristic element in Early and Middle Miocene faunas of the Old World. Between roughly 20 and 10 million years ago (Ma), they evolved in Africa and the Indian subcontinent and spread some 16.5 Ma to Europe, northern Asia and China (VAN DER MADE, 1996).

NICOLET (1844a) was the first to publish on a listriodont. He described a first upper incisor (Pl. 1, fig. 2), that he found in 1838 in La Chaux-de-Fonds. He mentioned the tooth in a discussion on fossil giraffes and noted that the groove that divides the tooth in two lobes resembles the "incisive externe" (lower canine) of giraffes, which has a similar groove. Later, Vacek (1900) tentatively assigned a listriodont incisor to the giraffe *Helladotherium*. However, Nicolet believed the incisor to belong to "*Lophiodon*" found by Lartet in Simorre (southern France), according to Nicolet, also in the year 1838. A skull from Simorre (figured by BLAINVILLE, 1847) shows the association of "giraffe-like" incisors and tapir-like molars.

NICOLET (1844b) gave a further description of the material. He considered the material as *Lophiodon*, a Palaeogene tapir, apparently because of the lophodont structure of the molars. Lartet and also BLAINVILLE (1847) considered the animal from Simorre a tapir and LYDEKKER (1868) described the first listriodont from the Indian subcontinent as *Tapirus Pentapotamiae*. NICOLET (1844b) noted the resemblance of the incisors to those of a wild boar, which is surprising, since their resemblance to those of tapirs lead LEINDERS (1977) to interpret the *Listriodon* dietary adaptation as similar to those of tapirs. In particular the lower incisors (Pl. 1, figs. 4-5) are morphologically much closer to those of the tapirs than those of the living suids.

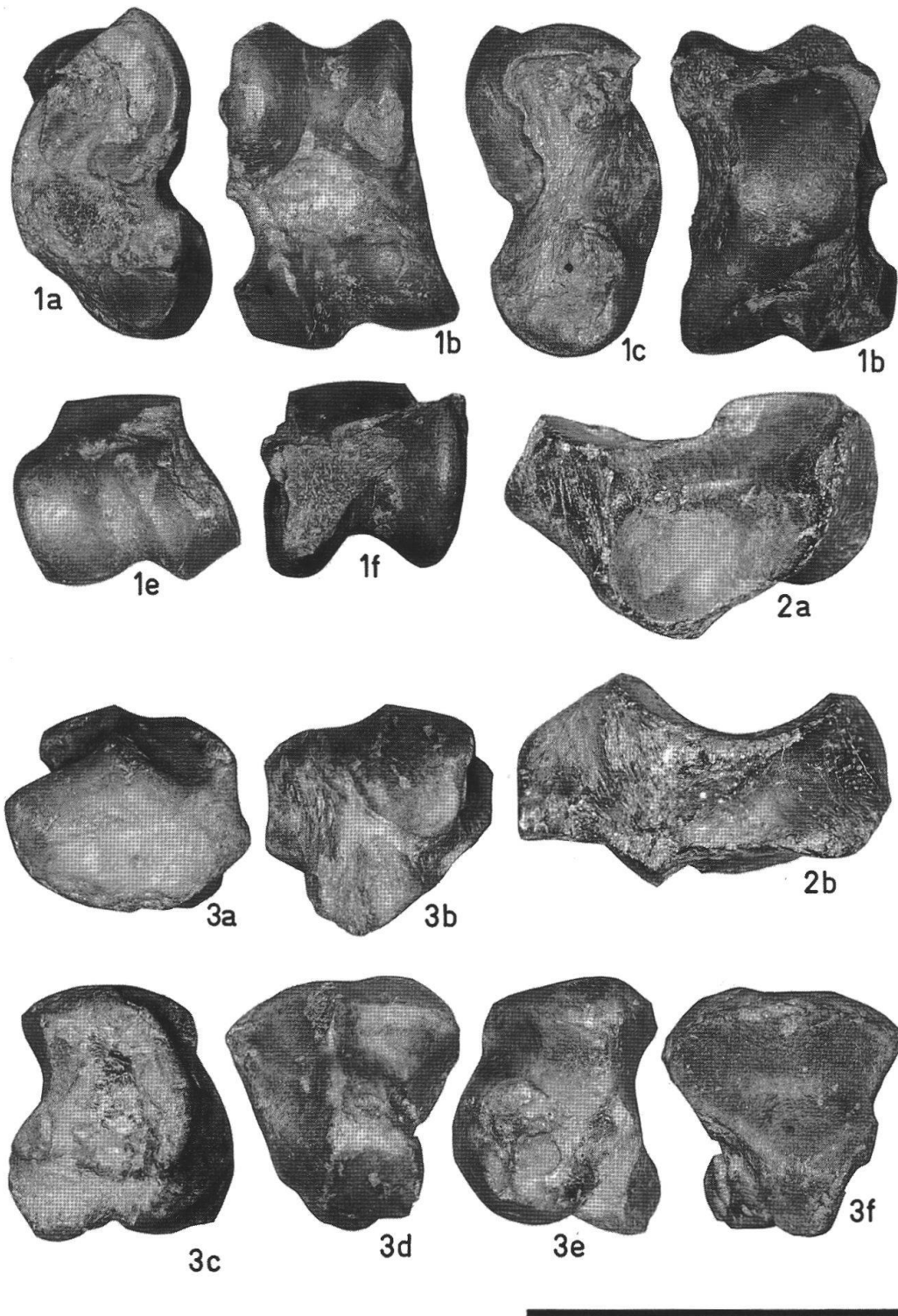
Von MEYER (1846) became convinced that the animal from La Chaux-de-Fonds (and from Simorre) was indeed a pig and no tapir and that it had nothing to do with *Lophiodon*; he introduced the name *Listriodon splendens* for these fossils. In the same paper, he also introduced the names *Calydonius trux* and *Calydonius tener* (Pl. 1, fig. 1) for the suid canines from La Chaux-de-Fonds.

A recent revision of the listriodonts (VAN DER MADE, 1996) recognizes 5 listriodont genera and some 25 species. Wide incisors with low crowns are typical for all of them and in nearly all lineages, still wider incisors evolved parallel. Lophodont teeth, as in tapirs, evolved at least twice. Incisor morphology, enamel thickness, lophodonty and tooth wear suggest that listriodonts were folivores. They may have ingested large quantities of leaves and may have had a "grazing" type of feeding. However, their low crowned teeth suggest that they did not eat grass, which is very abrasive and which usually is eaten by species with high-crowned cheek teeth. Different listriodont lineages in Africa,



**Plate 1:** *Listriodon splendens* from La Chaux-de-Fonds.

1) MHNC 48 - Left  $C^m$ , posterior view. 2) MHNC 9aua - Left  $I^1$ , labial and apical views. 3) MHNC -- - Right cuboid, internal, external and distal views. 4) MHNC 6 - Right  $I_1$ , distal and labial views. 5) MHNC 10x - Left  $I_3$ , apical and labial views. 6) MHNC -- - Left calcaneus, anterior and external views. The bar represents 5 cm for figures 1 & 6 and 6.7 cm for figures 2-5.



**Plate 2:** *Listriodon splendens* from La Chaux-de-Fonds.

1) MHNC -- - right astragalus, external, anterior, internal, posterior, distal and proximal views. 2) MHNC -- - Left navicular, proximal and external views. 3) MHNC -- - Right magnum, anterior, posterior, internal, proximal, external and distal views. The bar represents 5 cm for figure 1 and 6.7 cm for figures 2 & 3.

Europe, China and the Indian Subcontinent disappeared in a short period following the spread of open grasslands.

Estimated body weights of the listriodonts vary between 8 kg for *Lopholistriodon moruoroti* and over 3000 kg for *Kubanochoerus mancharensis*. *Kubanochoerus* is a peculiar listriodont, in which the females has small protuberances above the orbits and the males, in addition to these, a large "horn" in the middle of the frontals. The "horn" was directed forward and was probably not covered by keratin.

The increasing width of the incisors and increasing size of the canines in the different lineages have stratigraphic value. The incisors of *L. splendens* suggest a position for La Chaux-de-Fonds between the older sample from La Grive and younger samples from Sant Quirze and Castell de Barberà.

Though the fossils collected by Nicolet were the first described listriodont remains and constitute the type material of *Listriodon splendens*, type species of *Listriodon*, type genus of the Listriodontinae, the material was not often object of study. There are descriptions by BAYLE (1856) and STEHLIN (1899/1990). Stehlin and I figured

some of the dental material (STEHLIN, 1899/1990; VAN DER MADE, 1996, Pl. 41, figs. 1-14). None of the paratype bones have ever been figured, even though the listriodont ankle joint morphology has been interpreted as representing a particular cursorial specialisation (LEINDERS, 1976). Figures of the paratype astragalus (Pl. 2, fig. 1), cuboid (Pl. 1, fig. 3), navicular (Pl. 2, fig. 2) and calcaneus (Pl. 1, fig. 6) are provided here. Also the magnum may turn out to have a phylogenetically important character. The anterior end of that bone may touch the unciform (as in the more derived suids) or not (as in a hyotheriine like *Chleuastochoerus* Pearson, 1928). In *Listriodon*, the magnum has a facet for the unciform that reaches the anterior end of the bone (Pl. 2, fig. 3). Measurements of the specimens are given elsewhere (VAN DER MADE, 1996, tables 6-19).

#### ACKNOWLEDGEMENTS

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