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Tarsal diversity in the earliest Eocene mammal fauna of Dormaal, Belgium

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ABSTRACT. Mammal teeth bring important information regarding phylogeny and diet. However, postcranial elements, although poorly studied for small Paleogene mammals, can provide other significant data. The purpose of this study is to associate tarsal bones with dental specimens for a systematic identification. We thus chose the Belgian locality of Dormaal (Tienen Formation, Belgium) that has yielded the earliest Eocene mammals of Europe. This particularly rich fauna, dated between 55.5 and 55.8 Ma, occurred during the Paleocene-Eocene Thermal Maximum, a key period in the mammal evolution. It is composed by archaic mammals ("condylarths", arctocyonids, plesiadapiforms, "insectivorans"…) and also by earliest modern taxa (primates, rodents, carnivoraforms, artiodactyls …), representing about 14,000 dental specimens. 488 tarsal bones are studied according to three methods: morphology, relative abundance and relative size. 12 morphotypes of astragali and 18 of calcanei are discriminated and most of them are identified at the level of species (e.g. the marsupial *Peratherium constans*), genus or family (e.g. ischyromyid rodents). New perspectives in phylogeny and paleoecology are proposed for further studies implying tarsal bones.

KEYWORDS: PETM, Tienen Formation, postcranial, astragalus, calcaneus.

1. Introduction

Teeth are generally the most studied elements in mammal paleontology: highly mineralized, they represent the most preserved part of the skeleton. In the majority of cases, they are used for the identification of species and can also provide important information about diet and paleoenvironment. However, tarsal elements, although poorly studied for small Paleogene mammals, are widely recognized as holding a strong functional and sometimes phylogenetic significance (e.g. Zack et al., 2005). They display some complementary characters that are not submitted to the same selective pressures than teeth and can indeed provide additional information. Actually, the pattern of a tooth is generally characteristic of a particular taxon, but some convergences for an adaptation to a similar diet can be found in other taxa. Tarsal bones, not directly linked with diet, can retain phylogenetic features of the taxon. They are not automatically submitted to strong convergences: even for an adaptation to a similar locomotion, the numerous possibilities for tarsal articulation offer a large range of morphological patterns (e.g. two different morphologies for a similar arboreal locomotion in *Mixodectes* and *Chriacus*, in Szalay & Lucas, 1996), from whose phylogenetic hypothesis can be tested. The study of tarsal bones enables to add some characters in phylogenetic matrices (e.g. Godinot et al., 1996; Hooker, 2001), decreasing biases created by potential dental convergences. However, tarsal bones need to be associated to the corresponding dental remains for a systematic identification, so most of the described tarsal bones are known from rare complete or partial skeletons preserving teeth (Hooker, 2001). Consequently, and despite their great interest, very few is known about the tarsal diversity within a same fauna, especially for small mammals.

Our study has for aim to develop a methodology allowing to identify isolated astragali and calcanei of Paleogene mammal faunas. We have chosen the very rich earliest Eocene Dormaal fauna (Tienen Formation, Flemish Brabant, Belgium) that is known based on species represented by numerous dental remains.

2. Dormaal: a key locality from a key period in mammal evolution

The stratotype of the Dormaal Sand Member, exhibiting a cyclic sedimentation pattern of fluviatile origin, is dated between 55.5 and 55.8 Ma and represents the lower part of the Tienen Formation (Casier, 1967; Berggren & Aubry, 1996; Smith & Smith, 1996). Its stratigraphic position has been revised on the basis of sedimentology and micropaleontology (Steurbaut et al., 1999), ichtyology (Smith et al., 1999), and mammalian biochronology and isotopic stratigraphy (Smith, 2000; Smith et al., 2006). According to the paleobotanic association, the Dormaal palaeoriver system was bordered by warm-temperate to humid subtropical forests (Fairon-Demaret & Smith, 2002). The Dormaal mammal association defines the reference level MP7 of the mammalian biochronological scale for the European Paleogene that has yielded the earliest Eocene mammals of Europe (Schmidt-Kittler, 1987). Importantly, it is one of the richest Paleogene mammal fauna that occurred during the Paleocene-Eocene Thermal Maximum (PETM), a key period in mammal evolution (Smith, 2000). This event, discovered by Kennett & Stott (1991), is one of the most abrupt global warming (Zachos et al., 1993) and is characterized by at least 5° rise in deep-sea temperature in less than 10 ka (Zachos et al., 2008). The recovery to initial values was more gradual and the entire event lasted less than 170,000 years (Zachos et al., 2008). The PETM is characterized by a significative negative Carbon Isotope Excursion (CIE) of 2.5‰ – 4.5‰ observed in marine and terrestrial records (Kennett & Stott, 1991; Koch et al., 1992; Magioncalda et al., 2004).

Several important events are related to the PETM, like an important dissolution of seafloor carbonate (Thomas et al., 1999; Schmitz et al., 1997), a mass extinction of benthic foraminifera (Thomas, 1998), and also the widespread proliferation of numerous taxa, like exotic planktic foraminifera taxa (Kelly et al., 1996; Lu et al., 1998), the dinoflagellate *Apectodinium* (Crouch et al., 2001), or the colonization of thermophile plants (Wing et al., 2005; Tiffney, 1994). Several important intra and intercontinental migrations have also occurred (e.g. Woodburne et al., 2009) as the dispersal and subsequent radiations and turn-overs of Northern Hemisphere land mammals (Koch et al., 1992, 1995; Clyde & Gingerich, 1998; Beard & Dawson, 1999). PETM species were notably smaller in size than the related species present just before or after the event, with a loss of weight around 50 to 60% (Gingerich 1989, 2003; Strait, 2004). Moreover, the Paleocene-Eocene transition marks the appearance of modern mammal taxa such as Primates, Perissodactyla, Artiodactyla, Rodentia, Carnivoraformes, Hyaenodontida, Chiroptera and Cetacea. They replace, during Eocene, more primitive taxa that were most diversified during Paleocene such as Multituberculata, "Condylarthra", Plesiadapiformes, Oxyaenodonta, Procreodi, Acreodi and Cimolesta.

The particularly rich fauna of Dormaal is constituted by a mix of archaic and modern mammals (Table 1). The association is dominated by the louisinid "condylarth" *Paschatherium dolloi*, the arctocyonid procreodi *Landenodon woutersi*, the herpetotheriid marsupial *Peratherium constans*, ischyromyid rodents, the "miacid" carnivoraform *Dormaalocyon latouri*, the erinaceomorph insectivore *Macrocranion vandebroeki*,

Order	Family	Species	% sp.	N
Marsupialia	Herpetotheriidae	*Peratherium constans*	5.88	349
Rodentia	Ischyromyidae	*Microparamys nanus*	1.30	77
		Paramys anacingularis	0.02	1
		Paramys sp.	0.81	48
		Pseudoparamys n. sp.	0.30	18
		cf. *Pseudoparamys* sp.	0.25	15
		Meldimys sp.	0.08	5
		Euromys ? *metacingularis*	1.06	63
		Indeterminate	2.58	153
Cimolesta	Apatemyidae	*Apatemys teilhardi*	0.67	40
	Pantolestidae	*Palaeosinopa russelli*	0.13	8
Hyaenodontida		*Prototomus minimus*	0.35	21
		Prototomus girardoti	0.02	1
		Arfia gingerichi	0.15	9
		Galecyon morloi	0.07	4
Oxyaenodonta		*Oxyaena woutersi*	0.02	1
		Palaeonictis gigantea		-
Carnivora	Miacidae	*Dormaalocyon latouri*	2.68	159
		Gracilocyon solei	0.08	5
Lipotyphla	Adapisoriculidae	*Bustylus* sp.	0.02	1
		Remiculus cf. *deutschi*	0.05	3
		Remiculus delsatei	0.15	9
	Amphilemuridae	*Macrocranion vandebroeki*	3.17	188
		Macrocranion germonpreae	0.07	4
	Nyctitheriidae	*Leptacodon dormaalensis*	0.96	57
	Family indet.	*Wyonycteris richardi*	0.91	54
		Gen. et sp. indet.		-
Plesiadapiformes	Plesiadapidae	*Platychoerops georgei*		-
Primates	Omomyidae	*Teilhardina belgica*	5.22	310
Procreodi	Arctocyonidae	*Landenodon woutersi*	1.85	110
Condylarthra	Louisinidae	*Paschatherium dolloi*	69.55	4127
		Paschatherium yvetteae	0.17	10
		Paschatherium sp. 1	0.17	10
		Paschatherium sp. 2	0.17	10
		Teilhardimys musculus	0.08	5
		Louisinidae n. gen. n. sp.	0.24	14
		Gen. et sp. indet.	0.47	28
	Family indet.	Gen. et sp. indet.	0.05	3
	Phenacodontidae	*Phenacodus teilhardi*	0.03	2
Artiodactyla	Dichobunidae	*Diacodexis gigasei*	0.12	7
Indeterminate			0.07	4

Table 1. Faunal list of Dormaal mammals (modified from Smith, 1999). Relative abundance of each taxon is indicated as **% sp.** and number of dental remains as **N**.

and the omomyid primate *Teilhardina belgica* (Smith & Smith, 1996; Smith, 1999, 2000). It is worth noticing that the genus *Teilhardina*, the oldest euprimate known from Asia, Europe and North America, has undergone a rapid geographic dispersal associated with important morphological character evolution during the PETM (Smith et al., 2006).

3. Material and methods

3.1. Dormaal mammal specimens

The tarsal bones here studied are represented by 209 astragali and 279 calcanei respectively. These 488 specimens have to be compared with the 14,000 dental specimens that were collected from Dormaal. Among them, about 4,500 belong to RBINS collections (including the G. Wouters and D. Delsate collections), about 2,000 were collected by P. Gigase and more than 7,000 by R. Smith. Between 1989 and 1990, R. Smith collected 24 tons of fossiliferous sediments (Smith & Smith, 1996) that were screenwashed on meshes of 0.85 mm in order to collect all the mammal diversity.

3.2. Methods

In order to associate tarsal bones with dental remains of Dormaal taxa, three independent methods are used, following Cifelli

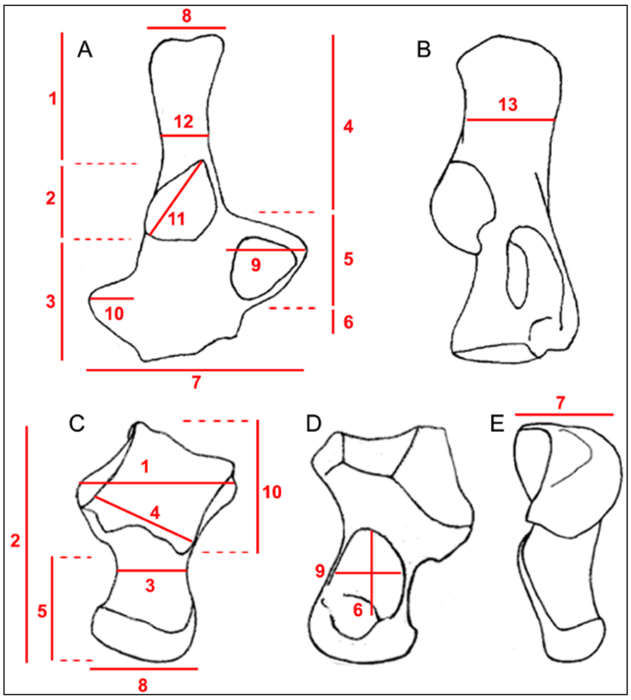

Figure 1. Measurements taken on calcaneus (A, B): 1-proximo-distal length from the proximal border of the calcaneus to the proximal border of the ectal facet, 2-proximo-distal length of the ectal facet, 3-proximo-distal length from the distal border of the ectal facet to the distal border of the calcaneus, 4-proximo-distal length from the proximal border of the calcaneus to the proximal border of the sustentaculum, 5- proximo-distal length of the sustentaculum, 6-proximo-distal length between the distal border of the sustentaculum and the medio-distal border of the calcaneus, 7-medio-lateral width of the calcaneus, 8-medio-lateral width of the proximal part of the tuber calcanei, 9-medio-lateral width of the sustentaculum, 10-medio-lateral width of the peroneal tubercle, 11-maximal length of the ectal facet, 12-minimal width of the tuber calcanei, 13-ventro-dorsal depth of the tuber calcanei. Measurements taken on astragalus (C, D, E): 1-maximal medio-lateral width of the astragalus, 2-maximal proximo-distal length of the astragalus, 3-minimal medio-lateral width of the neck, 4-minimal length between trochlea's condyles, 5-proximo-distal length from the distal border of the trochlea to the distal border of the astragalus, 6-proximo-distal length of the sustentacular facet, 7-ventro-medial depth of the trochlea, 8-medio-lateral width of the navicular facet, 9-medio-lateral width of the sustentacular facet, 10-proximo-distal length of the trochlea.

Table 2. Data used for the construction of linear regression models (Fig. 2A-B) in the frame of relative abundance study. Length and width, in millimeters, represent the measurements taken in a specimen, or the mean of several specimens of a species, according to the availability of bibliographical data.

Species	astragalus length	calcaneus length	m2 length	m2 width	Source	Reference
Afrodon gheerbranti	3.24	4.29	1.92	1.15	De Bast et al., 2012 ; Smith et al., 2010	1
Alcidedorbignya inopinata	10.79		5.37	3.92	de Muizon et al., 1998	2
Arctocyon primaevus	28.50	52.50	12.80	11.30	Russell, 1964	3
Arfia shoshoniensis	19.95	34.95	9.05	5.22	Gingerich & Deutsch, 1989	4
Asionyctia guoi		2.47	1.31	0.90	Missiaen & Smith, 2005 ; Missiaen et al., 2006	5
Bustylus folieae	2.24	2.76	1.41	0.94	De Bast et al., 2012	6
Bustylus marandati	1.81	2.35	1.23	0.82	De Bast et al., 2012 ; Smith et al., 2010	7
unnamed Condylarthra	8.08		4.21	4.26	de Muizon et al., 1998	8
Eomylus bayanulanensis	3.10	4.25	1.85	1.88	Missiaen & Smith, 2008 ; Missiaen et al., 2006	9
Gazinocyon vulpeculus	20.33	32.90	8.33	4.73	Polly, 1996	10
Miacis exiguus	14.20		4.13	3.09	Gingerich, 1983	11
Molinodus suarezi	8.06		3.70	2.80	de Muizon et al., 1998	12
Notoparamys costilloi	20.00	28.40	4.60	4.46	Rose & Koenigswald, 2007	13
Palaeonictis gigantea	29.90		9.95	6.12	Solé et al., 2011	14
Palaeostylops iturus	4.90	8.60	3.53	1.76	Missiaen & Smith, 2008 ; Missiaen et al., 2006	15
Plesiadapis cookei	13.02	18,8	6.32	5.56	Boyer, 2009	16
Plesiadapis rex	7.94		4.89	4.56	Boyer, 2009	17
Prodinoceras efremovi		69.35	16.00	12.50	Missiaen & Smith, 2008 ; Missiaen et al., 2006	18
Prolimnocyon atavus		20.60	6.90	4.50	Gebo & Rose, 1993	19
Prototomus martis	14.10		7.40	4.70	Gingerich & Deutsch, 1989	20
Pseudictops lophiodon		24.15	5.15	5.45	Missiaen & Smith, 2008 ; Missiaen et al., 2006	21
Pucanodus gagnieri	5.95		2.60	2.50	de Muizon et al., 1998	22
Rhombomylus turpanensis	8.38	13.07	3.57	4.72	Meng et al., 2003	23
Tiuclaenus minutus	5.80		2.50	1.70	de Muizon et al., 1998	24
Tribosphenomys minutus	2.10	3.05	0.95	0.96	Missiaen & Smith, 2008 ; Missiaen et al., 2006	25
Tritemnodon strenuus	24.00	38.30	9.00	5.30	Egi, 2001	26
Uintacyon rudis	16.50		4.30	3.17	Gingerich, 1983	27
Zionodon satanus	7.90	14.00	3.50	2.70	Dunn & Rasmussen, 2009	28
Zionodon walshi	8.80		3.80	2.90	Dunn & Rasmussen, 2009	29
Teilhardimys reisi	4.20	8.70	2.64	2.11	Tabuce et al., 2006	30

(1983): morphology, relative size and relative abundance. Astragali and calcanei are also associated by physical adjustment between them.

3.2.1. *Morphology*

Morphological comparisons are mostly made on the basis of reference collections, casts and literature. After the discrimination of several morphotypes according to the global morphology of specimens, 10 different measurements on astragalus and 13 measurements on calcaneus are taken with a graduated stereo microscope (Fig. 1), encompassing the major characters of tarsal bones. They are then computed under a Principal Component Analysis (PCA) with the freeware R (R Development Core Team 2011). Log-shape ratio approach (Mosimann, 1970) is used in order to avoid the size effect and to analyze only morphology.

3.2.2. *Relative abundance*

The relative abundance is based on the number of dental specimens of each species comparing to the total number of specimens (Table 1). Only the R. Smith collection is used for the count of teeth, its collecting methodology ensuring to obtain the entire fossil material, whatever the size of the specimens. Count is realized only on diagnostic teeth (upper and lower P4-M3 for placentals and upper and lower M1-M4 for marsupials) that represent a total of 5,934 specimens. Tarsal bones being significantly less numerous than teeth, count of astragali and calcanei is realized on the whole collections.

Compatibility between relative abundance of teeth and tarsal bones morphotypes is considered as acceptable when the difference remains under 30%. A threshold between 30 and 60% is considered as less probable but the compatibility is not excluded. Over 60%, the difference between relative abundances is supposed too important and the compatibility is excluded.

3.2.3. *Relative size*

Molar size is highly correlated with body size (e.g. Kay, 1975; Gingerich, 1977). In order to associate teeth and tarsal bones by relative size, comparison is made with 30 different species phylogenetically related to order, family or genus present in the Dormaal fauna, on the basis on bibliographical data (Table 2). Extant species are not used because of their derived tarsal morphology in comparison with Paleocene-Eocene taxa. Two linear regression models are thus constructed for the study of the covariation between the logarithm of m2 area (maximal length multiplied by maximal width of the tooth) and the logarithm of the length of calcaneus (Fig. 2A), and then astragalus (Fig. 2B).

A second step is the construction of another linear regression model associating teeth, astragali and calcanei of Dormaal species that were already published or identified during this study (Fig. 2C ; Table 3). This model is more adjusted to the Dormaal fauna, the previous one encompassing species of Europa, Asia and South America. This second model enables to refine the identifications made with the first model, when the morphology, relative size and abundance are not sufficient to select only one species for a tarsal morphotype.

4. Discrimination of morphotypes

Twelve morphotypes of astragali and 18 of calcanei previously determined by their global morphology are also discriminated by multivariate analysis, on the PCA computed on measurements taken as described in Figure 1 (Fig. 3).

On PCA made on astragali (Fig. 3A-B), PC1 encompasses 36.7% of variance and is strongly correlated with measurements 7, 3 and 5. It discriminates efficiently the morphotype A3, displaying a very long neck and a deep trochlea. PC2 (Fig. 3A) supports 16.5% of the variance and is more correlated with measurements 6 and

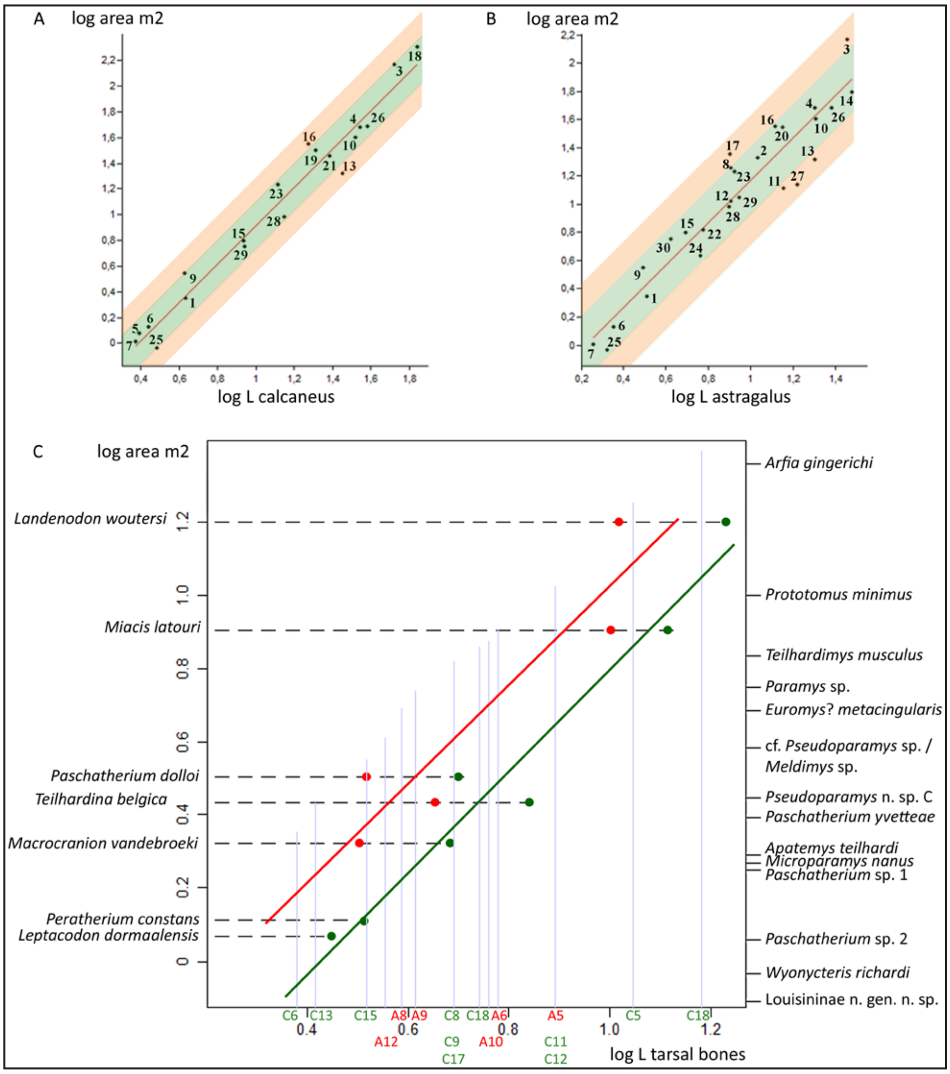

Figure 2. Size adjustment models between log of m2 area (length * width) and log of proximo-distal length of calcaneus (A) and astragalus (B). These models enable to test the compatibility in size between m2 and tarsal bones of Dormaal fauna. Green zone indicates a good compatibility and orange zone a less probable. Out of these zones, species defined by teeth and morphotypes of tarsal bones are considered as not compatible. Details of species used for the construction of linear models (on the basis of bibliographical data) are indicated in Table 2. r² = 0.97 for calcaneus (A) and r² = 0.90 for astragalus (B). A second size-adjustment model (C) includes two linear regression models for astragalus (in red) and calcaneus (in green). Log area of m2 are indicated vertically, for species used for the calibration of models (on the left) and for species for which tarsal bones morphotypes could match (on the right) (see Table 3 for raw data). Log of proximo-distal length of tarsal bones morphotypes are indicated horizontally. r² = 0.98 between m2 and calcaneus; r² = 0.93 between m2 and astragalus; r² = 0.99 between astragalus and calcaneus.

Species	**length m2**	**width m2**	**length astragalus**	**length calcaneus**
Peratherium constans	1.50	0.86		3.26
Microparamys nanus	1.36	1.36		
Paramys sp.	2.47	2.28	7.80	11.10
Pseudoparamys n. sp.	1.75	1.60		
cf. *Pseudoparamys* sp.	2.10	1.80		
Meldimys sp.	2.00	1.95		
Euromys ? metacingularis	2.23	2.18		
Apatemys teilhardi	1.83	1.06	3.40	4.90
Prototomus minimus	4.12	2.43		
Arfia gingerichi	6.90	3.45		
Dormaalocyon latouri	3.38	2.41	10.10	12.97
Macrocranion vandebroeki	1.66	1.26	3.20	4.83
Leptacodon dormaalensis	1.28	0.91		2.81
Wyonycteris richardi	1.19	0.78		
Teilhardina belgica	1.84	1.48	4.51	6.93
Landenodon woutersi	4.80	3.30	10.40	16.96
Paschatherium dolloi	1.99	1.60	3.29	5.00
Paschatherium yvetteae	1.73	1.42		
Paschatherium sp. 1	1.50	1.18		
Paschatherium sp. 2	1.22	0.94		
Teilhardimys musculus	2.95	2.33		
Louisinidae n. gen. n. sp.	1.00	0.78		

Table 3. Raw data used for the construction of the second linear regression model (Fig. 2C) in the frame of relative abundance study. Length and width, in millimeters, represent the mean of the measurements taken in each species present in Dormaal. Length of tarsal bones is indicated for species used for the construction of linear models. Length and width of m2 are indicated for all Dormaal species, for the comparison with morphotypes.

9, then 4. This axis discriminates efficiently the morphotype A9, displaying a small sustentacular facet and a very asymmetrical trochlea. PC3 (Fig. 3B), supporting 11.2% of variance, provides less information than the two first principal components for species discrimination. This axis is mainly correlated with measurement 10 and to a lesser extent with measurement 9, which is also shared with PC2. A light gradation can be noticed: morphotypes 1, 2, 3, 6 and 9 (that display a small proximo-distal length of trochlea relatively to the whole bone, and for some of them a small width of sustentacular facet), then 7, 8, 10 and 11 (for which the length of the trochlea represents approximatively half of the proximo-distal length of the bone) and finally 4, 5 and 12 (with a quite long trochlea, and a sustentacular facet nearly as long as wide).

Because of the consequent number of damaged specimens (mostly on the peroneal tubercle), calcaneus morphotypes 4, 9, 10, 13, 16 and 17 cannot be included in the PCA, this analysis requiring the globality of measurements for a better discrimination of morphotypes (Fig. 3C-D). The first principal component of the PCA (Fig. 3C) includes 57.2% of total variance and is highly supported by measurements 6 and 7. Measurements 1, 4, 8 and 9 are also relatively correlated with PC1. Two morphotypes displaying a peculiar shape are highly discriminated by PC1: morphotypes C3 (with an extremely long distal part of the bone, reaching almost the proximo-distal half of the calcaneum) and C14 (quite broad, with a very high sustencaculum, reaching the distal extremity of the bone). PC2, with 20.3% of the variance (Fig. 3C-D), shows more gradation. It is mainly supported by

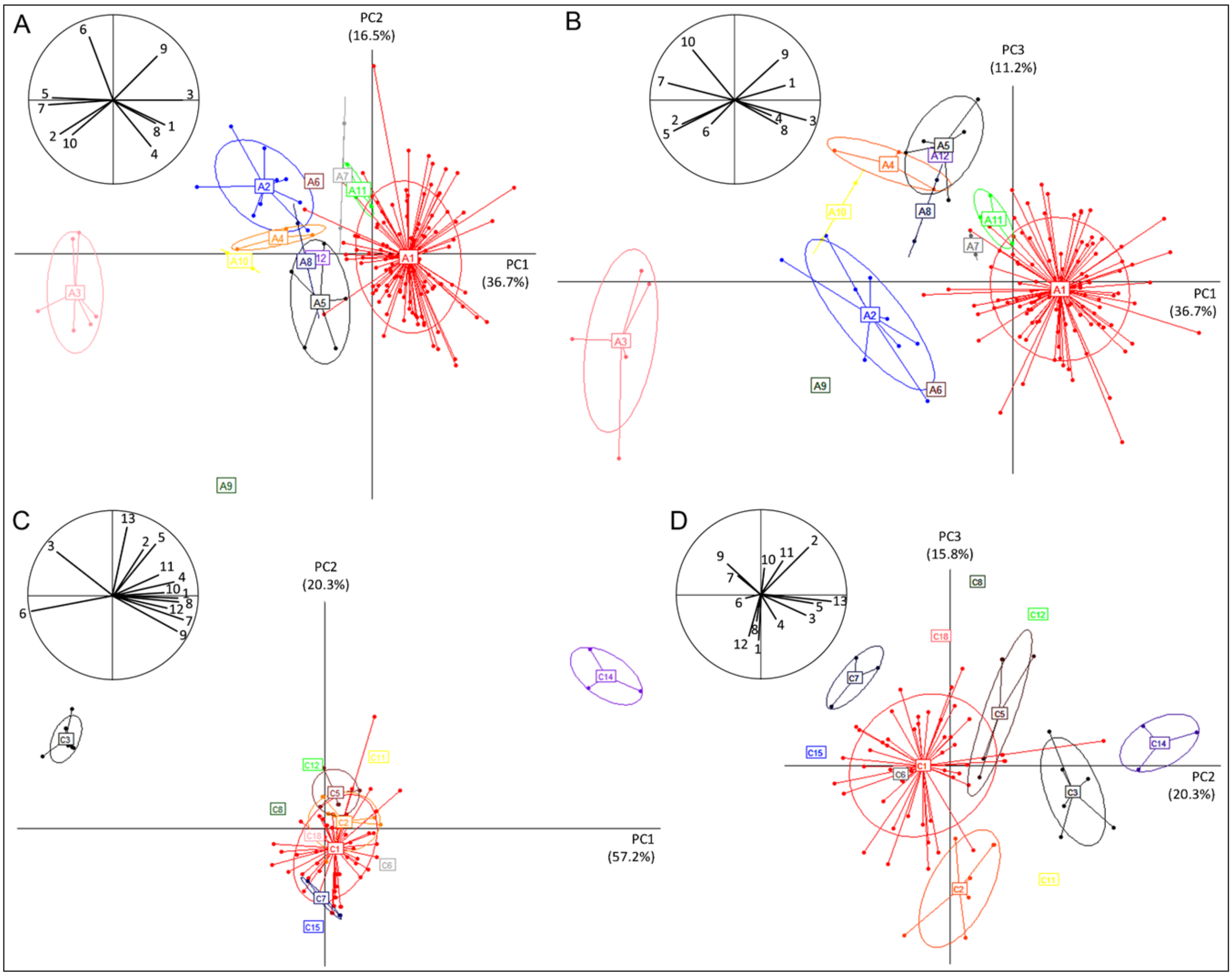

Figure 3. PCA computed with the log-shape ratio approach (Mosimann, 1970) on measurements taken on astragalus along PC1 and PC2 (A), PC1 and PC3 (B) and on calcaneus along PC1 and PC2 (C), then PC1 and PC3 (D) (see Fig. 1 for details of measurements).

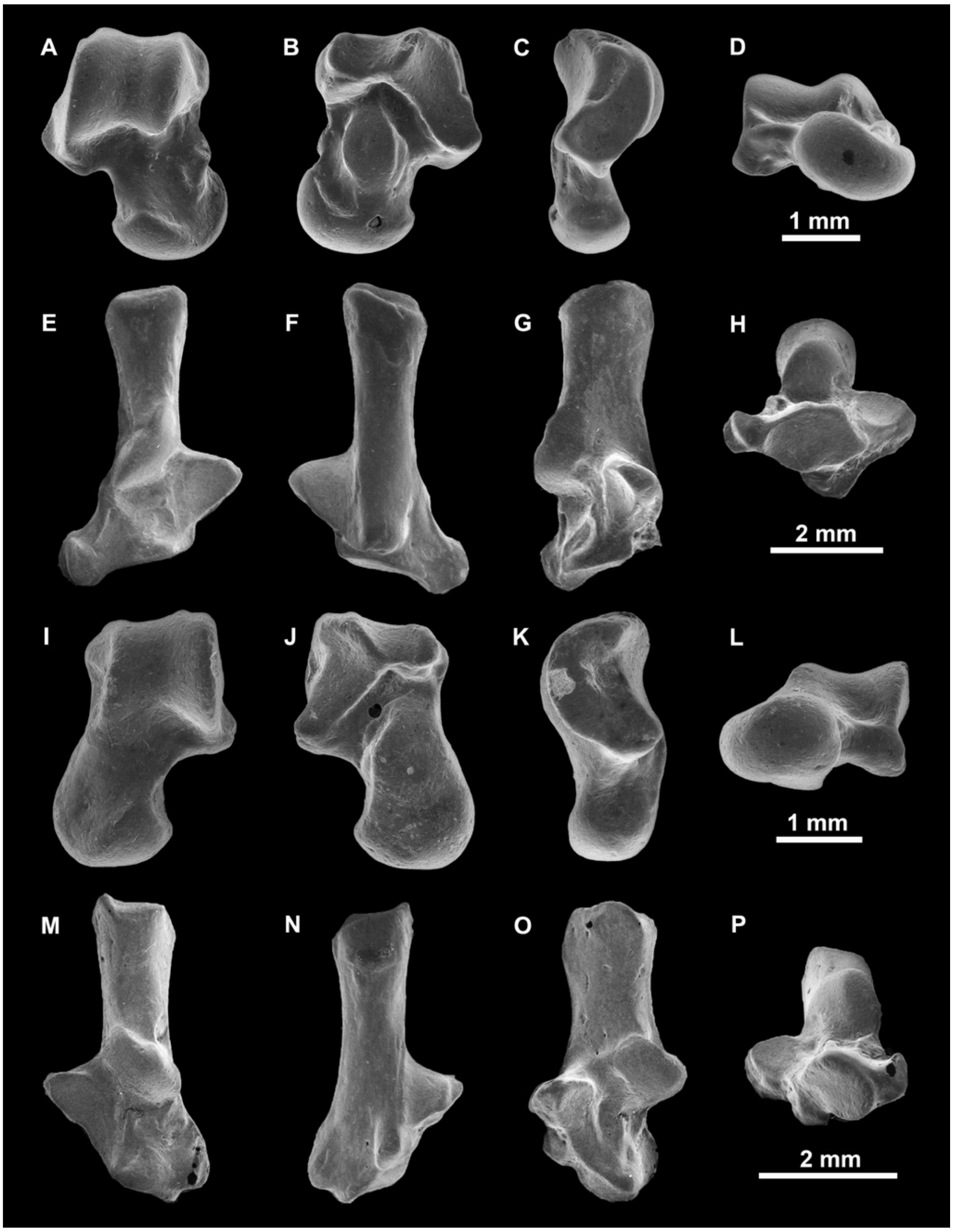

Figure 4. Tarsal bones of ***Paschatherium dolloi*** (A-H) (morphotypes A1: specimen IRSNB M1281 and C1: specimen IRSNB M1253 modified from Godinot et al., 1996) and ***Macrocranion vandebroeki*** (I-P) (morphotypes A2: specimen IRSNB M1282 and C2: specimen IRSNB M1251 modified from Godinot et al., 1996). Astragalus (A-D, I-L) and calcaneus (E-H, M-P) are represented in dorsal (A, E, I, M), ventral (B, F, J, N), lateral (C, K), medial (G, O) and distal (D, H, L, P) views.

measurement 13 then 5, 2 and 3, the latter being also partially shared with PC1. Morphotypes C15 (with proximo-distally small sustentacular and ectal facets, and long peroneal tubercle) and C14 (already well discriminated by PC1) are the most extreme along this axis. PC3, with 15.8% of variance (Fig. 3D), is mostly correlated with measurements 1 (shared with PC1), 2 (shared with PC2) and 12. The extreme morphotypes are C2 (with a proximo-distally small ectal facet and quite strong and long tuber calcanei) and C8 (with a proximo-distally longer ectal facet). Morphotypes are well discriminated along PC2 and PC3 (Fig. 3D), the information discriminating morphotypes C3 and C14 being supported mainly on PC1.

5. Identification of the morphotypes according to morphology, relative size and relative abundance

The discriminated morphotypes are then compared to Dormaal species on the basis of recognized typical morphologies for each taxonomic group and submitted to relative size and abundance analyses. The latter can be divided in three groups.

The first group is composed of some taxa displaying a very low abundance that do not match with any of the morphotypes and their tarsal bones can be thus considered as absent in the studied Dormaal collections. This is the case for Artiodactyla (e.g. Rose, 1982), Phenacodontidae (e.g. Rose, 1996), Oxyaenodonta (Szalay, 1977; Denison, 1938; Matthew, 1915), Plesiadapidae (e.g. Szalay & Decker, 1974; Gunnell, 1989), Adapisoriculidae (Smith et al., 2010) and Pantolestidae (Rose & Koenigswald, 2005).

The second group is represented by morphotypes A5, A8, C5, C8, C12, C18 that all display the Paramyine rodent-like morphology (Hooker, 2001; Meng et al., 2003; Rose & Chinerry, 2004; Szalay, 1985). It remains difficult to identify these morphotypes at the species or genus level, even with the second relative size model (Fig. 2C) until the systematic study based on numerous isolated dental specimens is not finished.

The third group contains morphotypes that can be easily identified by the association of the three methods. This is especially the case for species that are represented by abundant tarsal bones such as the three species from Dormaal that have already been described: the abundant louisinid "condylarth" *Paschatherium dolloi* (morphotypes A1 and C1, Fig. 4A-H) (Godinot et al., 1996), the amphilemurid insectivore *Macrocranion vandebroeki* (morphotypes A2 and C2, Fig. 4I-P) that is significantly more abundant than *Macrocranion germonpreae* (Table 1) (Smith & Smith, 1995; Godinot et al., 1996); and finally the omomyid primate *Teilhardina belgica* (morphotypes A3 and C3, Fig. 5A-H) (Gebo et al., 2012). All three species are identified based on morphology, relative size and relative abundance. The other morphotypes that can be referred to species will not all be detailed here because several of them will be described in systematic

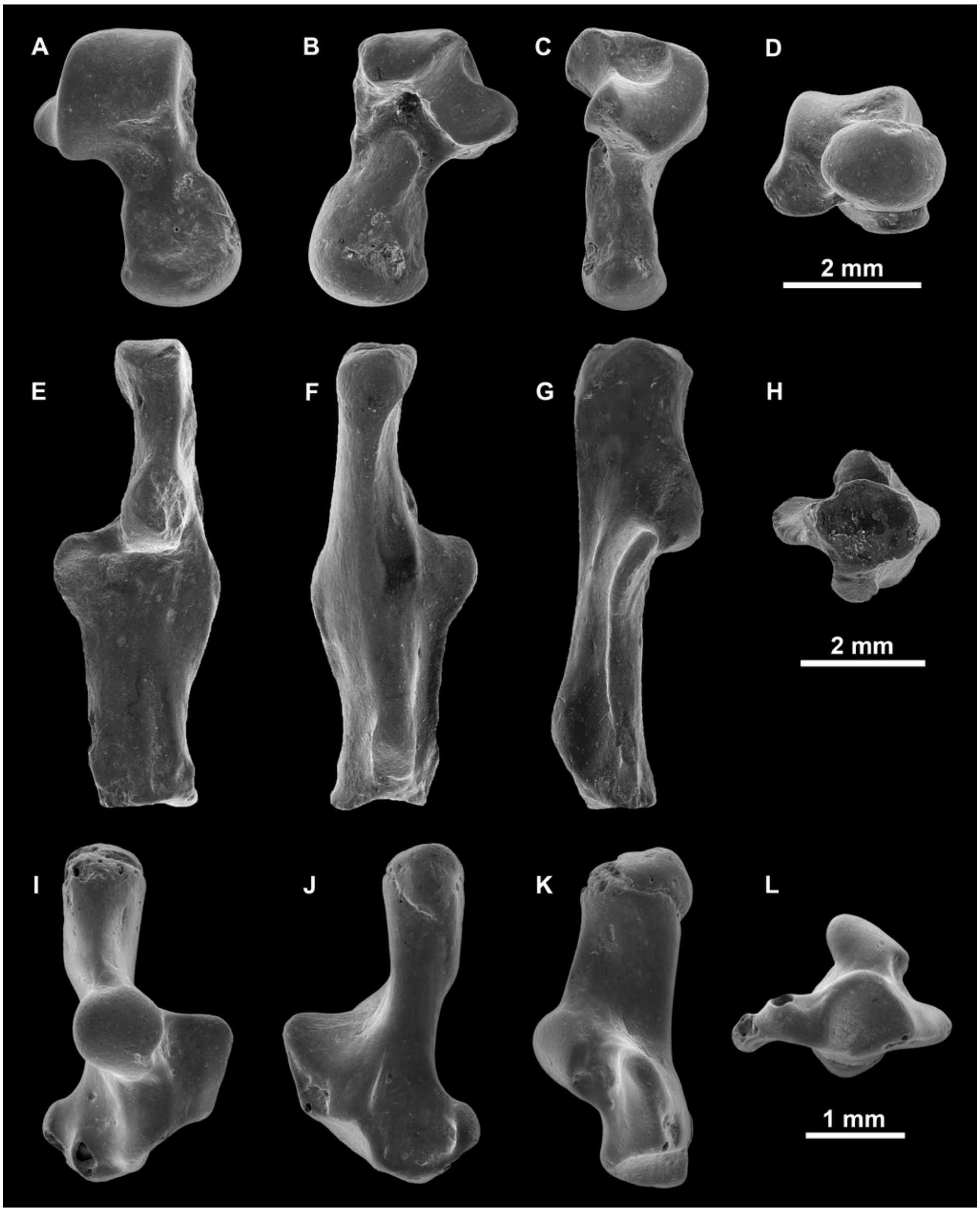

Figure 5. Tarsal bones of ***Teilhardina belgica*** (A-H) (morphotypes A3: specimen IRSNB M1235 and C3: specimen IRSNB M1236) and ***Peratherium constans*** (I-L) (morphotype C14: specimen IRSNB M1329). Astragalus (A-D) and calcaneus (E-L) are represented in dorsal (A, E, I), ventral (B, F, J), lateral (C), medial (G, K) and distal (D, H, L) views.

studies that are beyond the scope of the present methodological paper. However, three morphotypes taken to exemplify the efficiency of the methodology are here identified and commented.

Morphotype C14 displays a very particular morphology with a distorted tuber calcanei, a very rounded ectal facet, a proximo-distally extended peroneal tubercle that is situated more distally than the curved sustentacular facet, the latter extending until the distal border of the calcaneum. This morphology is typical for a scansorial Marsupialia (e.g. Szalay & Sargis, 2001; Rose, 2006). The very small size and high abundance of this morphotype confirm that it belongs to the herpetotheriid *Peratherium constans* (Fig. 5 I-L), which is the only marsupial present in Dormaal.

Morphotype C7 that presents nearly the same size that C14 shows a different outline with a straight tuber calcanei and a medio-laterally compressed ectal facet, characteristic of a placental mammal. The sustentacular facet, displaying a nearly rectangular shape, begins proximally at the level of the distal border of the ectal facet. The square peroneal tubercle is not in a distal position. The cuboid facet is rounded with a medial peak, and slightly inclinated medio-laterally. This morphology corresponds to a nyctitheriid insectivore (Hooker, 2001). The very small size and the weak abundance of this morphotype are in agreement with *Leptacodon dormaalensis* (Fig. 6A-D).

Morphotypes A4 displays a smooth trochlea (displaying a sharp lateral crest and a greatly blunt medial crest) with an astragalar foramen and a well-developed squatting facet. The surface for articulation with the distal tibia is broad and smooth. The sustentacular facet is rounded, slightly longer than wide. The navicular facet is much wider than the neck, dorso-ventrally compressed and medio-laterally oriented in distal view. This morphology is typical for a carnivoraform mammal (e.g. Heinrich & Houde, 2006 ; Spaulding & Flynn, 2009 ; MacIntyre, 1966) and is thus here referred to the species *Dormaalocyon latouri* (Fig. 6E-H) based on its greater size and abundance than the other miacid *Gracilocyon solei* (Table 1), which is about 25% smaller and very rare.

6. Discussion

It is important to associate the three methods we use in the present paper to obtain more probable results, some bias being inherent to each method (Solé et al., in press). It is particularly difficult to identify species belonging to groups for which the tarsal morphology is still unknown except if the relative abundance is high. *Paschatherium dolloi* that represents about 70% of the Dormaal fauna is one of the rare examples that have been identified only based on abundance and size (Godinot et al., 1996). Size-dependent bias is mostly related to the sampling: teeth count is realized only on R. Smith collection while tarsal bones count is done on the whole collections, encompassing more morphotypes, tarsal bones being much less numerous than teeth in vertebrate remains, and being more fragile than the more mineralized teeth. Screenwashing of old RBINS collections has been done on meshes of 2 mm, excluding very small bones (only found in

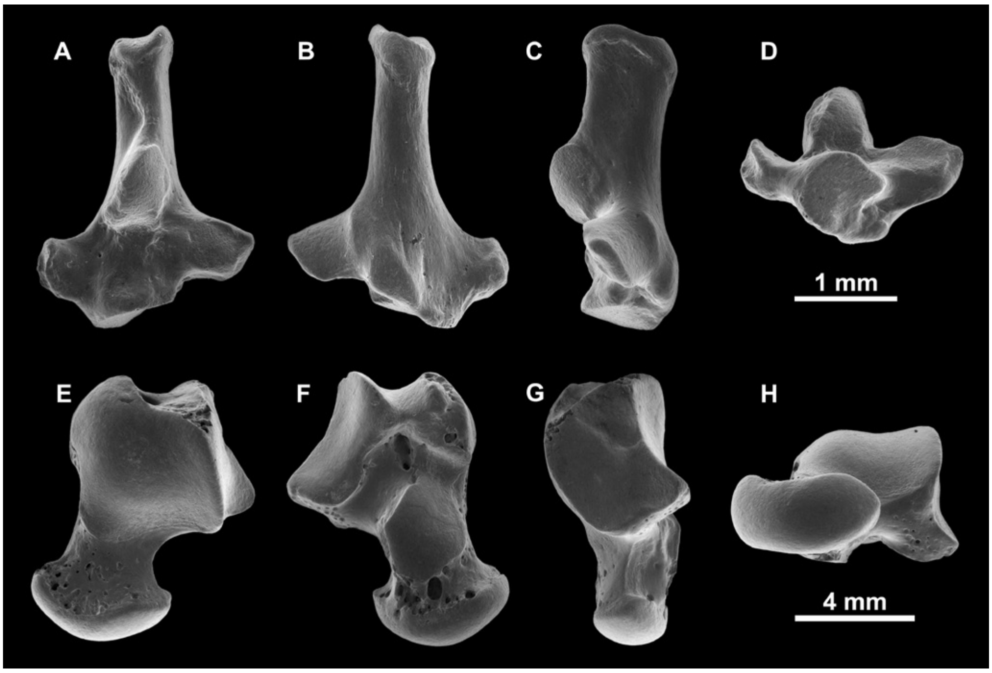

Figure 6. Calcaneum of ***Leptacodon dormaalensis*** (A-D) (morphotype C7: specimen IRSNB M1330) and astragalus of ***Dormaalocyon latouri*** (E-H) (morphotype A4: specimen IRSNB M2113 modified from Solé et al., in press) represented in dorsal (A, E), ventral (B, F), medial (C), lateral (G) and distal (D, H) views.

R. Smith and P. Gigase collections). Another size-dependent bias is related to the granulometric sorting due to local taphonomic conditions of the Dormaal deposits that preserved much more small and middle-sized mammal remains than large mammal remains (Smith, 1999). Large mammal species are indeed represented by only one tooth of Oxyaenodonta and two teeth of Phenacodontidae in R. Smith collection. However, Pantodonta, Acreodi and Perissodactyla, absent in Dormaal are present in the contemporaneous deposits of Erquelinnes in south Belgium (Dollo et al., 1924; Missiaen et al., this volume). Moreover, in comparison with isolated corresponding molars, astragali are about two times larger and calcanei are about three times larger. A significant bias in relative abundance can also be related to the numerous unidentified teeth, often due to their high wear.

In conclusion, this study enables to associate tarsal bones with species known by dental remains. Some of them are identified with certainty by means of the association of the three methods described previously. Others are assigned to higher taxonomical ranks and require further investigations for being identified at species level.

This work opens new perspectives for further studies implying tarsal bones. Comparison with other fossil taxa could improve knowledge about tarsal bones synapomorphies, and enables to identify derived characters in different taxonomic groups. Tarsal bones characters of Dormaal species could be assessed in an ecological and evolutionary framework before their use in phylogenetic analysis as proposed by Salton and Szalay (2004). Locomotion can also be inferred from tarsal bones characters, as well as other postcranial bones (Day & Jayne, 2007; Ladevèze et al., 2010; Smith & Smith, 2012). It provides supplementary information on paleoecology and paleoenvironments (e.g. Smith et al., 2006), revealing a direct relationship between mammal evolution and climatic changes. The association of high increase in temperatures during PETM, expansion of tropical forests, decrease of sea level and competition between archaic and first modern mammal faunas has led to important adaptive radiations and migrations. Study of tarsal bones enables to better understand changes of ecological niches in this frame.

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