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Hipparion primigenium from Höwenegg/Hegau, FRG

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Hipparion from the Vallesian (upper Miocene) of Höwenegg is referred to *H. primigenium* (von Meyer) and compared with local samples of that species from other parts of Europe and from North Africa.

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1. Introduction

The upper Miocene fossil locality Höwenegg is famous for being the only locality in the Old World which has yielded complete skeletons of *Hipparion* (Tobien 1959, Tobien & Jörg 1959). *Hipparion* from Höwenegg has not been formally described, but Forstén (1968:15) referred it to *H. primigenium* (see also Gromova 1952:310). More data than available to me in 1968, i.e. the Höwenegg collections kept in the Hessisches Landesmuseum in Darmstadt and in the Geological-Paleontological Institute of the University of Freiburg, support my earlier opinion: the *Hipparion* from Höwenegg, with its low-crowned, strongly plicated cheek teeth and massive limbs, belongs to *H. primigenium*. This species was widely distributed in Europe and North Africa, where in the Vallesian upper Miocene it was the sole representative of its genus.

Nothing indicates that the *Hipparion* sample from Höwenegg is heterogeneous (Tables 1-3). I therefore refer it in toto to *H. primigenium*. In this paper I compare Höwenegg *H. primigenium* with local samples of that species from the Western Palearctic. For characterization of the latter see Forstén (1968, 1972, 1978a & b, 1982, 1983). The measurements on the skull, jaw, and limb bones used here are taken according to Gromova (1952).

I wish to thank Prof. S. Kuss and Dr. W. v. Koenigswald for showing me the collections in their care.

2. Diagnosis of *Hipparion primigenium* (von Meyer, 1829)

Diagnosis (Forstén 1968:15, emended): Middle sized to large. Metapodials massive; MT III often lacking a facet against the external cuneiform. Preorbital fossa simple, oval to pear-shaped, situated rather far from the eye. Cheek teeth relatively low crowned. Uppers mostly richly plicated; protocone oval, often quite flat. Lowers with well developed cingular elements. Upper Miocene.

3. Description and comparison

3.1. Skull

I have seen four skulls from Höwenegg (three skulls in Darmstadt: 54/F4 G1, M 55/L & 58/VI, and a cast of a fourth in the Humboldt Museum, Berlin, DDR). All four are crushed, but in two skulls an oval pear-shaped preorbital fossa with a wide posterior pocket is visible. It extends from a level with M^2 to about P^3. Plotted on orbit-fossa distance against P^2-orbit distance, these two skulls fall in with skulls referred to *H. primigenium* (Forstén 1983, fig. 1 & p. 692). When compared with the latter for skull size and proportions, the Höwenegg specimens are characterized by a long snout and diastema, but short nasal

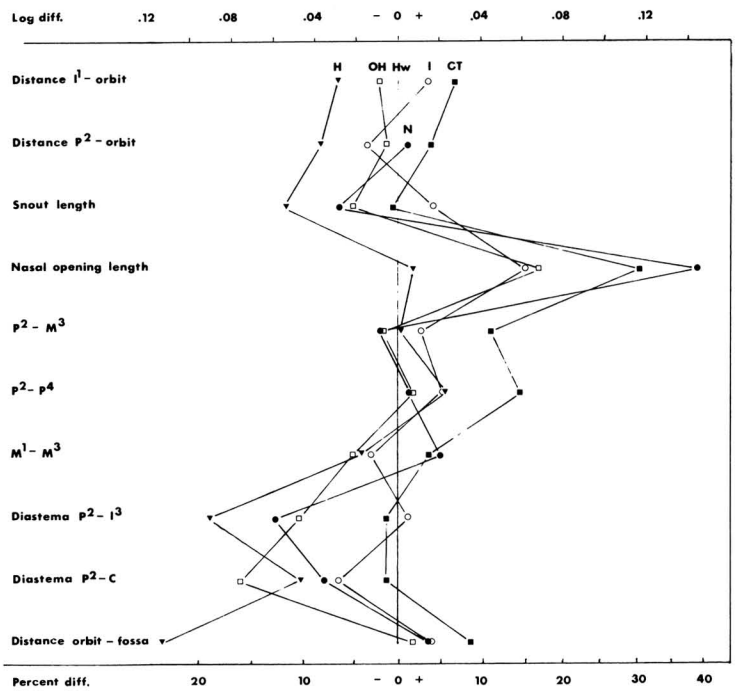

Fig. 1. Ratio diagram showing relative size of the skull in samples of *Hipparion primigenium*. Standard of comparison Höwenegg (Hw, means). Other samples are Oued el Hammam (OH, means), Nesebr (N, means), Hostalets (H, single skull), Inzersdorf (I, means), and Can Trullas (CT, single skull).

opening (Fig. 1). The nasal opening ends at a level 1-2 cm in front of P^2. The diastema is long also in the jaw, as is the symphysis (Fig. 2).

3.2. Teeth

Hipparion primigenium from Höwenegg cannot be compared for detailed dental size, since isolated teeth measureable at the crown base are too scarce, but the tooth rows are long (Tables 1-2, Figs. 1-2). In the uppers, mean protoconal length ($N = 15$, $\bar{x} = 0.758 \pm 0.017$) and plication count ($N = 9$, $\bar{x} = 30 \pm 2.3$) do not differ from those in local samples of *H. primigenium* (e.g. Forstén 1978b, Table 1).

In the lowers the protostylid is almost always present. An ectostylid occurs in the premolars of two jaws (Freiburg Nos. 264 & 265, and 381), but in none of the molars. The ectoflexid is often deep, not only in the molars but also in the premolars, reaching into the metaconid-metastylid stalk.

3.3. Limbs

Compared for the means of 12 limb bone measurements (MC III and MT III total length, proximal and distal breadth, phalanx 1 dorsal length and mid-shaft width, phalanx 2 volar length and mid-shaft width, and astragalus articular breadth and height) with some local samples of *H. primigenium*, Höwenegg is similar to Eppelsheim, the type locality of the species (Fig. 4). Two out of a total of twelve MT III from Höwenegg lack a facet for the inner cuneiform.

In *H. primigenium* from Höwenegg the tibia is long in relation to MT III length, the radius short in relation to MC III length; Gromova (1952: 173) considers these primitive traits in *Hipparion*. Also, the femur is long. A relatively long tibia characterizes *H. primigenium* in those samples where this bone is preserved (Fig. 3: P1, G1). In some stratigraphically younger species of *Hipparion*, e.g. Turolian *H. mediterraneum* Roth & Wagner, *H. moldavicum* Gromova, and *H. verae* Gabunia, the tibia is shortened (Fig. 4: P2, G2). This is still more pronounced in

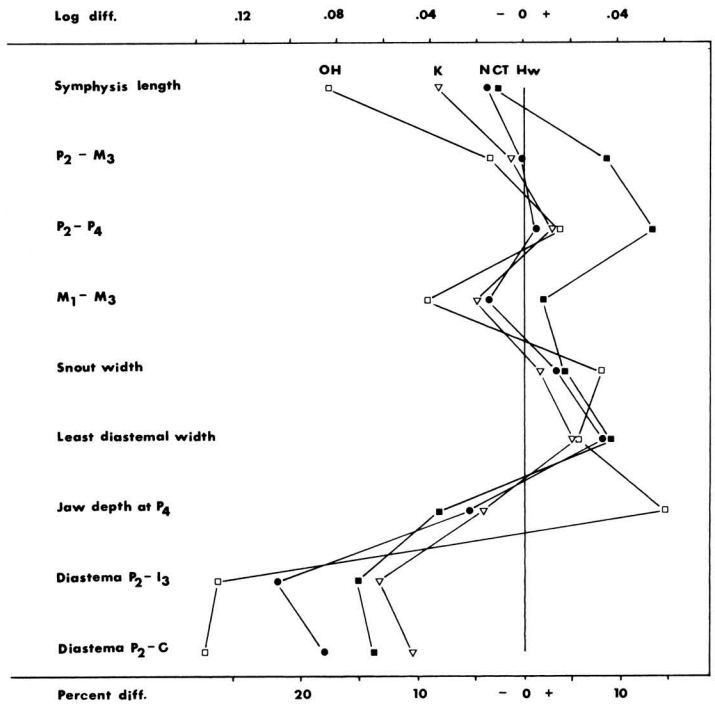

Fig. 2. Ratio diagram showing relative size of the mandible in samples of *H. primigenium*. Standard of comparison Höwenegg (Hw, means). Other samples are Oued el Hammam (OH, means), Kalfa (K, means), Nesebr (N, means), and Can Trullas (CT, single jaw).

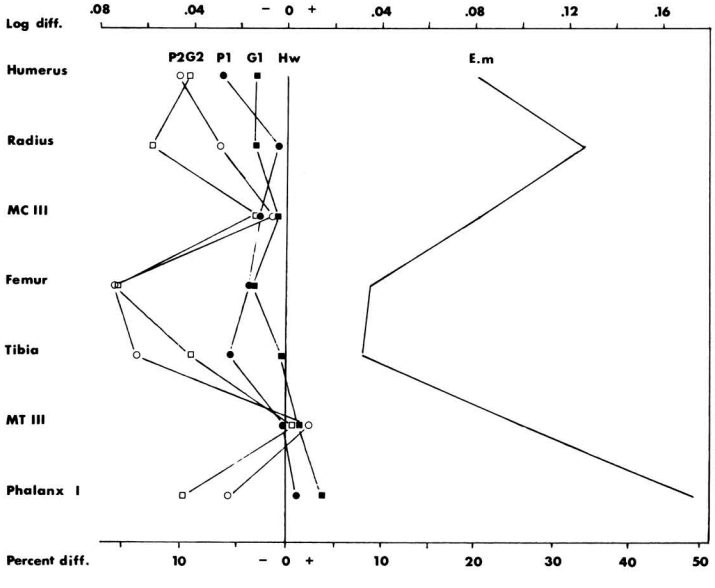

Fig. 3. Ratio diagram showing relative lengths of the limb bones in samples of *Hipparion* and *Equus* (means). Standard of comparison Höwenegg (Hw). Other samples are *H. primigenium* from Pikermi and Grebeniki (P1 & G1), *H. mediterraneum* from Pikermi (P2), *H. verae* from Grebeniki (G2), and *Equus mosbachensis* v. Reich. (E.m) from Mosbach.

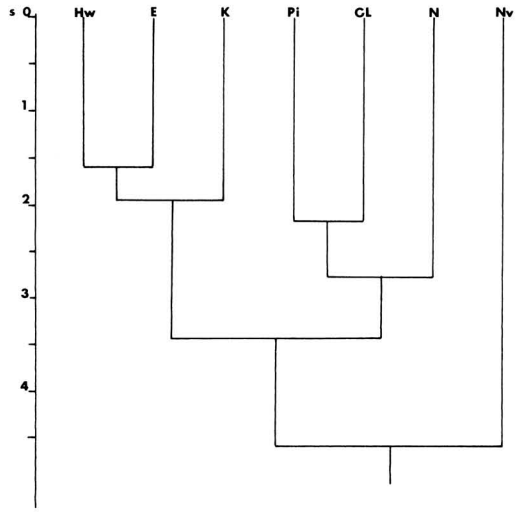

Fig. 4. Phenogram of UPGMA clustering constructed using the means of 12 limb bone measurements (see text) in samples of *H. primigenium*. Distance scale in standard deviation units. Samples used are Höwenegg (Hw), Eppelsheim (E), Kalfa (K), Polgardi (Pi), Can Llobateres (CL), Nesebr (N), and Nombrevilla (Nv).

hipparions with caballoid teeth (Old World *Neohipparion*). The hind limbs in these Pliocene forms take on the proportions of those of most monodactyl horses, in which the tibia is short in relation to MT III (Fig. 4: E.m). The femur becomes shorter simultaneously with the tibia. In all hipparions, the radius remains relatively short compared with MC III, in contrast to the monodactyl horses, in which the radius is long.

The intra-limb proportions in *Hipparion* probably influenced the angulation of the limbs, the type of locomotion, and, ultimately, the type of habitat preferred. According to Gromova's (1952) analysis of the limb bones of the genera *Hipparion* and *Equus*, the limbs in *Hipparion* were more angulated than those of *Equus*. In *H. primigenium* the front limbs were relatively short (humerus + radius + MC III length 78 cm), the hind limbs long (femur + tibia + MT III length 103 cm), compared with *Equus* of approximately the same size, e.g. *E. przewalskii* Polj., in which the front and hind limbs are more equal in length (front limb 80 cm, hind limb 95 cm; according to Gromova 1949, Tables VIII, IX, X and XII, Eisenmann 1979, Table 6). The hind limbs in *H. primigenium* must have been well-angulated or the animal would have been overbuilt.

Table 1. Statistiscs on the skull of *H. primigenium*, Höwenegg.

	N	Range	Mean ± *SE*
Distance I^1-orbit	2	29.2, 29.8	29.5
" P^2-orbit	2	16.5, 17.2	16.8
Nasal opening length	2	8.65, 9.00	8.83
Length P^2-M^3	3	14.9-15.5	15.3 ± 0.19
" P^2-P^4	3	7.45-8.40	8.08 ± 0.17
" M^1-M^3	4	6.87-7.45	7.14 ± 0.12
Diastema I^3-P^2	2	10.4, 11.1	10.76
" P^2-C	2	6.18, 6.50	6.34
Distance orbit-fossa	2	4.50, 4.60	4.55

Renders (1984) recently interpreted the fast gait of *Hipparion*, documented in the form of fossil footprints, as a running walk. The *Hipparion* represented by the fossil footprints may have had limb proportions different from those of *H. primigenium*, i.e. more *Equus*-like, with relatively shorter hind limbs, in which case its locomotion is directly comparable to that in *Equus* (Renders 1984: 180). With other limb proportions, e.g. with the hind limbs considerably longer than the front limbs as in *H. primigenium*, other modes of locomotion are possible.

Žegallo (1978:66-67, Fig. 46) compared the proportions of the hind limbs of *H. primigenium* from Höwenegg with those of certain artiodactyls, e.g. *Capreolus*, which according to Gambaryan (1974) use a "lunging" gallop as the main mode of locomotion. They also prefer closed to semi-closed forest or brush country, or hilly country. Žegallo (1978:67) also found traits in common in the proportions of the hind limbs of *H. primigenium* and the tapir, the latter with a primitive "ramming" type of gallop. He believed this mode of locomotion to typify animals in semi-closed brush country.

4. Conclusions

Hipparion primigenium from Höwenegg adds little of novelty to the picture of *Hipparion* in the Old World. It is a conventional early representative of its species. However, the sample from Höwenegg is important because it allows a more detailed characterization than heretofore of the size, proportions, and qualitative morphology of the

Table 2. Statistics on the jaw of *H. primigenium*, Höwenegg.

	N	Range	Mean ± *SE*	*s*	*V*
Length I_1-gonion	1	41.5			
Symphysis length	4	8.40-9.70	9.03 ± 0.27	0.54	5.97
Length P_2-M_3	2	15.5, 15.6	15.55		
" P_2-P_4	2	7.45, 7.65	7.55		
" M_1-M_3	3	7.70-7.88	7.81 ± 0.06	0.10	1.23
Snout width	2	4.58, 4.98	4.78		
Diastemal least width	2	2.80, 3.05	2.93		
Diastema I_3-P_2	3	9.90-12.56	11.00 ± 0.8	1.39	12.60
" P_2-C	4	8.12-11.09	9.11 ± 0.68	1.35	14.85
Depth of jaw at P_4	4	6.60-7.24	6.81 ± 0.15	0.30	4.35

Table 3. Statistics on the limb bones of *H. primigenium*, Höwenegg.

	N	Range	Mean ± *SE*	*s*	*V*
Humerus length	3	26.0-30.9	28.13 ± 1.45	2.51	8.90
Radius length	6	27.0-30.0	28.25 ± 0.40	0.98	3.45
MC III length	14	21.0-22.2	21.59 ± 0.11	0.42	1.96
" proximal breadth	15	3.77-4.20	4.02 ± 0.03	0.12	3.10
" distal breadth	14	3.41-4.00	3.71 ± 0.03	0.12	3.32
Femur length	3	40.5-42.2	41.57 ± 0.54	0.93	2.24
Tibia length	6	35.8-39.0	37.37 ± 0.62	1.51	4.05
MT III length	17	23.0-25.1	24.39 ± 0.16	0.64	2.62
" proximal breadth	15	4.13-4.74	4.35 ± 0.05	0.21	4.83
" distal breadth	17	3.50-4.14	3.81 ± 0.05	0.19	4.99
Phalanx 1 dorsal length	37	5.59-6.31	5.90 ± 0.03	0.21	3.56
" 1 mid-shaft width	37	2.58-3.30	3.01 ± 0.03	0.20	6.61
Phalanx 2 volar length	38	3.53-4.30	3.90 ± 0.03	0.18	4.62
" 2 mid-shaft width	38	2.94-3.40	3.16 ± 0.02	0.12	3.80
Astragalus articular breadth	10	4.05-4.74	4.40 ± 0.07	0.21	4.77
" height	10	5.47-5.97	5.72 ± 0.05	0.17	2.92

species, the earliest described in the genus. Other forms of *Hipparion*, geographically distant or stratigraphically younger, can be shown to resemble *H. primigenium* morphologically, thus to taxonomically equal it and probably to share similar ecology with it.

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