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| Zeitschrift: | Eclogae Geologicae Helvetiae |
| Herausgeber: | Schweizerische Geologische Gesellschaft |
| Band: | 80 (1987) |
| Heft: | 3 |
| Artikel: | New Theridomyidae (Rodentia, Mammalia) in the Oligocene Molasse of Switzerland and Savoy |
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| Kapitel: | Subfamily Issiodoromyinae |
| DOI: | https://doi.org/10.5169/seals-166036 |

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Table 7: Measurements of the $M_{1/2}$ of *Blainvillimys stehlini* n. sp. from Mümliswil-Hardberg (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|----|-----------------------|-----------|-----------|------|-------|
| 4 | 10 | Sinusid height | 0,50–1,75 | 1,24 | 0,41 | – |
| | 9 | Length | 2,17–2,58 | 2,31 | 0,13 | 5,56 |
| | 9 | Width | 2,00–2,42 | 2,13 | 0,13 | 6,57 |
| | 8 | Sinusid length | 1,67–2,20 | 1,83 | 0,16 | 8,79 |
| | 9 | Extrasinusid distance | 0,16–0,28 | 0,21 | 0,03 | 15,06 |
| | 9 | Crown height | 1,33–2,75 | 2,01 | 0,56 | – |

715, Fig. 6 and 7) considered the material of *Blainvillimys* of Mümliswil-Hardberg as a new species: first as the genus *Archaeomys*, afterwards as *Blainvillimys*. The specimen NMB: UM 2407 (P_4 sin.) and UM 2424 (unworn fragment of $M_{1/2}$) show a very superficial pseudogruben, where the III synclinid is only a slight notch. But, no one specimen shows a typical tubular III synclinid. Ninety six percent of the lower teeth show a graben or semigraben (none a sinusid with a tubular III synclinid). In the process of wear this rare pseudogruben shows a longer “sinusid” with a wide notch on the lingual border. The Pearson variation coefficient of the length of $M_{1/2}$ (9 specimens) show a normal value of V (5,56), in spite of the few number of specimens. The comparison by the Student t-test of the sample of *Blainvillimys blainvillei* of Antoingt (4 specimens) with the sample of *B. stehlini* n. sp. of Mümliswil-Hardberg (8 specimens) for the length of $M_{1/2}$ did not show significant differences. But the Student t-test show highly significant differences for sinusid length ($N = 11$) and for the width/sinusid length ratio ($N = 12$).

Measurements in the Tables 3–8.

Statistical test in the Tables 54 and 56.

Table 8: Measurements of the M_3 of *Blainvillimys stehlini* n. sp. from Mümliswil-Hardberg (Switzerland)

| SW | N | Sinusid length | Length | Width | Sinusid length | Extrasinus distance | Crown height |
|----|---|----------------|--------|-------|----------------|---------------------|--------------|
| 3 | 1 | 1,08 | 1,92 | 1,83 | 1,50 | 0,17 | 1,75 |
| 5 | 1 | 0,42 | 2,17 | 2,00 | 1,92 | 0,17 | 0,58 |

Subfamily *Issiodoromyinae* (SCHLOSSER 1884)

Genus *Issiodoromys* CROIZET, in BLAINVILLE 1840

Type species. – *Issiodoromys pseudanema* GERVAIS 1848–52.

Stratigraphic range. – Oligocene, Upper “Chattien”. From Fornant-7 to Rickenbach assemblage zones in the faunal province of Switzerland and Savoy (see ENGESSER & MAYO 1987).

Geographical distribution. – Central and West Europe.

Previous diagnoses. – CROIZET 1840, in: BLAINVILLE, p. 931–32; GERVAIS 1848–52, p. 27 and 47, explanation to Fig. 6 and 8; POMEL 1854, p. 39–40; LYDEKKER 1885, p. 252; ZITTEL 1891–93, p. 525; VIRET 1929, p. 85; WINGE 1941, p. 22–23 and 131; FREUDENBERG 1941, p. 137; STEHLIN 1951, p. 69, 74 and 247–48 in: STEHLIN & SCHAUB; SCHAUB 1953, p. 190 and 1958, p. 45; VIANEY-LIAUD 1976, p. 34.

Emended diagnosis. – Hypsodont [protohypodont] Issiodoromyinae. Broad infraorbital foramen. Ascending ramus of anterior zygomatic process with very concave anterior

border. Masseteric apophysis of the anterior zygomatic process with masseteric ridge and horizontal foramen laterally to the ridge. External alveolar border of the maxilla in front of M^2-M^3 , perpendicular to the abrasive surface of the teeth. Mandible with very elongated longitudinal masseteric ridge and deep tubular masseteric sulcus. Teeth with very elongated lobules. P^4 with normal to atrophied anterior labial root. M^1-M^2 with atrophied labial roots. M^3 with semiatrophied labial roots. Enamel in the labial border of the upper teeth or in the lingual of the lower ones reduced or missing in the lobules. Lower teeth with two or three roots.

Subgenus *Issiodoromys*. (*Issiodoromys*) CROIZET

Issiodoromys (*Saboyanomys*) n. subg.

Issiodoromys (*Issiodoromys*) CROIZET, in BLAINVILLE 1840

Type species. – *I. (Issiodoromys) pseudanema* GERVAIS 1848–52.

Stratigraphic range. – Oligocene, Upper “Chattien”. Upper the Fornant-6 to Rickenbach assemblage zones, in faunal province of Switzerland and Savoy (see ENGESSER & MAYO 1987).

Geographical distribution. – Central and West Europe.

Diagnosis. – Issiodoromyinae without enamel in the lobules on the labial border of the crown in the upper teeth or on the lingual border of the lowers. Lower border of the anterior zygomatic process with short and narrow masseteric apophysis and ridge. Maxilla with broad infraorbital canal on the base, strongly vaulted and with a highly developed external ridge. Anterior alveolar foramen in the base of the infraorbital canal. Posterior border of incisive foramen in front of the posterior prism of P^4 . P^4 smaller than M^1 or M^2 and very inclined to M^1-M^3 . Most of the I syncline in P^4 opened. Crown of P^4-M^3 : quadrangular in SW-1 to 3; subcylindrical starting from SW-4. Sinus rectum, blunt, short and broad in P^4-M^3 in SW-3. In M^1-M^3 sinus very elongated, curved and sharp starting from SW-4. All teeth with sinus and sinusid, open lingually and labially respectively and closed inside by cellular cement. M^1-M^2 with atrophied labial roots. P^4 with normal to semiatrophied anterior labial root. Lingual root with narrow base. M^3 with two semiatrophied labial roots or only one posterior semiatrophied labial root, somewhat laminated. Lower teeth with long roots without indication of atrophy.

I. (*Saboyanomys*) n. subg.

Type species. – *I. (Saboyanomys) weidmanni* n. subg. n. sp.

Stratigraphic range. – Oligocene, Upper “Chattien”, from Fornant-7 to Rickenbach assemblage zones (see ENGESSER & MAYO 1987).

Geographical distribution. – Central and West Europe.

Diagnosis. – Issiodoromyinae with fine enamel layer on the lobules of the crown in the upper teeth and partially on the lower. Lobules of medium size on the labial border of the upper teeth and on the lingual border of the lower. Maxilla with broad and scarcely vaulted infraorbital canal. External ridge slightly developed. Small maxillary height from the labial alveolar border to the dorsal border of the external ridge. Posterior border of

Table 9: Measurements of the P⁴ of *Issiodoromys (Saboyanomys) weidmanni* n. subg. n. sp. from Ruisseau du Bey (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|-------|
| 1 | 3 | Length | 1,58–2,00 | 1,72 | 0,24 | 14,10 |
| | 2 | Width | 1,25–1,42 | 1,34 | 0,12 | 9,00 |
| 3 | 3 | Sinus height | 3,87–4,33 | 4,07 | 0,24 | 5,83 |
| | 5 | Length | 1,60–1,83 | 1,71 | 0,09 | 5,05 |
| | 5 | Width | 1,48–1,68 | 1,58 | 0,09 | 5,87 |
| | 3 | Crown height | 4,17–4,75 | 4,42 | 0,30 | 6,78 |
| 4 | 6 | Sinus height | 2,83–4,17 | 3,57 | 0,54 | 15,04 |
| | 7 | Length | 1,67–1,83 | 1,74 | 0,06 | 3,20 |
| | 7 | Width | 1,50–1,83 | 1,69 | 0,11 | 6,79 |
| | 6 | Crown height | 3,17–4,50 | 3,88 | 0,51 | 13,26 |
| 5 | 3 | Sinus length | 1,83–3,08 | 2,61 | 0,68 | – |
| | 4 | Length | 1,58–1,75 | 1,71 | 0,09 | 4,98 |
| | 4 | Width | 1,33–2,58 | 1,77 | 0,56 | – |
| | 3 | Crown height | 2,17–3,67 | 3,00 | 0,76 | – |

the incisive foramen in front of the posterior prism of P⁴. P⁴ slightly smaller than M¹ or M²; very inclined toward M¹–M² and with semiatrophied to vestigial anterior labial roots, according to species. I syncline of P⁴ closed. M¹–M³ with two atrophied to vestigial roots. P⁴–M³ with lingual root slightly broader than crown cylinder and with the tendency to reduction. Lower teeth lingually concave towards the middle of the crown and with a tendency toward atrophy in the roots.

Differential diagnosis. – *I. (Saboyanomys)* n. subg. differs from *I. (Issiodoromys)* in the following characters:

Table 10: Measurements of the M^{1/2} of *Issiodoromys (Saboyanomys) weidmanni* n. subg. n. sp. from Ruisseau du Bey (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|-------|
| 1 | 1 | Length | – | 1,90 | – | – |
| | 1 | Width | – | 1,17 | – | – |
| 2 | 1 | Sinus height | – | 4,75 | – | – |
| | 2 | Length | 1,75–1,92 | 1,84 | – | – |
| | 2 | Width | 1,42–1,50 | 1,46 | – | – |
| 3 | 1 | Sinus height | – | 5,50 | – | – |
| | 3 | Length | 1,75–2,08 | 1,86 | 0,19 | 10,24 |
| | 3 | Width | 1,33–1,67 | 1,47 | 0,18 | 11,96 |
| | 1 | Crown height | – | 5,83 | – | – |
| 4 | 8 | Sinus height | 4,33–6,00 | 5,36 | 0,55 | 10,31 |
| | 9 | Length | 1,75–2,08 | 1,89 | 0,11 | 5,83 |
| | 8 | Width | 1,33–1,83 | 1,59 | 0,20 | 12,27 |
| | 5 | Crown height | 5,41–6,25 | 5,87 | 0,39 | 6,60 |
| 5 | 9 | Sinus height | 1,75–4,58 | 3,57 | 0,48 | – |
| | 9 | Length | 1,58–1,92 | 1,78 | 0,09 | 5,37 |
| | 8 | Width | 1,50–2,08 | 1,81 | 0,18 | 9,72 |
| | 7 | Crown height | 2,17–5,16 | 4,10 | 1,26 | – |

Table 11: Measurements of the M^3 of *Issiodoromys (Saboyanomys) weidmanni* n. subg. n sp. from Ruisseau du Bey (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|-------|
| 2 | 2 | Length | — | 1,75 | — | — |
| | 2 | Width | 1,33–1,58 | 1,46 | 0,18 | 12,15 |
| 3 | 4 | Sinus height | 3,25–4,42 | 3,73 | 0,52 | 13,95 |
| | 4 | Length | 1,75–2,00 | 1,85 | 0,11 | 5,69 |
| | 6 | Width | 1,42–1,75 | 1,59 | 0,13 | 8,15 |
| | 4 | Crown height | 3,67–4,58 | 4,00 | 0,41 | 10,29 |
| 4 | 8 | Sinus height | 2,67–4,00 | 3,36 | 0,43 | 12,88 |
| | 5 | Length | 1,83–1,92 | 1,87 | 0,05 | 2,64 |
| | 5 | Width | 1,58–1,83 | 1,67 | 0,10 | 5,88 |
| | 6 | Crown height | 3,83–4,17 | 3,88 | 0,29 | 7,59 |
| 5 | 2 | Sinus height | 1,25–2,08 | 1,67 | 0,59 | — |
| | 2 | Length | — | 2,00 | — | — |
| | 2 | Width | 2,00–2,25 | 2,13 | 0,18 | 8,32 |
| | 2 | Crown height | 2,08–2,33 | 2,21 | 0,18 | 8,02 |

- presence of enamel on the lobules of the crown,
- larger size of the P^4 ,
- different morphology of P^4 in unworn stage,
- smaller lobules on the labial border of the upper teeth and lingual border of the lowers,
- lower maxillary height from the labial alveolar border to the dorsal border of the infraorbital canal ridge,
- stronger tendency towards atrophy of the labial roots in P^4 ,
- broader lingual root than crown cylinder in the upper molars,
- tendency toward atrophy of the roots in the lower teeth.

Table 12: Measurements of the P_4 of *Issiodoromys (Saboyanomys) weidmanni* n. subg. n sp. from Ruisseau du Bey (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|----------------|-----------|-----------|------|-------|
| 1 | 1 | Length | — | 1,92 | — | — |
| | 1 | Width | — | 1,08 | — | — |
| 3 | 1 | Sinusid height | — | 3,25 | — | — |
| | 1 | Length | — | 1,75 | — | — |
| | 1 | Width | — | 1,75 | — | — |
| | 1 | Crown height | — | 3,75 | — | — |
| 4 | 2 | Sinusid height | 2,08–2,58 | 2,33 | 0,35 | 15,17 |
| | 2 | Length | 2,08–2,17 | 2,13 | 0,06 | 2,99 |
| | 2 | Width | — | 1,50 | — | — |
| | 2 | Crown height | 2,50–3,00 | 2,75 | 0,35 | 12,86 |
| 5 | 2 | Sinusid height | 0,75–2,08 | 1,41 | 0,94 | — |
| | 1 | Length | — | 2,08 | — | — |
| | 2 | Width | 1,42–1,67 | 1,55 | 0,18 | 11,44 |
| | 2 | Crown height | 1,00–2,67 | 1,84 | — | — |

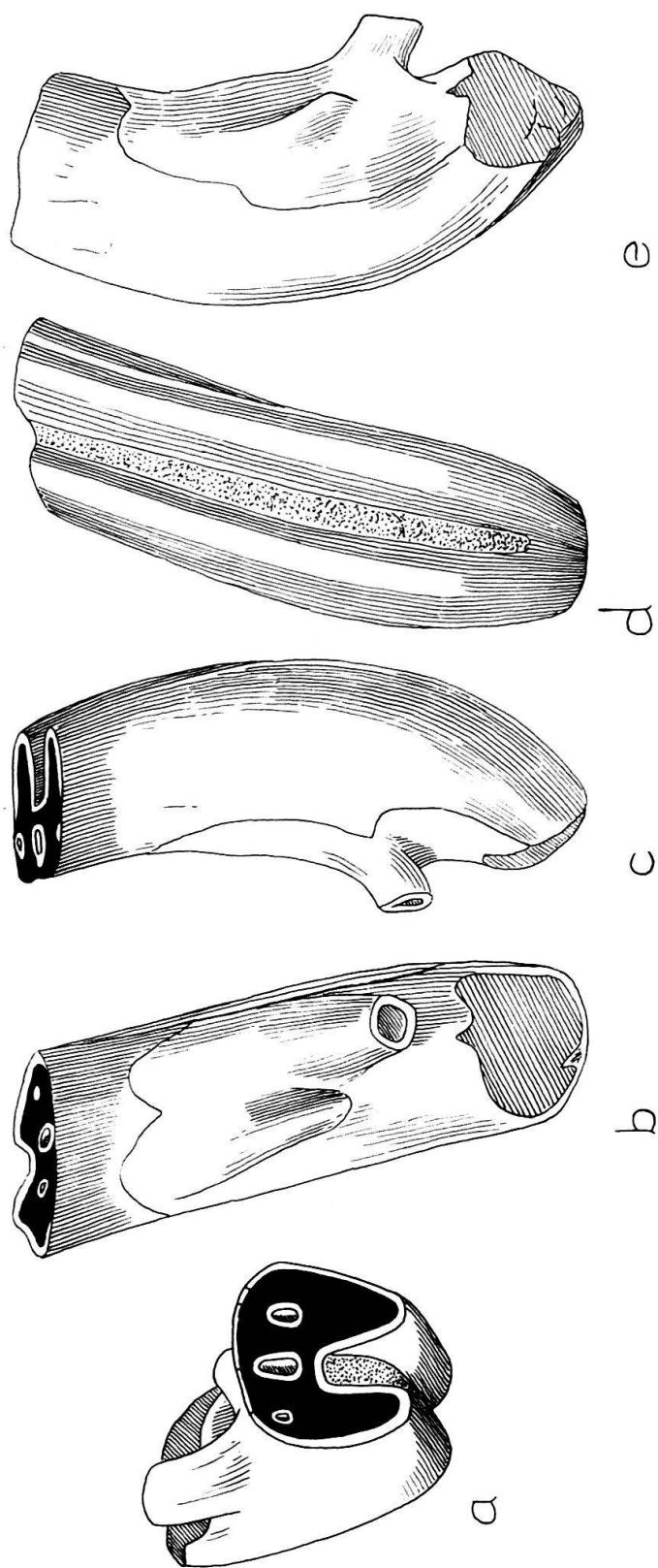


Fig. 15. *Issiodromys (Saboyanomys) weidmanni* n. sp. MGL 46368. P^4 dex (invers.). Holotype. Ruisseau du Bey, Switzerland. a = occlusal view. b = labial view. c = anterior view. d = posterior view. e = lingual view. — All figures $\times 12,5$.

I. (Saboyanomys) weidmanni n. subg. n. sp.

Fig. 15

Derivatio nominis. – After the geologist Dr. Marc Weidmann (Lausanne), principal collector of the material.

Holotype. – MGL 46368. P⁴ dex. in SW-3.

Measurements of the Holotype. – Sinus height: 4,33 · Length: 1,75 · Width: 1,58 · Sinus length: 0,92 · Extrasinus distance: 0,67 · Curvature radius: 4,20 · Crown height: 4,75 · Anterior lobule height: 0,50 · Posterior lobule height: 0,67 · Crown height above anterior lobule: 0,75; above posterior lobule: 0,67.

Paratypes. – SW-1: P⁴. – NMB: RB 1, 2 and 7; M². – NMB: RB 19; M³. – NMB: RB 36. P₄. – MGL 46331; M₁. – NMB: RB 23. SW-2: M¹. – MGL 46309; M². – NMB: RB 17; M³. – NMB: RB 37; MGL 46303; P₄. – NMB: RB 42f; M₃. – NMB: RB 43; MGL 46350. SW-3: P⁴. – MGL 46365 and 46370; NMB: RB 3 and 8; M¹. – MGL 46308 and 46314; M². – MGL 46364. M³. – NMB: 39f and 40; MGL 46321, 46325, 46327 and 46332. P₄. – NMB: RB 42f; M₁. – MGL 46323, 46326, 46344 and 46366; NMB: RB 27; M₃. – MGL 46351. SW-4: P⁴. – MGL 46307, 46313, 46317 and 46367; NMB: RB 4–6; M¹. – MGL 46304–06, 46310–11; NMB: 10 and 15; M². – MGL 46287 and NMB: RB 18; M³. – NMB: RB 33, 34, 35, 40 and 41f; MGL: 46335, 46339f and 46348; P₄. – MGL 46336 and NMB: RB 39. M₁. – MGL 46312, 46322, 46328, 46330, 46338, 46346 and 46374. NMB: RB 25, 26, 28, 30 and 32; M₃. – MGL: 46352, 46357 and 46362; NMB: RB 44. SW-5: P⁴. – MGL 46289, 46316 and 46361; NMB: RB 9; M¹. – NMB: RB 11–14 and 16. M². – MGL 46263; NMB: 20–22; M³. – NMB: RB 38 and 41. P₄. – 46328, 4633 (e) and 46369. M₁. – NMB: 24, 26 and 29; MGL: 46329, 46341, 46342, 46345, 46347, 46354, 46356, 46379 and 46383.

Type locality. – Ruisseau du Bey, North of Mathod, Switzerland (see JORDI 1955, p. 34). However, the list of the fauna offered by JORDI does not belong to Ruisseau du Bey.

Other locality. – Fornant-7.

Table 13: Measurements of the M_{1/2} of *Issiodoromys (Saboyanomys) weidmanni* n. subg. n. sp. from Ruisseau du Bey (Switzerland)

| SW | N | | range | X | S | V |
|----|----|----------------|-----------|------|------|-------|
| 1 | 1 | Length | – | 1,75 | – | – |
| | 1 | Width | – | 1,25 | – | – |
| 3 | 4 | Sinusid height | 4,92–5,67 | 5,19 | 0,34 | 6,48 |
| | 5 | Length | 2,25–2,58 | 2,43 | 0,15 | 6,08 |
| | 3 | Width | 1,67–1,83 | 1,77 | 0,09 | 5,20 |
| | 2 | Crown height | 5,00–5,25 | 5,12 | 0,18 | 3,45 |
| 4 | 12 | Sinusid height | 3,67–5,00 | 4,53 | 0,45 | 10,01 |
| | 11 | Length | 2,17–2,58 | 2,39 | 0,13 | 5,38 |
| | 8 | Width | 1,67–2,00 | 1,76 | 0,11 | 6,33 |
| | 12 | Crown height | 4,33–5,50 | 4,89 | 0,39 | 7,96 |
| 5 | 12 | Sinusid height | 1,92–4,83 | 3,55 | 1,01 | – |
| | 11 | Length | 2,17–2,58 | 2,33 | 0,14 | 6,03 |
| | 9 | Width | 1,50–2,17 | 1,88 | 0,19 | 9,99 |
| | 12 | Crown height | 3,00–5,17 | 3,94 | 0,97 | – |

Table 14: Measurements of the M_3 of *Issiodoromys (Saboyanomys) weidmanni* n. subg. n. sp. from Ruisseau du Bey (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|----------------|-----------|-----------|------|-------|
| 2 | 2 | Length | 2,00–2,08 | 2,04 | 0,06 | 2,77 |
| | 2 | Width | 1,33–1,58 | 1,46 | 0,18 | 12,15 |
| 3 | 1 | Sinusid height | — | 4,33 | — | — |
| | 1 | Length | — | 2,33 | — | — |
| | 1 | Width | — | 1,75 | — | — |
| | 1 | Crown height | — | 4,67 | — | — |
| 4 | 4 | Sinusid height | 3,75–4,25 | 3,98 | 0,23 | 5,77 |
| | 2 | Length | 1,75–2,17 | 1,96 | 0,30 | 15,15 |
| | 3 | Width | 1,67–3,42 | 2,25 | — | — |
| | 4 | Crown height | 3,92–4,50 | 4,27 | 0,25 | 5,78 |

Type formation. – Untere bunte Mergel (Lower Motley Marls).

Stratum type. – Layer 2 of the JORDI profile (1955, p. 34, Fig. 10).

Stratigraphic range. – Oligocene, Upper “Chattien”, assemblage zone of Fornant-7 (see ENGESER & MAYO 1987).

Geographical distribution. – The same as of the Subgenus.

Diagnosis. – Species of small size and with low hypsodonty. Mean of curvature radii: $P^4 = 4,20$; $M^1 = 3,86$; Boundary of sinus height in SW-4: $M^1 = 6,08–5,16$; $M^2 = 6,00–5,25$. Height of anterior lobule: $M^1 = 0,36–0,40$; $M^2 = 0,58–0,83$; $M_{1/2} = 2,08$. P^4 with a scarcely semiatrophied anterior labial root. Labial roots of M^1 atrophied, lingual roots large and not atrophied. Lower roots large and slightly semiatrophied.

Discussion. – In the stratum 7 from the Fornant profile (see WEIDMANN 1982, p. 18–21, Fig. 5 and 6 in: JUNG) some material of this species was found. It is somewhat less evolved with a slightly lower crown height but of equal size. This is an indication of the gradual chronocinal evolution, and it cannot be separated into different species or even as a subspecies. The comparison (by the Student t-test) of the sample of Ruisseau du Bey with the sample of Fornant-7 for the lengths of P^4 in SW-3, 4 and 5 (19 specimens) showed not significant differences.

Measurements in the Tables 9–14.

Statistical test in the Tables 54–56.

Table 15: Measurements of the P^4 of *Issiodoromys (Saboyanomys) oppligeri* n. subg. n. sp. from Fornant-6 (France)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|-------|
| 3 | 2 | Sinus height | 4,50–4,58 | 4,54 | 0,06 | 1,25 |
| | 2 | Length | 1,83–2,17 | 2,00 | 0,24 | 12,02 |
| | 2 | Width | 1,50–1,92 | 1,71 | 0,30 | 17,38 |
| | 2 | Crown height | 4,83–4,92 | 4,88 | 0,06 | 1,31 |
| 4 | 4 | Sinus height | 3,67–4,00 | 3,82 | 0,17 | 4,47 |
| | 4 | Length | 2,00–2,08 | 2,02 | 0,04 | 1,98 |
| | 4 | Width | 1,67–1,92 | 1,79 | 0,11 | 5,98 |
| | 2 | Crown height | 4,08–4,25 | 4,17 | 0,12 | 2,89 |
| 5 | 5 | Sinus height | 2,67–3,75 | 3,22 | 0,44 | 13,74 |
| | 3 | Length | 1,83–2,00 | 1,92 | 0,09 | 4,44 |
| | 5 | Width | 1,67–1,83 | 1,73 | 0,09 | 5,05 |
| | 4 | Crown height | 3,08–4,50 | 3,69 | 0,72 | — |

Table 16: Measurements of the $M^{1/2}$ of *Issiodoromys (Saboyanomys) oppligeri* n. sp. from Fornant-6 (France)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|-------|
| 1 | 1 | Length | — | 1,75 | — | — |
| | 1 | Width | — | 1,17 | — | — |
| 2 | 1 | Length | — | 1,83 | — | — |
| | 1 | Width | — | 1,42 | — | — |
| 3 | 2 | Length | — | 2,08 | — | — |
| | 2 | Width | 1,67–1,83 | 1,75 | 0,11 | 6,46 |
| 4 | 3 | Sinus height | 5,41–6,00 | — | — | — |
| | 3 | Length | 1,83–2,08 | 1,97 | 0,13 | 6,48 |
| | 3 | Width | 1,75–1,83 | 1,80 | 0,05 | 2,56 |
| 5 | 8 | Sinus height | 1,25–4,58 | 3,21 | 1,15 | — |
| | 8 | Length | 1,92–2,33 | 2,08 | 0,13 | 6,37 |
| | 7 | Width | 1,75–2,33 | 2,26 | 0,24 | 10,73 |
| | 7 | Crown height | 2,17–5,00 | 3,88 | 0,95 | — |

Table 17: Measurements of the M^3 of *Issiodoromys (Saboyanomys) oppligeri* n. sp. from Fornant-6 (France)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|-------|
| 1 | 1 | Length | — | 1,75 | — | — |
| | 1 | Width | — | 1,33 | — | — |
| 2 | 1 | Sinus height | — | 4,58 | — | — |
| | 4 | Length | 1,67–1,84 | 1,75 | 0,07 | 3,96 |
| | 4 | Width | 1,67–2,08 | 1,77 | 0,21 | 11,57 |
| | 1 | Crown height | — | 4,67 | — | — |
| 3 | 2 | Sinus height | 3,58–4,42 | 4,00 | 0,59 | 14,85 |
| | 2 | Length | 1,83–2,83 | 2,33 | 0,71 | — |
| | 2 | Crown height | 4,42–4,75 | 4,59 | 0,23 | 5,09 |
| 4 | 2 | Sinus height | 2,33–3,25 | 2,79 | 0,65 | — |
| | 2 | Length | 2,20–2,25 | 2,23 | 0,04 | 1,59 |
| | 2 | Width | 2,08–2,50 | 2,29 | 0,30 | 12,97 |
| | 1 | Crown height | — | 3,25 | — | — |
| 5 | 5 | Sinus height | 1,75–3,33 | 2,57 | 0,74 | — |
| | 3 | Length | 2,00–2,08 | 2,03 | 0,05 | 2,28 |
| | 3 | Width | 2,00–2,17 | 2,08 | 0,09 | 4,08 |
| | 4 | Crown height | 2,50–4,08 | 3,29 | 0,71 | — |

I. (Saboyanomys) oppligeri n. sp.

Fig. 16

Synonymy. —1984 *Issiodoromys* n. sp. MAYO, p. 15 and 23 in: ENGESER et al.

Derivatio nominis. — After Mr. Daniel Oppliger (Basel), fossil vertebrate preparator at NMB and one of the collectors of this material.

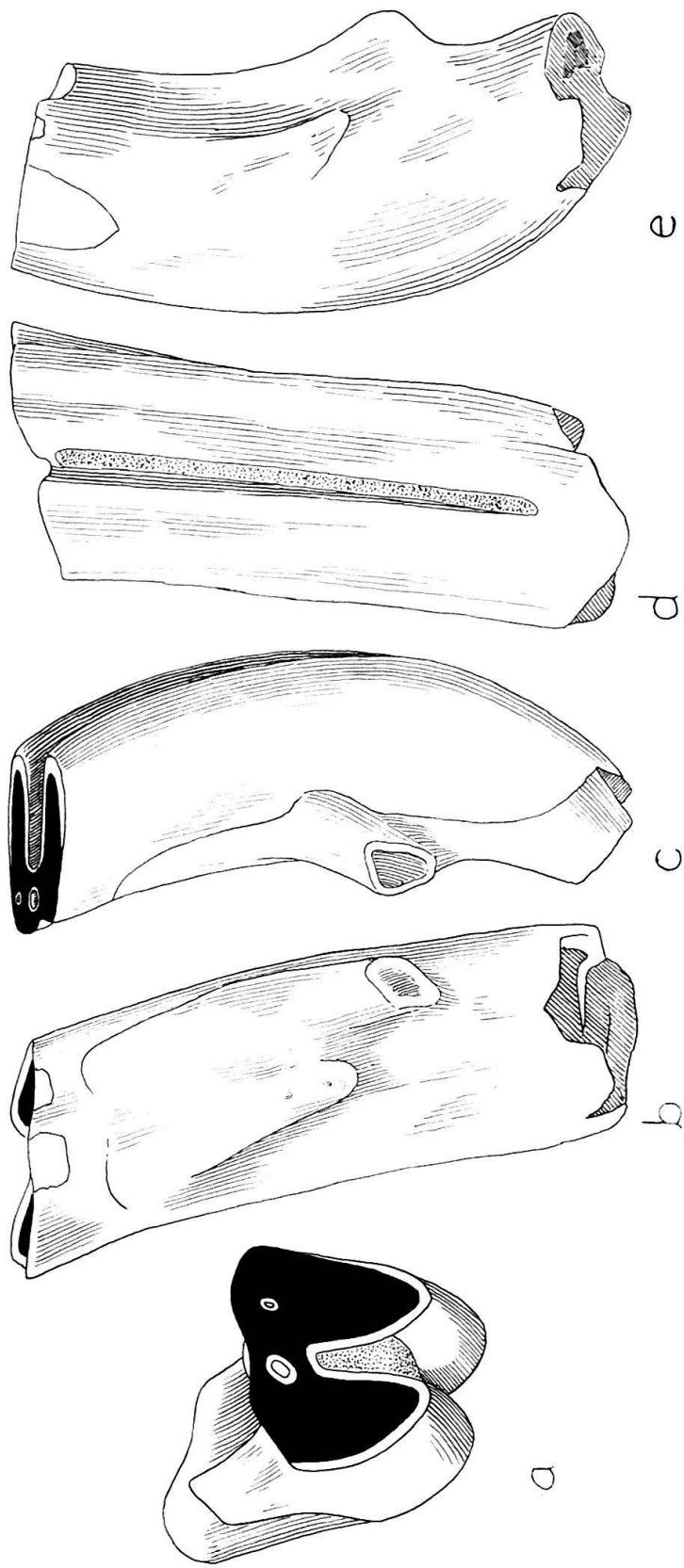


Fig. 16. *Issiodoromys (Saboyanomys) oppigeri* n. sp. NMB: Sav 202. P^4 dex (invers.). Formant-6, Savoy, France. a = occlusal view. b = labial view. c = anterior view. d = lingual view. e = posterior view. All figures $\times 12,5$.

Table 18: Measurements of the P_4 of *Issiodoromys (Saboyanomys) oppligeri* n. sp. from Fornant-6 (France)

| SW | N | | range | \bar{X} | S | V |
|----|---|----------------|-----------|-----------|------|-------|
| 4 | 4 | Sinusid height | 2,33–4,33 | 3,33 | 0,82 | — |
| | 2 | Length | 2,00–2,17 | 2,06 | 0,10 | 4,77 |
| | 2 | Width | 1,33–1,58 | 1,46 | 0,18 | 12,15 |
| | 2 | Crown height | 2,67–3,50 | 3,09 | 0,59 | 19,02 |
| 5 | 4 | Sinusid height | 1,25–1,75 | 1,46 | 0,21 | 14,33 |
| | 1 | Length | — | 2,33 | — | — |
| | 4 | Width | 1,42–1,67 | 1,57 | 0,13 | 8,02 |
| | 4 | Crown height | 1,83–2,25 | 2,00 | 0,21 | 10,29 |

Holotype. — NMB: Sav 202, P^4 dex. in SW-3 terminal.

Measurements of the Holotype. — Sinus height: 4,50 · Length: 21,7 · Width: 1,92 · Sinus length: 1,25 · Extrasinus distance: 0,67 · Curvature radius: 3,60 · Crown height: 4,83 · Height of the lobules not observable.

Paratypes. SW-1. — M^1 : NMB: Sav 203; M^3 : NMB: Sav 204; SW-2. — M^2 : NMB: Sav 205; M^3 : NMB: Sav 206–209. SW-3. — P^4 : NMB: Sav 210–211; M^1 : NMB: Sav 210–213; M^3 : NMB: Sav 214–215; P_4 : NMB: Sav 216; M_3 : NMB: Sav 217. SW-4. — NMB: Sav 218–221; M^2 : NMB: Sav 222–224; M^3 : NMB: Sav 225–227; P_4 : NMB: Sav 228–230; $M_{\frac{1}{2}}$: NMB: Sav 231–235; M_3 : NMB: Sav 236. SW-5. — P^4 : NMB: Sav 237–241; M^1 : NMB: Sav 242–248; M^2 : NMB: Sav 249; M^3 : NMB: Sav 250–254; P_4 : NMB: Sav 255–258; $M_{\frac{1}{2}}$: NMB: Sav 259–273; M_3 : NMB: Sav 274–276.

Type locality. — Le Fornant, High Savoy, near to Frangy (France).

Type formation. — Molasse rouge (Red Molasse).

Stratum type. — Layer 6 of the profile of Le Fornant river. See WEIDMANN (1982, pl. 18–21, Fig. 5 and 6, in: JUNG).

Stratigraphic range. — Upper Oligocene, assemblage zone of Fornant-6 (see ENGESSER & MAYO 1987).

Geographical distribution. — The same as of the Subgenus.

Diagnosis. — Species of larger size and more hypodontic than *I. (Saboyanomys) weidmanni*. Mean of curvature radii: $P^4 = 3,9$; $M_{\frac{1}{2}} = 4,13$. Boundary of sinus height viewed in SW-4: $M^2 = 6,00–5,45$; $M_{\frac{1}{2}} = 5,33–4,92$; in SW-5: $M^1 = 4,58$ and $M_{\frac{1}{2}} = 5,00$. Height of anterior lobule: $M_{\frac{1}{2}} = 0,92$; $M_{\frac{1}{2}} = 2,42$. Upper teeth with more atrophied roots and lowers with more semiatrophied roots than in *S. (Saboyanomys) weidmanni*. Lower teeth with slipping crest.

Table 19: Measurements of the $M_{1/2}$ of *Issiodoromys (Saboyanomys) oppligeri* n. sp. from Fornant-6 (France)

| SW | N | | range | \bar{X} | S | V |
|----|----|----------------|-----------|-----------|------|-------|
| 4 | 6 | Sinusid height | 4,92–5,33 | 5,09 | 0,17 | 3,25 |
| | 6 | Length | 2,33–2,50 | 2,43 | 0,12 | 5,03 |
| | 6 | Width | 1,58–2,00 | 1,79 | 0,17 | 9,75 |
| | 2 | Crown height | 5,00–5,50 | 5,25 | 0,35 | 6,73 |
| 5 | 15 | Sinusid height | 1,33–5,00 | 3,51 | 1,13 | — |
| | 14 | Length | 2,08–2,75 | 2,47 | 0,20 | 7,97 |
| | 12 | Width | 1,67–2,17 | 1,85 | 0,21 | 11,20 |
| | 14 | Crown height | 1,83–5,50 | 4,02 | 1,01 | — |

Table 20: Measurements of the M_3 of *Issiodoromys (Saboyanomys) oppligeri* n. sp. from Fornant-6 (France)

| SW | N | | range | \bar{X} | S | V |
|----|---|----------------|-----------|-----------|------|-------|
| 3 | 1 | Sinusid height | — | 4,67 | — | — |
| | 1 | Length | — | 2,25 | — | — |
| | 1 | Width | — | 1,42 | — | — |
| | 1 | Crown height | — | 4,92 | — | — |
| 4 | 2 | Sinusid height | 3,67–4,33 | 4,00 | 0,47 | 11,67 |
| | 2 | Length | 2,17–2,42 | 2,31 | 0,18 | 7,70 |
| | 2 | Width | 1,75–2,00 | 1,88 | 0,18 | 9,43 |
| | 2 | Crown height | 4,08–4,75 | 4,42 | 0,47 | 10,73 |
| 5 | 3 | Sinusid height | 1,83–3,75 | 2,67 | 0,98 | — |
| | 3 | Length | 2,25–2,42 | 2,30 | 0,10 | 4,26 |
| | 1 | Width | — | 1,58 | — | — |
| | 3 | Crown height | 2,67–4,00 | 3,25 | 0,68 | — |

Differential diagnosis. – *I. (Saboyanomys) oppligeri* n. sp. differs from *I. (Saboyanomys) weidmanni* n. subg. n. sp. in the following characters:

- longer P^4 and $M_{\frac{1}{2}}$,
- higher hypsodonty,
- different mean of the curvature radii,
- different height of the lobules,
- more atrophied roots in upper teeth and more semiatrophied in lowers,
- slipping crest in lingual roots of the lower teeth.

Discussion. – The Student t-test showed the highly significant difference between the samples of *I. (Saboyanomys) oppligeri* n. sp. from Fornant-6 and *I. (Saboyanomys) weidmanni* n. subg. n. sp. in the length of all the P^4 in SW-3 and 4 (15 specimens), and of the $M_{\frac{1}{2}}$ in SW-3, 4 and 5 (35 specimens). Also, the sinus height of the $M_{\frac{1}{2}}$ in SW-3 and 4 (18 specimens) showed a significant difference of 5%. Nevertheless, the length of the $M_{\frac{1}{2}}$ did not show a significant difference. That can be accounted by the greater length of the P_4 and by the special morphological function of the crown construction of $M_{\frac{1}{2}}$ relating to the M_3 .

Measurements in the Tables 15–20.

Statistical test in the Tables 54 and 56.

I. (Saboyanomys) rickenbachensis n. sp.

Fig. 17

Derivatio nominis. – After Rickenbach, type locality of the species.

Holotype. – NMB: UM 625 (P^4 dex.) in SW-4.

Table 21: Measurements of the P^4 of *Issiodoromys (Saboyanomys) rickenbachensis* n. sp. from Rickenbach (Switzerland)

| SW | Sinus height | Length | Width | Crown height |
|----|--------------|--------|-------|--------------|
| 1 | — | 1,50 | 1,25 | — |
| 2 | — | 1,58 | 1,25 | — |
| 4 | 4,83 | 1,83 | 1,75 | 4,92 |

Table 22: Measurements of the $M^{1/2}$ of *Issiodoromys (Saboyanomys) rickenbachensis* n. sp. from Rickenbach (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|----|--------------|-----------|-----------|------|-------|
| 2 | 3 | Length | 1,83–2,00 | 1,92 | 0,09 | 4,44 |
| | 3 | Width | 1,42–1,58 | 1,47 | 0,09 | 6,27 |
| 3 | 2 | Length | 2,00–2,17 | 2,09 | 0,12 | 5,76 |
| | 2 | Width | 1,58–1,67 | 1,63 | 0,06 | 3,92 |
| 4 | 2 | Length | 2,00–2,08 | 2,04 | 0,06 | 2,77 |
| | 3 | Width | 1,67–1,75 | 1,70 | 0,04 | 2,56 |
| 5 | — | Sinus height | — | > 6,33 | — | — |
| | 10 | Length | 1,83–2,17 | 1,80 | 0,17 | 8,24 |
| | 11 | Width | 1,42–2,25 | 1,80 | 0,25 | 14,10 |

Measurements of the Holotype. — Sinus height: 4,83 · Length: 1,83 · Width: 1,75. Sinus Length: 1,25. Extrasinus distance: 0,33 · Crown height: 4,92 · Curvature radius: 4,80.

Paratypes. — SW-1: P⁴. — NMB: UM 2831. SW-2: P⁴: NMB: Rick 1. M^{1/2}. — NMB: UM 355, HR 259. M³. — NMB: UM 1282; Rick 3. P₄. — NMB: UM 1974. SW-3: M^{1/2} NMB: HR 181; UM 1083. M³. — NMB: UM 1310a; M_{1/2}. — NMB: HR 1003; Rick 25. SW-4. — M^{1/2}. — NMB: UM 1080, 1299; Rick 4. M³. — NMB: UM 560, 7119, 1904 and 140. P₄. — NMB: UM 1094, 1909 and 354; HR 265. M_{1/2}. — NMB: UM 628; Rick 26. M₃. — NMB: HR 1001; Rick 34. SW-5: P⁴. — Rick 24; M^{1/2}. — NMB: UM 620, 626, 3200, 621, 2125, 2658, 625 and 2661; Rick 19–11, 2 and 22. M³. — NMB: Rick 32, 33. P₄. — NMB: UM 1935 and 2659. M_{1/2}. — NMB: UM 2112, 6160, 1301, 1309, 1302, 1034, 654, 1091, 6159, 676; Rick 27–30. M₃. — NMB: UM 656 and 1914. Maxillary fragment: NMB: UM 1282 (P⁴–M³; P⁴ in SW-3, M¹–M² in SW-4 and M³ in SW-2).

Hypodigm. — In addition to Holotypes and Paratypes the following specimens: P⁴: NMB: UM 2381 in SW-1 and UM 109f in SW-4. M_{1/2}: NMB: HR 907.

Type formation. — Molasse alsacienne.

Stratum type. — Knauriger Sandstein (Concretionary Sandstone). See KEHRER (1922, p. 22) and profile in KFSNMB.

Stratigraphic range. — Oligocene, Upper “Chattien”, assemblage zone of Rickenbach (see ENGESSER & MAYO 1987).

Table 23: Measurements of the M^3 of *Issiodoromys (Saboyanomys) rickenbachensis* n. sp. from Rickenbach (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|--------------|-----------|-----------|------|------|
| 3 | 1 | Length | — | 2,00 | — | — |
| | 1 | Width | — | 1,58 | — | — |
| 4 | 2 | Sinus height | 4,67–4,92 | 4,80 | 0,18 | 3,69 |
| | 3 | Length | 1,83–2,00 | 1,94 | 0,10 | 5,05 |
| | 3 | Width | 1,58–1,83 | 1,72 | 0,13 | 7,42 |
| | 2 | Crown height | — | 5,00 | — | — |
| 5 | 1 | Sinus height | — | 4,75 | — | — |
| | 1 | Length | — | 2,00 | — | — |
| | 1 | Width | — | 1,83 | — | — |
| | 1 | Crown height | — | 5,00 | — | — |

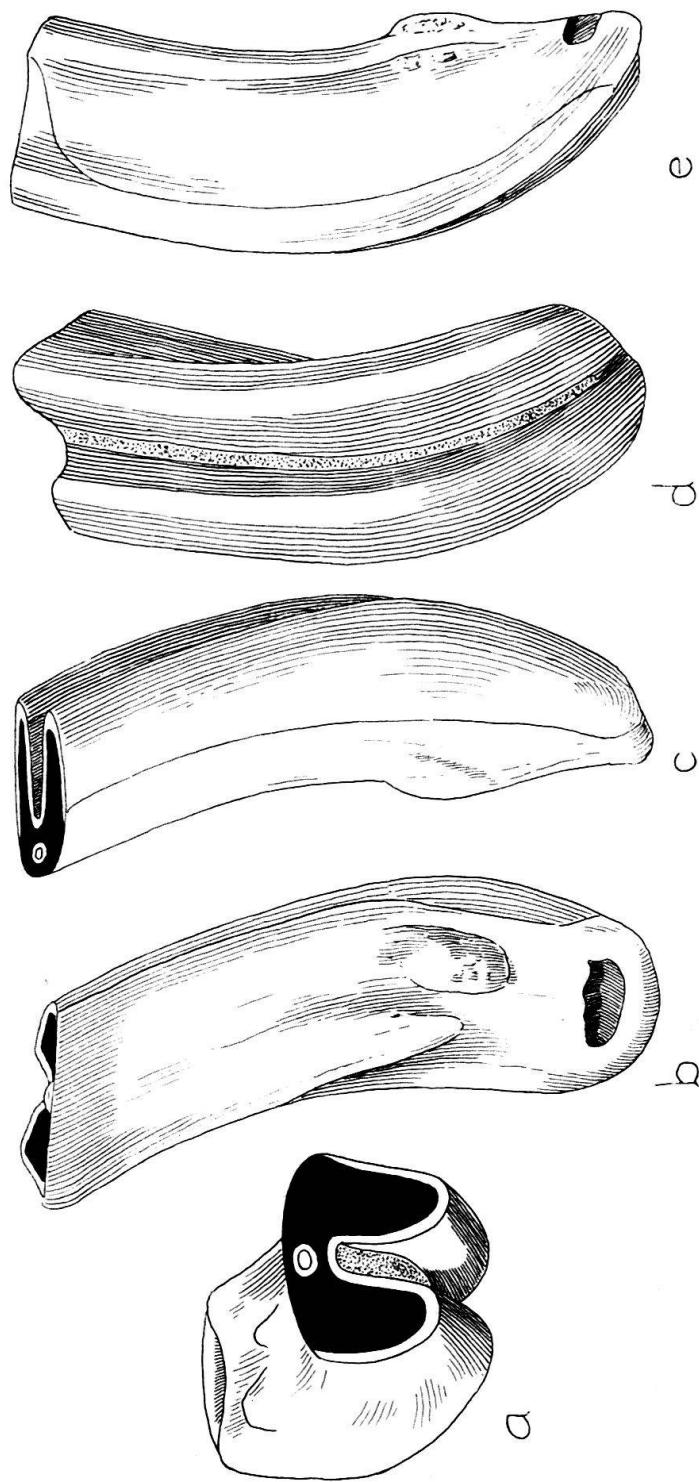


Fig. 17. *Issiodoromys (Saboyanomys) rickenbachensis* n. sp. NMB: UM 625. P^4 dex (invers). Holotype. Rickenbach, Switzerland. a = occlusal view. b = labial view. c = anterior view. d = posterior view. e = lingual view. — All figures $\times 12,5$.

Table 24: Measurements of the P_4 of *Issiodoromys (Saboyanomys) rickenbachensis* n.sp. from Rickenbach (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|----------------|-----------|-----------|------|-------|
| 4 | 3 | Sinusid height | 4,17–5,50 | 4,75 | 0,68 | 14,34 |
| | 4 | Length | 1,75–2,25 | 2,02 | 0,23 | 11,36 |
| | 4 | Width | 1,33–1,58 | 1,46 | 0,14 | 9,92 |
| | 2 | Crown height | 4,42–4,92 | 4,67 | 0,35 | 7,57 |
| 5 | 2 | Sinusid height | 1,50–3,17 | 2,34 | — | — |
| | 1 | Length | — | 2,00 | — | — |
| | 1 | Width | — | 1,42 | — | — |
| | 2 | Crown height | 2,08–3,50 | 2,79 | — | — |

Geographical distribution. – Central Europe.

Diagnosis. – Species of the same size, but more hypodont than *I. (S.) oppligeri*. Mean of curvature radii: $M^{\frac{1}{2}} = 4,00$. Boundary of the sinus height viewed in SW-5: 6,17. Height of anterior lobule in $M^{\frac{1}{2}} = 0,58–0,67$. Height of posterior lobule: $M^{\frac{1}{2}} = 0,42–0,58$. $M_{\frac{1}{2}} = 1,25–3,58$. Enamel borders of the crown thick. P^4 with two vestigial labial roots. $M^{\frac{1}{2}}$ with fully atrophied labial roots. Lower teeth with fully atrophied lingual roots and vestigial labial root.

Differential diagnoses. – *I. (Saboyanomys) rickenbachensis* n. sp. differs from *I. (Saboyanomys) weidmanni* n. subg. n. sp. in the following characters:

- larger size,
- very high hypodonty,
- different mean of curvature radii,
- different boundaries of sinus and sinusid height,
- different thickness of the enamel borders,
- different height of the anterior and posterior lobules,
- vestigial labial roots in P^4
- fully atrophied labial roots in $M^{\frac{1}{2}}$,
- vestigial and fully atrophied roots in lower teeth.

From *I. (Saboyanomys) oppligeri* n. sp. in the:

- higher hypodonty,

Table 25: Measurements of the $M_{1/2}$ of *Issiodoromys (Saboyanomys) rickenbachensis* n.sp. from Rickenbach (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|----|----------------|-----------|-----------|------|------|
| 3 | 2 | Length | 2,17–2,42 | 2,30 | 0,17 | 7,70 |
| | 2 | Width | 1,33–1,50 | 1,42 | 0,12 | 8,50 |
| 4 | 2 | Length | 2,17–2,33 | 2,25 | 0,11 | 5,03 |
| | 2 | Width | 1,58–1,67 | 1,63 | 0,06 | 3,92 |
| 5 | 9 | Sinusid height | 2,92–6,50 | 4,27 | 1,14 | — |
| | 11 | Length | 2,25–2,75 | 2,43 | 0,13 | 5,22 |
| | 12 | Width | 1,50–2,08 | 1,79 | 0,17 | 9,56 |
| | 9 | Crown height | 3,33–6,67 | 4,78 | 1,09 | — |

In addition:

- the same seven characters as by *I. (Saboyanomys) weidmanni* n. subg. n. sp., starting from character number three (“different mean of curvature radii”).

Measurements in the Tables 21–26.

Statistical test in the Tables 54–56.

Table 26: Measurements of the M_3 of *Issiodoromys (Saboyanomys) rickenbachensis* n.sp. from Rickenbach (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|----------------|-----------|-----------|------|------|
| 4 | 1 | Sinusid height | – | 5,17 | – | – |
| | 2 | Length | 1,12–1,20 | 1,16 | 0,06 | 4,88 |
| | 2 | Width | 1,83–2,00 | 1,92 | 0,12 | 6,28 |
| | 1 | Crown height | – | 5,33 | – | – |
| 5 | 1 | Sinusid height | – | 4,08 | – | – |
| | 2 | Length | – | 1,16 | – | – |
| | 2 | Width | 1,83–2,08 | 1,96 | 0,18 | 9,04 |

Genus *Nesokerodon* SCHLOSSER 1884

Type species. – *Nesokerodon quercy* SCHLOSSER 1884.

Stratigraphic range. – Lower to Middle Oligocene, from Balm to Aarwangen assemblage zones in the faunal province of Switzerland and Savoy (see ENGESSER & MAYO 1987).

Geographical distribution. – Central and West Europe.

Previous diagnoses. – SCHLOSSER 1884, p. 16–20; LYDEKKER 1885, p. 253; ZITTEL 1891–93, p. 525; VIRET 1929, p. 85.

Emended diagnosis. – Semihypsodont Issiodoromyinae. Maxilla very expanded labially in front of P^4 ; external border against M^2 – M^3 lies perpendicular to the abrasive surface of the crown; labial and lingual alveolar borders very slightly separated; external alveolar border softly curved; infraorbital canal wide to very wide. Ascending ramus of anterior zygomatic process with very concave anterior border. Ventral surface of the masseteric apophysis of the anterior zygomatic process with a relatively wide masseteric fossa. Vertical foramen inside fossa. Posterior border of incisive foramen in front of the contact between P^4 and M^1 . Palatine vault with a groove. Posterior palatine foramen in front of M^2 . Teeth with low to high semihypsodonty. Upper teeth: with subrounded crown on unworn surface; semihypsodonty of slight to moderate sagittal rotation; wear widespread to complete occlusal surface of crown; antyclines and some synclines soon disappear with abrasion; labial border of the crown vertical, or slightly inclined with respect to the labial roots; enamel height in labial border small; lobules very short. P^4 – M^3 with normal labial roots. M^1 and M^2 with labial roots emerging from the labial border of the crown. Lingual root: bent slightly along its length; labial-lingually convex and wide in the posterior half; concavity of its labial border shallow and narrow, without a horizontal space between the labial and lingual roots below the crown. Mandible: with inclined short

shelflike masseteric ridge relatively near to the alveolar border. Lower and upper masseteric ridges; or without lower, but with short and slightly prominent longitudinal masseteric ridge. Without longitudinal masseteric sulcus. Lower teeth with or without anterisusid; with II, III and IV synclinids; with pseudograbens (rarely without) and two roots. P_4 of equal or larger size than the lower molars.

Differential diagnoses. – *Nesokerodon* differs from other *Issiodoromyinae* genus in the following characters:

From *Issiodromys* CROIZET in the:

- different infraorbital canal,
- vertical external ridge of infraorbital canal,
- presence of a masseteric fossa on ventral surface of masseteric apophysis of the anterior zygomatic process,
- presence of a vertical foramen inside masseteric fossa,
- presence of semihypsodonty,
- presence of normal labial roots in the upper teeth,
- presence of very small lobules,
- small crown height on the labial border of the upper teeth and on the lingual border of the lowers,
- presence of a barrel form in the crown of the upper teeth,
- presence of a narrow and shallow pseudograbens in the upper teeth,
- wider and deeper synclines and synclinids,
- transversal ridge in a more median position on the crown surface of the upper and lower teeth,
- presence of shelflike masseteric ridge in the mandible,
- presence of an angular upper masseteric ridge on the mandible,
- presence of an angular lower masseteric ridge on the mandible,
- absence of a longitudinal sulcus on the mandible.

From *Pseudolitomys* LAVOCAT 1952, in the:

- greater maxillary height dorsally to M^2-M^3 ,
- different infraorbital canal (proportionally deeper and more closed in comparison),
- presence of a groove in the palatine vault,
- comparatively shorter palatine vault,
- different position of the incisive foramen,
- reduced synclines.

From *Elfomys* HARTENBERGER 1971 in the:

- comparatively shorter palatine vault,
- much longer incisive foramen,
- higher semihypsodonty,
- absence of brachydont teeth,
- reduction or absence of the bunodont traces in the teeth,
- much better formed antyclines and antyclinids,
- more developed and deeper synclines and synclinids,
- tendency to increase in size,
- more developed and deeper pseudograbens,

- absence of teeth without pseudograben in the upper teeth,
- absence of wrinkled enamel in the teeth.

Discussion. – PALMER (1904, p. 458) designated as type species of *Nesokerodon* (SCHLOSSER 1884 to “*Issiodromys*” *minor* FILHOL 1877. This species cannot be accepted as the type species of the genus according to the Article 167g of the Int. Code of Zoological Nomenclature (see SCHLOSSER 1884, p. 15). The reintroduction of the genus *Nesokerodon* SCHLOSSER 1884 is recommended because of the discovery of *Issiodromys* CROIZET as an invader of the Molasse basin of Switzerland and Savoy, and also it is polyphyletic (see ENGESSER et al. 1986; ENGESSER & MAYO 1987; MAYO 1987 and more details in MAYO 1987a).

Table 27: Measurements of the D⁴ and P⁴ of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| Tooth | SW | N | | range | \bar{X} | S | V |
|----------------|----|---|---------------------|-----------|-----------|------|------|
| D ⁴ | | 3 | Sinus height | 0,17–0,50 | 0,30 | 0,12 | – |
| | | 3 | Length | 1,50–1,60 | 1,53 | 0,04 | 3,77 |
| | | 3 | Width | 1,17–1,25 | 1,20 | 0,03 | 3,86 |
| | | 3 | Crown height | 0,58–0,92 | 0,77 | 0,12 | – |
| P ⁴ | 1 | 2 | Sinus height | – | 1,33 | – | – |
| | | 2 | Length | 1,33–1,42 | 1,38 | 0,06 | 4,63 |
| | | 2 | Width | – | 1,17 | – | – |
| | | 2 | Crown height | 1,75–1,83 | 1,79 | 0,06 | 3,16 |
| 4 | | 1 | Sinus height | – | 0,58 | – | – |
| | | 1 | Length | – | 1,50 | – | – |
| | | 1 | Width | – | 1,50 | – | – |
| | | 1 | Sinus length | – | 0,50 | – | – |
| | | 1 | Extrasinus distance | – | 1,00 | – | – |
| | | 1 | Crown height | – | 1,08 | – | – |

Nesokerodon balmensis n. sp.

Fig. 18

Synonymy. –

- 1941 *Oltinomys* sp. STEHLIN, p. 213 and 219 in: ERNI.
 1966 *Pseudolitinomys* sp. II. THALER, p. 91.
 1976 *Elfomys* sp. VIANEY-LIAUD, p. 21 and 24, in part.
 1976 *Elfomys medius* VIANEY-LIAUD, p. 25 and 32, Table 6; 89 and 93, Fig. 45 and 46, in part.
 1979 *non Elfomys medius* VIANEY-LIAUD, p. 227.

Derivatio nominis. – After Balm, type locality of this species.

Holotype. – NMB: Blm 210. P⁴ sin. in SW-1.

Measurements of the Holotype. – Sinus height: 1,40. Length: 1,04. Width: 1,00. Crown height: 1,80. Width between the paracone and protocone: 0,90.

Paratypes. – D⁴. – NMB: Blm 205; NMO: Blm 81 and 82; D₄. – NMB: Blm 242; NMO: Blm 73. SW-1: P⁴. – NMB: Blm 93. M¹. – NMB: Blm 30 and 208. NMO: Blm 76, 79 and 89. M². – NMB: Blm 88 and 91. M³. – Blm 25, 50 and 80. NMO: Blm 72, 85 and 86. P₄. – NMB: Blm 192. M₁. – NMB: Blm 23, 187, 193, 198 and 200. NMO: Blm 98 and 125f. M₂. – NMB: Blm 190. SW-2: M¹. – NMB: Blm 32f, 201, 204 and 209. NMO: Blm 77f and 130. M². – NMB: Blm 27, 29, 33e, 78, 90 and 128. NMO: Blm 74f, 72f. M³. –

Table 28: Measurements of the M¹ of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|---------------------|-----------|-----------|------|------|
| 1 | 5 | Sinus height | 1,25–1,50 | 1,37 | 0,10 | 7,03 |
| | 5 | Length | 1,33–1,50 | 1,42 | 0,09 | 6,00 |
| | 5 | Width | 1,00–1,17 | 1,08 | 0,09 | 7,84 |
| | 5 | Crown height | 1,75–2,00 | 1,83 | 0,12 | 6,46 |
| 2 | 5 | Sinus height | 1,17–1,33 | 1,22 | 0,07 | 5,87 |
| | 5 | Length | 1,42–1,58 | 1,50 | 0,06 | 3,77 |
| | 5 | Width | 1,17–1,25 | 1,22 | 0,04 | 3,60 |
| | 4 | Crown height | 1,67–1,83 | 1,75 | 0,07 | 3,73 |
| 4 | 1 | Sinus height | — | 0,75 | — | — |
| | 1 | Length | — | 1,33 | — | — |
| | 1 | Width | — | 1,58 | — | — |
| | 1 | Sinus length | — | 0,58 | — | — |
| | 1 | Extrasinus distance | — | 1,08 | — | — |
| | 1 | Crown height | — | 1,17 | — | — |

NMB: Blm 25, 71, 75f and 87. P₄. – NMB: Blm 107. M₁. – NMB: Blm 124, 196 and 199. NMO: Blm 101, 104, 105, 116, 117 and 123. M₃. – NMB: Blm 189. NMO: Blm 110. SW-3: M¹. – NMO: Blm 127 (e). M². – NMB: Blm 21. M³. – NMB: Blm 202. NMO: Blm 84. P₄. – NMB: Blm 108. M₁. – NMB: Blm 19 and 24. NMO: Blm 97, 100, 106, 113, 114 and 122. M₃. – NMB: Blm 121 and 191. NMO: Blm 94, 109, 111 and 112. SW-4: P⁴. – NMB: Blm 206. M¹. – NMB: Blm 28. M². – NMB: Blm 129. M³. – NMB: Blm 83. M₁. – NMB: Blm 22, 115 and 188. NMO: Blm 102 and 120. SW-5: P⁴. – NMO: Blm 103 (e). P₄. – NMO: Blm 126.

Table 29: Measurements of the M² of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|---------------------|-----------|-----------|------|-------|
| 1 | 2 | Sinus height | 1,17–1,33 | 1,25 | 0,11 | 9,05 |
| | 2 | Length | 1,36–1,42 | 1,39 | 0,04 | 3,05 |
| | 2 | Width | 1,08–1,25 | 1,17 | 0,12 | 10,32 |
| | 1 | Crown height | — | 1,58 | — | — |
| 2 | 5 | Sinus height | 1,20–1,33 | 1,27 | 0,06 | 4,46 |
| | 8 | Length | 1,33–1,58 | 1,46 | 0,08 | 5,24 |
| | 7 | Width | 1,25–1,50 | 1,33 | 0,10 | 7,26 |
| | 5 | Crown height | 1,42–2,00 | 1,70 | 0,21 | 12,21 |
| 3 | 1 | Sinus height | — | 1,08 | — | — |
| | 1 | Length | — | 1,50 | — | — |
| | 1 | Width | — | 1,33 | — | — |
| | 1 | Sinus length | — | 0,33 | — | — |
| | 1 | Extrasinus distance | — | 1,08 | — | — |
| | 1 | Crown height | — | 1,50 | — | — |
| 4 | 1 | Sinus height | — | 0,83 | — | — |
| | 1 | Length | — | 1,42 | — | — |
| | 1 | Width | — | 1,50 | — | — |
| | 1 | Sinus length | — | 0,50 | — | — |
| | 1 | Extrasinus distance | — | 1,00 | — | — |
| | 1 | Crown height | — | 1,17 | — | — |

Table 30: Measurements of the M^3 of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|---------------------|-----------|-----------|------|-------|
| 1 | 6 | Sinus height | 1,00–1,33 | 1,18 | 0,15 | 12,84 |
| | 6 | Length | 1,16–1,25 | 1,19 | 0,04 | 3,05 |
| | 6 | Width | 1,08–1,25 | 1,19 | 0,08 | 6,32 |
| | 6 | Crown height | 1,00–1,67 | 1,38 | 0,26 | 18,67 |
| 2 | 2 | Sinus height | 0,83–1,08 | 0,96 | 0,18 | 18,51 |
| | 4 | Length | 1,17–1,42 | 1,23 | 0,13 | 10,14 |
| | 3 | Width | 1,25–1,33 | 1,27 | 0,05 | 3,62 |
| | 2 | Crown height | 1,25–1,33 | 1,29 | 0,06 | 4,39 |
| 3 | 2 | Sinus height | 0,58–1,08 | 0,83 | 0,35 | – |
| | 2 | Length | 1,33–1,42 | 1,38 | 0,06 | 4,63 |
| | 1 | Width | – | 1,44 | – | – |
| | 2 | Sinus length | 0,42–0,50 | 0,46 | 0,06 | 12,30 |
| | 1 | Extrasinus distance | – | 1,08 | – | – |
| | 2 | Crown height | 1,00–1,42 | 1,21 | 0,30 | – |
| 4 | 1 | Sinus height | – | 0,67 | – | – |
| | 1 | Length | – | 1,42 | – | – |
| | 1 | Width | – | 1,67 | – | – |
| | 1 | Sinus length | – | 0,58 | – | – |
| | 1 | Extrasinus distance | – | 1,17 | – | – |
| | 1 | Crown height | – | 1,08 | – | – |

Definition of the stage of wear. – Upper teeth: see p. 1005. Lower teeth: Some specimens in SW-1 have no pseudogruben. For this reason they have no SW-2. For the rest see p. 1005.

Type locality. – Balm on the shores of the brook of Balm, Canton of Solothurn, Switzerland (see ERNI 1941, Fig. 3 and KFSNMB).

Stratum type. – See ERNI 1941, p. 211–212.

Stratigraphic range. – Rupelien, Lower Oligocene, assemblage zone of Balm (see ENGESSER & MAYO 1987).

Geographical distribution. – Central Europe.

Diagnosis. – *Nesokerodon* of small size. Upper teeth with shallow pseudogruben and cusped 2 and 4 antyclines. P^4 : somewhat larger than M^1 or M^2 . Antyclines 1 and 5 as cingulum, incipient I and IV synclines. The first one completely open. M^1 – M^2 pentaantycline. Space between lingual and labial roots of crown inclined and cusped. Lower teeth: P_4 with shallow pseudogruben; posterior part of the crown wider than the anterior. M_4 : tetraantyclinid; with antesisinusid; very shallow pseudogruben and only in some part of the teeth; 2 and 4 antyclines cusped; 5 antyclinid as a cingulum. M_3 : larger than M_4 , antyclinid 4 more cusped than 2; antyclinid 5 generally as a cingulum. Average thickness of enamel border in the upper teeth: 0,04–0,08.

Table 31: Measurements of the D_4 and P_4 of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| Tooth | SW | Sinusid height | Length | Width | Sinusid length | Extrasinusid distance | Crown height |
|-------|----|----------------|--------|-----------|----------------|-----------------------|--------------|
| D_4 | | 0,40 | 1,76 | 1,00–1,08 | 0,33–0,42 | 0,67 | 0,72 |
| P_4 | 1 | 1,00 | 1,50 | 0,92 | – | – | 1,33 |
| P_4 | 2 | 0,92 | – | 1,08 | – | – | 1,17 |
| P_4 | 3 | 0,83 | 1,60 | 0,92 | 0,33 | 0,58 | 1,25 |
| P_4 | 5 | 0,25 | 1,67 | 1,42 | 0,58 | 0,75 | 0,75 |

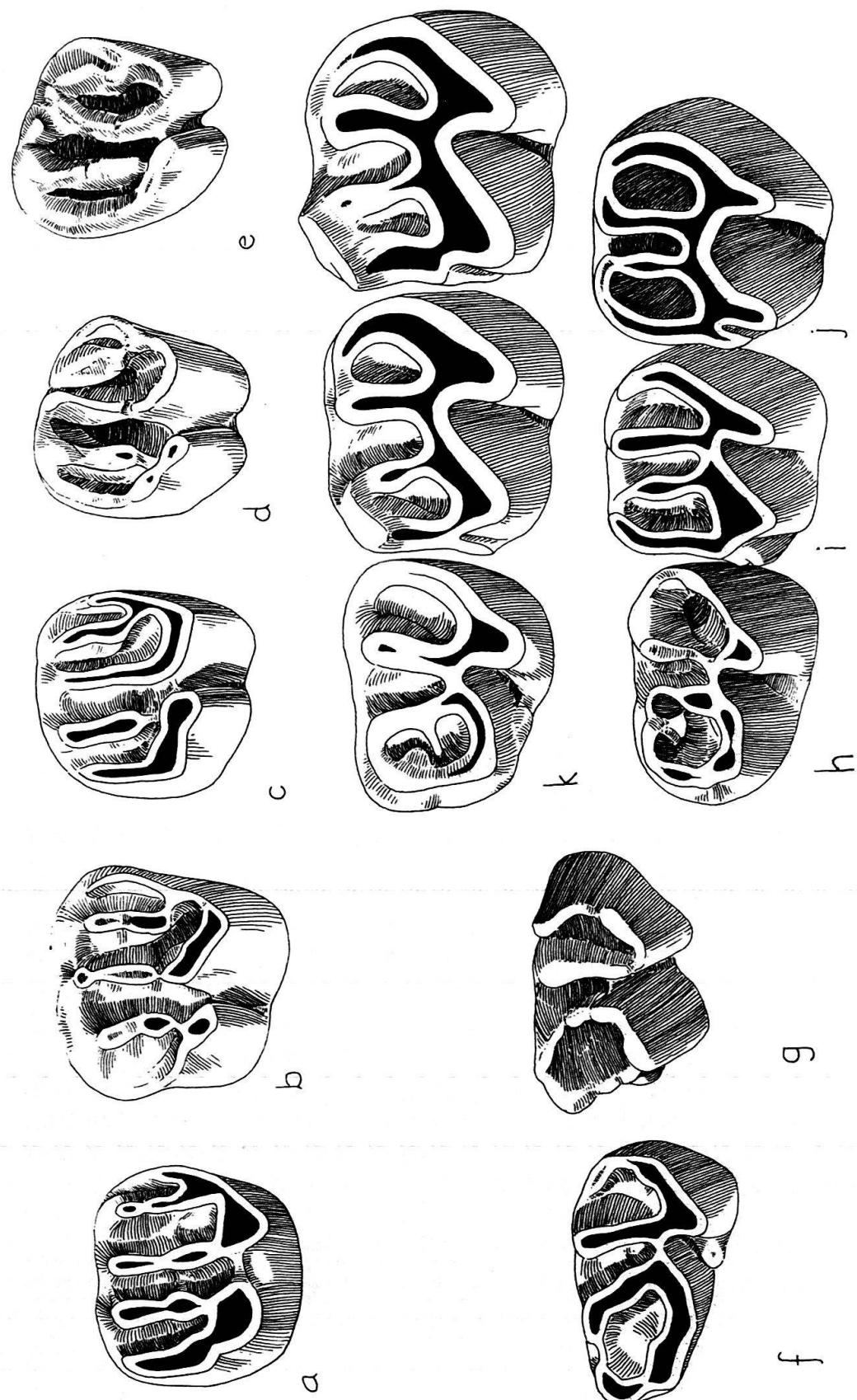


Fig. 18. *Nesokerodon balmensis* n. sp. and *Nesokerodon medius* (VIANNEY-LIAUD 1976). *Nesokerodon balmensis* n. sp.: a = NMB: Blm 82. D^4 dex (invers.). Paratype. b = NMB: Blm 210. P^4 sin. Holotype. c = NMB: Blm 204. M^1 sin. Paratype. d = NMB: Blm 88. M^2 sin. Paratype. e = NMB: Blm 25. M^3 sin. Paratype. f = NMB: Blm 242. D_4 sin. g = NMB: Blm 190. M_3 dex (invers.). Paratype. h = NMB: Blm 108. P_4 sin. Paratype. i = NMB: Blm 100. $M_{1/2}$ sin. Paratype. j = NMB: Blm 188. $M_{1/2}$ sin. Paratype. k = LPVUM: PLA-24. P_4-M_2 sin. Holotype. La Plante 2, Quercy, France. — All figures $\times 12.5$. Balm, Switzerland. *Nesokerodon medius* (VIANNEY-LIAUD 1976); k = LPVUM: PLA-24.

Differential diagnoses. – *Nesokerodon balmensis* n. sp. differs from *Nesokerodon nanus* (THALER 1969) in the:

- larger size,
- higher semihypsodonty,
- more detached presence of bunodont appearance,
- more developed syncline I in P⁴.

From *Nesokerodon medius* (VIANEY-LIAUD 1976) in the:

- smaller size,
- lower semihypsodonty,
- less reduced synclines,
- not so thick enamel borders,
- more detached presence of bunodont appearance,
- less developed pseudograben in M₁ and M₂.

Discussion. – VIANEY-LIAUD (1976, p.21) emended the diagnosis of *Elfomys* HARTENBERGER 1971 including in this genus *N. medius* and *N. balmensis* n. sp. (she could not separate these two last species). Unfortunately she excluded in this procedure some important characters of *Elfomys* s. st. or included other ones which do not contain the

Table 32: Measurements of the M_{1/2} of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| SW | N | | range | X̄ | S | V |
|----|---|-----------------------|-----------|------|------|-------|
| 1 | 7 | Sinusid height | 1,08–1,50 | 1,33 | 0,15 | 11,50 |
| | 7 | Length | 1,42–1,58 | 1,49 | 0,06 | 3,71 |
| | 7 | Width | 0,92–1,08 | 0,99 | 0,07 | 7,28 |
| | 6 | Crown height | 1,25–1,75 | 1,57 | 0,18 | 11,39 |
| 2 | 9 | Sinusid height | 1,00–1,33 | 1,18 | 0,16 | 9,77 |
| | 9 | Length | 1,36–1,58 | 1,49 | 0,08 | 5,36 |
| | 9 | Width | 1,00–1,17 | 1,07 | 0,07 | 6,27 |
| | 8 | Crown height | 1,42–1,58 | 1,50 | 0,06 | 4,03 |
| 3 | 8 | Sinusid height | 0,92–1,33 | 1,07 | 0,12 | 11,17 |
| | 8 | Length | 1,42–1,58 | 1,50 | 0,06 | 4,33 |
| | 8 | Width | 1,00–1,17 | 1,11 | 0,08 | 6,86 |
| | 8 | Sinus length | 0,33–0,50 | 0,45 | 0,06 | 13,27 |
| | 8 | Extrasinusid distance | 0,58–0,75 | 0,68 | 0,07 | 9,81 |
| | 8 | Crown height | 1,33–1,58 | 1,46 | 0,14 | 9,56 |
| 4 | 4 | Sinusid height | 0,67–1,00 | 0,83 | 0,15 | 18,15 |
| | 4 | Length | 1,32–1,67 | 1,49 | 0,14 | 9,54 |
| | 4 | Width | 1,25–1,42 | 1,33 | 0,05 | 5,21 |
| | 3 | Sinusid length | 0,58–0,67 | 0,61 | 0,05 | 8,52 |
| | 4 | Extrasinusid distance | 0,67–0,83 | 0,75 | 0,07 | 8,71 |
| | 4 | Crown height | 1,08–1,42 | 1,23 | 0,17 | 14,20 |
| 5 | 1 | Sinusid height | – | 0,25 | – | – |
| | 1 | Length | – | 1,58 | – | – |
| | 1 | Width | – | 1,75 | – | – |
| | 1 | Sinusid length | – | 0,83 | – | – |
| | 1 | Extrasinusid distance | – | 0,83 | – | – |
| | 1 | Crown height | – | 0,67 | – | – |

Table 33: Measurements of the M_3 of *Nesokerodon balmensis* n. sp. from Balm (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|-----------------------|-----------|-----------|------|-------|
| 1 | 1 | Sinusid height | — | 1,33 | — | — |
| | 1 | Length | — | 1,50 | — | — |
| | 1 | Width | — | 1,00 | — | — |
| | 1 | Crown height | — | 1,50 | — | — |
| 2 | 2 | Sinusid height | 1,33–1,42 | 1,38 | 0,06 | 4,63 |
| | 2 | Length | 1,58–1,75 | 1,67 | 0,12 | 7,22 |
| | 2 | Width | 1,08–1,17 | 1,13 | 0,06 | 5,66 |
| | 2 | Crown height | — | 1,58 | — | — |
| 3 | 6 | Sinusid height | 0,92–1,17 | 1,06 | 0,09 | 8,08 |
| | 6 | Length | 1,33–1,59 | 1,47 | 0,10 | 6,92 |
| | 6 | Width | 1,00–1,50 | 1,18 | 0,19 | 16,39 |
| | 6 | Sinusid length | 0,36–0,58 | 0,48 | 0,09 | 19,21 |
| | 6 | Extrasinusid distance | 0,50–0,58 | 0,53 | 0,04 | 7,45 |
| | 6 | Crown height | 1,17–1,42 | 1,32 | 0,10 | 7,39 |

species of the Eocene at all (more details in MAYO 1987a). For this reason, and because the characters of *N. nanus*, *N. medius* or *N. balmensis* n. sp. fit together better with those of *Nesokerodon* SCHLOSSER 1884, they are included in this genus. The $M_{\frac{1}{2}}$ of the Holotype of *N. medius* VIANEY-LIAUD, (LPVUM, PLA 24) – the only specimen from the fissure filling of La Plante-2 which belongs without doubt to *N. medius* – appears larger and has a greater crown height than the teeth of *N. balmensis* n. sp. from Balm. The comparison by the Student-t test of the sample of *N. balmensis* n. sp. (27 specimens) with the type of *N. medius* for the length of $M_{\frac{1}{2}}$ (2 specimens), showed great significant differences. It is also necessary to take into account that the Pearson's coefficient of variation of *N. medius* from La Plante-2 for the $M_{\frac{1}{2}}$ (41 specimens) is 8,83% (after VIANEY-LIAUD 1976, p.85, Table 20). However, the coefficient for the same teeth of *N. balmensis* n. sp. (29 specimens) is only 5,17. This result, using statistical methods, suggests that in the carstic fissure filling of La Plante-2 there is a heterochronic mixture of specimens of different ages. VIANEY-LIAUD (letter of 30.1.1985) wrote me that the measurements of Table 6 (1976, p. 32) belong to Balm and not to Montalbán.

Measurements in the tables: 27–33.

Statistical test in the tables: 54 and 56.

Nesokerodon aarwangerensis n. sp.

Fig. 19

Synonymy. –

- 1914 *Nesokerodon quercyi* STEHLIN, p. 183.
 1966 *Issiodoromys pseudanema* THALER, p. 203, Table 9.
 1969 *Issiodoromys pseudanema* HUGUENEY, p. 200.
 1976 *Issiodoromys quercyi* VIANEY-LIAUD, p. 60 in part, 68 and 70, Table 17, Fig. 35.
 1983 *Issiodoromys quercyi* MAYO, p. 903, Fig. 55.

Holotype. – NMB: Aw 62, left maxillary fragment with D^4 – M^2 . M^1 in SW-2 and M^2 in SW-1.

Measurements of the Holotype. – Sinus height: $D^4 = 0,58$; $M^1 = 4,83$; $M^2 = > 4,00$. Length: $D^4 = 2,67$; $M^1 = 2,08$; $M^2 = 1,92$. Width: $D^4 = 1,92$; $M^1 = 1,83$; $M^2 = 1,50$. Si-

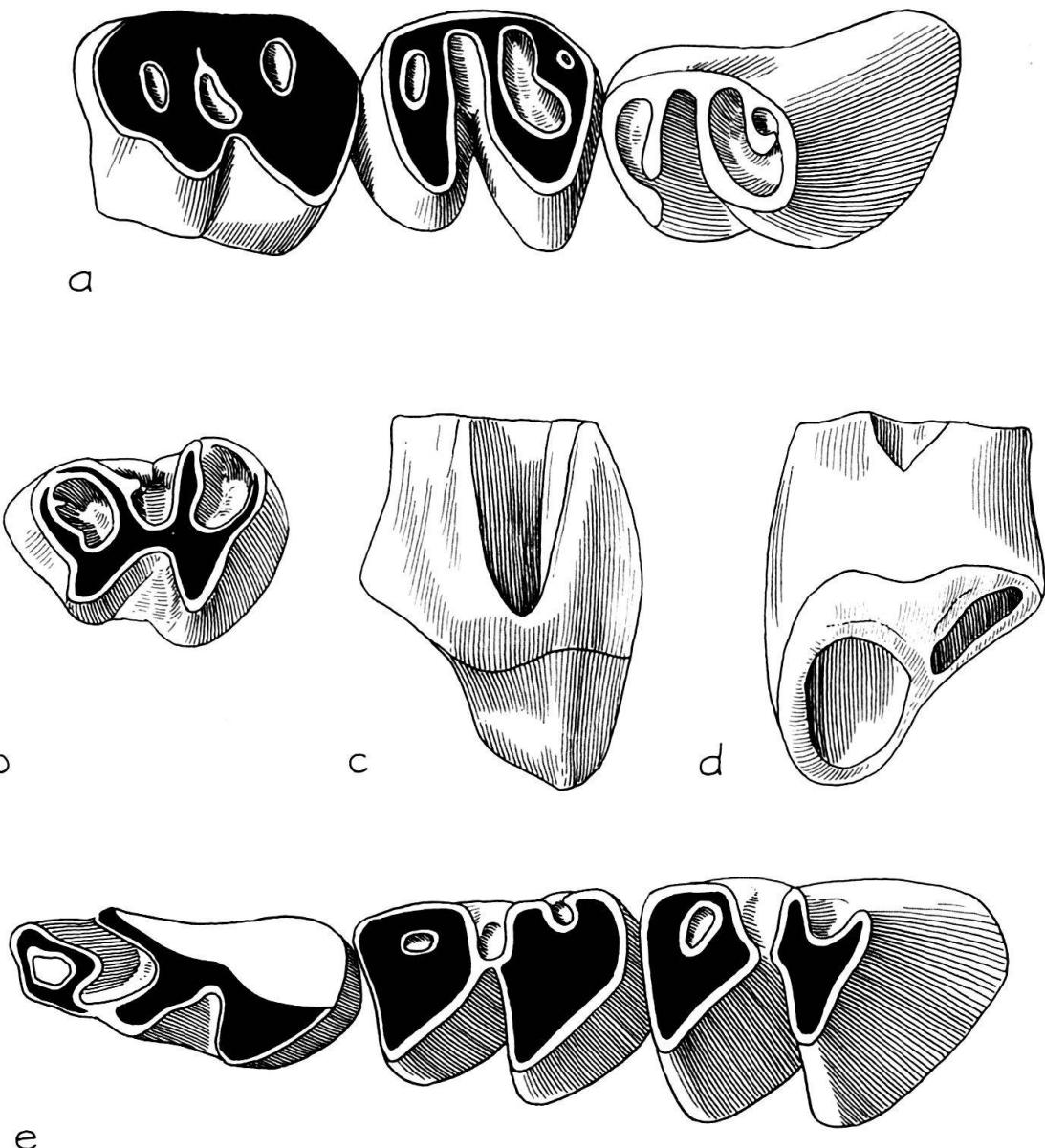


Fig. 19. *Nesokerodon aarwängensis* n. sp. a = NMB: Aw 62. D⁴-M² sin. Holotype. b = NMB: Aw 63. P₄ sin. Paratype. c = labial view. d = lingual view. e = NMB: Aw 61. D₄-M₂ dex (invers.). Paratype. Aarwangen 1, Switzerland. – All figures $\times 12,5$.

nus length: D⁴ = 0,58. Extrasinus distance: D⁴ = 1,08. Crown height: D⁴ = 1,00; M¹ = 5,00. Maxillary height in front of P⁴ between alveolar border and infraorbital crest: 3,08.

Paratypes. – NMB: Aw 61; right mandibular fragment with D₄-M₂. M₁ in SW-3 and M₂ in SW-2. NMB: Aw 63 (P₄) in SW-3.

Type locality. – Aarwangen-1, (see KFSNMB).

Type formation. – Aarwangen Molasse (see MARTIN 1906, p. 98; HEIM & HARTMANN 1919, p. 68; BAUMBERGER 1927, p. 560 and HABICHT 1987, p. 8–11).

Stratigraphic range. – Oligocene, Lower “Chattien”, assemblage zone of Aarwangen-1 (see ENGESSER & MAYO 1987).

Geographical distribution. – Central Europe.

Diagnosis. – Teeth with high semihypsodonty. Upper teeth with very bent crown labially-lingually. Very high maxilla in front of P⁴. M¹-M² with very short labial crown height, relative to the lingual one. Very small lobules. IV syncline very reduced. II syncline without a labial aperture. Mandible with longitudinal masseteric ridge moderately well developed. Lower teeth lingually concave to the crown base. P₄ large and molars very inclined to forward.

Differential diagnosis. – *Nesokerodon aarwicensis* n. sp. differs from *Nesokerodon quercyi* in the following characters:

- more elevated maxillary height in front of P⁴,
- larger size of the teeth,
- higher semihypsodonty,
- labially-lingually more bent upper crown,
- wider sinus,
- IV syncline very reduced, better developed masseteric ridge on the mandible,
- more forwardly inclined lower teeth,
- presence of a marked angle between the anterior border of the crown and anterior root in the lower molars,
- deeper concavity on the lingual border of the lower molars,
- greater size of P₄,
- thicker cellular cement on the sinusid.

Table 34: Measurements of the cheek teeth of *Nesokerodon aarwicensis* n. sp. from Aarwangen-1 (Switzerland)

| Tooth | SW | Sinus(id) height | Length | Width | Sinus(id) length | Extrasinus(id) distance | Crown height |
|----------------|----|---------------------|--------|--------|---------------------|----------------------------|--------------|
| D ⁴ | – | 0,58 | 2,67 | 1,92 | 0,58 | 1,08 | 1,00 |
| M ¹ | 2 | 4,83 | 2,08 | 1,83 | – | – | 5,00 |
| M ² | 1 | – | 1,92 | 1,50 | – | – | – |
| D ₄ | – | 0,25 | ~ 3,17 | ~ 1,50 | – | – | 0,67 |
| P ₄ | 3 | 2,00 | 2,17 | 1,58 | 0,67 | 0,92 | 2,50 |
| M ₁ | 4 | 3,42 | 2,50 | 1,67 | 1,00 | 0,50 | 3,58 |
| M ₂ | 3 | 4,00 | 2,25 | 1,67 | – | – | 4,17 |

Discussion. – STEHLIN (1914, p. 183) determined the Issiodoromyinae material of Aarwangen-1 as *Nesokerodon quercyi* SCHLOSSER 1884. THALER (1966, p. 203, Table 9) and HUGUENY (1969, p. 200) identified this material as *Issiodoromys pseudanema* GERVAIS 1848–52 on the basis of its considerable crown height. VIANEY-LIAUD (1976, p. 60, 68 and 70, Table 17, Fig. 35) and MAYO (1983, p. 903, Fig. 55) considered that it belongs to *I. quercyi*. Nevertheless, the better preparation of the material allowed it to be described as a new species.

Measurements in the Table 34.

Oensingenomys n. gen.

Synonymy. – See type species.

Type species. – *Oensingenomys ravellensis* n. gen. n. sp.

Stratigraphic range. – Oligocene, Lower “Chattien”, from Oensingen to Boningen assemblage zones (see ENGESSER & MAYO 1897).

Geographical distribution. – Central Europe.

Diagnosis. – Semihypsodont Issiodoromyinae with strong sagittal rotation in the upper teeth. Very high maxilla dorsal to P^4 , but compressed on M^2-M^3 . Deep and narrow infraorbital canal and with a high external ridge. Long palatine vault. Posterior border of incisive foramen in front of posterior prism of P^4 . Posterior palatine foramen in front of contact between M^2 and M^3 . Choanae opened in front of first prism of M^3 . Posterior maxillary foramen behind M^3 , relatively far from maxillary border. Upper teeth with strongly dissimilar abrasion. Tooth rows much more curved than in *Nesokerodon*. Distance between lingual and labial alveolar borders in M^2-M^3 greater than in *Nesokerodon*. Lingual half of upper teeth in the early stage of wear more abraded than the opposite side. Occlusal surface convex in the labial half and concave in the lingual half. The antycline and syncline weakly worn. Labial border of upper crown and of lingual root very bent. Normal labial roots of upper teeth with the base in the lower part of the crown. Lingual roots very short, strongly bent and with a tendency to lamination. Crown base with a broad space between labial and lingual roots. Mandible: with slightly to moderately prominent anterior masseteric ridge, parallel to cheek teeth and hold of the alveolar border; broad to very broad ventral part of mandible below the masseteric ridge, owing to pneumatic process. Upper and lower angular masseteric ridges behind the anterior

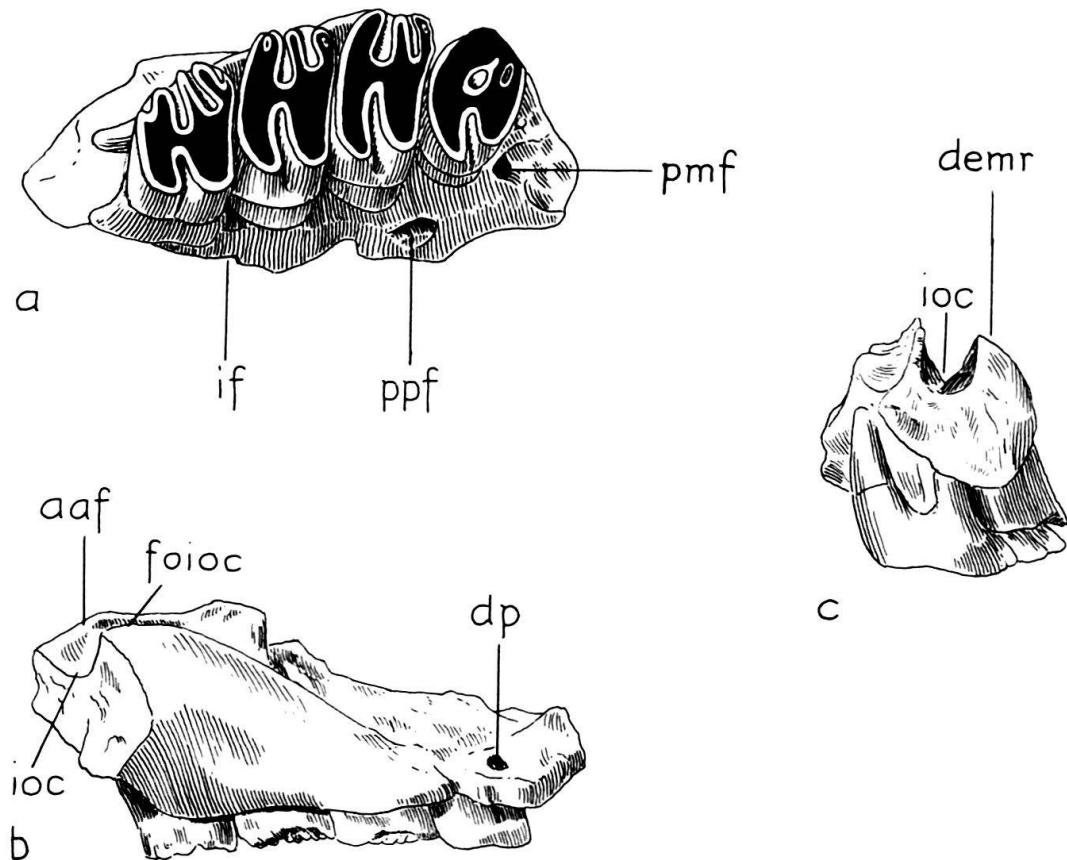


Fig. 20. *Oensingenomys ravelensis* n. gen. n. sp. NMB: UM 486. Left maxillary fragment with P^4-M^3 . Holotype. a = ventral view. b = labial view. c = frontal view. Oensingen, Switzerland. – All figures $\times 3$.

masseteric ridge. Upper angular masseteric ridge with a very slight groove. M_3 with three roots. M_1 or M_2 with two or three roots. P_4 smaller than molars.

Differential diagnoses. — *Oensingenomys* n. gen. differs from *Issiodoromys* in the following characters:

- presence of semihypsodonty,
- different morphology of the maxilla,
- deeper and not vaulted infraorbital canal,
- presence of masseteric fossa on the ventral surface of the masseteric apophysis of the anterior zygomatic process,
- different length of the palatine vault,
- slightly different position of the posterior border of the incisive foramen,
- different position of the anterior border of the choanae,
- different position of the posterior palatine foramen,
- absence of posterior maxillary sulcus on the external border of the maxilla behind M^3 ,
- vertical external ridge of the infraorbital canal,
- presence of vertical foramen inside the masseteric fossa of the masseteric apophysis of the maxilla,
- compressed maxilla dorsally to M^2-M^3 ,
- strongly curved tooth row,
- longer distance between the labial and lingual alveolar border of the maxilla beside M^2 ,
- different morphology of the mandible,
- absence of the long longitudinal masseteric ridge,
- absence of a deep sulcus above the masseteric ridge,
- absence of teeth with atrophied roots,
- presence of synclines and anticyclines, very weakly worn in advanced stage of wear,
- unequal abrasion of the occlusal surface of the upper teeth,
- upper teeth much wider in fully worn stage,
- broader and shorter lobules.

From *Nesokerodon* in the:

- different morphology of the maxilla,
- much deeper and narrower infraorbital canal,
- larger maxillary height in front of P^4 ,
- low maxillary height dorsally to M^2-M^3 ,
- different length of the palatine vault,
- slightly different position of the posterior border of the incisive foramen,
- different position of the anterior border of the choanae,
- different position of the posterior palatine foramen,
- absence of posterior maxillary sulcus on the external border of the maxilla behind M^3 ,
- very bent tooth row and labial alveolar border of the maxilla,
- larger distance between the lingual and labial alveolar border in the maxilla beside M^2 ,
- presence of a protuberance of bone on the labial border of the maxillary alveolus below the crown,
- different morphology of the mandible,
- different masseteric ridges,
- deep position of the masseteric ridge with reference to the alveolar border,

- very broad ventral part of the mandibular ramus below the masseteric ridge,
- pneumatic process of the mandible,
- absence of the shelflike masseteric ridge,
- horizontal position of the anterior masseteric ridge,
- different position of the lower angular masseteric ridge, and its absence below the anterior masseteric ridge,
- dissimilar abrasion of occlusal surface of the upper teeth,
- convex part of the occlusal crown surface on the synclines and antyclines,
- upper teeth much wider in advanced worn stage,
- presence of very weakly worn synclines and antyclines in the advanced state of wear,
- presence of a broad space below the upper crown, between the labial and lingual roots,
- more inclined labial border of the upper crown,
- more bent upper tooth rows,
- more bent lingual roots in the upper teeth,
- tendency towards lamination of the lingual roots of the upper teeth,
- more concave or laminated lingual roots in the upper teeth,
- absence of barbel form in the crown of the upper teeth,
- labial roots of the upper teeth with their base in the lower part of crown,
- M_3 with three roots,
- M_1 and M_2 with two or three roots.

Oensingenomys ravelensis n. gen. n. sp.

Fig. 20–21

Synonymy. –

- 1914 *Nesokerodon minor* STEHLIN; p. 18.
 1951 *Issiodoromys minor* STEHLIN, p. 71 and 72, Fig. 90 and 92.
 1966 *Issiodoromys minor* THALER, p. 201 and 203, Table 9.
 1976 *Issiodoromys cf. pauffiensis* VIANEY-LIAUD, p. 55 and 57, Table 13b, in part; non Fig. 32a, b and d; only Fig. 32c.
 1981 *Issiodoromys minor* HUGUENY, p. 64.
 1982 *Issiodoromys aff. pauffiensis* VIANEY-LIAUD, p. 691.
 1982 *Issiodoromys minor* MAYO, p. 710.
 1983 *Issiodoromys minor* MAYO, p. 905 and 907.
 1984 *Issiodoromys pauffiensis* MAYO, p. 26, in: ENGESSER et al.

Table 35: Measurements of the P^4 of *Oensingenomys ravelensis* n. gen. n. sp. from Oensingen (Switzerland)

| SW | N | | range | \bar{X} | S | V |
|----|---|---------------------|-----------|-----------|------|-------|
| 3 | 1 | Sinus height | – | 1,33 | – | – |
| | 1 | Length | – | 1,75 | – | – |
| | 1 | Width | – | 1,92 | – | – |
| | 1 | Sinus length | – | 0,83 | – | – |
| | 1 | Extrasinus distance | – | 1,08 | – | – |
| | 1 | Crown height | – | 1,75 | – | – |
| 4 | 2 | Sinus height | – | 0,50 | – | – |
| | 2 | Length | 1,83–1,92 | 1,88 | 0,06 | 3,39 |
| | 2 | Width | 2,25–2,42 | 2,33 | 0,12 | 5,15 |
| | 2 | Sinus length | – | 1,00 | – | – |
| | 2 | Extrasinus distance | 1,25–1,33 | 1,29 | 0,06 | 4,39 |
| | 2 | Crown height | 0,92–1,17 | 1,05 | 0,18 | 16,92 |

Table 36: Measurements of the $M^{1/2}$ and M^3 of *Oensingenomys ravellensis* n. gen. n. sp. from Oensingen (Switzerland)

| Tooth | SW | N | | range | \bar{X} | S | V |
|-----------|----|---|---------------------|-----------|-----------|------|------|
| $M^{1/2}$ | 2 | 1 | Sinus height | — | 2,42 | — | — |
| | | 1 | Length | — | 1,50 | — | — |
| | | 1 | Width | — | 1,67 | — | — |
| | | 1 | Crown height | — | 2,75 | — | — |
| $M^{1/2}$ | 3 | 1 | Sinus height | — | 1,50 | — | — |
| | | 1 | Length | — | 1,75 | — | — |
| | | 1 | Width | — | 2,08 | — | — |
| | | 1 | Sinus length | — | 1,00 | — | — |
| | | 1 | Extrasinus distance | — | 1,08 | — | — |
| | | 1 | Crown height | — | 2,08 | — | — |
| $M^{1/2}$ | 4 | 4 | Sinus height | 0,33–0,58 | 0,44 | 0,13 | — |
| | | 4 | Length | 1,75–1,92 | 1,83 | 0,07 | 3,79 |
| | | 4 | Width | 2,67–2,92 | 2,81 | 0,10 | 3,70 |
| | | 4 | Sinus length | 1,33–1,58 | 1,48 | 0,11 | 7,13 |
| | | 4 | Extrasinus distance | 1,25–1,33 | 1,31 | 0,04 | 3,05 |
| | | 4 | Crown height | 0,58–1,08 | 0,83 | 0,24 | — |
| M^3 | 2 | 1 | Sinus height | — | 1,75 | — | — |
| | | 1 | Length | — | 1,50 | — | — |
| | | 1 | Width | — | 1,42 | — | — |
| | | 1 | Crown height | — | 2,25 | — | — |

Holotype. – NMB: UM 486, left maxillary fragment with P^4 – M^3 . All teeth in SW-3.

Measurements of the Holotype. – Sinus height: $P^4 = 0,50$; $M^1 = 0,58$; $M^2 = 0,50$; $M^3 = 0,33$. Length: $P^4 = 1,92$; $M^1 = 1,83$; $M^2 = 1,83$; $M^3 = 1,83$. Width: $P^4 = 2,42$; $M^1 = 2,67$; $M^2 = 2,83$; $M^3 = 2,33$. Sinus length: $P^4 = 1,00$; $M^1 = 1,33$; $M^2 = 1,50$; $M^3 = 0,92$. Extrasinus distance: $P^4 = 1,33$; $M^1 = 1,33$; $M^2 = 1,33$; $M^3 = 1,25$. Crown height: P^4 – $M^3 = 7,17$. Distance between lingual and labial alveolar borders over M^2 : 3,83. The same measurements dorsally between the wall of the skull and the labial maxillary border: 2,50. Width of the infraorbital canal: 0,83. Anterior border of the alveolar foramen dorsally in near position to lower anterior crown border of P^4 . Height of the maxilla in front of P^4 between the alveolar border and crest of the infraorbital canal: 3,58. Frontal depth of the infraorbital canal (without fossa): 0,92.

Paratypes. – All in the collection of the NMB. D_4 . – UM 7163. SW-1: P_4 . – UM 6855. SW-3: P^4 . – UM 2189. M^1 . – UM 491, UM 7164f, M^2 . – UM 7165. $M_{1/2}$. – UM 468, 492, 2193, 6853 and 6854. SW-4: $M_{1/2}$. – UM 496 and 2192. Maxillary fragments: UM 226 (P^4 – M^2 : in SW-3) and UM 6851 (M^2 – M^3 in SW-2). Mandibular fragments: UM 2929

Table 37: Measurements of the D_4 and P_4 of *Oensingenomys ravellensis* n. gen. n. sp. from Oensingen (Switzerland)

| Tooth | SW | Sinusid height | Length | Width | Sinusid length | Extrasinusid distance | Crown height |
|-------|----|----------------|--------|-------|----------------|-----------------------|--------------|
| D_4 | – | – | 2,87 | 1,25 | 0,42 | 0,75 | – |
| P_4 | 1 | 1,42 | 1,42 | 0,92 | – | – | 1,92 |
| P_4 | 2 | 1,17 | 1,67 | 1,25 | – | – | 1,58 |
| P_4 | 3 | 1,08 | 1,75 | 1,33 | 0,58 | 0,67 | 1,42 |
| P_4 | 4 | 0,50 | 2,00 | 1,50 | 1,16 | 0,58 | 1,17 |

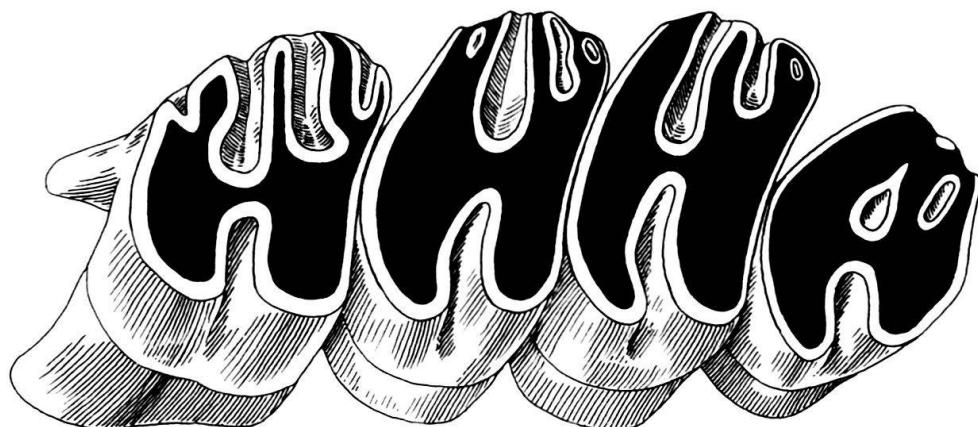


Fig. 21. *Oensingenomys ravelensis* n. gen. n. sp. NMB: UM 486. P⁴–M³ sin. Holotype. Oensingen, Switzerland.
— × 12,5.

(P₄–M₃; P₄ and M₃ in SW-3; M₂ in SW-4; M, f); UM 495 (P₄–M₁; P₄ in SW-2 and M₂ in SW-3).

Hypodigm. – In addition to the Holotype and Paratype the specimen UM 228 f.

Type locality. – Oensingen-Ravellen (Canton of Solothurn, Switzerland). See STEHLIN (1914, p. 180); BAUMBERGER (1923, p. 36–38, Fig. 15); MAYO (1980, p. 1096–97, Fig. 1 and 1982, p. 714–18, Fig. 8 and 9).

Type formation. – Oensingen limestone. See BAUMBERGER 1923, p. 36–38 and 1927, p. 554–56, Fig. 4 and 5; WAIBEL & BURRI 1961, p. 187–88 and MAYO 1980, p. 1096–97, Fig. 1 and 1982, p. 714–18, Fig. 9.

Stratum type. – Lacustrine limestone of brown colour with 2,5 m of thickness. 2,3 m above the Eocene siderolitic Formation.

Stratigraphic range. – Oligocene, Lower “Chattien”, assemblage zone of Oensingen (see ENGESER & MAYO 1987).

Geographical distribution. – Faunal province of Switzerland and Savoy.

Diagnosis. – Species of small size and medium semihypsodonty. Maxilla with a very deep infraorbital canal. Infraorbital canal with a deep fossa in its base. Anterior alveolar foramen partially open at the base of the canal, inside the anterior border of the fossa. Anterior alveolar foramen dorsal to base of anterior border of P⁴. Labial alveolar border of maxilla almost parallel to occlusal surface of M²–M³. Sinus or sinusid without cellular cement. Lingual roots anterior-posteriorly narrow.

Discussion. – STEHLIN (1914, p. 18 and 1951, p. 71–72, Fig. 90 and 92) determined the material of *Oensingenomys ravelensis* n. gen. n. sp. as *Nesokerodon* or *Issiorodomys minor* SCHLOSSER 1884. He described the strong increase of the occlusal surface in the upper worn teeth as a normal sagittal rotation of the semihypsodontic teeth. THALER (1966, p. 201 and 203, Table 9) maintained this opinion. VIANEY-LIAUD (1976, p. 55, 57 and 59, Fig. 32 and Table 13b) observed that the teeth of Oensingen are greater in size than those of *Nesokerodon minor*. For this reason she considered with some doubt, this material as *Issiodromys cf. pauffiensis* VIANEY-LIAUD 1976. HUGUENEY (1981, p. 64) identified it as *I. minor*. Later VIANEY-LIAUD (1982, p. 691) determined this material as *I. aff. pauffiensis*. MAYO (1982, p. 710 and 1983, p. 905 and 907) indicated that it belonged to a different

Table 38: Measurements of the $M_{1/2}$ and M_3 of *Oensingenomys ravellensis* n. gen. n. sp. from Oensingen (Switzerland)

| Tooth | SW | N | | range | \bar{X} | S | V |
|-----------|----|---|-----------------------|-----------|-----------|------|-------|
| $M_{1/2}$ | 3 | 6 | Sinusid height | 1,58–2,08 | 1,79 | 0,17 | 9,59 |
| | | 6 | Length | 1,68–2,08 | 1,96 | 0,15 | 7,64 |
| | | 6 | Width | 1,33–2,33 | 1,63 | 0,37 | – |
| | | 6 | Sinusid length | 0,58–0,83 | 0,72 | 0,10 | 14,51 |
| | | 6 | Extrasinusid distance | 0,67–0,83 | 0,73 | 0,06 | 8,80 |
| | | 6 | Crown height | 1,92–2,42 | 2,16 | 0,18 | 8,27 |
| $M_{1/2}$ | 4 | 3 | Sinusid height | 0,75–1,25 | 1,00 | 0,25 | – |
| | | 3 | Length | 2,00–2,17 | 2,08 | 0,09 | 4,08 |
| | | 3 | Width | 1,60–2,00 | 1,84 | 0,21 | 11,50 |
| | | 3 | Sinusid length | 0,83–1,17 | 1,03 | 0,18 | 17,16 |
| | | 3 | Extrasinusid distance | 0,75–0,92 | 0,81 | 0,10 | 12,17 |
| | | 2 | Crown height | 1,08–1,50 | 1,29 | 0,30 | – |
| M_3 | 3 | 1 | Sinusid height | – | 1,00 | – | – |
| | | 1 | Length | – | 2,25 | – | – |
| | | 1 | Width | – | 1,83 | – | – |
| | | 1 | Sinusid length | – | 0,92 | – | – |
| | | 1 | Extrasinusid distance | – | 0,83 | – | – |
| | | 1 | Crown height | – | 1,08 | – | – |

taxon to *I. minor*. MAYO (1984, p. 26, in: ENGESSER et al.) considered it may be *I. pauffiensis* VIANEY-LIAUD, 1976. Nevertheless, a painstaking preparation and more detailed examination of this material has permitted its separation as a new genus and species.

Measurements in the Tables 35–38.

Oensingenomys huerzeleri n. sp.

Fig. 22

Derivatio nominis. – After Dr. Johannes Hürzeler (Basel), collector of the material.

Holotype. – NMB: UM 3775, left maxillary fragment with P^4 – M^3 , P^4 and M^3 in SW-2 and M^1 and M^2 in SW-3.

Measurements of the Holotype. – Sinus height: $P^4 = 2,42$; $M^1 = 2,50$; $M^2 = 3,17$; $M^3 = 2,58$. Length: $P^4 = 2,08$; $M^1 = 2,25$; $M^2 = 2,42$; $M^3 = 1,75$. Width: $P^4 = 1,92$; $M^1 = 2,42$; $M^2 = 2,50$; $M^3 = 1,92$. Sinus length: $P^4 = 0,75$; $M^1 = \sim 1,17$; $M^2 = \sim 1,17$. Extrasinus distance: $M^1 = 1,17$; $M^2 = 1,25$. Length of P^4 – $M^3 = 8,50$.

Paratypes. – All the material in the collections of NMB. SW-2: M^4 . – UM 5052. SW-3: P^4 . – UM 5065 and 6038 f. M^3 . – UM 3780. $M_{1/2}$. – UM 5052. SW-4: M^4 . – UM 3779, 5056 f, 5063 f, 5064 f and 5066 f. Mandibular fragments: UM 5051 (P_4 – M_3 : P_4 and M_3 in SW-3; M_1 and M_2 in SW-4). UM 3776 (P_4 – M_3 : P_4 and M_3 in SW-3 and M_1 and M_2 in SW-4).

Hypodigm. – In addition to the Holotype and Paratype the specimen UM 6039 (D_4e).

Type locality. – Boningen (Canton of Solothurn, Switzerland). See KFSNMB.

Type formation. – Aarwangen Molasse (see HABICHT 1987, p. 8–11).

Stratum type. – Green-gray lacustrine marls bed of ca. 40 cm thickness, with mollusc shells, below a hard limestone bed of 50 cm thickness.

Table 39: Measurements of the upper check teeth of *Oensingenomys huerzeleri* n. sp. from Boningen (Switzerland)

| Tooth | SW | N | | range | \bar{X} | S | V |
|-----------|----|---|---------------------|-----------|-----------|------|-------|
| P^4 | 3 | 2 | Sinus height | 2,42–3,42 | 2,92 | 0,71 | – |
| | | 2 | Length | 2,08–2,17 | 2,13 | 0,06 | 2,99 |
| | | 2 | Width | 1,92–2,08 | 2,00 | 0,11 | 5,66 |
| | | 2 | Sinus length | 0,75–0,92 | 0,84 | 0,12 | 14,40 |
| | | 1 | Extrasinus distance | – | 1,08 | – | – |
| | | 1 | Crown height | – | 2,92 | – | – |
| $M^{1/2}$ | 3 | 2 | Sinus height | 2,50–3,17 | 2,84 | 0,47 | 16,71 |
| | | 2 | Length | 2,25–2,42 | 2,34 | 0,12 | 5,15 |
| | | 2 | Width | 2,42–2,50 | 2,46 | 0,06 | 2,30 |
| | | 2 | Sinus length | – | 1,17 | – | – |
| | | 2 | Extrasinus distance | 1,17–1,25 | 1,21 | 0,06 | 4,68 |
| | | 2 | Crown height | 3,42–3,92 | 3,67 | 0,35 | 9,63 |
| $M^{1/2}$ | 4 | 5 | Sinus height | 1,25–3,00 | 2,33 | 0,70 | – |
| | | 5 | Length | 2,25–2,50 | 2,38 | 0,10 | 4,03 |
| | | 1 | Width | – | 2,83 | – | – |
| | | 3 | Sinus length | 1,42–1,50 | 1,45 | 0,03 | 3,19 |
| | | 1 | Extrasinus distance | – | 1,42 | – | – |
| | | 5 | Crown height | 1,75–3,50 | 2,80 | 0,69 | – |
| M^3 | 2 | 1 | Sinus height | – | 2,58 | – | – |
| | | 1 | Length | – | 1,75 | – | – |
| | | 1 | Width | – | 1,92 | – | – |
| | | 1 | Crown height | – | 3,00 | – | – |

Stratigraphic range. – Oligocene, top of Lower “Chattien”, assemblage zone of Boningen (see ENGESER & MAYO 1987).

Geographical distribution. – Central Europe.

Diagnosis. – Species of large size and high semiphysodonty. Labial border of the maxilla in front of M^2 – M^3 not parallel to occlusal surface. Upper teeth: with very broad and short lobules; very broad space below the crown between labial and lingual roots and very laminated lingual roots. Sinus relatively open and with cellular cement. Mandible with anterior masseteric ridge of moderate size (below P_4 and M_1) in very deep position relating to the alveolar border. Very broad ventral part of the mandible below the masseteric ridge owing to pneumatic process.

Differential diagnosis. – *O. huerzeleri* n. sp. differs from *O. ravellensis* n. gen. n. sp. in the following characters:

- larger size,
- higher semiphysodonty,
- different labial border of the maxilla in front of M^2 – M^3 ,
- broader space below the crown between labial and lingual roots,
- more laminated lingual roots,
- sinus with cellular cement,
- more opened sinus,
- longer anterior masseteric ridge,
- more pneumatic mandible.

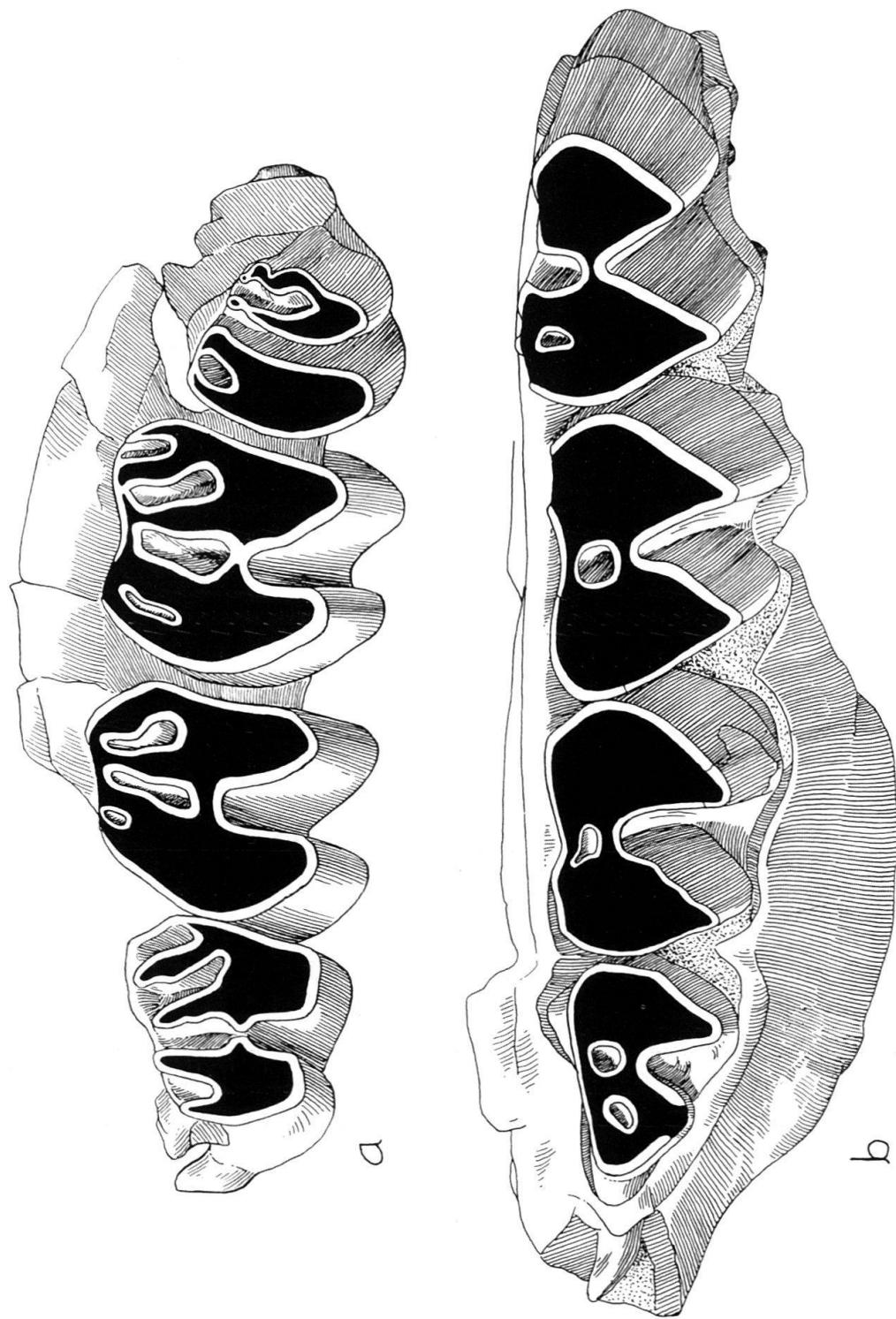


Fig. 22. *Oensisgenomys huertzleri* n. sp. a = NMB: U.M. 3775. Left maxillary fragment with P^4 - M^3 . Holotype. b = NMB: U.M. 5051. P_4 - M_3 sin. Paratype. Boningen, Switzerland. - All figures $\times 12.5$.

Discussion. – STEHLIN identified the teeth of this species as *Issiodoromy quercyi* SCHLOSSER 1884 (1928, labels). THALER (1966, p. 203) – with doubts – HUGUENEY (1969, p. 200, Fig. 116) and VIANEY-LIAUD (1976, p. 60, 67 and 69, Table 16d, Fig. 34 and 1979, p. 215 and 227) were of the same opinion. Nevertheless, a painstaking preparation of the material permitted its separation as a new species.

Measurements in the Tables 39–40.

Table 40: Measurements of the lower cheek teeth of *Oensingenomys huerzelei* n. sp. from Boningen (Switzerland)

| Tooth | SW | N | | range | \bar{X} | S | V |
|-----------|----|---|-----------------------|-----------|-----------|------|-------|
| P_4 | 3 | 2 | Sinusid height | 0,92–1,58 | 1,25 | 0,47 | – |
| | | 2 | Length | 1,83–2,08 | 1,96 | 0,18 | 9,04 |
| | | 2 | Width | 1,42–1,50 | 1,46 | 0,06 | 3,87 |
| | | 2 | Sinusid length | – | 0,83 | – | – |
| | | 2 | Extrasinusid distance | 0,42–0,58 | 0,50 | 0,11 | – |
| | | 2 | Crown height | 1,58–2,00 | 1,79 | 0,30 | 16,59 |
| P_4 | 4 | 1 | Sinusid height | – | 1,25 | – | – |
| | | 1 | Length | – | – | – | – |
| | | 1 | Width | – | 1,58 | – | – |
| | | 1 | Sinusid length | – | 0,83 | – | – |
| | | 1 | Extrasinusid distance | – | 0,50 | – | – |
| | | 1 | Crown height | – | – | – | – |
| $M_{1/2}$ | 2 | 1 | Sinusid height | – | 3,00 | – | – |
| | | 1 | Length | – | 2,75 | – | – |
| | | 1 | Width | – | 1,92 | – | – |
| | | 1 | Sinusid length | – | 1,17 | – | – |
| | | 1 | Extrasinusid distance | – | 0,75 | – | – |
| | | 1 | Crown height | – | 3,25 | – | – |
| $M_{1/2}$ | 3 | 2 | Sinusid height | 1,92–2,92 | 2,42 | 0,71 | – |
| | | 2 | Length | 2,42–2,50 | 2,46 | 0,06 | 2,30 |
| | | 2 | Width | – | 1,83 | – | – |
| | | 2 | Sinusid length | 1,08–1,17 | 1,13 | 0,06 | 5,66 |
| | | 2 | Extrasinusid distance | – | 0,75 | – | – |
| | | 2 | Crown height | 2,17–3,17 | 2,67 | 0,71 | – |
| $M_{1/2}$ | 4 | 7 | Sinusid height | 1,17–2,50 | 1,77 | 0,56 | – |
| | | 7 | Length | 2,33–2,75 | 2,50 | 0,15 | 5,88 |
| | | 7 | Width | 1,75–2,08 | 1,89 | 0,12 | 6,09 |
| | | 7 | Sinusid length | 1,08–2,25 | 1,38 | 0,41 | – |
| | | 7 | Extrasinusid distance | 0,42–0,83 | 0,62 | 0,13 | – |
| | | 6 | Crown height | 1,58–3,00 | 2,25 | 0,56 | – |
| M_3 | 3 | 2 | Sinusid height | 2,17–2,75 | 2,46 | 0,41 | 16,67 |
| | | 2 | Length | 2,42–2,67 | 2,55 | 0,18 | 6,95 |
| | | 2 | Width | – | 2,00 | – | – |
| | | 2 | Sinusid length | 1,00–1,08 | 1,04 | 0,06 | 5,44 |
| | | 2 | Extrasinusid distance | 0,50–0,75 | 0,63 | 0,18 | – |
| | | 1 | Crown height | – | 3,17 | – | – |

Subfamily *Archaeomyinae* LAVOCAT 1952

Genus *Toeniodus* POMEL 1854

Synonymy. –

- 1854 *Toeniodus* POMEL, p. 36 (correct original spelling Art. 32 cii).
 1859 *Taeniodus* GERVAIS, p. 31 (incorrect emendation of the original spelling).