

# Taxonomic revision of the genus *Leptoplesictis* (Viverridae, Mammalia) with description of new fossils from Grillental VI (Namibia) and Moratilla 2 (Spain)

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**Abstract :** The early Miocene locality of Grillental VI (21-19 Ma) has yielded an interesting assemblage of fossil carnivores, including a new mandible of the small viverrid classified as *Leptoplesictis senutae* Morales *et al.* 2008, which permits a better idea of the species to be obtained. In addition an unpublished mandible from the Spanish locality Moratilla 2, provisionally identified as *Leptoplesictis aurelianensis* Schlosser, 1888, gives us the possibility to make direct comparisons between these fossils, which, because of their small dimensions have not been well figured in the literature. Comparisons are made with mandibles of *Leptoplesictis filholi* Gaillard 1899, from the French locality of La Grive-Saint-Alban curated at the NHMUK, London, upon which Forsyth Major, 1903, based the new genus *Leptoplesictis*. The result is that the less hypercarnivorous African species can be segregated into a different genus from *Leptoplesictis*, for which a new genus is proposed, *Dunictis* nov. gen., with *Dunictis senutae* (Morales *et al.* 2008) as the type species, which is from Grillental VI, Namibia. Contrary to general opinion, the European forms of *Leptoplesictis* do not constitute a homogeneous assemblage, but instead comprise two divergent lineages. The first of these, from the locality of La Grive-Saint-Alban, represented by *Leptoplesictis filholi* Gaillard, 1899, has a less-reduced m/2, a robust m/1 and gracile premolars, which is joined by a second species of the genus, *Leptoplesictis peignei* from the late middle Miocene of Thailand, which even though it has relatively more robust premolars, shows an overall morphology which is closer to this genus than to any other. The second lineage is characterised by strong reduction of the m/2, a very sectorial m/1 and more robust premolars, for which we propose a new genus *Forsythictis* nov. gen., of which the type species is *F. ibericus* from the locality of Moratilla 2, and which includes the classic species *Forsythictis aurelianensis* (Schlosser, 1888) and the poorly known species *Forsythictis atavus* (Beaumont, 1973).

**Key Words :** Carnivora, Feliformia, Viverridae, Miocene, Africa, Eurasia, Biochronology, Biogeography

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## Introduction

There has been a certain amount of debate about the systematic classification of the various species of Early Miocene African Feliformia. The problem was particularly grave when attempts were made to relate the fossil feliformes in the broad sense, to the extant families, Viverridae and Herpestidae, and with the extinct family, Stenoplesictidae. The separate family status of Herpestidae from Viverridae is currently widely accepted, supported as it is by a wide range of morphological and biomolecular characters (Hunt, 1989; Hunt & Tedford, 1993; Veron,

2010; Eizirik *et al.* 2010; Nyakatura & Bininda-Emonds, 2012; Zhou *et al.* 2017). However, the skeletal differences between these families, except for the more derived tympanic bulla of Herpestidae, are difficult to determine. In addition, the fossil remains available from the Early Miocene of Africa are predominantly represented by more or less complete dentognathic material. The dentitions of some extant herpestids and viverrids show a really notable abundance of adaptations, occupying a broad range which includes many species of hypocarnivores and hypercarnivores, with

highly diverse adaptations (carnivores, myrmecophages, piscivores, frugivores, etc.). Under these circumstances it is difficult to establish clear criteria based solely on the dentition to distinguish the extant families, but as was pointed out above, this is the situation with which we are confronted in the present state of knowledge of the African early Miocene fossil record. A particularly complex case concerns the genus *Leptoplesictis* Forsyth Major, 1903, considered to belong either to

Herpestidae or to Viverridae, which had a vast geographic distribution during the early and middle Miocene of the Old World (Beaumont, 1973; Schmidt-Kittler, 1987; Roth, 1988; Morales *et al.* 2008; Grohé *et al.* 2020). The description of new fossils from the early Miocene of Grillental VI (Namibia) and from the beginning of the middle Miocene of Moratilla 2 (Spain) attributed to *Leptoplesictis* prompts us to undertake a revision of the taxonomic status of this genus.

### Geological Context and Age

Grillental VI is located in the fossiliferous valley-fill sediments of the Northern Sperrgebiet, Namibia, which are faunally similar to East African sites such as Songhor, Koru and Napak and to other Sperrgebiet sites such as Langental, Elisabethfeld and Grillental I-V, that are

attributed to the Early Miocene (East African Faunal Set I, Pickford, 1981, 1986) dated about 21-19 Ma (Pickford & Senut, 2003). Moratilla 2 is located in the Calatayud-Teruel Basin, Spain, dated about 15.8 Ma (Lower Middle Aragonian, local zone Db (Van der Meulen & Daams, 1992; Daams *et al.* 1999).

### Material and Methods

The new material from Grillental (GT) described herein is curated at the Earth Science Museum of the Geological Survey of Namibia (GSN Windhoek, Namibia). The specimen from Moratilla 2 is curated at the Museo Nacional de Ciencias Naturales (MNCN)-CSIC, Madrid. Specimens from La Grive-Saint-Alban, France are curated in the Natural History Museum (London) (NHMUK).

The teeth were measured with a Nikon Measuroscope 10 5x microscope with an incorporated micrometer. Scans were made by the Servicio de Técnicas No Destructivas: Microscopía Electrónica and Confocal and Espectroscopía del MNCM-CSIC, Madrid. Images of Tomographic Scans were obtained with VGStudio MAX 3.0 software.

### Systematic Palaeontology

#### Order Carnivora Bowdich, 1821

#### Suborder Feliformia Kretzoi, 1945

#### Family Viverridae Gray, 1821

#### Genus *Dunictis* nov.

**Type species** :- *Dunictis senutae* (Morales *et al.* 2008)

**Locality** :- Grillental VI, Sperrgebiet, Namibia.

**Age** :- Early Miocene.

**Derivatio nominis** :- From “dune”, a geomorphological entity common at Grillental.

**Holotype** :- GT VI 1'06, right mandible with p/1-m/2.

**Included species** :- *Dunictis rangwai* (Schmidt-Kittler, 1987); *Dunictis peignei* (Grohé *et al.* 2020) and (?)*Dunictis mbitensis* (Schmidt-Kittler, 1987)

**Diagnosis** :- Viverridae of small dimensions, with reduced m/2, m/1 large in comparison with the premolar series, with compressed paraconid lower than the protoconid, tall metaconid, almost as high as the paraconid; broad talonid comprised of similar-sized peripheral cuspids which surround a deep central valley; p/4 with cusps aligned oblique to the long axis of the mandible and the talonid enlarged, lingually closed by a tall lingual cristid, strong in the type

**Differential diagnosis** :- *Dunictis* differs from *Leptoplesictis* Forsyth Major (1903) by the less sectorial character of the premolar row, with short, more robust premolars, and with greater lingual development of the talonid. The m/1 is

species, but weaker in other species of the genus; p/3 with cuspids aligned along a mesio-distal axis of the mandible, p/3 with weak anterior cuspid, talonid broadening disto-lingually similar to that of the p/4, but smaller; p/2 lacking mesial cuspid, with small distal accessory cuspid and vestigial talonid, but similar in shape to those of the p/3 and p/4, uniradicate p/1 separated by a diastema from the p/2.

also more robust, differing from that of the type species *L. filholi* (Gaillard, 1889) by the less-developed cuspids and its peripheral position which results in a larger talonid valley.

#### **Species *Dunictis senutae* (Morales et al. 2008)**

##### **Synonymy** :-

2008 *Leptoplesictis senutae* Morales et al. p. 303.

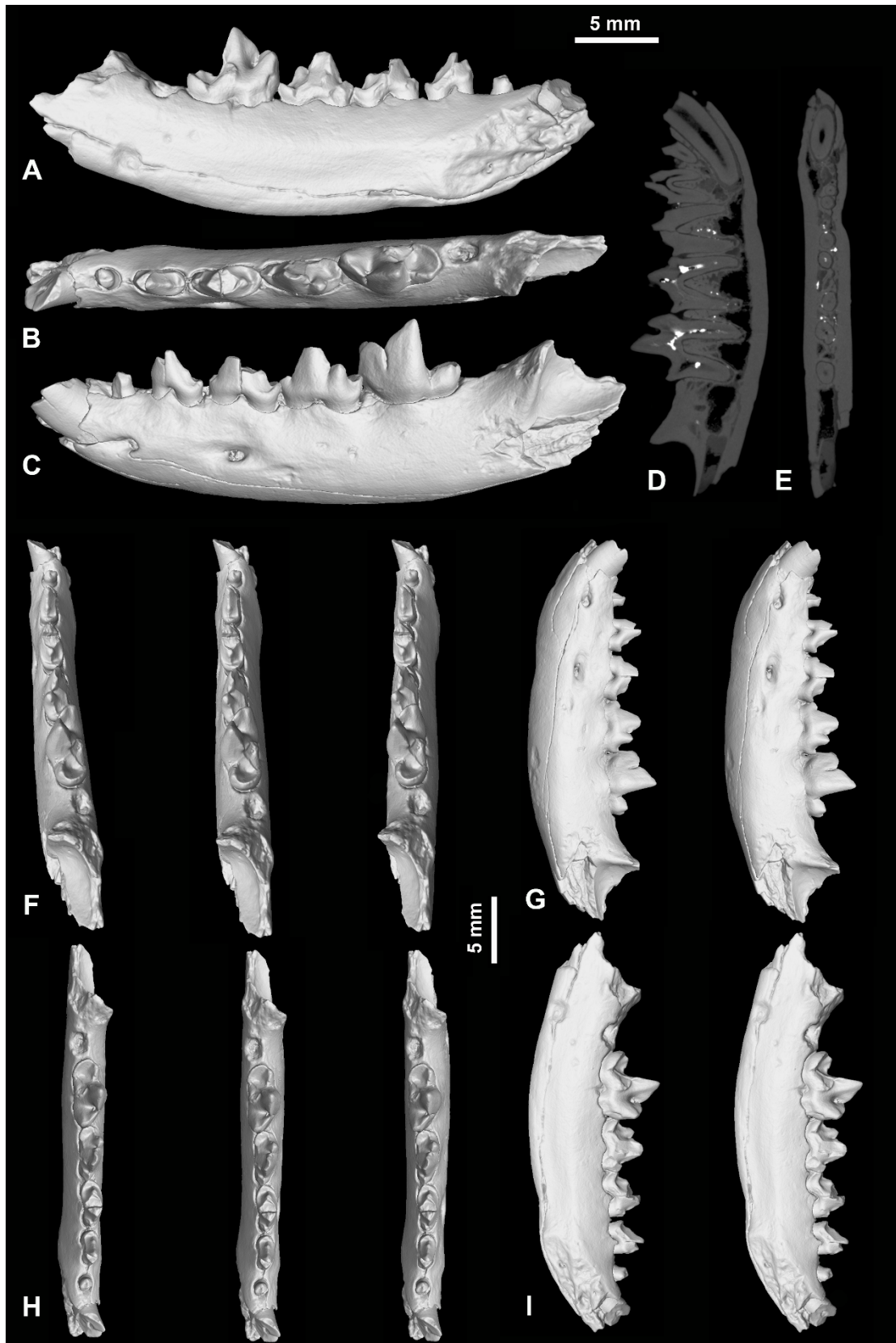
2010 *Leptoplesictis senutae* Werdelin & Peigné, p. 630.

##### **Description of new material**

GT VI 5'18 is a left mandible lacking the ascending ramus (Fig. 1). The m/2 is lost, but its alveolus indicates that it was reduced in dimensions and was uniradicate. The m/1 has a tall trigonid, with a quite mesio-buccally compressed paraconid, the protoconid is taller than the paraconid and is also compressed such that its mesial and disto-lingual cristids are sharp and form a cutting blade. The metaconid is partly broken, but judging from its base it must have been well-developed (similar to the m/1 in the holotype GT VI 1'06). The talonid is short (ca 31% of the total length of the tooth) and broad, with a deep valley, somewhat displaced lingually, surrounded by a crestiform hypoconid which continues as a peripheral cristid extending to the base of the metaconid in which the hypoconulid and entoconid are indistinguishable.

The p/4 is an elongated tooth with a large main cuspid, the accessory mesial cusplet is relatively small, the distal accessory cuspid

larger and taller. These three cusps are aligned with each other but are oblique (ca 20°) to the long axis of the jaw. Buccally, the talonid is short, but lingually it is well developed and is closed by a tall lingual cristid which terminates at mid-height of the main cuspid, without forming a separate cuspid (analogous to the position of the metaconid in the m/1). The p/3 has the cuspids aligned along the mesio-distal axis of the mandible, the mesial accessory cusplet is weak, the talonid is disto-lingually broadened similar to the morphology described for the p/4, but more reduced. The p/2 has no mesial cusplet, the distal accessory cusplet is very small and the talonid is vestigial, although similar in form to those of the p/3-p/4. The p/1 is eroded. It has a single tiny root. The canine is strong but the crown is damaged. Its transverse section is oval, quite compressed and its root is long, extending into the mandible as far as the base of the p/2.

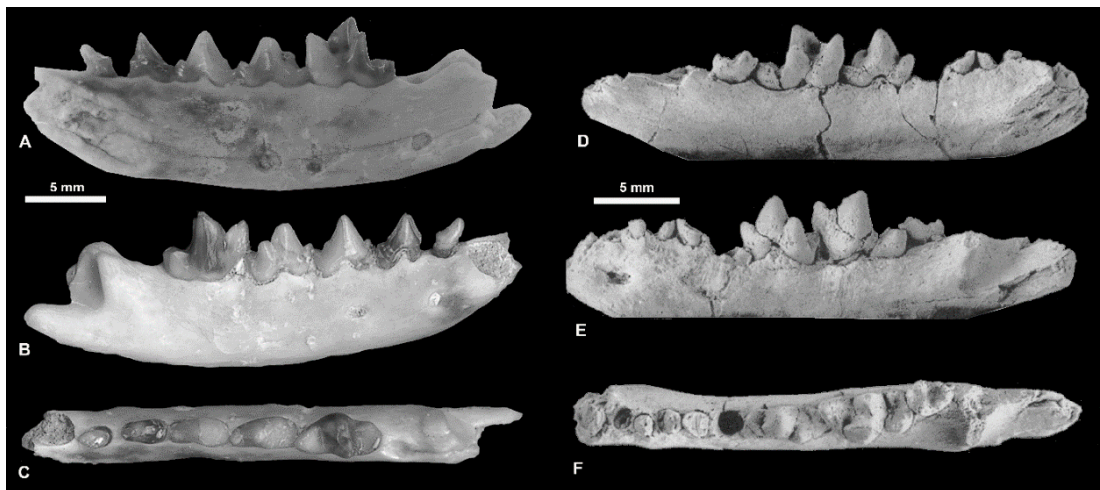


**Figure 1.** GSN GT VI 5'18, *Dunctis* nov. gen. *senutae* (Morales *et al.* 2008) from Grillental VI, Namibia, right mandible with canine root, p/1-m/1 and alveolus of m/2. A) lingual view, B) occlusal view, C) buccal view D) mesio-distal cross section, E) transverse section near the base of the tooth roots, F) occlusal stereo pairs (oblique distal view), G) buccal view (stereo pair), H) occlusal stereo pairs, I) lingual view (stereo pair).

## Discussion

*Dunictis senutae* was originally related by Morales *et al.* (2008) to *Leptoplesictis rangwai* and *Leptoplesictis mbitensis* (Fig. 2) based on the morphology of its p/4, in which the strong development of the talonid stands out, as does the alignment of the cusps oblique to the long axis of the mandible, as was pointed out by Schmidt-Kittler (1987). The three species share the m/1 with short talonid, formed of a hypoconid endowed with an anterior cristid and a peripheral entoconid. The presence of a uniradicate, reduced p/1 is another feature shared by *D. senutae* and *L. rangwai* (Fig. 2) but the condition of this tooth is unknown in *L. mbitensis* (Morales *et al.* 2008). However, *D. senutae* differs from *L. rangwai* by the smaller dimensions of the m/2 (represented only by its alveolus in *D. senutae*), the more compressed and sectorial morphology of the trigonid of the m/1 and of the premolars, although it is only possible to affirm this for the p/4, but judging from the alveoli of the p/3-p/2 in the holotype mandible of *L. rangwai* it is probable that the two premolars were more robust than those of *D. senutae*. Because of the hypercarnivorous morphology of the Grillental species, Morales *et al.* (2008) related it to *Leptoplesictis aurelianensis*, and suggested a generic distinction between these species and the less sectorial ones *L. rangwai* and *L. mbitensis*. However, the generic separation between

*Dunictis senutae* and *Leptoplesictis filholi*, added to the taxonomic re-evaluation of *Leptoplesictis aurelianensis*, drastically changes the scenario, reducing the morphological variation which *a priori* could justify the generic distinction between *L. rangwai* and *Dunictis senutae*. For this reason we propose that the former species should be transferred to the same genus, and be classed as *Dunictis rangwai* (Schmidt-Kittler, 1987). It is more difficult to extend the proposition to *L. mbitensis*, which has a short p/4 with a subtriangular occlusal outline, a large talonid which has developed a lingual cuspid adjoining the mesio-buccal accessory cusplet, thereby approaching this p/4 to the situation in *Orangictis gariensis* Morales *et al.* (2001). The morphology of the m/1 is difficult to interpret, because in the holotype, the protoconid is broken, the metaconid being almost as tall as the paraconid, and the two cusps are joined basally. According to Schmidt-Kittler (1987) the m/1 is morphologically very close to that of *D. rangwai*, and is thus distinct from the morphology in *O. gariensis*. In the meantime we propose to leave it in an open taxonomic position as (?)*Dunictis mbitensis* (Schmidt-Kittler, 1987), the same as for the Langental species (?)*Dunictis namibiensis* (Morales *et al.* 2008).



**Figure 2.** Comparison of GSN GT VI 1'06, the holotype left mandible of *Dunictis* nov. gen. *senutae* (Morales *et al.* 2008) from Grillental VI, Namibia, with KNM RU 15990, the holotype left mandible of *Dunictis rangwai* (Schmidt-Kittler, 1987) from Rusinga, Kenya. A-C) *Dunictis* nov. gen. *senutae* mandible with p/1-m/2, A) lingual view, B) buccal view, C) occlusal view. D-F) *Dunictis rangwai* mandible with p/4-m/2 and roots of canine-p/3, D) lingual view, E) buccal view, F) occlusal view.

## Genus *Leptoplesictis* Forsyth Major, 1903

**Type species** :- *Leptoplesictis filholi* (Gaillard, 1899).

**Diagnosis** :- Forsyth Major (1903), Roth (1988), Werdelin & Peigné (2010).

### Notes on the taxonomy of *Leptoplesictis* Forsyth Major, 1903

*Leptoplesictis* was proposed by Forsyth Major (1903) who based his diagnosis on five mandibles from La Grive-Saint-Alban, France, curated at the NHMUK (previously abbreviated BMNH) (Fig. 3), for the similar-sized fossils ascribed to the species described by Gaillard (1889) as *Herpestes filholi*, and the smaller ones to a second species which he named *Leptoplesictis minor*. Forsyth Major (1903) did not discuss the new genus in depth, limiting his remarks to its proximity to *Stenoplesictis* from the Phosphorites of Quercy by the slenderness of its teeth, “*but its other characters assign to it decidedly a position within Viverridae*”. Previously Schlosser (1888) defined a new species *Stenogale aurelianensis*, on the basis of descriptions and figures of a mandible called *Plesictis* by Gervais (1867-69) from Suevres, France, which he related to an edentulous mandible from La Grive-Saint-Alban identified as *Mustela* sp. by Filhol (1888). Mayet (1908) followed the identification by Schlosser (1887-88) without adding any new data, and ignoring the work of Gaillard (1899) who described *Herpestes filholi* from the locality of La Grive. Stehlin & Helbing (1925) proposed a new taxonomic combination *Herpestes aurelianensis* and pointed out that the preservation characters of the specimen indicate that it probably did not come from Suevres, but was more like fossils from Pontlevoy. These two authors discussed the relationships of *H. aurelianensis* to the fossils from La Grive attributed by Gaillard (1899) to *Herpestes filholi*, concluding that the differences that were observed between them could be explained by individual variation, and thus the species from La Grive would be a synonym of *H. aurelianensis*. They did not pronounce an opinion on the validity of *Leptoplesictis*, but evidently discounted keeping the species in *Herpestes*. This position was maintained by Viret (1951) in his monograph on the carnivores of La Grive, considering that the species present

in the locality should be called *Herpestes aurelianensis*, and therefore considered that *Leptoplesictis filholi* Gaillard (1899) and *Leptoplesictis minor* Forsyth Major (1903) were synonyms of the species defined by Schlosser (1888). Viret (1951) attributed a maxilla with P4/-M1/ and alveolus of M2/ to this species. Beaumont (1973) revalidated *Leptoplesictis* but only at the subgeneric rank, as *Herpestes (Leptoplesictis) aurelianensis*, in which he included two subspecies; *Herpestes (Leptoplesictis) aurelianensis atavus* for two molars from Vieux Collonges and *Herpestes (Leptoplesictis) aurelianensis aurelianensis* for the species from La Grive, a denomination that runs against the International Code of Zoological Nomenclature, in that the nominal subspecies must apply to *Leptoplesictis aurelianensis*, either with the type locality Suevres or alternatively Pontlevoy, but not La Grive. A thorough revision of the genus was undertaken by Roth (1988) who raised the subspecies from Vieux Collonges to species rank as *Leptoplesictis atavus*. However, she considered *Leptoplesictis filholi* Gaillard (1899) to be valid, and to be the type species of the genus and indirectly noted that it could not be *Leptoplesictis aurelianensis* Schlosser (1889). Prior to the study by Roth (1988) Schmidt-Kittler (1987) as discussed above, included two new species from the early Miocene of Kenya in the genus *Leptoplesictis*, *L. rangwai* and *L. mbitensis*, both from Rusinga. Morales *et al.* (2008) described two new species from Namibia, *L. senutae* from Grillental and *L. namibienses* from Langental. McKenna & Bell (1997) and Werdelin & Peigné (2010) included the genus in the family Herpestidae. A new species *Leptoplesictis peignei* from the late middle Miocene of Thailand was recently defined by Grohé *et al.* (2020), who expressed their conviction that the type species of the genus is *Leptoplesictis filholi* (Gaillard, 1899).

### Species *Leptoplesictis filholi* (Gaillard 1899)

#### Synonymy :-

- 1899 *Herpestes filholi* Gaillard, p. 62.  
1903 *Leptoplesictis filholi* Forsyth Major, p. 535.  
1925 *Herpestes aurelianensis* Stehlin & Helbing, p. 61.  
1951 *Herpestes aurelianensis* Viret, p. 76.  
1988 *Leptoplesictis filholi* Roth, p. 338.  
1999 *Leptoplesictis filholi* Ginsburg, p. 131.  
2012 *Leptoplesictis filholi* Peigné, p. 625.  
2020 *Leptoplesictis filholi* Grohé *et al.* p. 39.

**Type locality** :- La Grive-Saint-Alban, France.

**Age** :- Middle Miocene, Upper Aragonian (MN 6-7/8).

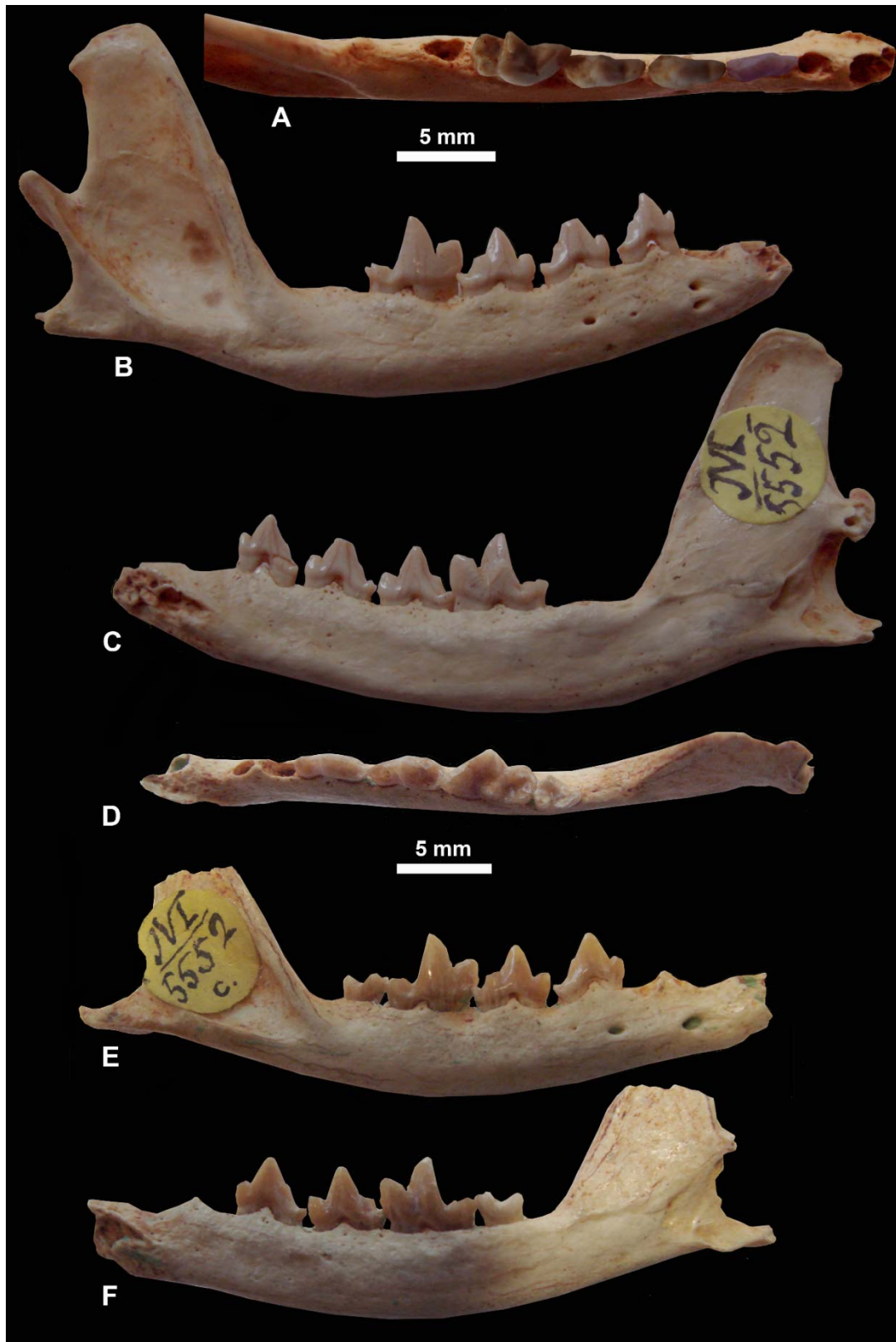
**Holotype** :- LGr 1372 mandible with p/3-m/2, figured by Gaillard 1899, pl. III, fig. 4.

**Diagnosis** :- Roth (1988).

#### Discussion

Inclusion of the species *Herpestes aurelianensis* in *Leptoplesictis* has caused a great deal of confusion in the taxonomy of the genus, considering that the type species of the genus, *L. filholi* is a synonym of the species described by Schlosser (1888), which is represented only by a mandible fragment containing m/1-p/4. The pooling of the two taxa into a single species greatly increased the range of intraspecific variation, to the extent of turning the genus into a waste-basket taxon. Roth (1988) as discussed above, separated out the two species and added a third *L. atavus*, which had been defined as a subspecies by Beaumont (1973). A detailed comparison between *Leptoplesictis filholi* from La Grive (including the material used by Forsyth Major, 1903) and the material from Petersbuch 2 (Germany) described by Roth (1988) as *Leptoplesictis aurelianensis*, together with an unpublished mandible from Moratilla 2 (Spain) and the holotype of *Herpestes aurelianensis* (Schlosser, 1888) figured by Mayet (1908) and Stehlin & Helbing (1925) shows clearly the

specific distinction between *Leptoplesictis filholi* and *Herpestes aurelianensis*, which could even extend to the level of the genus. *Leptoplesictis filholi* has a relatively robust m/1, in particular compared with the gracility and elongation of the premolars. The m/2, even though reduced, retains a complete trigonid and a narrow talonid. However, the forms included in *Leptoplesictis aurelianensis* are characterised by the great reduction of the m/2, the m/1s are elongated and bucco-lingually compressed, whereas the premolars (in the forms in which they are known) even though gracile, do not show the specialisation seen in *L. filholi*. It is evident that the divergence between the two species, even if they had a common ancestor, is sufficiently great to separate them at the generic level. In consequence, the European species of this genus, hitherto identified as *L. aurelianensis* and *L. atavus* must be removed from this genus, and for this reason a new genus is erected, for which we propose the name *Forsythictis* nov. gen.



**Figure 3.** *Leptoplesictis filholi* (Gaillard, 1888) and *Leptoplesictis minor* Forsyth Major (1903) from La Grive-Saint-Alban, France. Mandibles employed by Forsyth Major (1903) to diagnose the genus *Leptoplesictis*. NHMUK M-5552 right mandible of *Leptoplesictis filholi* with alveoli of the canine and p/1, complete p/2-m/1 and alveolus of m/2. A) occlusal view, B) buccal view, C) lingual view. NHMUK M-5552c right mandible of *Leptoplesictis filholi* (= *Leptoplesictis minor*) with alveoli of canine and p/2, and complete p/3-m/2. D) occlusal view, E) buccal view, F) lingual view.



### Species *Leptoplesictis peignei* Grohé *et al.* 2020

**Type locality** :- Mae Moh, Thailand.

**Age** :- Middle Miocene (ca. 13.2-13.4 Ma).

**Holotype** :- MM-51, fragment of mandible with alveolus of p/2, complete p/3-m/1, Grohé *et al.*

2020, Fig. 7.

**Diagnosis** :- Grohé *et al.* (2020)

#### Discussion

When erecting the species *Leptoplesictis peignei* from Thailand Grohé *et al.* (2020) pointed out the differences between it and *Leptoplesictis filholi*. In general *Leptoplesictis peignei* differs from *L. filholi* by the greater robusticity of the premolars. The morphology of the p/4 is very close to that of extant *Genetta genetta* L., and the same applies to the simple morphology of the p/3 and p/2, with the accessory cusplets greatly reduced, as in the extant form. The morphology of the m/1 of *L. peignei* is close to that of *Leptoplesictis filholi* and also close to that of *G. genetta*, with a reduced, bucco-lingually narrow talonid compared to the trigonid; which conserves the

tall and strong metaconid; in the talonid the hypoconid stands out from the rest of the cusplets, which are little different from each other and positioned disto-lingually. The differences between the species from Mae Moh, Thailand, and *Forsythictis* are marked, particularly by the more sectorial carnassial of the species of this genus. With respect to *Dunictis* the differences are also important, in particular in the construction of the talonid of the premolars, much larger and disto-lingually accentuated, while the m/1 shows distinct differences; in *Dunictis* the talonid is proportionally broader bucco-lingually and as a consequence, the talonid valley is larger.

#### Genus *Forsythictis* nov.

**Type species** :- *Forsythictis ibericus* nov. sp.

**Other species** :- *F. aurelianensis* and *F. atavus*.

**Diagnosis** :- Very small viverrid, lower post-canine dental series comprised of four premolars and two molars, with strong reduction of m/2; m/1 with clear sectorial tendency, elongated, trigonid narrow, metaconid variable depending on the species, very reduced in the type species, although well-

developed in other species of the genus. Where known, the premolars in the species are moderately elongated; p/4 with well-developed accessory distal and mesial cusplets, the disto-lingual expansion weakly developed; p/3 with a mesial accessory cusplet but the distal cusplet is variable, absent in the type species.

**Derivatio nominis** :- Dedicated to British palaeontologist Charles Immanuel Forsyth

Major.

#### Species *Forsythictis ibericus* nov.

**Holotype** :- (MNCN 87000) fragment of left mandible with alveolus of m/2 and complete m/1-p/3.

**Type locality** :- Moratilla 2, Zaragoza, Spain

**Age** :- Middle Miocene, Middle Aragonian MN 4 (local zone Dd).

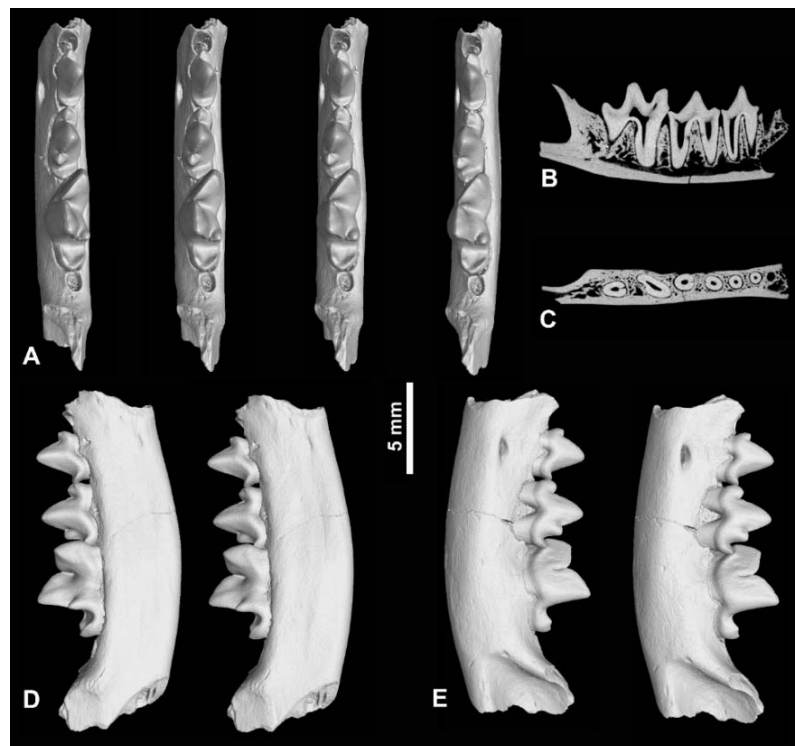
**Diagnosis** :- *Forsythictis* with metaconid of the m/1 greatly reduced, accessory cusps of the p/4 small, p/3 without a distal accessory cuspid.

**Derivatio nominis** :- From the Iberian Peninsula.

## Description

(MNCN-87000) is a fragment of left mandible with the alveolus of the m/2, and complete m/1-p/3 (Fig. 4). The mandible is deep and robust, lacking the ascending ramus, the symphysis and the alveolar part of the p/1 and the mesial root of the p/2. There is a strong mental foramen beneath the p/3. The distal root of the p/2 is clearly reduced in comparison with those of the p/3, and it is possible to discern that the canine root ends beneath the p/3. The p/3 is a simple tooth with a tall main cusp, a low, but well-developed mesial accessory cusplet, and no distal accessory cusplet, or if one is present it is a small talonid elevated distally. The p/4 has a well-developed distal accessory cusplet, and a more developed talonid somewhat

extended lingually, the mesial accessory cusplet is tall and strong. The m/1 has a paraconid which is quite a bit lower than the protoconid, but the two cusps are of similar length. The base of the paraconid has an ample contact with the lingual part of the talonid of the p/4. The metaconid is small, and is positioned at mid-height of the disto-lingual cristid of the protoconid, and barely stands out lingually. The talonid is low, small compared to the trigonid. The hypoconid, hypoconulid and entoconid are crestiform, being barely differentiated from each other and are located peripherally around the talonid valley. The alveolus of the m/2 is small, uniradicate and almost circular in section.



**Figure 4.** MNCN 87000, *Forsythictis* nov. gen. *ibericus*. nov. sp. from Moratilla 2, Spain. Left mandible with partial canine root, distal root of p/2, p/3-m/1 and alveolus of m/2. A) occlusal view (stereo pairs), B) mesio-distal cross section, C) transverse section near the base of the tooth roots, D) lingual view (stereo pair), E) buccal view (stereo pair).

## Discussion

The mandible from Moratilla 2, selected to be the holotype of *Forsythictis ibericus*, eliminates ambiguities in the taxonomy of *Leptoplesictis* as well as *Forsythictis*; which could occur if it were

secondary to *Forsythictis aurelianensis* (mandible from Suevres or from Pontlevoy). The latter mandible lacks the mesial premolars (p3-p/1), which, as was discussed above, are crucial for distinguishing between these two

genera. According to the illustrations published by Mayet (1908) and Stehlin & Helbing (1925) *F. aurelianensis* appears to have an m/1 that is somewhat less sectorial than that in the most complete mandible from Petersbuch 2, identified by Roth (1988) as *Leptoplesictis aurelianensis*. *Forsythictis ibericus* is clearly more advanced towards a hypercarnivorous adaptation, which is why they are here separated into two genera. This runs counter to

the affirmation by Viret (1951, p. 79) that “Grâce à un moulage de la mandibule de Pontlevoy, j’ai pu me convaincre que celle-ci a appartenu à un fort sujet d’H. filholi”. However, this supposed similarity seems improbable, a revision and more precise illustration of the mandible from Pontlevoy may aid in throwing light on the relation between the species included in *Forsythictis*.

### Species *Forsythictis aurelianensis* (Schlosser, 1889)

#### Synonymy :-

- 1889 *Stenogale aurelianensis* Schlosser, p. 153.
- 1908 *Stenogale aurelianensis* Mayet, p. 223.
- 1925 *Herpestes aurelianensis* Stehlin & Helbing, p. 59.
- 1951 *Herpestes aurelianensis* Viret, p. 76.
- 1958 *Herpestes aurelianensis* Mein, p. 51.
- 1987 *Leptoplesictis aurelianensis* Schmidt-Kittler, p. 105.
- 1988 *Leptoplesictis aurelianensis* Roth, p. 335.
- 1999 *Leptoplesictis aurelianensis* Ginsburg, p. 131.
- 2002 *Leptoplesictis aurelianensis* Ginsburg, p. 130.
- 2008 *Leptoplesictis aurelianensis* Morales *et al.* p. 303.
- 2020 *Leptoplesictis aurelianensis* Grohé *et al.* p. 39.

**Type locality** :- Suevres (Schlosser, 1888); Ginsburg (2002), Stehlin & Helbing (1925) wrote that the type locality was Pontlevoy.

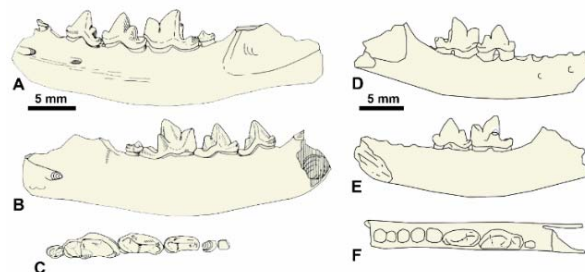
**Other localities** :- Petersbuch 2 and Erkertshofen 2, Germany (Roth, 1988), Artenay and Aerotrain, France (Ginsburg, 2002).

**Age** :- Middle Miocene, Middle Aragonian MN 4 (ca. 17-18 Ma).

**Diagnosis** :- Roth (1988).

**Differential diagnosis** :- *Forsythictis aurelianensis* differs from *F. ibericus* by the greater development of the metaconid of the m/1, which is displaced distally with respect to

the protoconid, the greater development of the accessory cusplets in the p/4 and the presence in p/3 of a well-developed distal accessory cusplet (Fig. 5).



**Figure 5.** Comparison between the mandible with alveolus of p/2 and complete p/3-m/2 of *Forsythictis* nov. gen. *aurelianensis* (Schlosser, 1887) from Petersbuch 2, Germany (after Roth, 1988) and the holotype of the species, a mandible with alveoli of p/1-p/3, complete p/4-m/1 and alveolus of m/2 (Pontlevoy 20) from Pontlevoy (after Stehlin & Helbing, 1925). A-C) *Forsythictis* nov. gen. *aurelianensis* from Petersbuch 2, A) buccal view, B) lingual view, C) occlusal view. D-F) *Forsythictis* nov. gen. *aurelianensis* from Pontlevoy, D) buccal view, E) lingual view, F) occlusal view.

**Table 1** Measurements (in mm) of the teeth of species of *Leptoplesictis*, *Forsythictis* and *Dunictis*. Data from : 1: Gaillard (1889) holotype of *Leptoplesictis filholi* Forsyth Major (1903). 2: measurements taken by the authors. 3: Roth (1988). 4: Peigné (2012). 5: measurements estimated by the authors in Viret (1951, Fig. 21). 6: Ginsburg (2002). \*alveolus measurement. \*\* Mandibles from La Grive identified as *Leptoplesictis minor* Forsyth Major (1903). (BLB – bucco-lingual breadth, MDL – mesio-distal length). (BSPG - Bayerische Staatssammlung für Paläontologie und Geologie, Munich; FSL - Faculty of Science, University of Lyon; GSN - Geological Survey of Namibia, Windhoek; MNHN - Muséum National d’Histoire Naturelle, Paris; NHMUK - Natural History Museum of the United Kingdom, London; SMNS - State Museum of Natural History, Stuttgart).

Species	Catalogue	Locality	c/1		p/2		p/3		p/4		m/1		m/2		Data source
			MDL	BLB	MDL	BLB	MDL	BLB	MDL	BLB	MDL	BLB	MDL	BLB	
<i>Leptoplesictis filholi</i>	MNHN LGr 1372	La Grive			3*		4		4.5		5	2.5	2.5	2	1
<i>Leptoplesictis filholi</i>	NHMUK M 5308	La Grive			3	1.1	3.1	1.5	3.5	1.6	4.5	2.5			2
<i>Leptoplesictis filholi</i>	NHMUK M 5552a	La Grive			3.3	1.1	3.6	1.3	3.5	1.7	5.1	2.4			2
<i>Leptoplesictis minor**</i>	NHMUK M 5552c	La Grive					3.5	1.3	3.8	1.6	4.7	2.6	2.4	1.6	2
<i>Leptoplesictis minor**</i>	NHMUK M 5552b	La Grive							3.6	1.6	4.4	2.6			2
<i>Forsythictis aurelianensis</i>	Pontlevoy 20	Pontlevoy							4.6		5.3				3
<i>Forsythictis aurelianensis</i>	BSPG 1976 XXII 3669	Petersbuch 2			2.9		3.7	1.4	4.5	2	5.6	2.5	1.6	1.2	3
<i>Forsythictis aurelianensis</i>	SMNS 44366	Petersbuch 2							4.7	2.1					3
<i>Forsythictis atavus</i>	FSL 65580 VxC	Vieux-Collonges									5.1	2.4			3
<i>Forsythictis atavus</i>	MNHN Sa 940	Sansan					3.3	1.3	3.6	1.5					4
<i>Forsythictis atavus</i>	MNHN Ss 5340	Sansan									4.7	2.5			3
<i>Forsythictis ibericus</i>	MNCN 87000	Moratilla 2					3.1	1.7	4.3	1.9	5.6	2.8			2
<i>Dunictis senutae</i>	GSN GT 10'06	Grillental VI			3.4	2	4.3	2.1	5	2.5	6	3	2*		2
<i>Dunictis senutae</i>	GSN GT 5'18	Grillental VI	3	2.5	2.9	1.6	3.9	1.8	4.9	2.2	5.5	2.8	1.5*	1.6*	2
? <i>Dunictis namibiensis</i>	GSN LT 30'07	Langental									8.3	4.4			2

Species	Catalogue	Locality	C1/		P2/		P3/		P4/		M1/		M2/		Data Source
			MDL	BLB	MDL	BLB	MDL	BLB	MDL	BLB	MDL	BLB	MDL	BLB	
<i>Leptoplesictis filholi</i>	MNHN LGr 1375	La Grive							5.1	3.3	2.7	5.1	0.7*	2.5*	5
<i>Forsythictis aurelianensis</i>	MNHN AR 2403	Artenay			2.8	1.65	4.5	2.2	7	3.65	2.7	5			6
<i>Forsythictis atavus</i>	FSL 65580 VxC	Vieux-Collonges									2.5	4.5			3

### Species *Forsythictis atavus* (Beaumont, 1973)

#### Synonymy :-

- 1973 *Herpestes (Leptoplesictis) aurelianensis atavus* Beaumont, p. 293.  
 1987 *Leptoplesictis atavus* Roth, p. 181.  
 1988 *Leptoplesictis atavus* Roth, p. 339.  
 1999 *Leptoplesictis atavus* Ginsburg, p. 131.  
 2012 *Leptoplesictis atavus* Peigné, p. 625.

**Type locality** :- Vieux Collonges, France

**Age** :- Middle Miocene, MN 5.

**Diagnosis** :- In Roth (1988).

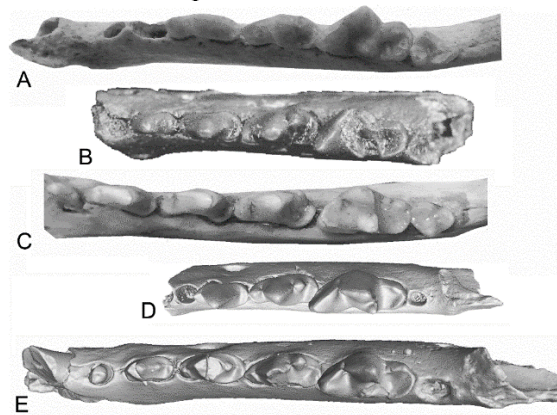
### Discussion

The species is so poorly represented that it is difficult to be precise about its validity, comprising the material described by Beaumont (1973) from Vieux Collonges (Mein, 1958), to

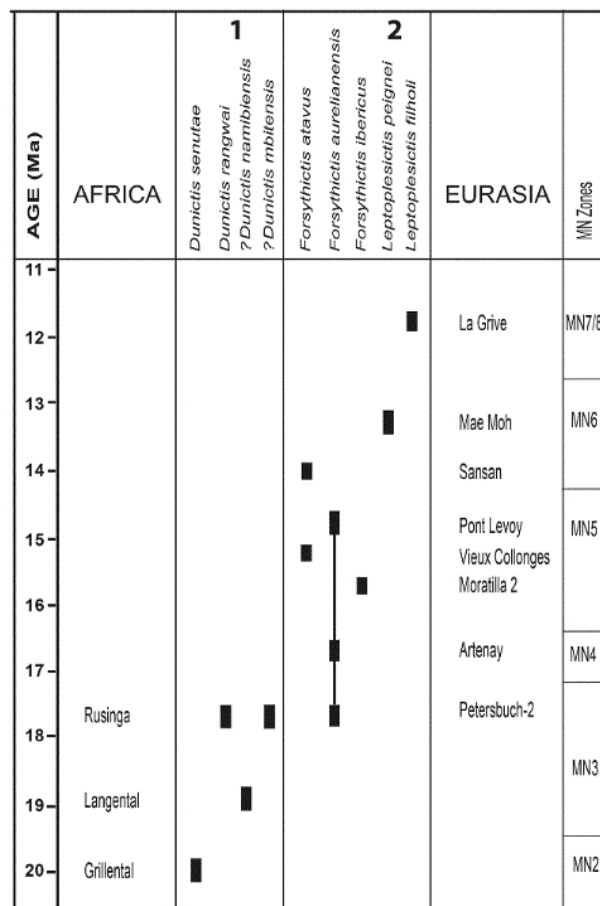
which Roth (1988) added a mandible from Sansan in which only the m/1 is preserved, that Ginsburg (1961) identified as *Herpestes aurelianensis*. Nevertheless, the size of the

alveolus of the m/2, is greater than that of *Forsythictis*, and the apparently greater robusticity of the m/1 could indicate a closer relationship to *Leptoplesictis filholi*. Peigné (2012) added a fragment of mandible with p/3-

p/4 to the hypodigm which could provide additional support in that, at least the fossils from Sansan resemble *Leptoplesictis filholi* from La Grive (Fig. 6).



**Figure 6.** Mandibles in occlusal views; A) NHMUK M 5552, *Leptoplesictis filholi* (Gaillard, 1888) from La Grive-Saint-Alban, France; B) MM-51, *Leptoplesictis peignei* Grohé *et al.* (2020) from Mae Moh, Thailand; C). *Genetta genetta* Linnaeus, 1758, extant from Spain; D) MNCN 87000, *Forsythictis* nov. gen. *ibericus* nov. sp. from Moratilla 2, Spain; E) GSN GT VI 5'18, *Dunictis* nov. gen. *senutae* (Morales *et al.* 2008) from Grillental VI, Namibia.



**Figure 7.** Biochronology of African and Eurasian Miocene localities, with the temporal ranges of the species of *Leptoplesictis*, *Forsythictis* and *Dunictis*. For correlations of African localities see Pickford (1986), Pickford & Senut (2003) and Werdelin & Peigné (2010); for European and Asian localities see Daams *et al.* (1999), Ginsburg (1999), Prieto & Rummel (2016) and Grohé *et al.* (2020). 1, African species. 2, Eurasian species. The time scale is from Hilgen *et al.* (2012).

## Conclusions

The revision of *Leptoplesictis* exposes the heterogeneity of the species previously included in the genus (Fig. 6) already evoked by Schmidt-Kittler (1987) and Morales *et al.* (2008), who reduced the content to two; the type species erected by Forsyth Major (1903) *Leptoplesictis filholi* (Gaillard 1899) from La Grive-Saint-Alban, France, and the recently defined *Leptoplesictis peignei* Grohé *et al.* (2020) from the middle Miocene of Thailand (Fig. 7). These two species are evidently affiliated with extant *Genetta*. The other species previously included in *Leptoplesictis*, exhibit important differences indicating that they represent distinct genera. On the one hand, the European species are herein classified in the genus *Forsythictis*, defined on the basis of a new species *F. ibericus* from the middle Miocene of Spain which is the type species, whilst the oldest named species *Stenogale aurelianensis* Schlosser (1888) is today called *Forsythictis aurelianensis*, and with some uncertainty, a third species is included, *F. atavus* Beaumont (1973) which is poorly known (Fig. 7). *Forsythictis* is characterised by a hypercarnivorous dental adaptation, more derived than that of *Leptoplesictis* but comparable to that of *Stenoplesictis cayluxi* Filhol (1880) or *Semigenetta mutata* (Filhol, 1891) even if the lower carnassial has a lower and more extended trigonid with slight reduction of the talonid compared to the species of *Stenoplesictis* (Peigné & De Bonis, 1999) or

of *Semigenetta* (Ginsburg, 1961). Finally, the African species – the oldest of the group studied herein (Fig. 7) are classified in a new genus *Dunictis* with *D. senutae* from Grillental, Namibia, as the type species, to which are transferred two species from Kenya previously attributed to *Leptoplesictis* by Schmidt-Kittler (1987); today known as *Dunictis rangwai* and with an element of doubt (?) *Dunictis mbitensis*. *Dunictis* is clearly less hypercarnivorous than *Forsythictis*. It also differs from *Leptoplesictis* in the morphology of the talonid of the m/1, in which the central basin is well developed and the talonid of the premolars which broaden distally forming a shallow valley.

The genera discussed in this paper have been included in the family Viverridae but conscious of the ambiguity of this classification expressed by Veron (2010) who wrote “*The relationships within the Viverridae have been long debated, largely due to their large diversity of forms and also because this family was a dumping ground for all ‘viverrid-like’ species of feliforms*”, a reflection that applies to the fossil forms, including those discussed herein. Without doubt, the three genera discussed in this contribution fall into a diffuse space comprising the grades “*Stenoplesictinae*” and “*Viverridae/Herpestidae*” which overlap, and as such they contribute to the resolution of one of the more interesting puzzles concerning the phylogeny and evolution of “*viverrid-like*” Feliformia.

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