Description of *Fahlbuschia* (Cricetidae) from various fissure fillings near La Grive-St. Alban (Isère, France)

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Fahlbuschia larteti (Schaub, 1925) is revised and described on the basis of new material from the fissure M at La Grive-St. Alban. A *Fahlbuschia* aff. *crusafonti* Agustí, 1978 is described from the La Grive fissure L3.

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Introduction

La Grive and St. Alban are two little villages, some 35 km east of Lyon, in the department Isère (France). In the surroundings of La Grive-St. Alban exists a number of outcrops of Bajocian limestone in topographically and geologically high blocks, that locally are called 'islands', like L'îsle d'Abeau, L'îsle Crémieu, etc. During most of the Cretaceous the area was submerged, and afterwards, during Late Cretaceous and Paleogene, karstification of the elevated blocks took place.

The rising sea level during the Neogene made an end to the active karst phase, and the existing fissures were filled in. Jourdan (1845) was the first to report fossil vertebrates from the fissures near La Grive-St. Alban, that were discovered during the construction of a rail-road. Until 1914 the limestone was exploited for rail-road ballast beds, and many finds of vertebrate fossils were reported by, among others, Depéret, Gaillard, and Forsyth Major. After 1914 exploitation of the limestone stopped, and hardly any new fossil material was found.

One of the authors of the present paper (P.M.) started prospecting the area of La Grive-St. Alban in 1962, and soon discovered various fossiliferous fissures, which led to the conclusion that most probably the ancient collections gathered by Depéret, Gaillard, etc., are a mixture of material from several fissures. It soon became obvious that the new material represented at least two different ages:
a 'classic' fauna, represented by the fissures, denominated M and L7 (attributed to MN unit 7), and a younger fauna, present in the fissures denominated L3 and L5 (attributed to MN 8).
In this terminology M stands for 'Carrière Milliat', St. Alban-de-Roche, and L represents the 'Carrière Lechartier' in La Grive.

Further prospecting in the area led to the discovery of:
two fissures in L'îsle d'Abeau, attributed to MN5 and MN6;
two fissures in L'îsle Crémieu: one at Vénérieux, attributed to MN7, and one at Crucillieux, of uncertain age;
a fissure north of La Grive, discovered in 1984 during the construction of road VP 24 (and denominated VP 24 for that matter), attributed to MN8, though containing a fauna different from L3 and L5.

Over the years many taxons have been described on the basis of holotypes in ancient collections from La Grive-St. Alban. This presents a problem, in view of the possibility, that these ancient collections contain a mixture of material from various fissures. In this respect it is important to draw the attention to a publication by Depéret (1894), which is a report of an excursion of the Société Géologique de France of August 20, 1894, in which he states, that the members of the Society have had ample opportunity to collect microvertebrate fossils in the Milliat quarry. In fact it may be assumed that a large part of the La Grive material in various old collections stems from this excursion. Furthermore we think, that the present-day fissure M coincides with the old fissure in the Milliat quarry, reported by Depéret.

METHODS

The measuring equipment and technique are as described by Freudenthal, 1966. The terminology used in the description of the molars is the one proposed by Mein & Freudenthal, 1971, amended by Freudenthal & Daams, 1988. Measurements are given in 0.1 mm units.

The new material is kept in the collections of the Faculté des Sciences, Lyon (FSL). Some older specimens, including the holotype of *F. larteti*, belong to the Musée des Sciences Naturelles, Lyon.

Descriptions

Fahlbuschia larteti (Schaub, 1925)
Pl. 1, figs. 1-9.

Lectotype — Maxilla sin. with M^1-M^3, nr. La Gr 145, Mus. Sci. nat., Lyon, Schaub, 1925, pl. 3, fig. 3. Measurements: M^1: 25.4 x 17.0; M^2: 18.9 x 16.5; M^3: 12.7 x 13.8.
Paralectotype — Mandibula sin. with M_1-M_3, nr. La Gr 144, Mus. Sci. nat., Lyon, Schaub, 1925, pl. 1, fig. 4. Measurements: M_1: 22.0 x 14.6; M_2: 19.0 x 15.6; M_3: 14.8 x 14.0.
Type-locality — La Grive-St. Alban, probably fissure M.
Other localities — In our opinion the occurrences in La Grive- St. Alban L7 and La Grenatière are certain, the presence in Mourel de l'Oreille is doubtful; all citations of *F. larteti* from other localities refer to other species.

Although Schaub did not define a holotype for *F. larteti*, it seems to be most logical to consider the above-mentioned specimens as the type-material for this species. Schaub also figured an isolated M^2, but this element would not be the best choice to serve as a type-specimen. Unfortunately the figured mandible and maxilla bear teeth that are rather worn, and do not give much information.

As explained above, we think that there is good reason to believe that our material from La Grive fissure M agrees with the classical La Grive fauna, and that the above-mentioned type- material may really come from this fissure. An extra argument is that among the fissures known nowadays only fissure M contains an abundant *Fahlbuschia* material. In all other fissures *Fahlbuschia* is rare or absent.

We therefore took 50 mandibles and 50 maxillas from La Grive M to serve as a basis for a revised description of *F. larteti*. The measurements of these specimens are found in the table below. A first morphological description was based on these 50 mandibles and maxillas too. But then it was realized that a majority of the teeth in these jaws was fairly worn, and an additional study was made of 50 isolated, less-worn, specimens of each element. These additional specimens were not measured.

Locality La Grive-St. Alban M

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	50	19.4	20.90	22.2	0.633	50	13.6	14.27	15.0	0.365
M_2	50	17.2	18.72	20.2	0.540	50	14.8	15.39	16.2	0.337
M_3	50	13.5	15.29	16.5	0.547	50	12.6	13.89	15.0	0.502
M^1	50	23.3	24.73	26.1	0.743	50	15.3	16.62	18.1	0.550
M^2	50	17.5	18.78	20.1	0.631	50	15.2	16.38	17.9	0.558
M^3	50	12.0	13.04	14.0	0.474	50	13.2	14.22	15.1	0.484
M_1-M_3	50	51.3	54.1	57.0						
M^1-M^3	38	51.5	54.2	56.8						

N.B. Only 38 complete maxillas were available. The remaining twelve were substituted by maxillas with M^1-M^2, and isolated M^3.

Revised diagnosis — M_1 with small anteroconid, reduced anterosinusid, and well-developed direct connection between metaconid and anteroconid. There may be a labial

spur on the anterolophulid, that points obliquely forward. Mesolophid short or absent. M_3 has the shape of a short triangle; the entoconid is small; on its occlusal surface two diverging crests may be visible. In M^1 the forked anterolophule may form a small funnel on the posterior wall of the anterocone. There is hardly ever a trace of an anterior protolophule; the posterior protolophule is generally oblique. The mesoloph is short. The metalophule is very much backwards. The outline of the tooth is smoothly convex, there is no clear constriction of the lingual wall between protocone and anterocone. M^2 has often an anterior protolophule, which is weaker than the posterior connection. The mesoloph is short or absent. There is always a posterior metalophule, rarely an anterior one.

Description

M_1 – Length/width ratio 1.46. The anteroconid is small, the anterosinusid small and shallow, rarely wide and open. The anteroconid is asymmetrical and lies lingually of the axis of the molar. There is a ridge descending from the anteroconid along the labial border of the molar, which may reach the basis of the protoconid. In 5 out of 50 specimens there is a small protrusion of the enamel at the basis of the antero-lingual wall of the anteroconid. The connection between metaconid and anteroconid, typical of *Fahlbuschia*, is strongly developed (27), weak (2), or absent (8), in the mandible specimens. In the less-worn, isolated specimens this connection is complete (20), incomplete (19) or absent (10). This means that the degree of wear has a considerable influence on the interpretation of this feature. In 28 out of 86 specimens the anterolophulid bears a labial spur, pointing obliquely forward, which may reach the anterior border of the tooth. In unworn teeth 4 out of 12 specimens show a superficial subdivision of the anteroconid into two points; this feature is bound to disappear with the slightest degree of wear. Metalophulid and hypolophulid are pointing forward. The valley between protoconid and metaconid is shallower than the valley between hypoconid and entoconid. The mesolophid is short or absent, generally nothing more than a vague inflation of the ectolophid. Only one specimen has a mesolophid of medium length. The sinusid is directed obliquely forward, open or blocked by a cingulum ridge descending from the protoconid. This cingulum ridge may form a kind of stylid in the entrance of the sinusid; sometimes it forms a broad shoulder, set off from the wall of the protoconid. The posterolophid reaches the entoconid, but the posterosinusid is often not really closed.

M_2 – Only in little worn specimens a trace of the lingual anterolophid and of the anterosinusid may be seen. The mesolophid is somewhat less developed than it is in M_1, and often absent. Only in one specimen it is short/medium (in this specimen

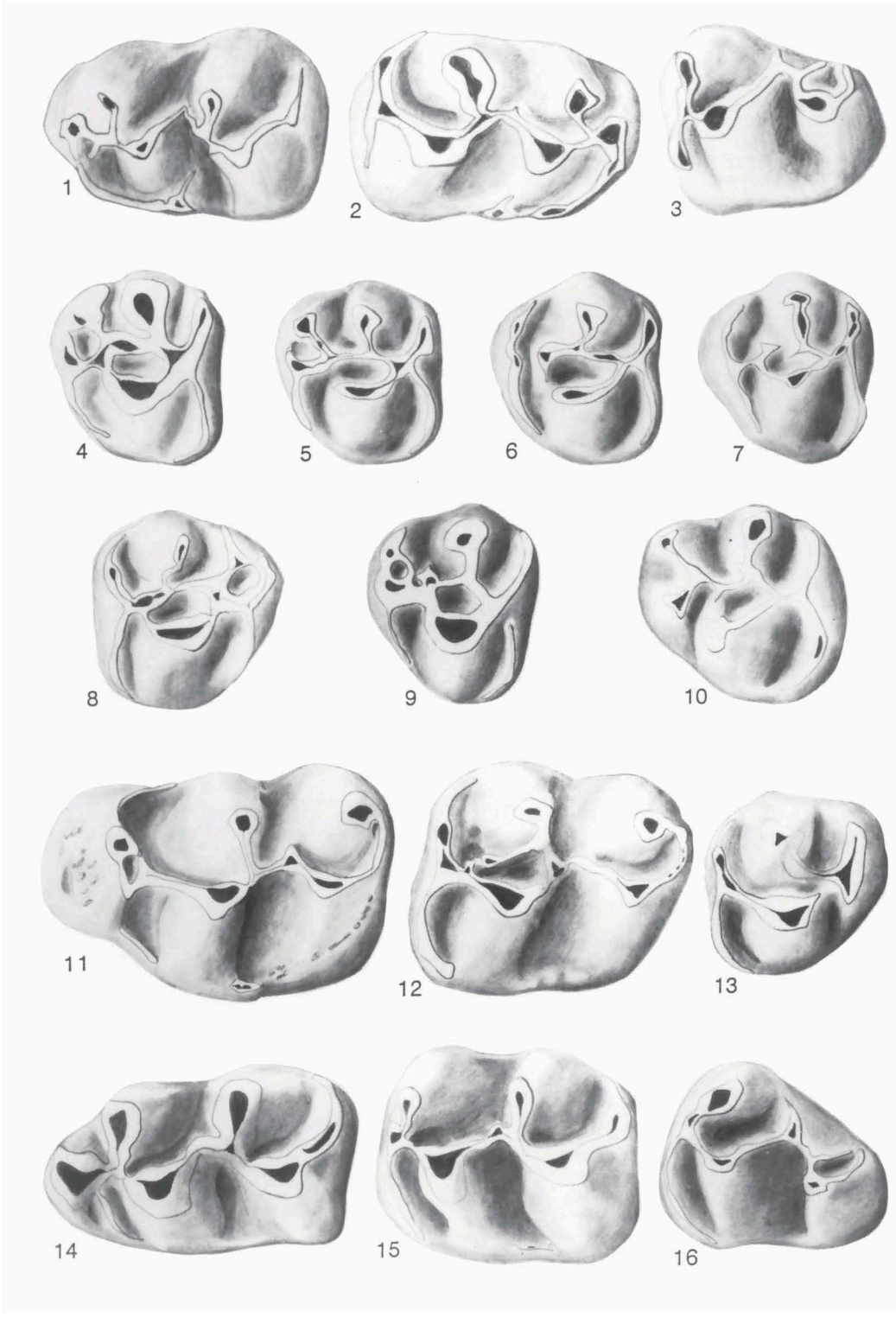
Plate 1

Fahlbuschia larteti Schaub, 1925
La Grive M
Fig. 1. M_1 sin., FSL 65 682.
Fig. 2. M_1 dext., FSL 65 683.
Fig. 3. M_3 sin., FSL 65 681.
Fig. 4. M^3 dext., FSL 65 676, morphotype 1.
Fig. 5. M^3 dext., FSL 65 678, morphotype 2.
Fig. 6. M^3 dext., FSL 65 679, morphotype 3.
Fig. 7. M^3 dext., FSL 65 680, morphotype 4.
Fig. 8. M^3 sin., FSL 65 677, morphotype 1.

La Grive L7
Fig. 9. M^3 dext., FSL 65 675.

Fahlbuschia aff. *crusafonti* Agustí, 1978
La Grive L3
Fig. 10. M^3 dext., FSL 65 674.
Fig. 11. M^1 sin., FSL 65 684.
Fig. 12. M^2 sin., FSL 65 685.
Fig. 13. M^3 sin., FSL 65 686.
Fig. 14. M_1 sin., FSL 65 689.
Fig. 15. M_2 sin., FSL 65 690.
Fig. 16. M_3 sin., FSL 65 688.

Plate 1



the M_1 also has a mesolophid of medium length; maybe this mandible belongs to a *Democricetodon* and not to *Fahlbuschia*). The sinusid is directed obliquely forward or slightly curved backwards, often blocked by a low cingulum ridge. In some cases there is an ectomesolophid pointing from the cingulum into the sinusid. The posterolophid may reach the entoconid, the posterosinusid is more closed than it is in M_1.

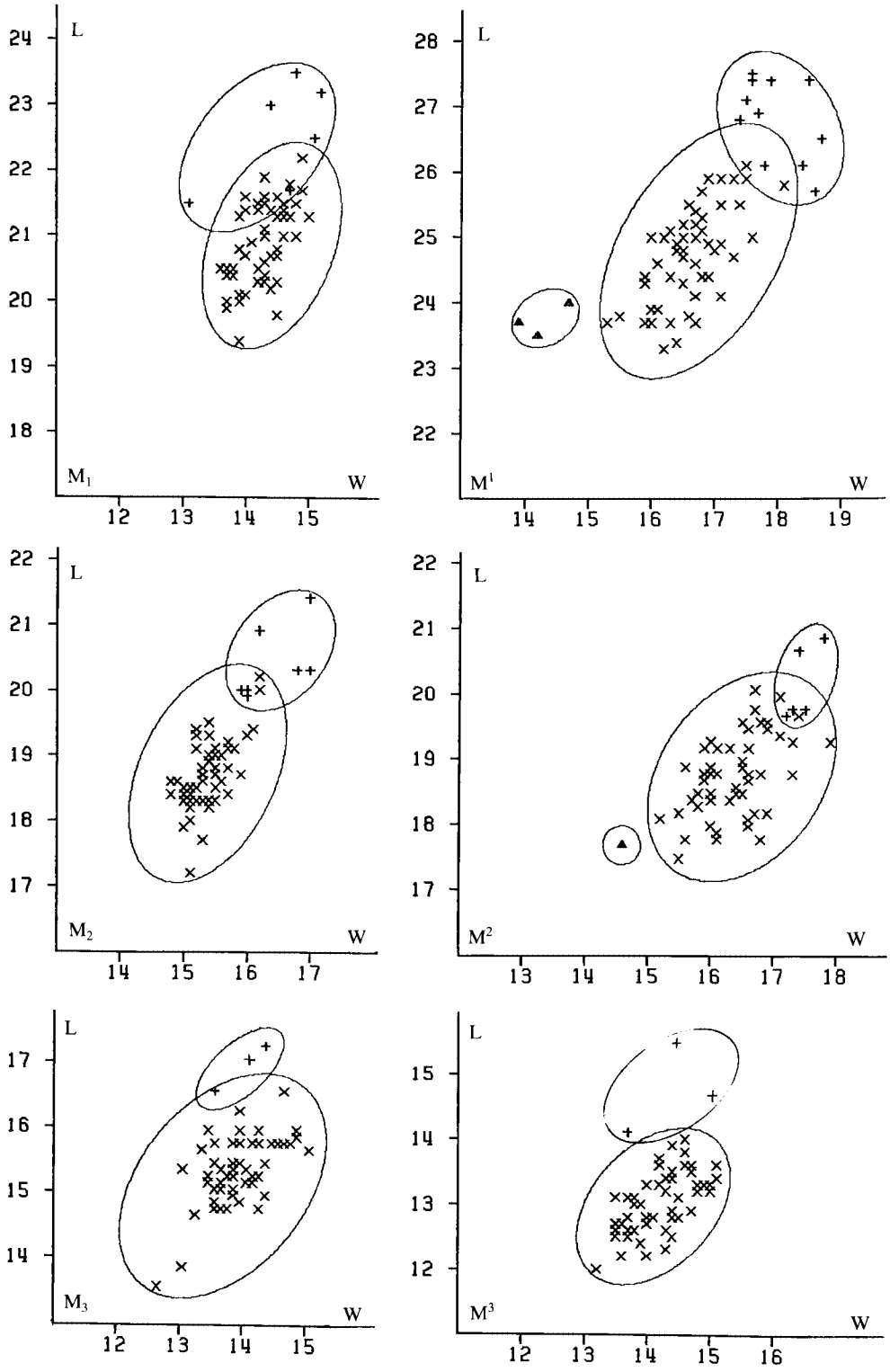
M_3 — The outline of this element is a short triangle. A small lingual anterolophid and a very small anterosinusid are often present, even in moderately worn specimens. The sinusid is curved backwards, narrow and long, blocked or open. The cingulum ridge descending from the protoconid is often somewhat inflated, forming some kind of a stylid or an ectomesolophid. The entoconid is a small flat area, generally not protruding forward; its lingual wall may be concave. In the little-worn specimens the entoconid may show some interesting details.In about 50 % of them its lingual wall is not only concave, but two diverging crests may be distinguished on the occlusal surface, forming a V that is lingually open. Evidently the posterior one of these crests is the hypolophulid, and the anterior one appears to be the mesolophid (see Pl. 1, fig. 7). Apparently the mesolophid in *F. larteti* has not disappeared, but it has fused with the hypolophulid and the entoconid into the generally flat area that is normally interpreted as being the entoconid. The mesosinusid is open, or closed at a low level. The posterosinusid is open or closed.

M^1 — In 16 out of 45 specimens there is an - often weak - cingulum at the anterolingual base of the anterocone. The anterocone is a curved, smooth crest with a labial cone. Among the medium-worn specimens on the maxillas some have a forked anterolophule; in the less-worn isolated specimens 28 out of 60 specimens have a forked anterolophule: the lingual branch is connected longitudinally to the anteroloph; the labial branch is short and broad, directed towards the anterocone, but generally not reaching it; if it reaches the anterocone it may close a small funnel on the hind wall of the anterocone. The anterior protolophule is absent (41), indicated (2), or present though weak (1). The posterior protolophule is transverse or - mostly - obliquely backward. The mesoloph is short, seldom of medium length. The sinus is transverse. All valleys are more or less blocked by cingulum ridges. The metalophule is placed very much backwards, but in little-worn specimens the posterosinus persists. Both the labial and the lingual border of the molar are smoothly convex. The anterocone is not set off from the rest of the molar by a constriction of the lingual border in front of the protocone.

M^2 — This description is based on the 50 little-worn specimens. The protolophule is posterior (19), posterior plus a trace of an anterior connection (10), or double (21). The sinus is transverse, the valleys are blocked. The mesoloph is short or absent. The metalophule is posterior; in 5 out of 50 specimens a weak anterior connection is present too. The posterosinus is somewhat larger than it is in M^1.

M^3 — For a detailed description of the M^3 of *Fahlbuschia* the reader is referred to Freudenthal & Daams (1988). In our material from La Grive M basically four morphotypes of M^3 are found, which are figured in Pl. 1, figs. 4-8. Morphotype 1 (30 specimens) is by far the most frequent. Morphotype 2 (3 specimens) differs from morphotype 1 by a slight interruption of the connection between protocone and hypocone (neo-entoloph), and a small incision in the posterior wall of the tooth, separating hypocone and metacone. Two specimens are intermediate between morphotypes 1 and 2: the posterior wall is continuous, but the neo-entoloph is slightly interrupted. In morphotypes 3 (5 specimens) and 4 (3 specimens) the posterior part of the tooth is much more

Fig. 1. Length/width diagrams of *Fahlbuschia* from La Grive-St. Alban. x *F. larteti* from La Grive M; + *F.* aff. *crusafonti* from La Grive L3; ▲ *Fahlbuschia* sp. from La Grive M.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reduced than it is in types 1 and 2. In type 3 the neo-entoloph is somewhat discontinuous, in type 4 it is continuous. In morphotype 5 (1 specimen) there is a small funnel in the connection between protocone and hypocone. The meaning of this feature has been treated by Freudenthal & Daams (1988). In a second group of 50 specimens the same morphotypes are repeated. In the entire population only one specimen shows a trace of a mesoloph. A very constant feature of the M^3 of *F. larteti* is the transversal position of the protolophule, connected to a longitudinal crest running from protocone to hypocone (the axioloph).

Locality La Grive-St. Alban L7

Apart from the La Grive M fissure, *F. larteti* has been found in the fissure La Grive L7. In this material the metaconid-anteroconid connection in M_1 is somewhat less-developed, but the difference is not significant. Also, the anterior protolophule of M^2 seems to be slightly better developed. The only real differences between the two populations appear in the M^3:

In the L7 fissure 5 out of 15 specimens have a trace of a mesoloph (see Pl. 1, fig. 9); in 1 specimen the axioloph is missing. Half the number of specimens are of morphotype 4; in morphotypes 1 and 2 the metalophule is more transverse than it is in fissure M.

L7 is considered to be older than fissure M. However, the differences between the M^3 of these two populations may not be interpreted as primitive versus modernized.

Fahlbuschia sp.

Locality La Grive-St. Alban M

Material and measurements
Maxilla with M^1-M^2: M^1 24.0 x 14.7, M^2 17.7 x 14.6.
Isolated M^1: 23.7 x 13.9, 23.5 x 14.2.

These specimens are too small for *F. larteti*. Furthermore the M^1 have an anterior protolophule; the metalophule is more transverse and the posterosinus larger than in *F. larteti*. In M^2 both the protolophule and the metalophule are double. None of the specimens has a mesoloph.

Several M_1 (20.1 x 13.3, 19.6 x 12.6, 18.2 x 12.7, 17.9 x 12.0) possibly belong to the upper teeth mentioned here. The metaconid-anteroconid connection is present (1) or absent (3), the mesolophid is absent (1) or short (3), the sinusid is open, the posterosinusid is open (2) or closed (2). In one specimen the metalophulid is interrupted.

It is not clear to which species these specimens should be attributed, and it is even not completely sure that all these specimens are from La Grive M (the maxilla with M^1-M^2 bears the indication La Grive M, 1965; in this case there is no doubt about its provenance). The upper teeth may belong to *F. freudenthali* Antunes & Mein, 1981, in view of the presence of the anterior protolophule. The length/width ratio of M_1, 1.49, is larger than it is in *F. freudenthali*, and falls in the range covered by *F. darocensis* Freudenthal, 1963.

Fahlbuschia aff. *crusafonti* Agustí, 1978
Pl. 1, figs. 10-16.

Locality La Grive-St. Alban L3

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	6	21.5	22.57	23.5	0.819	6	13.1	14.55	15.2	0.766
M_2	7	19.9	20.40	21.4	0.554	7	15.9	16.41	17.0	0.498
M_3	3	16.6	16.93	17.3	0.351	3	13.5	13.90	14.2	0.360
M^1	11	25.7	26.81	27.5	0.628	11	17.4	17.97	18.7	0.482
M^2	5	19.7	20.18	20.9	0.572	5	17.2	17.44	17.8	0.230
M^3	3	14.1	14.76	15.5	0.702	3	13.7	14.46	15.1	0.709

Description

M_1 — Length/width ratio 1.55. The anteroconid is fairly large, longitudinally lengthened in comparison with *F. larteti*. There is no descending lingual cingulum, and the labial ridge is weak. In 2 specimens there is a labial spur on the anterolophulid. The metalophulid is directed obliquely forward, a direct connection between metaconid and anteroconid is absent, the anterosinusid therefore is relatively large and wide. The mesolophid is absent. The posterolophid does not reach the entoconid, the posterosinusid remains open, as well as the sinusid.

M_2 — There is no lingual anterolophid. Only in one specimen the sinusid is closed by a cingulum ridge, and there is a short mesolophid. In the others the sinusid remains open and the mesolophid is absent.

M_3 — The entoconid is practically absent, the mesosinusid closed, the posterosinusid open (2) or closed (1).

M^1 — There is a cingulum at the antero-lingual base of the anterocone. The anterocone lies labially of the axis of the molar with a descending labial cingulum ridge to which the anterolophule is connected. The anterolophule may bear a labial spur, which forms a small funnel on the hind wall of the anterocone in 3 out of 6 specimens; this structure, which disappears rapidly with wear, exists also in *F. larteti*, but seems to be better developed in this population from L3. The protolophule is transversely posterior; one specimen shows a weak trace of an anterior protolophule. The mesoloph is absent or short. The metalophule is posterior. The posterosinus is small. The valleys are closed by weak cingulum ridges. The lingual border of the molar is strongly constricted between protocone and anterocone.

M^2 — The posterior protolophule is always present, the anterior one is incomplete (4) or complete (1). The sinus is open. The metalophule is posterior, and in one case there is an anterior connection too. In one specimen there is no metalophule. The mesoloph is absent.

M^3 — The reader is referred to Pl. 1, figs. 10 and 13.

Discussion

F. aff. *crusafonti* from fissure L3 is easily distinguished from *F. larteti* from fissure M by its larger size (Fig. 1). Further differences are:

the long anteroconid and wide anterosinusid in M_1,
the absence of the direct metaconid-anteroconid connection in M_1,
the posterolophid is shorter and the posterosinusid is not closed in M_1 and M_2,
the less-developed or absent cingulum structures in the sinusid of M_1 and M_2,
the smaller entoconid in M_3,
the better developed funnel on the hind wall of the anterocone in M^1,
the more frequent cingulum at the antero-lingual base of the anterocone of M^1,
the transverse posterior protolophule of M^1,
the more transverse metalophule of M^1,
the constricted outline of M^1.

F. aff. *crusafonti* from fissure L3 has many features in common with *F. crusafonti* from Sant Quirze and Hostalets de Pierola (Spain), e.g. its size, the shape of anteroconid and anterosinusid in M_1, and the open posterosinusid.

On the other hand, it presents differences too, like e.g.:
the smaller entoconid of M_3 as compared with the Spanish material,
the presence of a cingulum at the base of the anterocone of M^1,
the presence of a funnel on the hind wall of the anterocone of M^1,
the occasional occurrence of an anterior protolophule in M^1.

It is quite probable that the material from fissure L3 represents a new species different from *F. crusafonti.* However, both the material from L3 and the collection from Sant Quirze are rather poor, and the stated differences might disappear, were a more abundant material available. As far as Sant Quirze is concerned, extension of the collection, in collaboration with Dr J. Agustí, Sabadell, is being envisaged. This is the more important, since there exists a possibility, that the type-material of *F. crusafonti* contains two different species.

In the type-area of the Aragonian several localities, e.g. Solera and Carrilanga have yielded small collections of a large *Fahlbuschia* (see Freudenthal & Daams, 1988). This material has much in common with the material from L3, but unfortunately these collections are poor too.

An abundant material of a large *Fahlbuschia* is being collected at the new locality of Nombrevilla 2 (Zaragoza, Spain), recently discovered by Mr C. Langa from Daroca.

The largest *Fahlbuschia* described until now is *F. ultima* Antunes, Ginsburg & Mein, 1983 from Azambujeira (Portugal), but this species may belong to the genus *Renzimys* Lacomba, 1988.

Palaeoecology

Mein (1984) and Daams, Freudenthal & van der Meulen (1988) made an attempt to analyze the ecology of *Fahlbuschia.* One of the striking facts is, that *Democricetodon* and *Fahlbuschia* seem to be mutually exclusive. E.g. in a locality that seems to present all evidence of a wet environment like Sansan, *Democricetodon* is abundant, and *Fahlbuschia* is absent. Also in the fissure La Grive M, where *Fahlbuschia* is abundant, *Democricetodon* is rather scarce, in comparison with La Grive L7. On the other hand, important changes in humidity, as found by Daams et al. (1988) in the Spanish Aragonian are not reflected in the representation of *Fahlbuschia.*

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