PALÆO VERTEBRATA

ARTICLE

A pangolin (Manidae, Pholidota, Mammalia) from the French Quercy phosphorites (Pech du Fraysse, Saint-Projet, Tarn-et-Garonne, late Oligocene, MP 28)

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Abstract: Pangolins have never shown a high taxic diversity and their fossil record is scarce. We report here the first discovery of a partial humerus from late Oligocene deposits in Pech du Fraysse (MP28, France). The new specimen from Pech du Fraysse is described and compared to various extant and extinct species of pangolins. It shows a suite of morphological features very similar to the humeri discovered in Saint-André (MP 26), Solnhofen (Burdigalien), and Saulcet (Aquitanian), attributed here to *Necromanis franconica*. The description of the specimen from Pech du Fraysse allowed us to discuss the systematics of Paleogene and Neogene pholidotans. The differences between PFY 4051 and *N. franconica* on the one side, and *N. quercyi* on the other side, might be sufficiently important to justify a generic distinction. A comparison with extant species showed that *N. franconica* was likely terrestrial and fossorial based on its humeral morphology.

Keywords: Pangolin, Oligocene, Quercy phosphorites, Pech du Fraysse

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INTRODUCTION

The first excavations in the site of *Pech du Fraysse* (Saint-Projet, Tarn-et-Garonne, France) took place in 1967 within a specific action plan of the Laboratory of Paleontology in the Muséum national d'Histoire naturelle (MNHN, Paris, France; Crochet, 1971). Pech du Fraysse has since been used to define the mammalian standard level MP 28 (late Oligocene) at the *International Symposium on Mammalian Biostratigraphy and Palaeocology of the European Paleogene*, Mainz, 1987. In 1972, a pholidotan remain was collected *in situ*. This remain corresponds to a fragment of left humerus lacking the proximal epiphysis and a lateral portion of the distal epiphysis. The diaphysis is partially fractured but all the cristae and muscular insertion areas are well preserved as is usually the case for the material collected in this phosphate chamber (Laudet & Fosse, 2001). This chamber has a small karstic dome one to two meters long with a partially eroded surface (Fig. 1).

Extant pholidotans are restricted to Africa and southeastern Asia, but Cenozoic forms are known from Europe, northern America, Asia, and Africa (Gaudin *et al.*, 2009). The presence of a pholidotan in the fauna of Pech du Fraysse has previously been mentioned in the literature (Bonis *et al.*, 1973) under the generic attribution "cf. *Necromanis* sp. indet.", but the material has never been fully described. A detailed survey of the Pech du Fraysse collection, which includes several thousands of bony fragments collected over seven years (coll. MNHN, Paris and ISE-M, Université de Montpellier), has yet to identify any other mammalian remains attributable to a pholidotan. We present here the description of this bone that confirms the presence of pholidotans in Oligocene European deposits.

The systematics of extinct pholidotans has long been debated, even at a familial level. Szalay & Schrenk (1998) decided to place all extinct genera of Pholidota (i.e. *Eomanis*, *Patriomanis*, and *Necromanis*) in the family Patriomanidae. In contrast, Storch (2003) placed *Eomanis* (middle Eocene, Europe) in a new family, Eomanidae, and advocated for the removal of *Necromanis* from the Patriomanidae. Gaudin *et al.* (2006) also proposed that this family should be restricted to include only *Patriomanis* (late Oligocene, northern America) and the newly described *Cryptomanis* (late Eocene, Inner Mongolia, China). We follow the approach adopted in Storch (2003) and Gaudin *et al.* (2006) that recognized several families within the Pholidota. In their comprehensive morphology-based phylogenetic analysis, Gaudin *et al.* (2009) found strong support to distinguish *Necromanis* (Oligo-Miocene, Europe) from the Eocene European fossil genera (i.e., *Eomanis*, *Eurotamandua*, *Euromanis*), but failed to uncover unambiguous affinities with one of the two remaining families; *Necromanis* was considered to be a sister taxon to either Patriomanidae or to Manidae. This is interesting as over time several European genera have been questionably synonymised with *Necromanis*: *Leptomanis* Filhol, 1894, *Necrodasypus* Filhol, 1894, *Teutomanis* Ameghino, 1905, *Galliaetatus* Ameghino, 1905 (see Gaudin *et al.*, 2009). Such systematic results put into question the taxonomic attributions of these European Oligo-Miocene genera. The new discovery from Pech du Fraysse allows us to discuss the systematics of Paleogene and Neogene European pholidotans.

HISTORICAL BACKGROUND OF EUROPEAN DISCOVERIES

In 1875, for the first time, Gaudry detailed the presence of an edentate representative in France, which he believed was close to the Manidae, based on the discovery of two phalanges from a phosphate chamber near Caylux (Lot, Quercy). Gervais (1876) made reference to these specimens as well as to a humerus (an “extrémité inférieure” in the text) from the Filhol’s collection. Filhol (1894) addressed these concerns and considered the humerus to belong to the new genus and species *Necromanis quercyi*. The type specimen is a right humerus discovered in a phosphate chamber near Bach (Lot-et-Garonne, southwestern France). Filhol (1894) also described *Leptomanis edwardsi* from Larnagol (Lot, Quercy) on the basis of a partial skull. As often with the Quercy old collections, the exact location of the discovery remained unknown; the specimen is now stored at the MNHN.

Since then, several pholidotan remains were discovered in European sites, ranging from Eocene to Miocene in age (e.g. Quenstedt, 1885; Ameghino, 1905; Helbing, 1938; Koenigswald, 1969; Storch, 1978a, b). The material is extremely rare and consists mainly of humeri, which bear some of the diagnostic features of the group. The now reknown Messel Pit fossil site (MP 11, Lenz *et al*., 2014) yielded several complete *Eomanis waldi* skeletons, including the holotype of the species (Storch, 1978a, b; Koenigswald & Martin, 1990; Storch & Martin, 1994). To date, the only Paleogene fossils of Pholidota found in France are the aforementioned few well-preserved remains from Quercy (Bach and Larganol) attributed to *Necromanis quercyi* and *Leptomanis edwardsi*, and a proximal epiphysis of a humerus from Saint-André near Marseille (MP 26; Helbing, 1938; Emry, 1970), which was attributed to cf. *Teutomanis* by Emry (1970). In French Miocene deposits, several remains were reported from

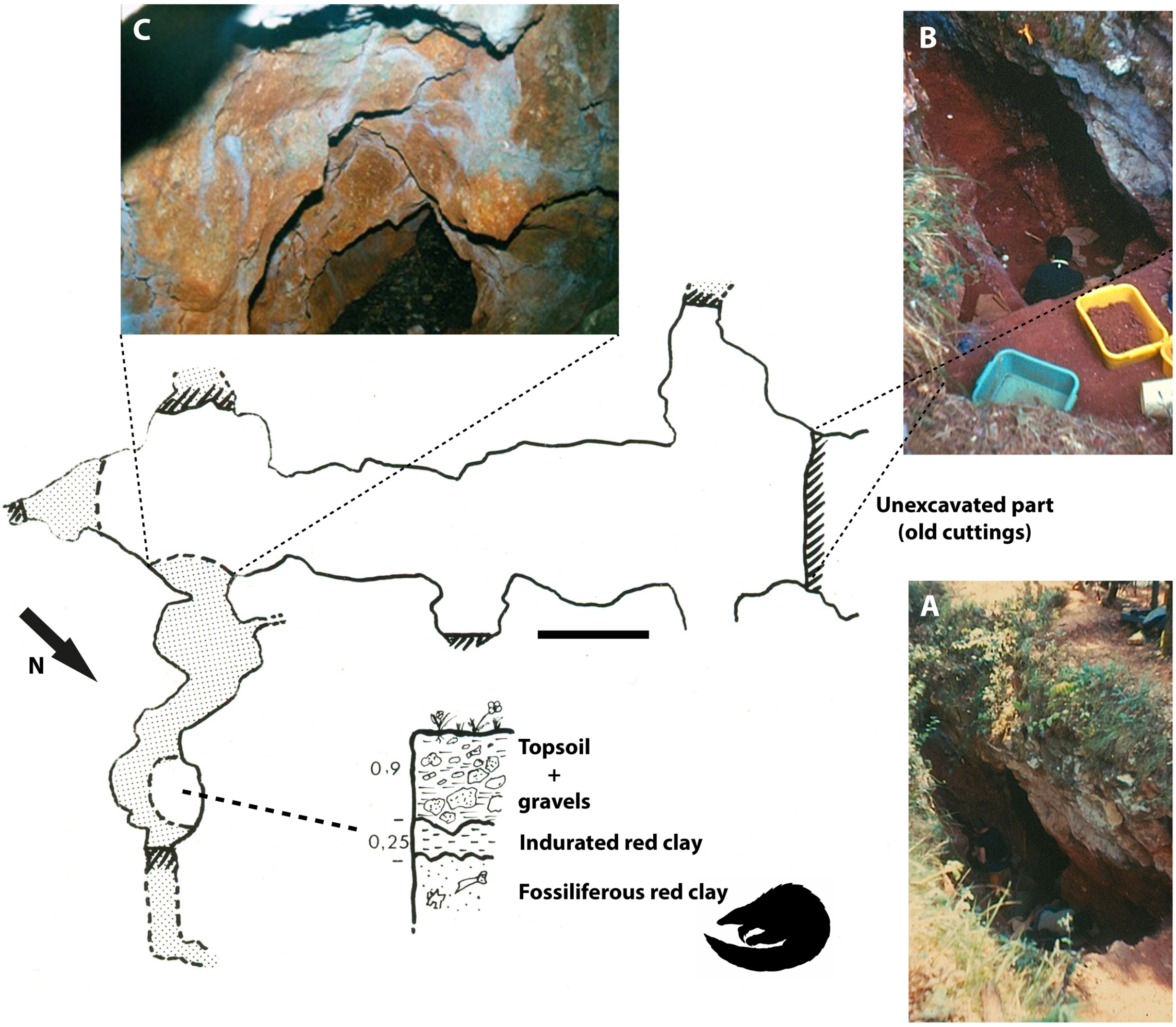

Figure 1. Schematic representation of the phosphate chamber of Pech du Fraysse (aerial view) and stratigraphic position of the red clays that yielded the fossil of pangolin described in this study. Grey areas represent galleries. (**A**) surface view of the phosphate chamber; (**B**) excavation in the main gallery (old phosphate exploitation site); (**C**) gallery where the humerus PFY 4051 was found. Scale bar = 1 m.

Mont-Ceindre (Lyon, France; Ameghino, 1905), Vieux Colonges (Lyon, France; Mein, 1958), La Grive Saint Alban (Lyon, France; Viret, 1951), and a radius was described from the Aquitanian of Montaigu-le-Blien (Allier, France; Helbing, 1938). In 1990, Koenigswald & Martin described a partial skeleton of *N. franconica* from Aquitanian deposits of Saulcet (Allier, France).

Several successive German discoveries confirmed the presence of manid representatives in Europe during the Miocene. First, in 1885, Quenstedt created the species *Lutra franconica*; the type specimen is a humerus discovered in the Burdigalian site of Solnhofen near Eichstätt, accompanied by a radius and an ulna. Schlosser (1904) made a passing mention of additional fragments including the distal portion of a humerus from the same site. Ameghino (1905) later identified some "edentate" ("édenté" in the text) features and proposed the new genus *Teutomanis* for this material. Several authors (Schlosser, 1907; Guth, 1958; Emry, 1970) have followed Ameghino's generic attribution, but Koenigswald (1969) decided to include it within the genus *Necromanis*. Second, from the same site of Solnhofen, *Teutomanis quenstedti* Ameghino, 1905 was described for the aforementioned distal portion of humerus. Then, Helbing (1938) published an astragalus and two calcanei (SMF M3379a, b, c) from Mainz-Weisenau (Germany) that he brought together with *Teutomanis*. Finally, Koenigswald (1969) created the species *N. parva* based on the distal portion of a humerus, a femoral diaphysis, and a proximal ulna from the Helvetian site of Wintershof-West. In the same paper, this author described *Necromanis* sp. material from the Oligocene of Gunzenheim (Germany; fragment of tibia) and Gaimerscheim (Germany; fragment of femur). He also considered *T. franconica* and *T. quenstedti* to be synonym taxa.

Institutional abbreviations: MNHN, Muséum National d'Histoire Naturelle, Paris, France; PFY, Pech du Fraysse, Université de Montpellier, Montpellier, France; SMF Senckenberg Research Institute and Natural History Museum Frankfurt.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PHOLIDOTA Weber, 1904
Family ?PATRIOMANIDAE Szalay & Schrenk, 1998
Genus *Necromanis* Filhol, 1894
Species *N.* cf. *franconica*

Referred material. PFY 4051, a partial left humerus, coll. Paléontologie, ISE-M, Univ. Montpellier. A 3D reconstruction of PFY 4051 was deposited in MorphoMuseum (M3#12 UM PFY 4051).

Age and occurrence. MP 28 (late Oligocene), Pech du Fraysse (Saint-Projet, Tarn-et-Garonne, France).

Description (Fig. 2 and 3)

The humerus PFY 4051, thought missing the proximal epiphysis and entepicondyle, is otherwise well-preserved. It is notably robust and the preserved part measures 61 mm in length (its estimated total length and width are respectively 85 mm and 35 mm). The broad, plate-like, deltopectoral crest projects well beyond the midshaft and is folded over the medial side of the diaphysis; it extends distally to the entepicondylar bridge and ends abruptly at the level of a well-defined groove for the passage of the tendon of the biceps muscle. The bicipital ridge extends from the posterior edge of the entepicondyle to the proximal diaphysis. The belly of the biceps muscle presumably laid along the deep, gutter-like depression defined between the bicipital ridge and the postero-medial side of the deltopectoral crest (Gaudin *et al.*, 2006). The orientation of the deltopectoral crest is anteromedian. The distal end of the deltoid tuberosity is flat and aligned with the midshaft. The entepicondyle is prominent and is separated distally from the trochlea by a distinct entepicondylar notch. The entepicondylar foramen is present. The proximal part of the lateral epicondyle and the capitulum are broken. The lateral epicondyle was prolonged proximally into a wide and robust supinator crest (=lateral supracondylar ridge). The profile of the trochlea is straight; it is sub-rectangular in anterior view. On the posterior side, the olecranon fossa is partially filled with sediment; it lies slightly above the trochlea and is more lateral than central. PFY 4051 shows a convex and dorsally extended articular surface of the trochlea in cranial view. The proximal part of the midshaft is sub-rectangular in section, the long axis being directed antero-posteriorly.

Comparisons

All the comparisons are limited by the preservation of the European material. The incomplete but well-preserved humerus PFY 4051 shows a suite of morphological features of pholidotan sensu stricto such as developed entepicondyle, the anteromedian orientation of the deltopectoral crest, the position and the shape of the entepicondylar foramen. Luckily, humeri are more common in the fossil record than other pholidotan remains, and partial or subcomplete ones are known from Eocene (*Eomanis*, Storch, 1978a,b; *Cryptomanis*, Gaudin *et al.*, 2006), Oligocene (*Necromanis,* Filhol, 1894; *Teutomanis*, Helbing, 1938), Miocene (*Teutomanis*, Schlosser, 1907; Viret, 1951; Guth, 1958; Emry, 1970; Koenigswald, 1969; Koenigswald & Martin, 1990), and Pliocene forms (*Manis*, Botha & Gaudin, 2007). The humerus of the patriomanid *Cryptomanis* (Gaudin *et al*., 2006) can be clearly discriminated from PFY 4051 in displaying a shorter deltopectoral crest, as well as a larger and longer entepicondyle, which is weakly flared at its tip. The humerus of *Patriomanis* clearly differs from PFY 4051 in showing a tapered entepicondylar process and a slender shaft with a mild deltopectoral crest (Emry, 1970).

PFY 4051 is overall quite similar to the type humeri of *Teutomanis franconica,* the specimen from Saint-André (Helbing, 1938; Emry, 1970), and the specimen from Saulcet (Koenigswald & Martin, 1990) both in size and morphology. In contrast, it is a lot bigger than the type humeri of *Necromanis quercyi* and *N. parva*. The type specimen of *N. franconica* (length is 84.5 mm, distal breadth 44 mm) is 1.5 time larger than that of *N. quercyi* (length is 62.2 mm, distal breadth 27.1 mm). The humerus of *Necromanis quercyi* can be clearly discriminated from PFY 4051 in showing a narrow distal epiphysis, an entepicondyle slightly distinct, slightly convex, and non straight-shape; a deltopectoral crest not as strongly folded over medially and a shallower medial concavity (Fig. 3 and Table 1). The olecranon fossa seems to be deeper and lower in *N. quercyi* (Koenigswald, 1969). The supinator crest of the latter is also more strongly projected laterally (from the diaphysis) than in *N. franconica*. The proximal epiphysis of *N. quercyi* shows a deeper muscle insertion groove than *N. franconica*, directly below the *caput humeri*. In *N. quercyi*, this muscle impression is interrupted dorsally by a crest running distally and merging into the *crista capitis* whereas it is uninterrupted in *N. franconica*. In *N. parva* and *N. franconica*, like in PFY 4051, a small notch is present and isolates the entepicondyle from the rest of the shaft (Table 1), which in turn makes the articulation more prominent. This entepicondylar notch is not observable on the specimen from Saint-André.

Compared to extant species, PFY 4051 shows an unusual combination of morphological features. It is clearly more robust than the humerus of *Manis culionensis*, *M. javanica*, *Phataginus tricuspis*, and *P. tetradactyla*. In contrast, some morphological features of PFY 4051 recall the morphology of the humerus of *M. crassicaudata*, *M. pentadactyla*, *Smutsia gigantea*, and *S. temminckii*, which show a broad deltopectoral crest that extends distally close to the entepicondylar bridge. However, its entepicondyle is less distinct and its deltopectoral crest is more projected medially. It clearly differs from *M. temminckii* that lacks an entepicondylar foramen, and from *M. gigantea* that shows a wider entepicondylar bridge.

DISCUSSION

Pholidotan systematics and the status of the genera *Necromanis* Filhol, 1894 and *Teutomanis* Ameghino, 1905

All living members of the order Pholidota are assigned to one family, the Manidae, representing eight extant species including the recent recognition of the Philippine pangolin as a distinct species (Gaubert & Antunes, 2005). There is, however, little consensus about the subdivision of the order at a generic level. Most of the classifications recognize only *Manis* as a valid genus, which is often subdivided at the subgeneric level (Jentink, 1882; Simpson, 1945; Ellerman & Morrison-Scott, 1951; Mohr, 1961; Meester, 1972; Meester *et al.*, 1986; Schlitter, 1993, 2005; Heath, 2013). However, several morphologists considered that such classifications underestimate the morphological diversity of the group; Pocock (1924) recognized as many as six genera (*Manis*, *Phatages*, *Paramanis*, *Uromanis*, *Smutsia*, and *Phataginus*). Other authors have suggested a subdivision of the Manidae into four (*Manis*, *Uromanis*, *Smutsia*, and *Phataginus*; Kingdon, 1997; McKenna & Bell, 1997), three (*Manis*, *Smutsia*, and *Phataginus*; Gaudin *et al.*, 2009) or two (*Manis* and *Phataginus*; Patterson, 1978; Corbet & Hill, 1991) extant genera. Literature supporting two subdivisions at a family level suggests the genus *Manis* is retained for Asian species, while African species are subdivided at a generic level to separate arboreal (*Phataginus* and *Uromanis*) and ground groups (*Smutsia*). Unfortunately, no large-scale molecular phylogeny exists for the extant representatives of the order. Such phylogeny would undoubtedly enable us to get crucial information about the divergence time between all these subgroups, especially considering that the late history of the group remains poorly known (e.g., Botha & Gaudin, 2007). Hence, new systematics studies are needed, not only to decipher the relationships between extinct representatives, but also to determine the taxonomy of extant species.

The humerus of Pech du Fraysse PFY 4051 (MP28) is assigned here to *Necromanis* cf. *franconica*. Some uncertainty remains, notably due to the greater development of the trochlea in cranial view compared to the holotype specimen of *N. franconica*. However, such a difference can be attributed to intraspecific variation. With respect to the morphological variation described in extant species (Pocock, 1924; Patterson, 1978; Corbet & Hill, 1991; Kingdon, 1997; McKenna & Bell, 1997; Gaudin *et al.*, 2006), following Emry (1970) and contra Koenigswald (1969), we consider that the differences between PFY 4051 and *N. franconica* on the one side, and *Necromanis*

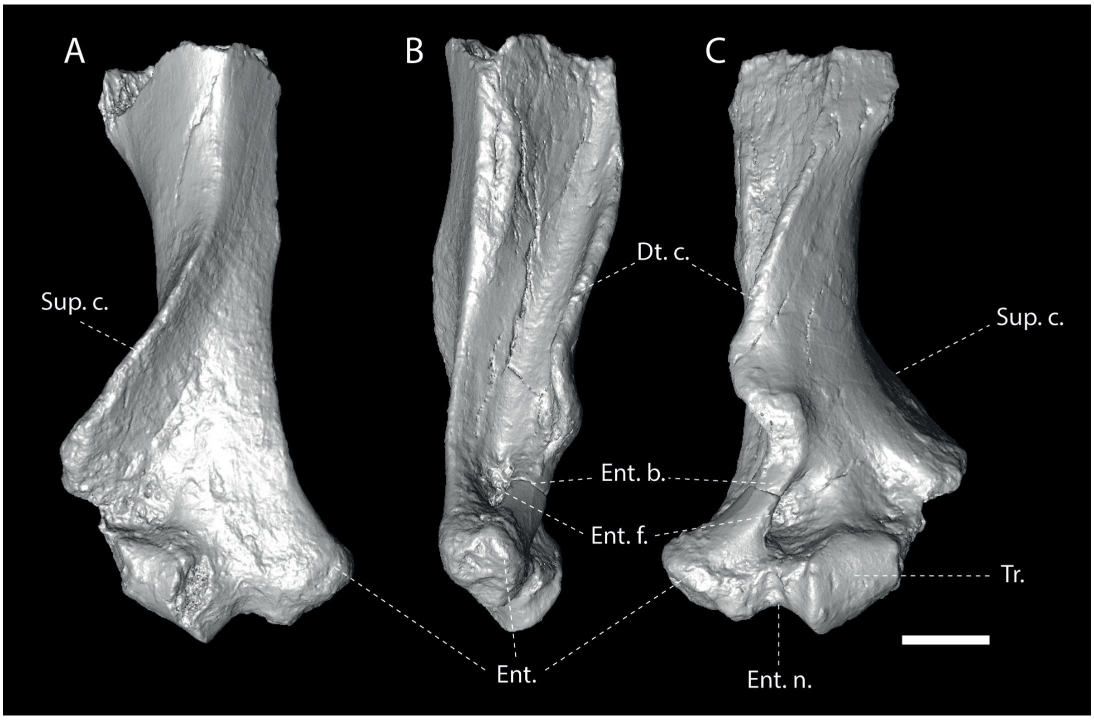

Figure 2. CT scan of the humerus from Pech du Fraysse (PFY 4051) in posterior (**A**), medial (**B**), and anterior (**C**) views. Scale bar = 1 cm. *Abbreviations*: Dt. c., deltopectoral crest; Ent., entepicondyle; Ent. b., entepicondylar bridge; Ent. f., entepicondylar foramen; Ent. n., entepicondylar notch; Sup. C., supinator crest; Tr., trochlea. Scale bar = 1 cm.

quercyi on the other side, might be sufficiently important to justify the original generic distinction between *Teutomanis* and *Necromanis*. However, discussing this generic distinction is out of the scope of this study since the material from Pech du Fraysse is too fragmentary to be included in a phylogenetical analysis. We included these characters in the comparative Table 1 but refrained perfoming a complete cladistic analysis just on the humerus because of the problems inherent to character pruning. The most comprehensive phylogenetic analysis of the order Pholidota was performed by Gaudin *et al.* (2009) (see Table 1). It includes a large number of cranial and postcranial characters coded on all extant species and on most fossil pangolins as well as on two well-known ?pholidotan palaeanodonts. Interestingly, Gaudin *et al*. (2009) followed Koenigswald (1969) and synonymised *Teutomanis* with *Necromanis* so that in their revision, the genus *Necromanis* includes *N. quercyi*, *N. parva* and *T. franconica* (apparently, *T. quenstedti* is synonymised to the latter). Nonetheless, Gaudin *et al.* (2009: material and methods, appendix 1 and acknowledgements) used specimens from the collections of the SMF to code their genus "*Necromanis*" in the data matrix. After investigation of one of us (T.L.), it appears that these specimens include the astragalus and calcanei (SMF M3379a, b, c) described by Helbing (1938) and referred to *Teutomanis franconica* (see also Koenigswald, 1969); a set of casts (SMF 2006/1-3) from the holotype and paratypes (humerus, ulna and radius) of *Teutomanis franconica*; and remains of several unpublished specimens (casts SMF 2010/1-9, 11, 12, 13-20, 22-39, 55-64) found at Herrlingen (Germany; MP29) and at Petersbuch (Germany; MN3, MN6) attributed to *Necromanis franconica* (according to the collection tags). The latter specimens correspond to the "extreme rich and complete" new specimens of *Necromanis* mentioned by Storch (2003: 56). Therefore, some character states do not reflect the discrete differences noticed between the type series of *Necromanis* and of *Teutomanis* (see Koenigswald, 1969: 66), and which should be coded as multistate characters if *Teutomanis* was synonymised with *Necromanis*. For instance, the presence of an entepicondylar notch is coded as present (character 215, state 2) for the genus *Necromanis*, although the holotype of *Necromanis quercyi* clearly lacks such structure, while it is present on the holotypes of *T. franconica* and *N. parva* (see Table 1). The unpublished specimens referred to *Necromanis franconica* (casts SMF 2010/1-9, 11, 12, 13-20, 22-39, 55-64) will not be included here as they are under study by other colleagues (Hoffmann comm. pers.). In that context, the re-evaluation of all remains attributed to *Necromanis* would then represent an interesting work opportunity for future investigations in order to clarify the systematics of Paleogene and Neogene pholidotans.

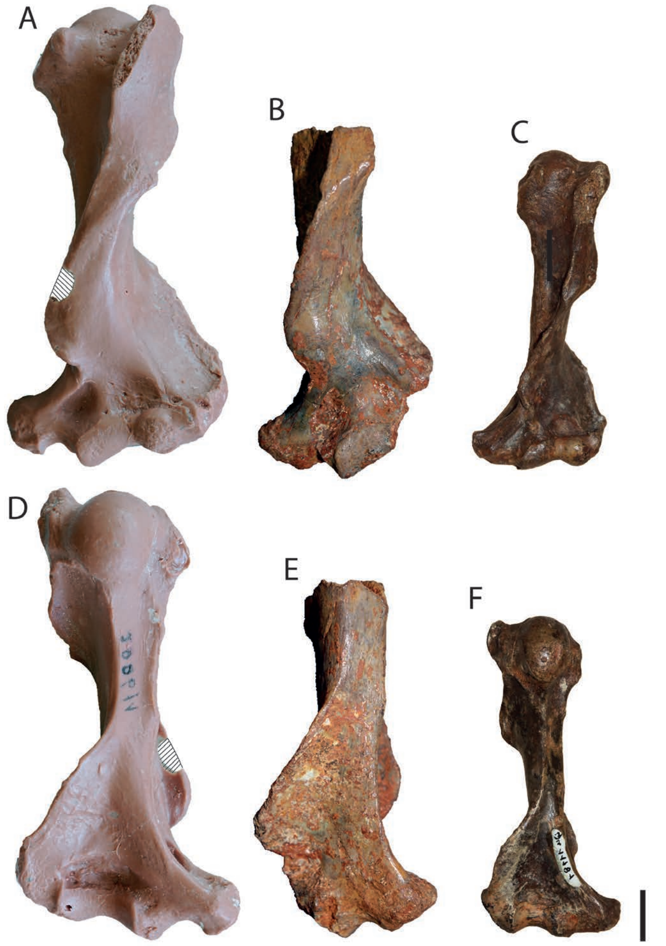

Figure 3. Comparative anterior (A, B and C) and posterior (D, E and F) views of the humeri of the type specimen of *Necromanis franconica* SMF 2006/1 (reversed here for easier comparison, **A** and **D**), the specimen from Pech du Fraysse PFY 4051 (**B** and **E**) and the type specimen of *N. quercyi* MNHN QU 11181 (reversed here for easier comparison, **C** and **F**). The hatched areas represent broken parts on the specimen of *N. franconica*. Scale bar = 1 cm.

The humerus of *Necromanis quercyi* can be clearly distinguished from other taxa, in particular PFY 4051, in showing: a narrow distal epiphysis, which is similar in size to *N. parva*; a small olecranon fossa narrower than the trochlea, a slightly individualized, slightly convex, and non-straight entepicondyle; a less bulb-like capitulum; a deltopectoral crest that is folded over medially to a lesser extent, no entepicondylar notch and has a shallower medial concavity (Table 1). All humeri described as *Necromanis franconica* share the following suite of morphological features: a large size associated with an overall robust morphology, with a broad, plate-like, deltopectoral crest projecting well beyond the midshaft and a prominent entepicondylar process separated from the trochlea distally by a small notch (Table 1). In summary, the species *N. franconica* is present in all the following localities, listed chronologically: Saint-André near Marseille, middle Oligocene MP 26; Pech du Fraysse, late Oligocene MP 28, PFY 4051; Saulcet, Aquitanian (Koenigswald & Martin, 1990); Montaigu, Aquitanian (Helbing, 1938); Mainz-Weisenau, Miocene (Helbing, 1938); Solnhofen, Burdigalian (Quenstedt, 1885); La Grive Saint Alban, Miocene (Viret, 1951). In this context, the status of *Necromanis parva* from Winterhof-West (Koenigswald, 1969) remains to be defined.

Paleobiological inferences

Within extant pholidotans, the habitat differentiation has occurred independently in both African and Asian lineages (Gaudin *et al*., 2009). This parallel evolution gives us a unique opportunity to separate the effect of phylogenetic and ecological constraints on morphological evolution of their humeri. One Asian (i.e., *M. crassicaudata*) and two African species (*M. temninckii* and *M. gigantea*) have a fossorial lifestyle; they show a robust humerus characterized by a broad deltopectoral crest that extends distally close to the entepicondylar bridge. In contrast, the other species (the Asian *M. javanica* and *M. culionensis*, and the African *M. tricuspis* and *M. tetradactyla*) have a more arboreal lifestyle; their humeri show a smaller deltopectoral crest that inserts further mesially from the entepicon-

Humerus characters (Gaudin *et al.*, 2009)	***Necromanis* sp. from Gaudin *et al.* (2009)**	***Necromanis quercyi* Filhol, 1894 HOLOTYPE**	***Necromanis franconica* Quenstedt, 1885 HOLOTYPE**	***Necromanis parva* Koenigswald, 1969 HOLOTYPE**	***Necromanis franconica* from Saulcet Koenigswald & Martin (1990)**	**PFY 4051**
Orientation of long axis of humeral head in posterior view (Character 205)	oriented distomedially	oriented proximodistally, or somewhat distolateral	oriented distomedially	-	-	-
Orientation of deltopectoral crest of humerus (Character 206)	canted medially at its distal end	canted medially at its distal end	canted medially at its distal end	canted medially at its distal end	canted medially at its distal end	canted medially at its distal end
Length of deltopectoral crest (Character 207)	extends >75% of the length of the humerus	extends >75% of the length of the humerus	extends >75% of the length of the humerus	-	extends >75% of the length of the humerus	-
Pulley for m. biceps brachii at distal termination of deltopectoral crest (Character 208)	present	present	present	present	present	present
Deep anterior groove between greater tubercle and lesser tubercle of humerus for head of m. biceps brachii (Character 209)	present	present	present	-	-	-
Large distinct deltoid crest extends across lateral surface of humerus (Character 210)	present	present	present	present	present	present
Distinct fossa for mm. infraspinatus and teres minor on lateral surface of humerus (Character 211)	absent	absent	absent	?	?	-
Width across humeral epicondyles (Character 212)	wide, >50% of length of humerus	intermediate width, 40–50% of length of humerus	wide, >50% of length of humerus	-	-	-
Length of entepicondyle (Character 213)	intermediate length, 30–40% of epicondylar width of humerus	intermediate length, 30–40% of epicondylar width of humerus	intermediate length, 30–40% of epicondylar width of humerus	intermediate length, 30–40% of epicondylar width of humerus	-	-
Position of proximal entepicondylar foramen (Character 214)	visible in anterior view	visible in anterior view	visible in anterior view	visible in anterior view	visible in anterior view	visible in anterior view
Entepicondylar notch (Character 215)	present	absent	present	present	-	present
Size and proximal extent of supinator crest (Character 216)	moderately developed, extends proximal to proximal opening of entepicondylar foramen but weakly flared laterally	well developed but lacking freestanding proximal extension, extends proximal to proximal opening of entepicondylar foramen and extends far lateral to humeral shaft	moderately developed, extends proximal to proximal opening of entepicondylar foramen but weakly flared laterally	moderately developed, extends proximal to proximal opening of entepicondylar foramen but weakly flared laterally	moderately developed, extends proximal to proximal opening of entepicondylar foramen but weakly flared laterally	moderately developed, extends proximal to proximal opening of entepicondylar foramen but weakly flared laterally
Form of supinator crest (Character 217)	flared laterally at its distal end, with well-developed anterior concavity	flared laterally at its distal end, with well-developed anterior concavity	flared laterally at its distal end, with well-developed anterior concavity	flared laterally at its distal end, with well-developed anterior concavity	flared laterally at its distal end, with well-developed anterior concavity	flared laterally at its distal end, with well-developed anterior concavity
Posterior surface of distal humerus between supinator crest and posterior edge of entepicondyle/entepicondylar foramen, proximal to olecranon fossa (Character 218)	concave	concave	concave	?	flat	flat
Distal edge of trochlea of humerus in anterior view (Character 219)	straight or slightly concave	straight or slightly concave	straight or slightly concave	straight or slightly concave	-	straight or slightly concave
Medial extent of radial fossa of humerus (Character 221)	extends over lateral half of trochlea	extends over lateral half of trochlea	extends over lateral half of trochlea	extends over lateral half of trochlea	extends over lateral half of trochlea	extends over lateral half of trochlea
Size of olecranon fossa of humerus (Character 222)	large, wider transversely than trochlea in posterior view	small, narrower transversely than trochlea	large, wider transversely than trochlea in posterior view	?	?	-
Relative proximal extent of greater and lesser tubercle of humerus (Character 223)	greater tubercle extends proximal to lesser	greater tubercle extends proximal to lesser	greater tubercle extends proximal to lesser	-	-	-
Position of proximal portion of lesser tubercle of humerus (Character 224)	extends anterolaterally, overlaps head in anterior view	extends anterolaterally, overlaps head in anterior view	extends anterolaterally, overlaps head in anterior view	-	-	-
Bicipital groove of humerus continuous with well-developed fossa anteromedial to greater tubercle (Character 225)	present	present	present	-	?	-
Orientation of greater tubercle of humerus relative to head in proximal view (Character 226)	divergent from head posterolaterally or approximately parallel to lateral surface of head	divergent from head posterolaterally or approximately parallel to lateral surface of head	divergent from head posterolaterally or approximately parallel to lateral surface of head	-	-	-

Table 1. Listing of characters and character states of the humerus used in Gaudin *et al*. (2009) applied to the holotype of *Necromanis quercyi*, the holotype of *Necromanis franconica*, the holotype of *Necromanis parva*, the specimen of *N. franconica* from Saulcet (Koenigswald & Martin, 1990), and the specimen PFY 4051 from Pech du Fraysse. "?", character unknown or character state not applicable; "-", undetermined characters due to the fragmentary nature of the specimen.

dylar bridge. The morphological differences between fossorial and arboreal pangolins imply differences between lever arm ratios at the level of the deltopectoral crest (Kardong, 2006). The output force is greater in the fossorial type since the relatively long deltopectoral crest favours large output force by moving the point of pivot (or fulcrum, here the humeral head) farther from the input force (i.e. the deltoid musculature; Shrivastava, 1962). Both *Necromanis quercyi* and *N. franconica* present a humerus characterized by a deltopectoral crest that extends distally close to the entepicondylar bridge. Following the interpretation of Koenigswald & Martin (1990), we postulate a terrestrial and fossorial mode of life for the two extinct species; fossoriality was probably more expressed in all representatives of *N. franconica* considering the even greater development of their deltopectoral crest but this feature might also be related to size since all extant fossorial forms tend to show bigger size.

CONCLUSION

Pangolins have never shown a high taxic diversity; their fossil record is limited and this new discovery from Pech du Fraysse documents an early stage of their presence in Europe. Their humerus bears several diagnostic features that could explain why it has been described so frequently in literature. However, other pholidotan bones, which are infrequently described, may have simply been overlooked in the fossil record. Nowadays, pangolins are restricted to tropical and equatorial areas of Africa and Asia. Their diet is composed mainly of insects, and in particular ants and termites. These ecological restrictions are in agreement with the climatic conditions proposed for Europe during the Oligo-Miocene. At that time, several species of pangolins lived in Europe as is the case today in equatorial areas. The specimen from Pech du Fraysse shows a suite of morphological features compatible with the humeri from Saint-André (MP 26), Solnhofen (Burdigalien), and Saulcet (Aquitanian), and was attributed to *Necromanis* cf. *franconica*. This taxon is without a doubt a distinct species compared to *N. quercyi*. We suggest that the generic synonymy between *Necromanis* and *Teutomanis* should be reinvestigated on the light of the differences between PFY 4051 and *N. franconica* on the one side, and *N. quercyi* on the other.

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