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Early Miocene ruminants of Wallenried (USM, Aquitanian / Switzerland): Sedimentology, biostratigraphy and paleoecology

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Key words: USM, Lower freshwater Molasse, Sedimentology, Aquitanian, Biostratigraphy, Artiodactyla, Paleoecology, Paleoclimatology

ABSTRACT

The Wallenried quarry, located 10 km north of Fribourg, presents certainly the best example of the Molasse grise de Lausanne-Formation (USM = Lower Freshwater Molasse, Aquitanian) in this area. Paleogeographically, Wallenried belongs to the «Genfersee-Schüttung» drainage system. Biostratigraphically, the abundant micromammals (Rodentia and Lagomorpha) and macromammals (Artiodactyla) place the studied interval in the European Mammal Neogene Zone MN2b.

The quarry section presents a set of typical lithofacies and architectural elements, which are interpreted as representing a meandering river.

The whole fauna shows a well equilibrated spectrum, with a good distribution between the freshwater, terrestrial and amphibian-living species. Among this fauna two large herbivore species, *A.* cf. *laugnacensis* and *Friburgomeryx* n.g. *wallenriedensis* n.sp. occur. They represent two primitive ruminants of moderate body weight, living in any kind of wooded habitats.

Most sedimentological and paleontological features observed at Wallenried suggest a subtropical humid climate with very few temperature variations and year-round humidity during the whole year. The drier season probably was short and never led to desiccation of the floodplain. The latter certainly had to be a complex of environments, between woodland and grassland, which fall under the umbrella term « savannah».

RESUME

La marnière de Wallenried, localisée 10 km au Nord de Fribourg, constitue certainement le plus bel exemple de la Formation de la Molasse Grise de Lausanne (USM = Molasse d'eau douce inférieure, Aquitanien) de la région. Paléogéographiquement on la place dans le système de drainage de la «Genfersee-Schüttung», alors que l'abondance de micromammifères (Rodentia et Lagomorpha) et de macromammifères (Artiodactyla) permet de dater le niveau mammalien européen MN2b.

Le profil sédimentologique de la marnière présente un ensemble typique de lithofacies et d'éléments architecturaux d'un système fluviatile à méandres.

La faune montre un spectre assez équilibré, avec une bonne distribution entre les espèces aux affinités aquatiques, dulcicoles et terrestres. Parmi cette faune, on retrouve deux espèces d'herbivores, *A.* cf. *laugnacensis* et *Friburgomeryx* n.g. *wallenriedensis* n.sp.. Elles représentent deux ruminants primitifs de taille moyenne, dont l'analyse dentaire indique une dentition typique sélénodonte, brachyodonte et broyeuse de feuilles. Ces deux artiodactyles devaient certainement vivre dans un environnement forestier au sens large, mais en aucun cas dans un environnement ouvert.

La plupart des caractéristiques sédimentologiques et paléontologiques observées à Wallenried désigne un climat subtropical humide avec peu de variations de température et une humidité présente durant la totalité de l'année. La saison sèche devait probablement être courte et ne jamais conduire à un assèchement complet de la plaine d'inondation. Cette dernière représentait certainement un complexe d'environnements, type paysage partiellement boisé, se rangeant sous le terme général de «savane».

ZUSAMMENFASSUNG

Der Steinbruch Wallenried, 10 km nördlich Fribourg gelegen, stellt das beste Beispiel für die Molasse grise de Lausanne-Formation (USM = Untere Süsswassermolasse, Aquitan) in der Gegend dar. Paläogeographisch zählt Wallenried zum Entwässerungssystem der «Genfersee-Schüttung». Die häufigen Funde von Kleinsäugern (Rodentia und Lagomorpha) sowie Grosssäugern (Artiodactyla) erlauben eine biostratigraphische Einordnung des untersuchten Zeitintervals in die Europäische Neogen Säuger Zone MN2b.

Das Steinbruchprofil enthält eine typische Faziesarchitektur, welche als Ablagerung eines mäandrierenden Flusses interpretiert wird.

Die gesamte Fauna zeigt ein ausgewogenes Artenspektrum zwischen Süsswasserformen, terrestrischen Formen und Formen mit amphibischer Lebensweise. In der Fauna enthalten sind auch zwei Vertreter der primitiven Wiederkäuer mit mittlerem Körpergewicht, *Andegameryx* cf. *laugnacensis* und *Friburgomeryx* n.g. *wallenriedensis* n.sp.. Als deren Lebensraum kann generell ein bewaldetes Habitat, auf keine Fall ein offenes Habitat, angenommen werden.

Die meisten sedimentologischen und paläontologischen Merkmale von Wallenried deuten auf ein subtropisches humides Klima mit ganzjährig geringen Schwankungen in Temperatur und Humidität. Die trockenere Jahreszeit war kurz und führte niemals zur Austrocknung der Überflutungsfläche. Letztere bestand sicherlich aus einem Komplex verschiedenartiger bewaldeter Habitate, welche unter dem Überbegriff «Savanne» zusammengefasst werden können.

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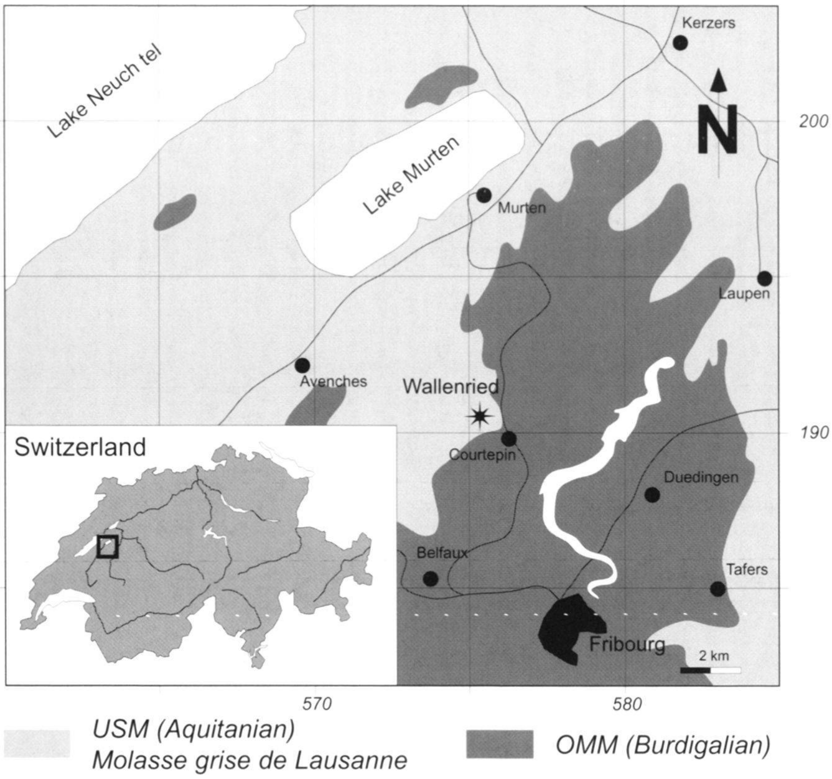

Fig. 1. Location map showing position and geological setting of Wallenried.
OMM = Obere Meeresmolasse = Upper Marine Molasse
USM = Untere Süsswassermolasse = Lower Freshwater Molasse

1. Introduction and geological background

The outcrop of Wallenried (574.45/192.45, Python 1996) is a quarry in the Plateau Molasse, located 10 km north of Fribourg (fig. 1). The salvaged material's sandy and marly components are exploited for the construction of bricks. The excavation is approximately 300 m wide and more than 40 m high, and altough only the top of this unit is exposed it certainly represents the best example of the Molasse grise de Lausanne-Formation (USM = Untere Süsswassermolasse = Lower Freshwater Molasse, Aquitanian) (Necker 1841, Habicht 1987, Weidmann 1996, Python et al 1998) in the Fribourg area. Paleogeographically (fig. 2) Wallenried belongs to the Aquitanian fluvial facies (Berger 1996), with a heavy mineral spectrum showing a strong influence of the «Genfersee-Schüttung» (Maurer 1983 a, b).

The USM of the Fribourg area was generally considered as azoic (Sieber 1959, Crausaz 1959, Becker 1972) except for rare mammal and helicid fragments (Ramseyer 1952, Hürzeler 1945). Berger (1985) published rich microfaunas and microfloras from neighbouring sections (Gottéron, Cournillens and Schiffenen). Additionally, a recent, detailed study (Becker 1996) discovered microflora and -fauna as well as the first recorded Artiodactyla in the Wallenried section.

2. Sedimentology

The quarry section (fig. 3 and 4) presents a set of typical lithofacies and architectural elements (lateral accretion and fining-up sequences), which are interpreted as representing «Sand-Bed Meandering River» to «Fine-Grained Meandering River», as defined by models 6 and 7 of Miall (1985, 1996). As Platt & Keller (1992), we adapted Miall's scheme (Miall 1985, 1996) in order to analyse the architectural elements more precisely. This led us to recognise 8 main architectural elements for this large outcrop. Their geometry, dimensions, and interpretations are defined below and summarised in tab. 1.

2.1 Architectural elements

Channel (CH)

We use the architectural element CH only for the indisputable sandy bedforms with channel shape and concave-up erosional base. It occurs as medium to coarse grained sandstones, with a thickness of 2–6 m and a lateral extension of up to 50 m. They are generally massive or trough cross bedded, with erosive bases outlined by mud clasts. Occasionally, the filling (channel) sandstones shows a fining-up trend towards the top of the bed, commonly interrupted by erosion surfaces. We can also observe internal erosion surfaces and lateral accretion macroform (see below and fig. 3).

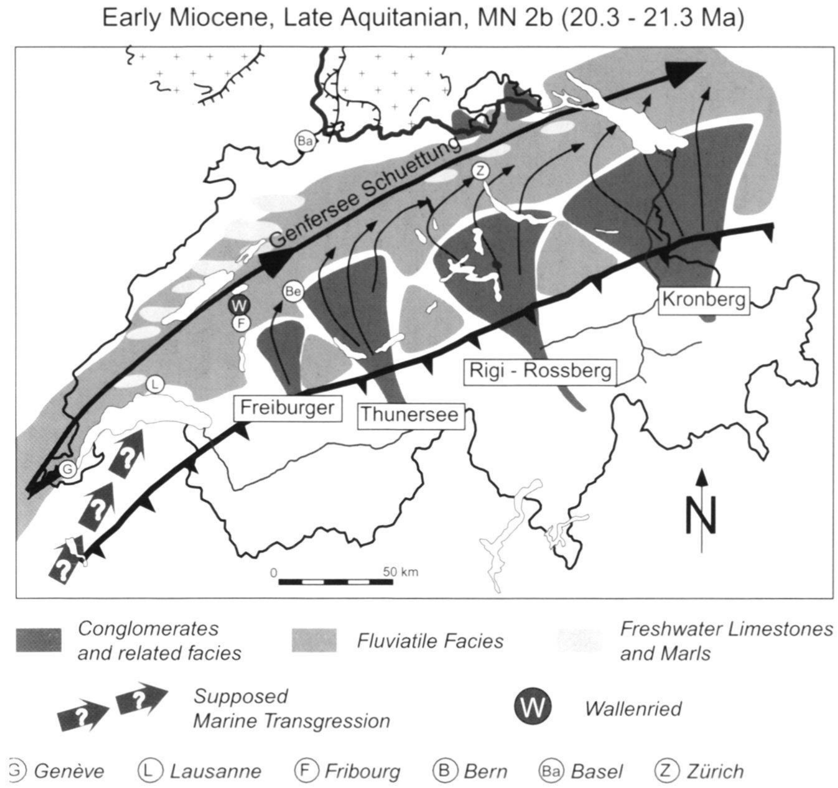

Fig. 2. Paleogeography of the Swiss Molasse basin of the Aquitanian, modified from Berger (1996).

Their geometry and the presence of low-angle cross-beds suggests deposition during lateral migration. The internal erosion surfaces and the presence of mud plugs indicate amalgamated bodies of complex genesis assigned to a meandering river.

Sandy bedform (SB)
This element is a general term used to define familiar flow-regime bedforms that take form in sand-dominated river systems and don't have obvious shape and structures allowing us to interprete them accurately. They can present a large range of sedimentary structures and could be interpreted as crevasse splay, bar tops, or as sand sheets in shallow rivers. They characteristically occupy the deeper portions of active channels wherever the bed load is predominantly sandy. The base and the top surface are commonly horizontal, but can show some concave-up and convex-up structures.

Lateral accretion (LA)
The lateral accretion deposits or point bars certainly represents the most characteristic feature of a fluvial sinusoidal regime. They develop on the insides of meander bends as the bend widens and migrates downstream. Surface flow impinges against the outer bank, where it maintains a cutbank by active erosion. Inside the LA we can commonly observe medium to coarse grained sandstones with trough cross-beds and low-angle cross-beds to horizontal laminations.

Levees (LV)
The levees are rarely observed in Wallenried and never really well developed. They should materialise the riverbanks on the concave side of the bend, and present bedded fine sandstones or siltstone up to few decimeters thick, intercalated with thin weakly mottled mudstones. Laterally discontinuous up to 10-30 meters, they constitute a wedged deposit, thinning and fining away from the channel margin. Bioturbation seems absent. This element represents short episodic flood events.

Crevasse channel (CR)
These medium to fine grained sandstones form small lenticular channel bodies up to 2 meters thick and a few meters wide with commonly no visible structures of migration. They cut through the concave side of the main channel bank or levee during the extraordinary flood.

Crevasse splay (CS)
The elements CS are the delta-like deposits which are formed near the margins of main channels and prograde from the crevasse channel to the floodplain. They are constituted of fine grained sandstones to siltstones with either weakly fine laminations or massive structure. It may reach 100×100 meters across and up to 1–2 meters thick. The crevasse splay deposits show convex-up structures in the distal part of the floodplain and concave-up in the proximal one.

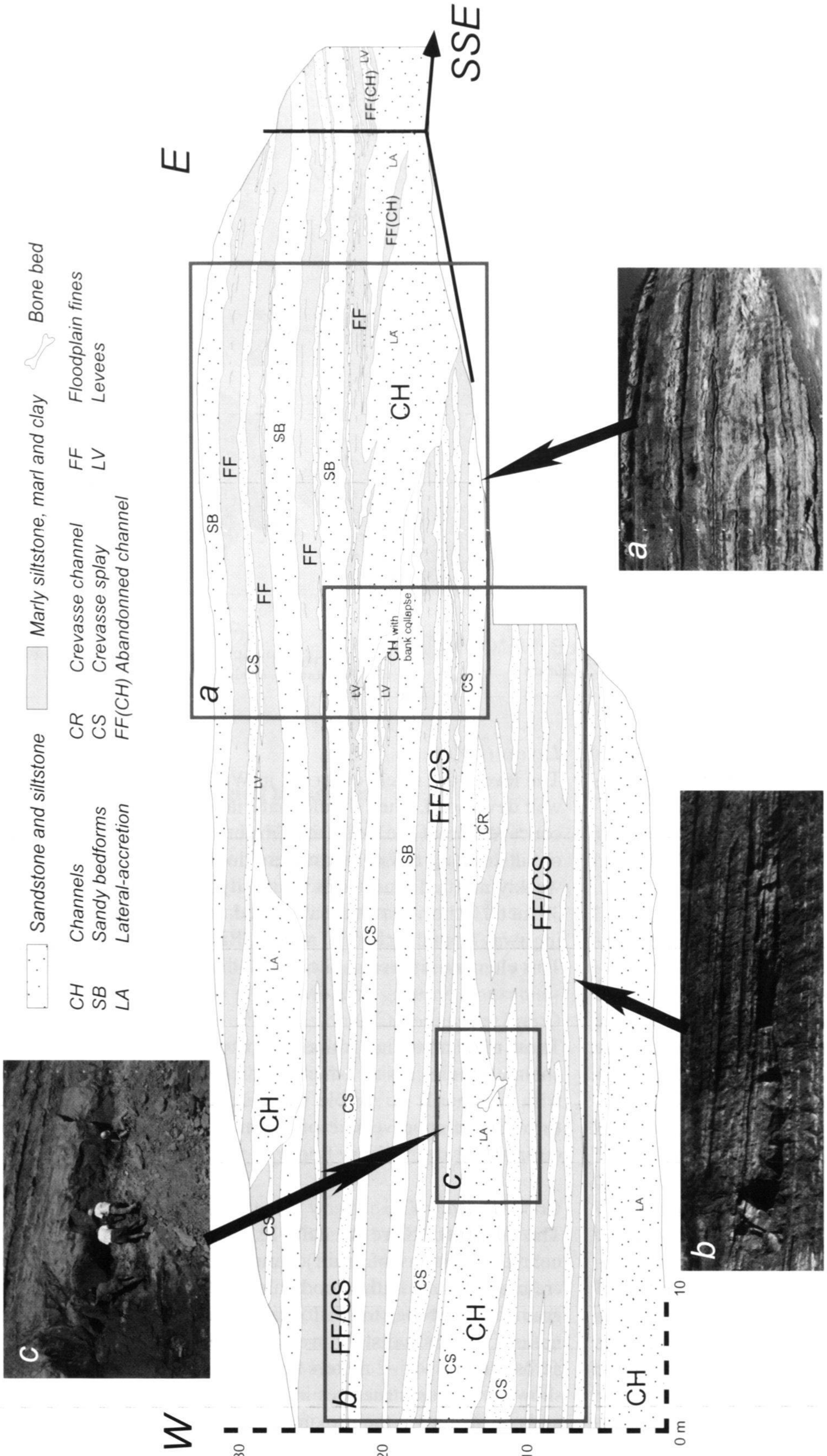

Fig. 3. Quarry section in the eastern part of the Wallenried outcrop.

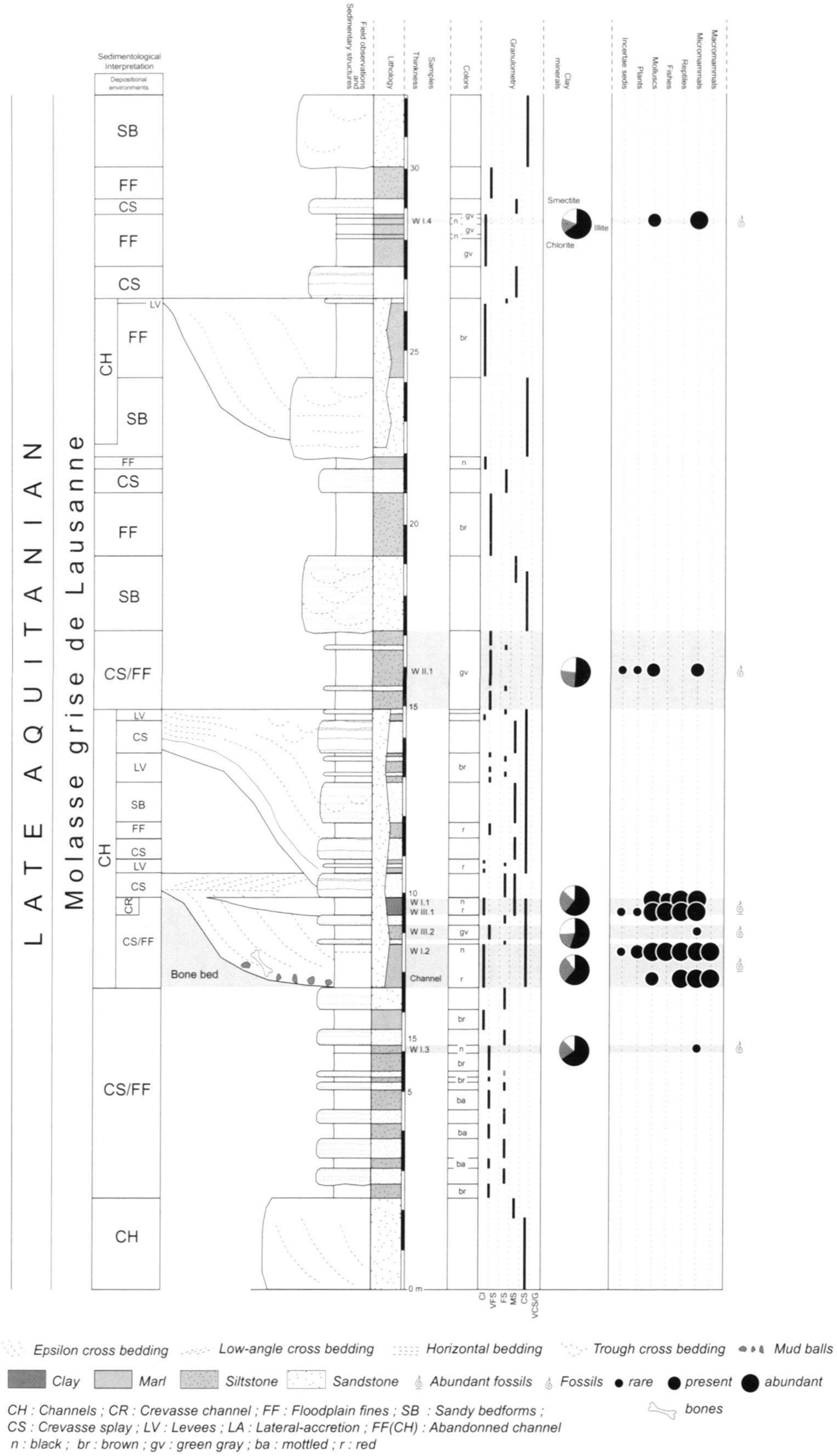

Fig. 4. Synthetic section of the 30 last m of the Wallenried outcrop.

Tab. 1. Lithofacies, sedimentary structures, interpretation and geometry of architectural elements of the Wallenried fluvial deposits.

Architectural Elements	Symbol	Lithofacies	Sedimentary structures	Geometry	Interpretation
Channels	CH	Sand, fine to coarse, sometimes with mud balls	Trough cross-beds Planar cross-beds Horizontal laminations Low-angle cross-beds Massive, or faint lamination	Finger, lens or sheet ; concave-up erosional ; scale and shape variable ; up to 5-6 m deep and up to 10s m width ; internal concave-up	3-D dunes 2-D dunes Pane-bed flow Scour fill Sediment-gravity flow deposit
Sandy bedforms	SB	Sand, fine to coarse, sometimes with mud balls	Trough cross-beds Planar cross-beds Horizontal laminations Low-angle cross-beds Massive, or faint lamination	Lens, sheet, blanket, wedge, occur as channel fills, crevasse splay ; up to 2-3 m thick and 100s m wide	3-D dunes 2-D dunes Pane-bed flow Scour fill Sediment-gravity flow deposit
Lateral-accretion	LA	Sand, fine to coarse, sometimes with mud balls	Trough cross-beds Planar cross-beds Horizontal laminations Low-angle cross-beds Massive, or faint lamination	Wedge, sheet, lobe ; characterized by internal lateral-accretion	3-D dunes 2-D dunes Pane-bed flow Scour fill Sediment-gravity flow deposit
Levee	LV	Sand, silt, mud	Fine lamination	Wedge up to 1-2 m thick, 10s m wide	Overbank flooding
Crevasse channel	CR	Sand, fine to medium	Broad shallow scours	Ribbon up to a few m wide, up to 2 m deep	Break in main channel margin
Crevasse splay	CS	Sand, silt	Fine lamination	Lens up to 100 X 100 m across, up to 1-2 m thick	Delta-like progradation from crevasse channel into floodplain
Floodplain fines	FF	Mud, silt	Fine lamination Massive	Sheet, may be many km in lateral dimensions, several m thick	Deposits of overbank sheet flow, floodplain ponds and swamps
Abandonned channel	FF(CH)	Silt, mud	Fine lamination Massive	Ribbon comparable in scale to active channel	Product of chute, neck cutoff or avulsion

Floodplain fines (FF)

Deposits of overbank fine sheet flow in the undrained areas and low relief of the floodplain. They occur like the crevasse deposits during extraordinary floods, but with a lower sedimentation rate and in a wider lateral extension, up to several kilometers. We are able to recover this element as silt or mud with seldom some faint, fine laminations. Especially towards the top of units, these laminations are commonly mottled as irregular red-grey-green, centimetre to decimetre large patches. Bedding-parallel colour banding on a 20–50 centimeters scale is also evident here, with the following common colour sequences: red, brown, dark, grey and grey-green.

The colours and especially the development of mottling records are characteristic of sediment subjected to repeated wetting and drying. Mottling is commonly associated with seasonally oscillating water tables.

Abandoned channel (FF (CH))

Abandoned channels, also called bayous, oxbows or billabongs, are common components of many fluvial styles, particularly the «sandy meandering river» and the «fine-grained meandering river».

These channels remain as ponds after a chute abandonment, a neck cut-off, or a simple avulsion. The mouth of the channel, at the cut-off, may gradually become silted up, leaving the abandoned channel to become progressively more undisturbed by turbulent whirlpool. Thus the waters of this elongate pond may become gradually more static, and slowly fills the abandoned channel with mud plugs.

2.2 *Fluvial style and environmental message*

The dominance of fine-grained sand and the observed association of swamp-channel-crevasse deposits in Wallenried are typical for a perennial river, but with seasonally dry and wet floodplains. The architectural elements and their sedimentary structures suggest migration of the meander belts, avulsions, channel abandonments, crevasse splays and, thus, fluctuations of discharge. The other arguments, like the LA architectural elements and fining-up sequences, confirm the presence of a meandering river. However it is difficult to show a clear link with a meandering river model of Miall (1985, 1996). Wallenried seems to be a compromise between the model 6 («Sand-Bed Meandering River») but with abandoned channels, even avulsions, and the model 7 («Fine-Grained Meandering River»), but with clearly Crevasse channel and Crevasse splay. With figure 5 we suggest a facies model slightly modified from Platt & Keller (1992) and adapted to Wallenried. The overbank deposits show stages of well-drained conditions (floodplain saturated or covered by water during significant parts of the annual cycle, showing backswamp and fine-grained grey-green sediments) and stages of poorly-drained conditions (marked water-table fluctuations with well-drained areas becoming relatively dry during extended periods of time and

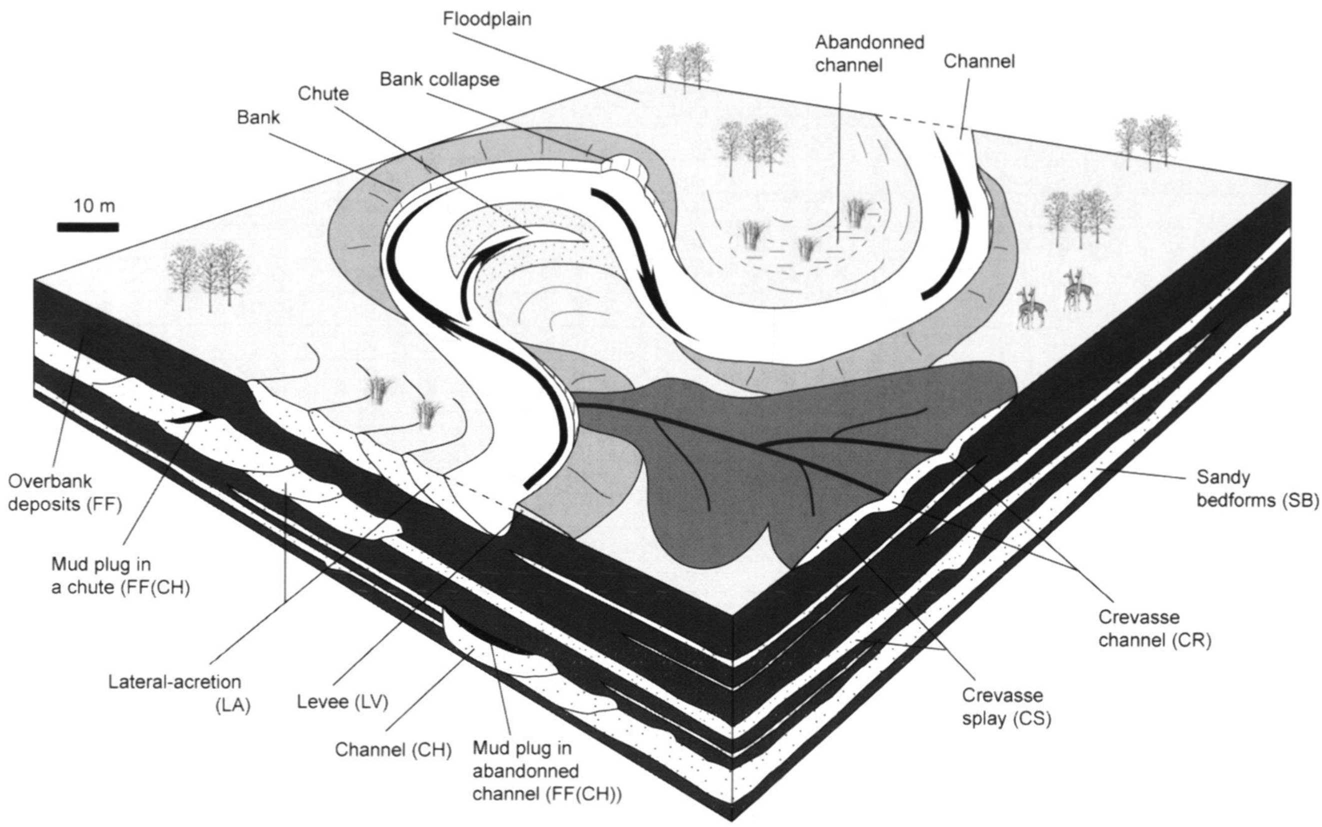

Fig. 5. Facies model adapted to Wallenried outcrop, modified from Platt and Keller (1992) and Miall (1996).

showing a red coloration). Nevertheless, it should not be forgotten that coloration does not necessarily correspond to the original environmental conditions, but to the earliest diagenesis (Behrensmeyer et al. 1992, Miall 1996).

Such environments generally occur either in tropical to subtropical systems (with wet-dry seasonality) or more rarely in temperate systems. To differentiate these systems we should find a relation in the figure of the overbank deposits. In particular the ponds and swamps occur more frequently in tropical areas and the crevasse deposits in the temperate areas. Most sedimentary and also paleontological (see below) features observed at Wallenried point to a subtropical humid climate with very few temperature variations and year-round humidity. The dry season was probably short and never led to desiccation of the floodplain.

3. Paleontology

3.1 Microfossils

More than 350 kg of sediment have been washed. The microfauna and microflora have been described in details by Becker (1996). We present here a short synthesis of the principal results (table 2, fig. 4).

Incertae sedis

Type 10 of Berger (1985). It could be a coprolith of worm or insect (Gregor 1978).

Flora & Invertebrates

Charophytes	Only two lychnothamnoid gyrogonites
Wood	Rare microscopic debris indet.
Fruit	Only one indefinite specimen with a form being suggestive of *Zanthoxylum*
Molluscs & Limacelles	Terrestrial gastropod fragments (Helicidae)

Small Vertebrates

Fishes	About thirty teeth of Cyprinidae, probably belonging to *Tarsichthys* sp.
Reptilians	Several crocodile teeth Fragments of turtle shield Abundant *Ophisaurus* osteoderm Various jaws of squamates and amphibians indet.

Tab. 2. Faunal list and accessory section levels of theWallenried outcrop. ✔ rare ✔✔ common ✔✔✔ abundant.

Fossils / Level		WI.1	WI.2	WI.3	WI.4	WII.1	WIII.1	WIII.2	Channel
Incertae sedis		✔	✔				✔		
Flora	Plant ind.					✔	✔		
	Fossil wood		✔✔			✔			
	Charophyta ind.		✔						
Invertebrata	Mollusca ind.	✔✔✔	✔✔✔		✔✔	✔✔	✔✔✔		
	Helicidae	✔✔	✔✔✔				✔✔✔		✔✔
	Limacelle						✔		✔✔
Fishes	Cyprinidae	✔✔	✔✔✔				✔✔✔		
	Fish's vertebra	✔	✔				✔		
Reptilia	Testudinata ind.								✔✔
	Squamata ind. and *Ophisaurus*	✔✔✔	✔✔✔				✔✔✔		✔✔✔
	Crocodilia ind.						✔		✔✔
Mammalia	Bones ind.	✔✔✔	✔✔✔	✔	✔✔✔	✔✔	✔✔✔	✔	✔✔✔
	Vertebra ind.		✔✔						✔
	Rodentia ind.	✔	✔				✔		✔
	Eomyidae ind.						✔		✔
	Gliridae ind.						✔		
	Peridyromys murinus						✔		
	Cricetidae ind.	✔	✔				✔		✔
	Eucricetodon aff. *gerandianus*	✔	✔						✔
	Lagomorpha ind.	✔✔✔	✔✔✔				✔✔		✔✔✔
	Prolagus praevasconiensis	✔✔	✔✔✔				✔		✔✔✔
	Artiodactyla ind.		✔						✔✔✔
	Andegameryx cf. *laugnacensis*		✔						✔✔✔
	Friburgomeryx n.g. *wallenriedensis* n.sp.		✔						✔✔✔

Micromammals — Numerous bone and teeth fragments:
Lagomorphs — *Prolagus praevasconiensis* RINGEADE
Rodents — *Eucricetodon* aff. *gerandianus* GERVAIS
Peridyromys murinus POMEL

3.2 Cervoid Ruminantia

Found by Becker (1996), these fossils have been studied by G. Rössner and are first published here.

All measurements are given in mm. The terminology of tooth crown elements and tooth measurement procedure mainly follows Rössner (1995).

Abbreviations:

APD = anterior-posterior diameter
aw = anterior width
l = lenght
w = width
pw = posterior width
TD = transversal diameter

Suborder Ruminantia SCOPOLI 1777
Ruminantia indet. (Fig. 6)
Wr. 11: right lower incisor weakly worn.

Description:
In buccal view the crown is posteriorly slightly inclined upwards and has a simple outline. The lack of enough complete fossil material and of studies on ruminant incisors make a more precise determination impossible. l = 2,7; w = 2,8.

Infraorder Pecora LINNAEUS 1758
Some specimens, namely part of a strongly worn lower tooth row, an incisor and several incomplete remains of manus and pes, cannot be determined exactly. The incisor and the distal parts of phalanges and metapodials show potentially diagnostic features, but because of the lack of identified and described material for comparison an exact determination is not possible. Therefore we decided to set up several "Pecora indet." determinations to indicate separable taxa among the fossils.

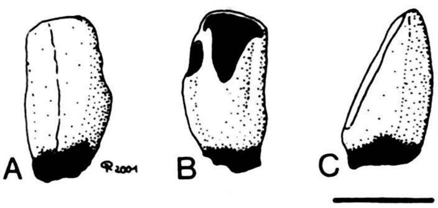

Fig. 6. Ruminantia indet. right lower incisor, Wr. 11. A, labial; B, lingual; C, posterior. Scale bar represents 4 mm.

Pecora indet. 1
Wr. 6: part of right mandibula with m1 to m3 strongly worn.

Description:
The remains of a right mandibula includes the three molars, but they are badly worn, so that only the lowest part of the teeth is preserved. An enamel band representing the remains of a central fossette is only present in the posterior part of m3. Moreover much of the exterior enamel casing of the teeth has been lost. In general the shape and a little of the morphology of brachyodont ruminant teeth is discernible. The m3 is the only tooth, which shows any detail: in the posterior part a low conical entoconid, a strong and low ectostylid and an anterior cingulid. Because of the strongly worn and badly preserved condition as well as the age-related compression of the tooth row, the following tooth measurements should be regarded as approximate: m1 l = 8,4; aw = 7,6; pw = 8,9. m2 l = 12,1; aw = 8,9; pw = 8,7. m3 l = –; aw = 8,7; pw = 9,0.

Pecora indet. 2 (Fig. 7)
Wr. 8: distal part of a phalange I.

Description:
The interdigital and exterior parts of the articular surface show nearly the same size and shape, except for a little more dorsal extension of the interdigital one. The median groove runs slightly from exterior to interdigital. The outline of the pulley is well rounded. The exterior ligament groove is rounded, the interdigital one elongated. The morphology differs clearly from tragulids in which the pulley is relatively shorter and wider and has a different shape of the articular surface. Within higher pecoran groups Cervidae show the most similar morphotype (see Köhler 1993). TD = 8,7; APD = 7,8.

Pecora indet. 3 (Fig. 8)
Wr. 9: distal part of a phalange I.

Interdigital and exterior articular surfaces of the pulley are closely similar in morphology and size and are visible in dorsal aspect. The outline shows a low, weakly compressed pulley.

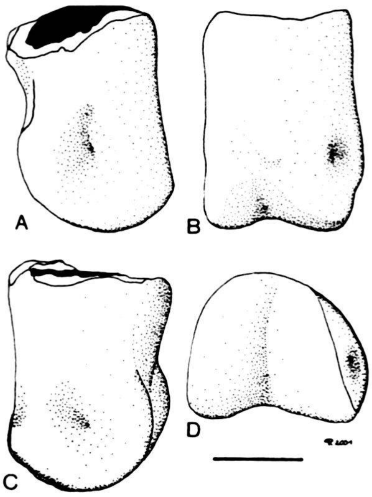

Fig. 7. Pecora indet. 2 distal part of phalange I, Wr. 8. A, external; B, dorsal; C, interdigital; D, distal. Black areas indicate sediment. Scale bar represents 5 mm.

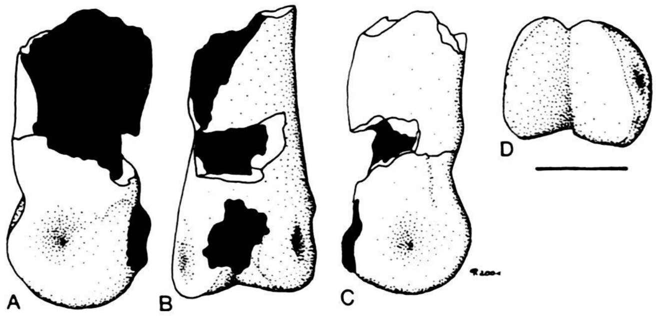

Fig. 8. Pecora indet. 3 distal part of phalange I, Wr. 9. A, interdigital; B, dorsal; C, external; D, distal. Black areas indicate sediment. Scale bar represents 5 mm.

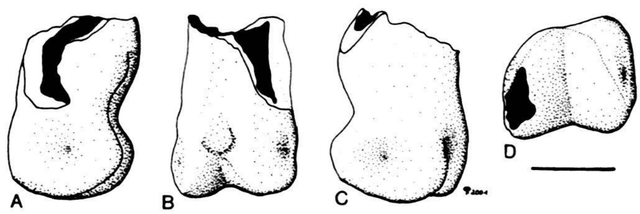

Fig. 9. Pecora indet. 4 distal part of phalange I, Wr. 10. A, interdigital; B, dorsal; C, external; D, distal. Black areas indicate sediment and corrosion. Scale bar represents 5 mm.

Both ligament grooves are rounded and relatively large in diameter. The median groove runs nearly tangentially. As in the case of Pecora indet. 2 Tragulidae can be excluded and Cervidae are the most similar. TD = 6,6; APD = 7,3.

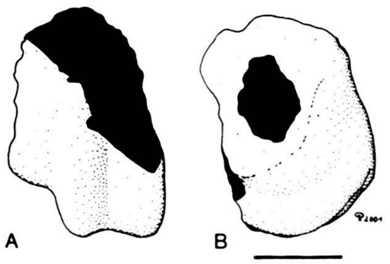

Fig. 10. Pecora indet. 5 distal pulley of right metapodium, Wr. 12. A, dorsal; B, external. Black areas indicate sediment. Scale bar represents 5 mm.

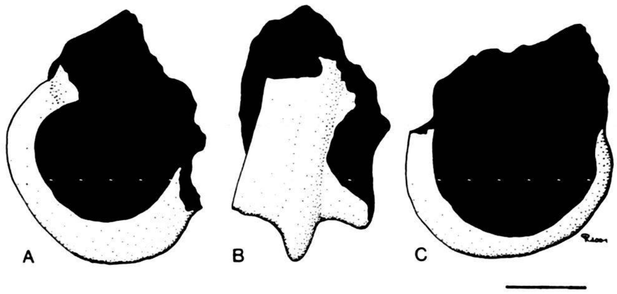

Fig. 11. Pecora indet. 7 distal pulley of left metapodium III or IV, Wr. 7. A, external; B, dorsal; C, interdigital. Black areas indicate sediment and corrosion. Scale bar represents 5 mm.

Pecora indet. 4 (Fig. 9)
Wr. 10: distal part of a phalange I.

Description:
In the articular surfaces, the shape of the outline and the ligament grooves, this resemble Pecora indet. 3 specimen Wr. 9. The median groove is oriented as in Pecora indet. 2 specimen Wr. 8. A clear tendon protuberance dorsomedially and a concave volar curvature proximally of the pulley differ from both. The morphology most resembles the Cervidae. TD = 7,1; APD = 7,3.

Pecora indet. 5 (Fig. 10)
Wr. 12: distal pulley of a right metapodium.

Description:
The metapodial keel is complete. It is relatively wide and flattened. Dorsally it runs slightly diagonally from proximoexterior to distointerdigital. The diameter of the outside part of the pulley is much smaller than the median one. The size may indicate a metapodium III or IV.

A tragulid clearly can be excluded because of the complete keel instead of an incomplete one. Furthermore higher pecorans show no diagonal running distal keels which converge. But exactly that feature is shown by a posterior cannonbone of "*Amphitragulus*" *lemanensis* pictured and determined by Viret (1929: Pl. XXIV, fig. 3, 7), which corresponds also in size. Because of the lack of complete skeletons in primitive pecorans of the Lower Miocene almost all identifications of postcranials remain questionable. Therefore we decided to leave this metapodial as Pecora indet. TD = 9,2, APD = 8,7.

Pecora indet. 6 (Fig. 11)
Wr. 7: distal pulley of a left metapodium III or IV.

Description:
A part of the symphysis directly above the interdigital side of the pulley indicates a metapodium III or IV. The keel is complete and slender, dorsally low and blunt and distally as well as palmarly/plantarly high and sharp. Hence in sectional view it is dorsodistally flattened. The diameter of the exterior part of the pulley is only a little smaller than the medial. The morphology excludes a tragulid and any higher pecoran. For primitive pecorans this type of morphology is not yet described or figured. TD = 8,8; APD = 12,5.

Superfamily Cervoidea GOLDFUSS 1820
Family Moschidae GRAY 1821
Friburgomeryx n. g.
wallenriedensis n. sp.
Plate 1/1–4
Holotype: part of right maxilla with M1 to M3 moderately to strongly worn, collection of the Naturhistorisches Museum Basel, Switzerland, Wr. 2.

Derivatio nominis: The genus is named after the city of Fribourg and the locality provides the name for the species.

Locus typicus : Wallenried section, Switzerland, USM, Early Miocene

Diagnosis: Small to medium sized ruminant with selenodontbrachyodont dentition with more conical than crescent-shaped cusps. The upper molars possess a neocrista and strong parastyle, paracone, and mesostyle as well as a strong, connected cingulum. The lower molars show a strong *Palaeomeryx*-fold and a rounded lingual wall of the metaconid-complex. The lower premolars include p1. They are wide and bulky and poorly molarized. On p3 a short postprotocristid and postprotoconulidcristid are developed. p2 has a short postprotocristid and entocristid.

Differential diagnosis: *Friburgomeryx* n. g. *wallenriedensis* n. sp. differs from
- *Pomelomeryx gracilis* by larger size, more conical than crescentic-shaped cusps, less molarized lower premolars, and strong connected cingulum in upper molars.
- *Pomelomeryx boulangeri* by larger size, presence of p1, less molarized lower premolars, and strong connected cingulum in upper molars.

- *Dremotherium* by lower crown height, more conical than crescentic-shaped cusps, less molarized lower premolars, presence of p1, and strong connected cingulum in upper molars.
- *Hydropotopsis* by lower crown height, more conical than crescentic-shaped cusps, less molarized lower premolars, and strong connected cingulum in upper molars.
- *Bedenomeryx* by smaller size than in *B. truyolsi* and strong connected cingulum in upper molars.
- *Amphitragulus* by strong connected cingulum in upper molars.
- *Oriomeryx* by smaller size than in *O. willii*, and strong connected cingulum in upper molars.

Tab. 3. Measurements of *Friburgomeryx* n.g. *wallenriedensis* n.sp. from Wallenried taken in mm (following Rössner 1995).

		l	aw	pw
1	M1	11.1	12.6	11.7
	M2	12.9		
	M3	12.0	13.7	8.4
2	M1	11.1		12.2
	M2	13,8	15,3	14,2
	M3	12.5	14.9	12.3
4	p1	7.8	3.2	
	p2	9.8	4.9	
	p3	10.3	5.8	
5	m1/2/3			8.7

Further material:

Wr. 1: part of right maxilla with M1 to M3, weakly to strongly worn.
Wr. 4: part of right mandibula with p1 to p3, moderatley to strongly worn.
Wr. 5: left m1 or 2 or 3, weakly worn but partially preserved.

Description:

The tooth crowns, brachyodont and selenodont though they are, show somewhat conical rather than fully crescentic cusps.

In the upper molars parastyle, paracone and mesostyle are strong elements. A neocrista is developed. Specimen Wr. 2 is surrounded anteriorly, lingually and posteriorly by a strong cingulum with an integrated entostyle. In specimen Wr. 1 this cingulum is strongly worn and only preserved in parts. The same specimen includes an M3 with a poorly developed metaconule, what results in a triangular shape of the whole tooth crown. Poorly developed metaconules in M3s are part of ruminant species variability (Rössner 1995: Abb. 7), and are irrelevant for making identifications.

The lower premolars are wide and bulky and a p1 is included in the row. Their tooth crown pattern is simple with only the centrally positioned elements of protoconid, praeprotocristid, protoconulid and *Palaeomeryx*-fold (especially for that see Rössner 1995: Abb. 124). The crown height is very low. The molarisation (elongated transversal crests with metaconid in p3 and p4) of p2 and p3 is poor with a short postprotocristid and without a metaconid in p3. The p2 has a short entocristid and no postprotoconulidcristid. The latter element of p3 is short, as deduced from the small inlet of the lingual enamel layer.

The lower molar possesses a strong *Palaeomeryx*-fold, a poor metastylid and a conical metaconid forming a rounded lingual wall of the metaconid-complex. Its incomplete condition with only the anterior part makes it impossible to determine its exact position in the row.

For measurements see table 3.

Discussion:

The brachyodont selenodont tooth morphology with more conical cusps and a poor molarisation of the lower premolars clearly indicate a primitive Oligo-Miocene representative of moschoid ruminants.

Today moschoid ruminants are generally seen as the stem-group of Cervoidea with elongated upper canines but without cranial appendages (Gentry & Hooker 1988, Janis & Scott 1987, Ginsburg et al. 1994). The number of species included in that taxon is controversial and therefore no agreement exists on its systematic position whether as family Moschidae of the superfamily Cervoidea or as superfamily Moschoidea. In Eurasia moschoid ruminants were abundant and widely distributed faunal elements from the Late Oligocene (Chattian, MP27/28) to the Early Miocene (Agenian and Early Orleanian, MN1-MN3). During the Early Miocene those primitive forms went extinct. The more evolved genus *Micromeryx* was the only survivor of moschoid ruminants in Europe from the Middle Miocene (Late Orleanian and Astaracian, MN5 – MN7+8) to the Late Miocene (Vallesian and Early Turolian, MN9 – MN11). Nowadays worldwide only the Asiatic genera *Moschus* (musk deer) and perhaps *Hydropotes* (Chinese water deer) represent this group of ruminants (Gentry et al. 1999: 231).

Primitive Moschidae of the European Oligo-Miocene comprise the currently valid genera *Dremotherium*, *Bedenomeryx*, *Amphitragulus*, *Pomelomeryx* and *Hydropotopsis* (Blondel 1997, Gentry et al. 1999: 231–233). The genus *Oriomeryx*, formerly positioned within the Moschidae, is now included in the Palaeomerycidae (Ginsburg et al. 2000: 622) but shows a similar tooth morphology. Therefore all these taxa are possible suppliers of the moschid tooth material from Wallenried. The genus *Pomelomeryx* can be excluded immediately, because its body size is too small and besides the premolars are more molarized and the upper molars show no strong cingulum. *Dremotherium* and *Hydropotopsis* possess more crescentic cusps and a larger crown height as well as more molarized lower premolars. In contrast *Bedenomeryx validus* (Dehm 1935), *B. truyolsi* (Ginsburg, Morales & Soria 1994), *Amphi-*

Tab. 4. Comparison of measurements of *Friburgomeryx* n.g. *wallenriedensis* n.sp, *Amphitragulus elegans*, *Oriomeryx major*, *Bedenomeryx validus*, and *Bedenomeryx truyolsi*. All measurements of the following specimens were taken by the author in mm according to Rössner (1995): *A. elegans:* UCBL FSL 213880 (original of Viret 1929 Pl. XXII, Fig. 4), UCBL FSL 213879 (original of Viret 1929 Pl. XXII, Fig. 3), UCBL FSL 213878 (original of Viret 1929 Pl. XXII, Fig. 2), NMB M. A. 7925, NMB M. A. 7926; *O. major:* MNHN moulage 568 (original of Viret 1929 Pl. XXIII, Fig. 10), UCBL FSL 213 886 (syntype of Viret 1929 Pl. XXIII, Fig. 9), MHNL St.-G. 677 (original of Viret 1929 Pl. XXIII, Fig. 10), MHNL St.-G. 677 (original of Viret 1929 Pl. XXIII Fig. 8), MNHN moulage 567 (original of Viret 1929 Pl. XXIII Fig. 9).
Measurements of *B. validus* from Jehenne (1991: Table 1-3), measurements of *B. truyolsi* from Ginsburg et al. (1994: Table 5 + 6).
MHNL = Musée Guimet d'Histoire Naturelle de Lyon; MNHN = Musée d'Histoire Naturelle Paris; NMB = Naturhistorisches Museum Basel, UCBL = Centre de Paléontologie stratigraphique et Paléoecologie, Université Claude Bernard Lyon.

		Amphitragulus elegans			*Oriomeryx major*			*Bedenomeryx validus*			*Bedenomeryx truyolsi*		
		Montaigu			Montaigu/St.-Gérand								
		l	aw	pw	l	aw	pw	l	aw	pw	l	aw	pw
	N	3	3	3	2	2	2	2	2		6	6	
m3	Max	18.5	8.7	8.5	20.9	10.7	10.4	19.1	10.5		21.0	10.0	
	Min	15.7	8.1	7.6	20.7	8.8	10.2	17.8	9.8		17.9	8.8	
	N	3	3	3	2	2	2	3	3		5	5	
m2	Max	12.7	9.1	9.5	14.5	10.8	10.5	12.1	10.4		13.0	10.3	
	Min	11.3	8.3	8.5	14.0	10.0	10.1	11.3	9.6		12.0	9.1	
	N	3	3	3	4	4	4	3	3		5	5	
m1	Max	11.0	7.8	9.0	13.4	10.0	10.3	11.0	8.9		12.8	9.3	
	Min	10.9	7.0	7.4	11.8	8.3	9.1	10.4	8.1		11.2	8.0	
	N	3	3		2	2		3	3		5	5	
p4	Max	11.0	6.8		11.2	6.7		11.7	7.6		12.4	8.6	
	Min	9.5	5.9		11.0	6.7		11.5	7.1		10.7	6.5	
	N	3	3		2	2		3	3		4	4	
p3	Max	10.0	5.2		10.5	5.7		12.2	7.5		11.2	6.6	
	Min	8.7	4.9		10.2	5.6		11.5	6.1		10.3	5.3	
	N	2	2					2	2		2	2	
p2	Max	8.6	4.0					10.9	5.5		9.5	5.7	
	Min	8.3	3.8					10.9	5.3		9.5	4.8	
	N	1	1								1	1	
p1	Max	5.0	2.5								5.4	3.2	
	Min	5.0	2.5								5.4	3.2	
	N	2	2	2				2	2		1	1	
M3	Max	11.2	12.9	11.7				11.8	13.7		15.5	15.5	
	Min	10.3	12.7	11.7				11.7	13.6		15.5	15.5	
	N	2	2	2				2	2				
M2	Max	11.8	13.5	13.0				12.4	15.0				
	Min	11.2	13.3	11.5				12.2	14.9				
	N	2	2	2	1	1	1	2	2		1	1	
M1	Max	10.5	11.6	11.6	12.0	13.1	13.2	10.9	12.4		13.6	13.9	
	Min	10.3	11.5	11.0	12.0	13.1	13.2	10.8	12.2		13.6	13.9	

tragulus elegans (Pomel 1853) and *Oriomeryx major* (Viret 1929) all show the more conical cusps and lower tooth crown height as well as less molarization of the lower premolars, which agree with the morphology of the Wallenried Moschidae. The existence of a p1 in the Wallenried Moschidae further correlates with the latter genera, the tooth being consistent in *A. elegans* (Viret 1929: Pl. XXII, Fig. 4), *O. major* (Viret 1929: Pl. XXIII, Fig. 9), and *B. truyolsi* (Ginsburg et al. 1994: Pl. 2, Fig. 2, 3) and occasional in *B. validus* (Jehenne 1988: 1995). The three species differ only slightly in size, with *O. major* and *B. validus* being of nearly similar size and most closely resembling the measurements of the Wallenried Moschidae (see table 4).

Amphitragulus major Viret 1929 was assigned by Ginsburg (1985) to be the type species of *Oriomeryx*, which can be differentiated from *Amphitragulus* only by a more lingually rounded P4 with a clear cingulum. A skull of *Oriomeryx* is not known.

The genus *Bedenomeryx* was established by Jehenne (1988) with the species *B. milloquensis* and *B. paulhiacensis*. The differences between *Oriomeryx* and *Bedenomeryx* are the more triangular shaped P2 and P3 the latter. Both species of

Tab. 5. Comparison of measurements of m1 of *Andegameryx*. All measurements of the following specimens were taken by the author in mm according to Rössner (1995): *A. andegaviensis* Pontigné, MNHN Fs 280 type specimen original to Ginsburg (1971: Fig. 1), MNHN Fs 362; *A. laugnacensis* Laugnac, MHNT no number, UPM no numbers, including type specimen original to Ginsburg & Morales (1989: Pl. 3 Fig. 1+2); *A. andegaviensis* Cetina de Aragon; MNCN 35205 original to Ginsburg et al. (1994: Pl. 1 Fig. 3), MNCN 35208.
MHNT = Muséum d'Histoire Naturelle Toulouse ; MNCN = Museo Nacional de Ciencias Naturales Madrid; UPM = Département des Sciences de la Terre, Université de Provence, Marseille.

	A. cf. *laugncensis* Wallenried			*A. andegaviensis* Pontigné			*A. andegaviensis* Cetina de Aragon			*A. laugnacensis* Laugnac			*A. serum* Wintershof-West		
	l	aw	pw	l	aw	pw	l	aw	pw	l	aw	pw	l	aw	pw
N	1	1	1	1	1	1	2	2	2	3	3	3	5	3	4
Max	12.0	7.5	7.9	9.4	6.2	6.7	10.8	8.3	8.5	12.6	8.0	8.3	9.6	5.5	6.8
Min	12.0	7.5	7.9	9.4	6.2	6.7	10.3	6.8	7.0	12.2	7.2	7.9	8.3	5.2	6.1

Bedenomeryx were synonymized by Ginsburg et al. 1994 with *Amphitragulus validus* from Dehm (1935), and so the species is named, according to the rules of priority, *B. validus* (Dehm 1935). A very well preserved skull of *B. validus* from La Milloque (MP29) shows typical characters, which separate this genus clearly from *Amphitragulus* and *Dremotherium*, but no comparison is possible with *Oriomeryx* for which no skull is available. Therefore the only known diagnostic features between *B.* and *O.* are developed in the upper premolars.

Unfortunately upper premolars are not preserved from Wallenried, what might have meant an unresolved identity for the documented Moschidae there. However, in the studied material an eyecatching character is the strong cingulum around the upper molars of specimen Wr.1 and specimen Wr. 2 which is known neither in *Bedenomeryx* nor *Oriomeryx*. It gives the specimens from Wallenried a special character, so that establishing a new genus is appropriate.

The lower cheekteeth of *Oriomeryx*, *Bedenomeryx*, and *Amphitragulus* are morphologically not distinguishable. Therefore the lower cheekteeth from Wallenried associated with *Friburgomeryx* n. g. *wallenriedensis* n. sp. might belong to one of those genera, but in the faunal context the presented determination seems most probable.

A strong connected cingulum of the upper molars is known in the primitive ruminant groups Tragulina and "Gelocidae" (Janis & Scott 1987: table 4). Further the enigmatic ruminant *Orygotherium* from the Middle Miocene of Eurasia (Rössner & Mörs, in press), whose phylogenetic relationships are unclear, developed a distinctive morphology of its upper molars with a very strong cingulum. Because no evolutionary approaches to this unique morphology are known and because *Orygotherium* is only known from lignitic sediments, ist characteristics are interpreted as a rapidly-evolved adaptation to a special food source.

Whether the Wallenried Moschidae represent a less evolved phylogenetic lineage of primitive moschoid ruminants, in which an additional plesiomorphic character of its gelocid forerunners lingered or whether they are higher evolved members of the family Moschidae, which adapted to more specialised life habits, perhaps as an ancestor of *Orygotherium*, cannot be answered at this point of investigation. Additional material from further localities is necessary to analyse the possible phylogenetic position of that taxon.

Family Andegamerycidae GINSBURG & MORALES 1989
Genus *Andegameryx* GINSBURG 1971
Andegameryx cf. *laugnacensis* GINSBURG & MORALES 1989
Plate 1/5
Wr. 3: part of a left mandibula with m1 moderately worn.

Description:

The general tooth morphology of the lower molar is brachyodont-selenodont with a low conical shaped metaconid and entoconid. The lingual wall lacks stylids. The *Palaeomeryx*-fold is poor. On the external wall a strong anterior cingulid, a poor posterior cingulid and a medium ectostylid are developed. The tooth can be firmly determined as an m1, because of the typical rounded shape of the anterior contact facet for a premolar and the wider anterior part of the tooth compared to the posterior (Rössner 1995: Tab. 47).

Discussion:

The systematic position of *A.* within the Pecora has still to be discussed, which is beyond the scope of this paper. But, because of its uncertain origin, a summary of the research history is given: in 1971 Ginsburg established the new European ruminant genus *Andegameryx* with the type species *A. andegaviensis* (type specimen is a left mandibula with p4 to m3, MNHN Fs 280) from the locality Pontigné (Maine-et-Loire) in France. Its characters include very poor or absent lingual stylids and a poor or absent *Palaeomeryx*-fold in the lower molars. He judged *A.* andegaviensis to be systematically positioned within Hypertragulidae and assigned *Bachitherium serum* Obergfell 1957 with it. Ginsburg & Morales (1989) established a new species, *A. laugnacensis*, and the family Andegamerycidae, which they set close to Bovidae, because of a metatarsal with a dorso-distally open gully attributed to *A.*. In 1994 Ginsburg et

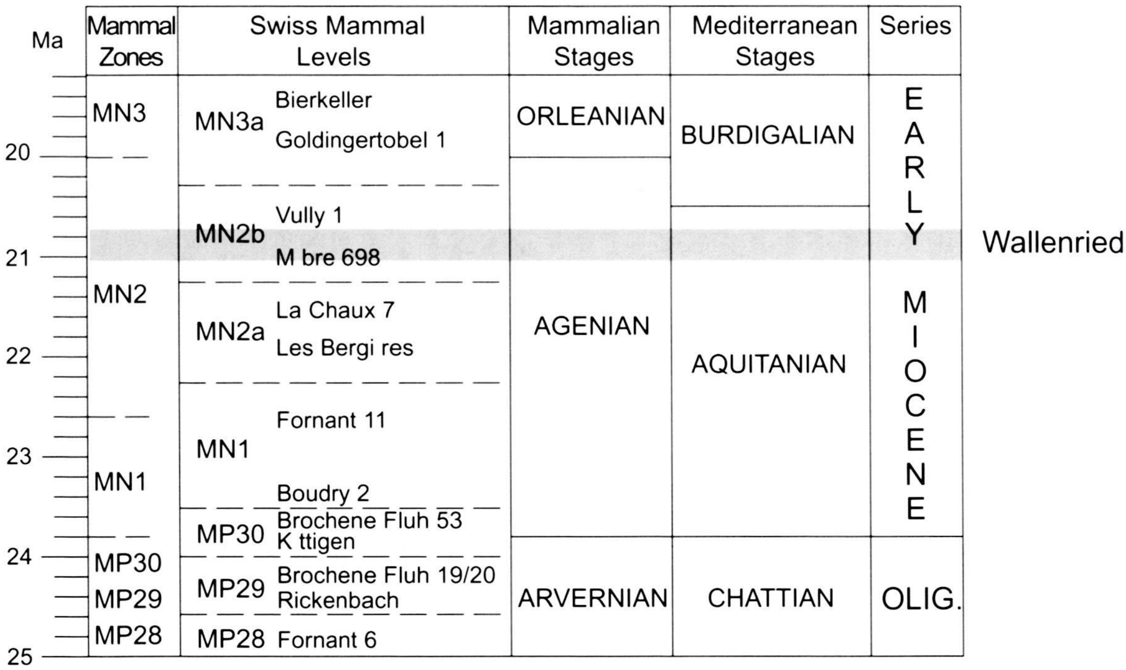

Fig. 12. European Early Miocene mammal biostratigraphy with correlation of Wallenried.
Column 1: "Mammal Zones" according to Steininger (1999)
Column 2: "Swiss mammal levels" (Engesser & Mödden 1997); correlation according to Kempf et al. (1997)
Column 3: "ELMMZ" = European Land Mammal Mega-Zones, according to Steininger (1999)
Column 4 & 5: "Mediterranean Stages" and "Series" according to Berggren et al. (1995), Hardenbol et al. (1998), Steininger et al. (1997)

al. rejected the Andegamerycidae and substituted it by a pecoran family Incertae sedis because of open and closed metatarsal gullies within the species. Gentry et al. (1999: 240f) placed it as possible Bovoidea and finally Ginsburg (1999:113) reinstated used the family Andegamerycidae.

The m1 of Wallenried undoubtedly displays the main characters of *A.* with absent lingual stylids and a poor *Palaeomeryx*-fold. By size it is most like *A. laugnacensis* from Laugnac (table 5). But, because neither the species variability at the localities being compared, nor the species variability at Wallenried is known, a definite determination is not yet possible. Thus, we decided to place it in *A.* cf. *laugnacensis*.

4. Biostratigraphy

The new and uncertain systematic status of the ruminants from Wallenried allow us only an approximate biostratigraphical frame. The biostratigraphical distribution of primitive Moschidae, which include *Friburgomeryx* n.g. *wallenriedensis* n.sp., occurs from the Late Oligocene (Chattian, MP27/28) to the Lower Miocene (Agenian and early Orleanian, MN1-MN3) in Europe. *Andegameryx* is known from the middle part of the Lower Miocene (Late Agenian and Early Orleanian, MN2 – MN3). *A. laugnacensis* is exclusively known from the latest Agenian (MN2b). Therefore, the associated occurrence of *Friburgomeryx* n.g. *wallenriedensis* n.sp. and *A.* cf. *laugnacensis* might indicate an age of MN2 or MN3.

This approximate biostratigraphy of ruminants is corroborated by the micromammals, especially by *Prolagus praevasconiensis* and *Eucricetodon* aff.*gerandianus*.

In fact *Eucricetodon* aff. *gerandianus* agrees with *Eucricetodon gerandianus* of the Swiss Mammal Level La Chaux 7, but has more evolved tooth shape. It is closer to *Eucricetodon gerandianus* of Mèbre 698, but still slightly more evolved. In contrast, the *Eucricetodon* of Vully 1 is manifestly bigger and more evolved. The species *Prolagus praevasconiensis*, quite absent in La Chaux, is identical to the one of Mèbre 698. For the final biostratigraphical result, we may place Wallenried in the top of the Swiss level La Chaux, between Mèbre 698 and Vully 1, certainly closer to Mèbre 698 (fig. 12) (Kälin 1997, Engesser & Möden 1997), what corresponds biochronologically to the European Mammal Neogene Zone MN 2b.

5. Taphonomy, paleoecology, paleobiology and paleoclimate

Bones are often deposited on point bars during waning flood stages. Prior to the onset of chemical decomposition, bones may have travelled many kilometers leading to characteristic sorting with abrasion and polish (Behrensmeyer et al 1992). The bone bed of Wallenried, despite a good state of general conservation, is a typical taphocenose with sorting of Artiodactyla jaw fragments.

The whole fauna of Wallenried shows a well balanced biological spectrum, with a good distribution of the freshwater species (Cyprinidae, charophytes), terrestrial species (mammals, *Ophisaurus*, gastropods) and partially aquatic species (crocodiles and certainly turtles).

Concerning the two large herbivore species, *A.* cf. *laugnacensis* and *F.* n. g. *wallenriedensis* n. sp., they should normally show a particularly good sensitivity to climatic variations (mobility is function of the primitive biomass availability) (Demarq et al. 1983). Regrettably no detailed palaeobiological or palaeoecological analysis of any of the hitherto known Lower Miocene ruminant species has been done and it is also beyond the scope of this study. In contrast to the extant representatives of the suborder Ruminantia at that time presumably only tropical or subtropical forest biomes were inhabited. Such biomes were more widely distributed than in later times, grassland biomes had not been and the general habitus of primitive ruminant groups, small to medium sized, did not vary too much. Several ecomorphological investigations on extant and fossil ruminants by different authors give sufficient background to make deductions. On that basis we can provide palaeobiological interpretations and palaeoecological conclusions.

The value of tooth morphology for indicating diet in mammalian herbivores has been the subject of various studies (e.g. Janis 1990a, 1995). Among the emerging Oligocene-Miocene ruminants the brachyodont-selenodont cheek teeth and the trend towards molarisation of the premolars must have aided the mastication of browse material in an unspecialised diet such as dicotyledonous leaves, shrubs, herbs, fruit and buds. This would correspond to the conditions prevailing at Wallenried. It is known that in extant browsers of wooded (= non-open) habitats, grasses can decline to less than 10% of the food consumed. Moreover ruminant browsers with their foregut fermentation are well-equipped to deal with food sources of restricted seasonal availability (Janis 1989).

Body mass can be predicted by whether proximal limb bones of arm and leg (Köhler 1993, Scott 1983, 1987, 1990) or cheek teeth (Janis 1990b, Legendre 1986), whilst Fortelius (1990) described postcrania the better reflectors. Since there are no femora or humeri from Wallenried only incomplete remains of teeth can be used to estimate body mass. With the methods described in Janis (1990b) the body weight of *Friburgomeryx* n.g. *wallenriedensis* n.sp. can be determined as approximately 20 to 25kg, comparable to extant *Muntiacus muntjak vaginalis* (Indian muntjac, Janis 1990b:260). For *Andegameryx* cf. *andegaviensis* the body weight is around 16kg, comparable to extant male *Muntiacus reevesi* (Chinese muntjac, Janis 1990b:260). The methods of Legendre (1986) give a weight estimate of about 30kg for the two species. Correlations between body weight and habitat are not known in general in extant Ruminantia, although these kinds of moderate body-mass are generally characteristic of quite closed habitats.

Köhler (1993) gave a detailed analysis of limb bone characters and their functional meaning in locomotion. Although the metapodial and digital remains from Wallenried are scarce they show some diagnostic morphological features. All phalanges I (specimens Wr 8, 9, 10) show a weak dorsal extension of the distal articular surface and relatively small lateral and interdigital ligament grooves. The parts of metapodial pulleys (specimens Wr. 6, 7) carry dorsally flattened and wide metapodial keels. The dorsal extension of the distal articular surface of phalange I indicates a straight-line-articulation of all three phalanges within a digit (Köhler 1993:21). The relative small size of its ligament grooves are typical for a flexor acentuated straight-line position of digits (Köhler 1993:23). Dorsally flattened metapodial keels without sharp edges allow splaying of the digits (Köhler 1993:22). All described characters and their functional morphology are typical for Köhler's (1993:21ff) ruminant foot type A found in humid wooded habitats with a moist and soft ground. Those ground conditions represent discontinuous and quickly changing requirements to locomotion. These are countered by a relatively moveable bauplan of manus and pes, allowing the digits to be splayed, and a comparatively large area of digit/ground-contact, given by a straight-line position of all three phalanges.

Finally the palaeobiological interpretations of the ruminant fauna from Wallenried confirm, what was said at the beginning about tropical to subtropical forest habitats, but do not provide more detailed information.

Concerning the small mammals, the Cricetidae and especially the Lagomorpha show adaptation for a relatively dry and hot climate, whereas the Gliridae confirm the presence of a vegetation cover (Berger 1985). However we should carefully notice the taphonomy of these small mammals, which is certainly linked with avian raptor pellets. Finally, from the presence of large reptilians (crocodiles and turtles) we can deduce a high and constant temperature (never below 15° C) all over the year.

The sedimentological and paleontological interpretations seem to indicate a subtropical climate with the onset of seasonal humidity. The floodplain must have been a complex of environments from open to forested plains, maybe a woodland, of a vegetation type ecologically and physiognomically intermediate between forest and grassland savannah, falling under the umbrella term "savannah" (Reed 1998).

6. Discussion: Wallenried in the pattern of climatic and ungulate evolution

In such a context of alluvial deposits, it is very important to place the outcrop in a regional and global setting and first of all to consider the taphonomy, with the aim of not interpreting biased paleoenvironments, paleoecology and paleoclimates.

In Wallenried, though the outcrop seems to present a subtropical environment with the onset of seasonality and the presence of primitive ruminants, the global context of climate and environment of early Miocene is considered as a short warming period (Janis 1989, Behrensmeyer et al 1992). This fact is confirmed by other Molasse grise de Lausanne localities, where we recover palm trees after their disappearance in the late Oligocene (Berger 1990). Thus, despite the overall cooling climate of the Miocene as a whole, the period of Wallenried represents a kind of early Miocene break in the relatively continuous evolution of cenozoic environments, climates and faunas in Eurasia. Actually the radiation of foregut Artiodactyla and the trend towards seasonality are momentarily stopped, as the trend towards a cooler and drier climate (Janis 1989). The development of lowstanding biomass vegetation types, including savannah, grassland and steppe is delayed in comparison with the lower latitudes and will occur only in mid-late Pliocene.

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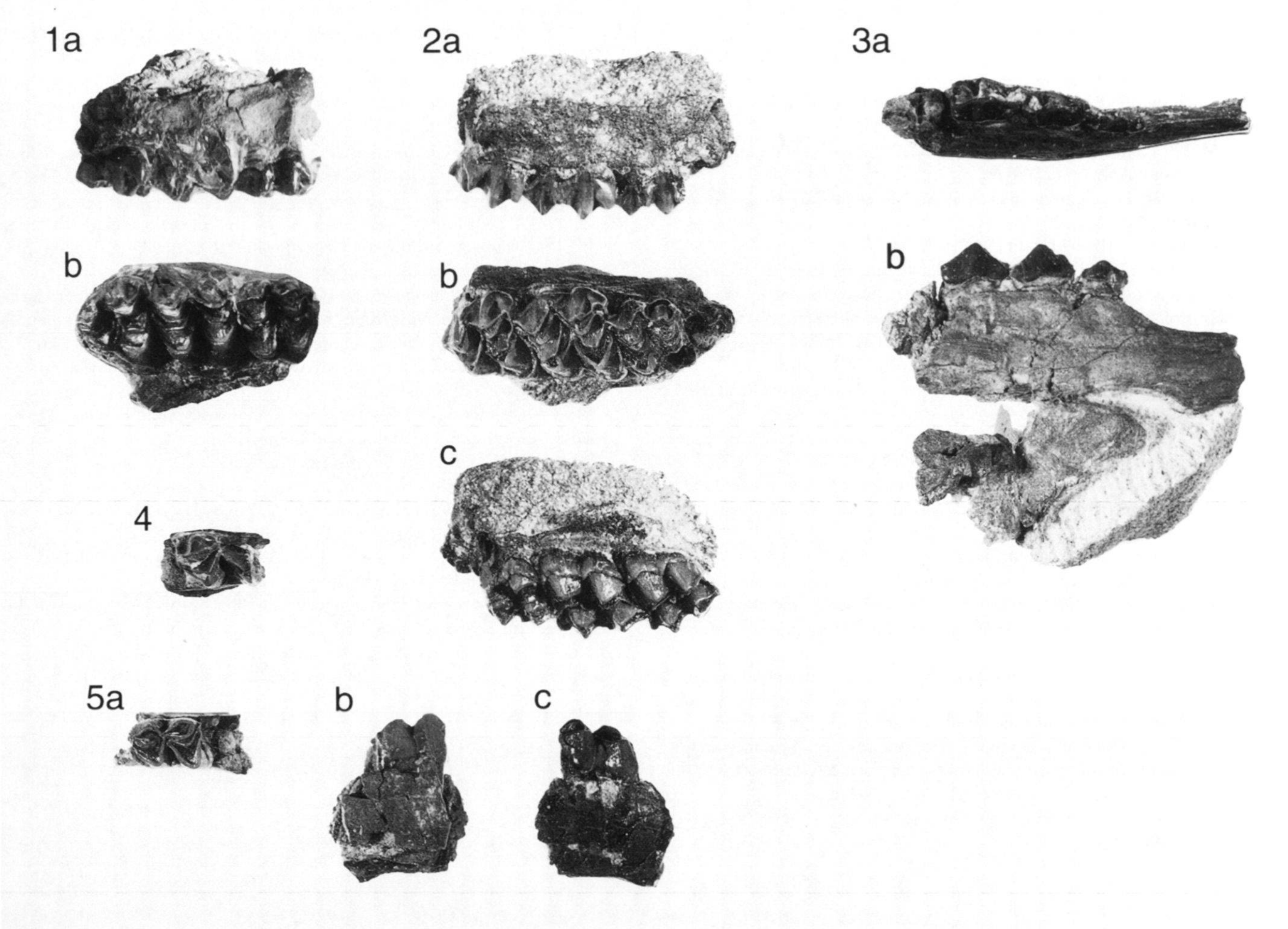

Plate 1

Friburgomeryx n.g. *wallenriedensis* n.sp
1: right maxilla with M1 to M3, Wr.1. a) labial; b) occlusal
2: holotype, right maxilla with M1 to M3, Wr.2. a) labial; b) occlusal; c) lingual.
3: left mandibula with p1 to p3, Wr.4. a) occlusal; b) labial;
4: left m1/2/3, Wr.5. Occlusal view.

Andegameryx cf. *laugnacensis*
5: left mandibula with m1, Wr.3. a) occlusal; b) lingual; c) labial.