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# A plastron fragment reveals a previously unrecorded turtle species in the Eocene of Messel Pit, Germany

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## Abstract

Depending on taxonomic opinion, between four and five turtle species are well attested for the Middle Eocene Messel Pit formation of Germany. Here, we describe specimen SMF ME-3495 from the Messel collection of the Senckenberg Museum in Frankfurt, which unambiguously corresponds to an additional turtle species. The specimen consists of a partial anterior plastral lobe that can be distinguished from other Messel turtle taxa on the basis of the presence of gular tubercles, an extensive epiplastral lip, narrow gulars that lap onto the entoplastron, and a sinuous gulo-humeral sulcus. The fragment is not sufficient to diagnose another contemporary European turtle taxon, but its epiplastral lip morphology is reminiscent of "ptychogasterid" geoemydids (Cryptodira). We also remark on bone corrosion consistent with "shell disease" and distinctive coloration.

## Key Words

Geoemydidae, *Gunnellichnus*, pathology, Ptychogasteridae, shell disease, Testudines

## Introduction

The Messel Pit quarry is a major Konservat-Lagerstätte with a rich sub-tropical flora and fauna preserved in black oil shale from the Middle Eocene (Lutetian, MP11) in the State of Hesse, Germany (Smith et al. 2018). An abundant fossil record of at least four turtle species is recognized for this site (Cadena et al. 2018). There is broad taxonomic agreement about three: the podocnemidid *Neochelys franzeni* Schleich, 1993 (Cadena 2015), the trionychid *Palaeoamyda messeliana* (Reinach, 1900) (Cadena 2016) and the carettochelyid *Allaeochelys crassesculpta* (Harrassowitz, 1922) (Joyce et al. 2012).

The taxonomy of the geoemydid turtles (Testudinoidea) from Messel is far more contentious: the number of potentially attested species ranges between one and four. A major cause for the divergence of opinions is the extensive intraspecific variation present in geoemydids in particular (Garbin et al. 2018), and in testudinoids in general (Joyce and Bell 2004). Two morphotypes of geoemydids were first considered as two species called *Ocadia messeliana* Staesche, 1928 and *Ocadia kehreri* Staesche, 1928, and later attributed by Hervet (2004a) to her new genera *Francellia* and *Euroemys*, respectively. Claude and Tong (2004) proposed a systematic treatment that synonymizes Hervet's genera into *Palaeoemys* and considers the two morphotypes as juvenile and adult forms of a single species: *Palaeoemys messeliana*. As some other authors before us (e.g., Cadena et al. 2018), we follow the latter assessment in this contribution, but the matter remains unsettled (Ascarrunz et al. 2021).

Other proposed geoemydids from Messel are more dubious. Hervet (2004a) identified as *Borkenia* aff. *oschkinisi* the Messel specimens SMNS 54849, SMNK 395, and IRSBN IG28502. However, those identifications were founded on subtle differences that could feasibly be encompassed in the extensive variation of the *Palaeoemys kehreri* morphotype. Indeed, Claude and Tong (2004) even posited that *Borkenia* as a whole is a possible junior synonym of *Palaeoemys*. In similar fashion, Hervet (2004a) tentatively referred the specimens HLMD-ME 7448 and BMNH R10869 to the geoemydid *Juvemys* sp., but this genus was also contested by Claude and Tong (2004) as a

junior synonym of *Palaeoemys*, and HLMD-ME 7448 is a small juvenile, which is difficult to contextualize due to the poorly understood ontogenetic variation of these taxa.

Here, we describe the Messel specimen SMF ME-3495, a partial anterior plastral lobe consisting of much of the epiplastra and the entoplastron. This limited material displays distinctive features that clearly lie outside the ranges of variation considered by previous authors for turtles from this site. Thus, SMF ME-3495 can be safely said to represent a distinct turtle species not previously recorded for Messel.

## Institutional abbreviations

**BMNH**, Natural History Museum, London (UK); **HLMD**, Hessiches Landesmuseum Darmstadt (Germany); **IRSNB**, Institut Royal des Sciences Naturelles de Belgique (Belgium); **SMNK**, Staatliches Museum für Naturkunde Karlsruhe (Germany); **SMF**, Senckenberg Museum Frankfurt (Germany); **SMNS**, Staatliches Museum für Naturkunde Stuttgart (Germany).

## Material

SMF ME-3495 (Fig. 1) is housed at the Senckenberg Museum, Frankfurt. It was found under the marker horizon *alpha* (Felder and Harms 2004) at the boundary between cells G8 and G9 of the site grid of Schaal and Rabenstein (2012), close to the "Turtle Hill," where numerous other turtle fossils have been collected. It was catalogued on the 9th of September 1999. In comparison to fragmentary, historic material, which was often collected as float from the surface, this specimen was collected directly from the sediments under controlled conditions. Its partial nature is therefore not a result of recent weathering, but rather of decay and disarticulation prior to deposition.

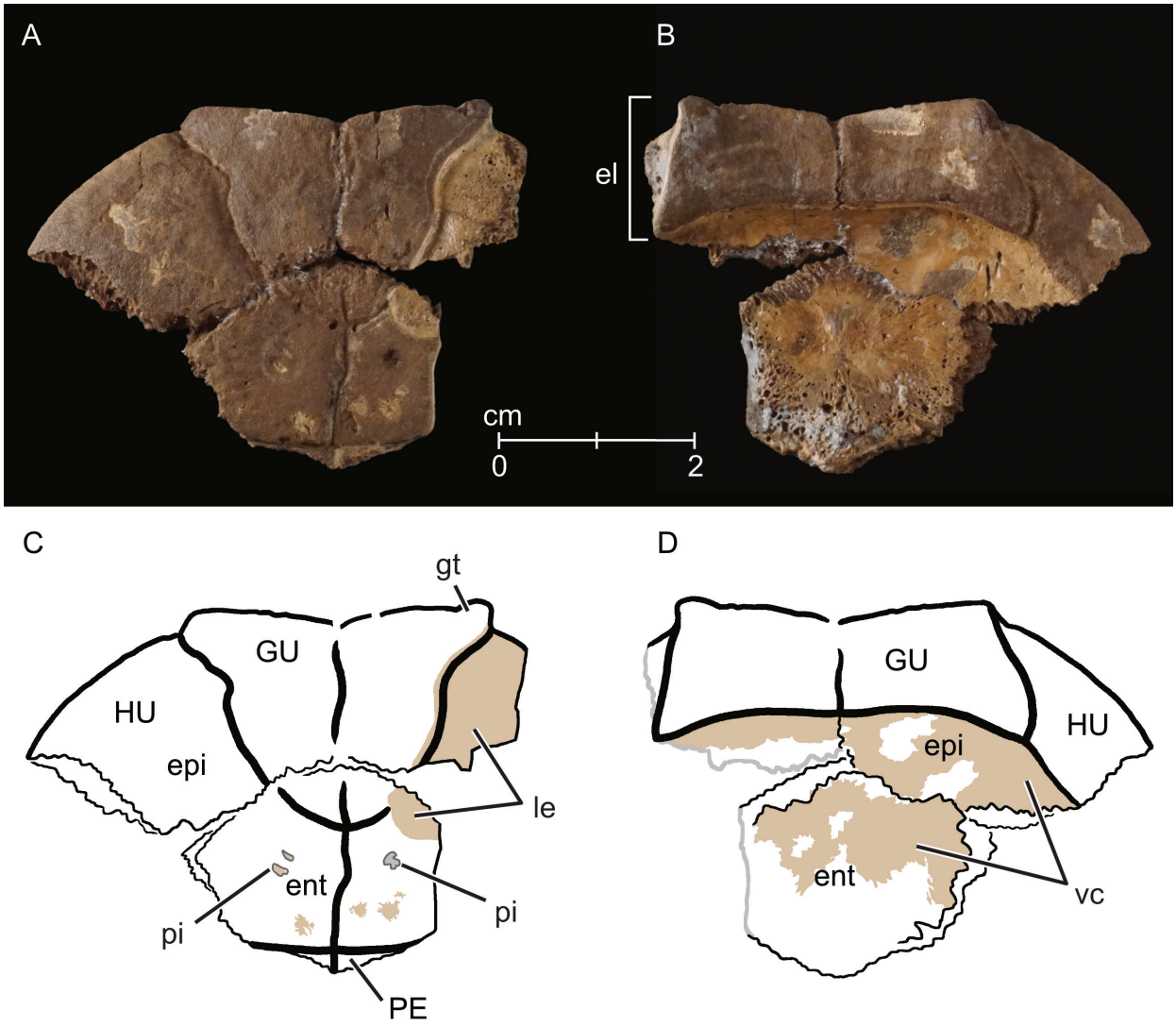


**Figure 1.** SMF ME-3495, undetermined "ptychogasterid", Middle Eocene (Lutetian, MP11), Messel Pit Formation, Germany. Photographs in ventral/external (**A**) and dorsal/visceral (**B**) views, with matching illustrations (**C** and **D**, respectively). Abbreviations: el, epiplastral lip; ent, entoplastron; epi, epiplastron; gt, gular tubercle; GU, gular scute; HU, humeral scute; le, large shell disease lesion; PE, pectoral scute; pi, pitting; vc, visceral coat. Colored areas correspond to light cream coloration discussed in the text.

# Description

SMF ME-3495 (Fig. 1) is a fragment of the anterior plastral lobe, consisting of much of the epiplastra and the entoplastron, preserved in a muted brown color like that of other Messel turtle material of similar size. The right epiplastron appears almost intact: cancellous bone is only exposed in gaps along the suture with the entoplastron and along the edge corresponding to the contact with the missing hyoplastron. The epi-hyoplastral suture is well-preserved, showing only some wear near the contact with the entoplastron. This suture displays a slight sinuous shape seen in many extant turtles (viz. *Geoemyda spengleri*, *Mauremys annamensis*, *Malayemys* spp.; pers. obs.) and its jagged edge is consistent with small sutural interdigitations. Sutural interdigitations are more salient on the visceral side. The left epiplastron preserves the entire region corresponding to the gular scute, but it is broken off, preserving only about a third of the region corresponding to the humeral scute.

On the ventral side, there is evidence of a large lesion in the humeral scute region encompassing the left epiplastron and a small semicircular portion of the entoplastron. The cortical bone is uniformly corroded away, beginning to expose a finely porous layer of cancellous bone. The affected area displays a light cream coloration and has smooth, well-defined boundaries. This kind of damage is consistent with a variety of "shell disease" pathologies (also informally known as "shell rot") caused by bacterial or fungal infections. Similar lesions have been reported for numerous other fossil turtles (e.g., Hutchison and Frye 2001; Guerrero and Pérez-García 2021, 2022, 2023, 2024; Zonneveld and Bartels 2023) and were recently grouped into the ichnotaxon *Gunnellichnus moghraensis* Zonneveld et al., 2022.

Other minor lesions are also present on the ventral face of the entoplastron: two small pits to the right of the inter-humeral sulcus and another to the left, and four small patches of cortical bone corrosion that display the same coloration as the large lesion, but are more superficial and have more jagged boundaries. The small pit on the left side of the entoplastron resembles the ichnotaxon *Karethraichnus* Zonneveld et al., 2022. Zonneveld and Bartels (2023) ascribed *Karethraichnus* to the action of ectoparasitic invertebrates such as ticks or leeches. Irregular whitish patches are scattered on the ventral and visceral sides of the epiplastra. They are faint at the center and more opaque at the periphery. These are likely taphonomic discolorations not associated with bone corrosion.

In ventral view, the anterior margins of the gular regions of the epiplastra are straight and form an angle of about 160° at the midline meeting point. In frontal view, these margins form a slight concavity that would have accommodated the head. In lateral view, there is an angle of about 150° between the planes of the entoplastron and the epiplastra. The latter are gently curved upwards.

The entoplastron appears complete on the right side. As with the epi-hyoplastral suture, the suture lines in the anterior and right regions of the entoplastron are well preserved considering that their overall shape is consistent with attested turtle anatomy and the appearance of its edges is consistent with interdigitations. The posterior edge of the entoplastron is overall well preserved as well, but some interdigitations are less pronounced and some wear cannot be ruled out. The left part of the entoplastron is broken off laterally. Slightly more than half of its medial side is preserved.

In ventral view, the gular scutes are about 1.2 times longer (= length of the inter-gular sulcus) than they are wide (= distance between the external end of the inter-gular sulcus and the external end of the gulo-humeral sulcus), and they clearly lap onto the entoplastron. They bear small tubercles at the margin with the humeral scutes, which accentuate the overall quasi-triangular shape of the scutes in ventral view. The gulo-humeral sulcus has a sinuous shape. At the level slightly anterior to half the medial length of the epiplastra, it distinctly bows into the gular, but more posteriorly, it bows more gently into the humeral, crossing the ento-hyoplastral suture. The curvature is such that the left and right gulo-humeral sulci meet the inter-gular sulcus at near-straight angles, forming together a parabolic section over the entoplastron.

The humero-pectoral sulcus crosses the entoplastron very near to its posterior edge. It is straight and forms an angle slightly smaller than 90° with the inter-humeral sulcus.

The anterior border of the visceral face of the plastron was also covered by the gular and humeral scutes, as is common in most testudinoids. This border is quite extensive, encompassing over 50% of the epiplastra. The part that is covered by the gular scutes is distinctly raised, forming a shelf or "epiplastral lip" (Fig. 1). This lip spans about 70% of the inter-epiplastral suture at the midline. The posterior border of the visceral face of the gular scutes is longer than the anterior border, defining a roughly trapezoidal outline. The anterolateral tubercles formed by the gular are visible in this view as well. The visceral area is covered by a material that forms a thin and patchy coat, irregularly colored in light cream and more orangish tones ("visceral coat" in Fig. 1). The posterior half of the entoplastron is textured by numerous fine foramina.

# Discussions

## Taxonomic status

Any affinities of SMF ME-3495 with the Messel pan-trionychians *Palaeoamyda messeliana* and *Allaeochelys crassesculpta* can be easily ruled out, because these soft-shelled turtles feature highly apomorphic plastral bone configurations with characteristic ornamentation and no plastral scute sulci (Joyce et al. 2012; Cadena 2016).

The Messel pleurodiran *Neochelys franzeni* differs from SMF ME-3495 (Fig. 2A) by the presence of extragular scutes, a single median gular, and a more anteriorly located humero-pectoral sulcus relative to the contact between the epi-hyoplastral suture with the entoplastron (Cadena 2015).

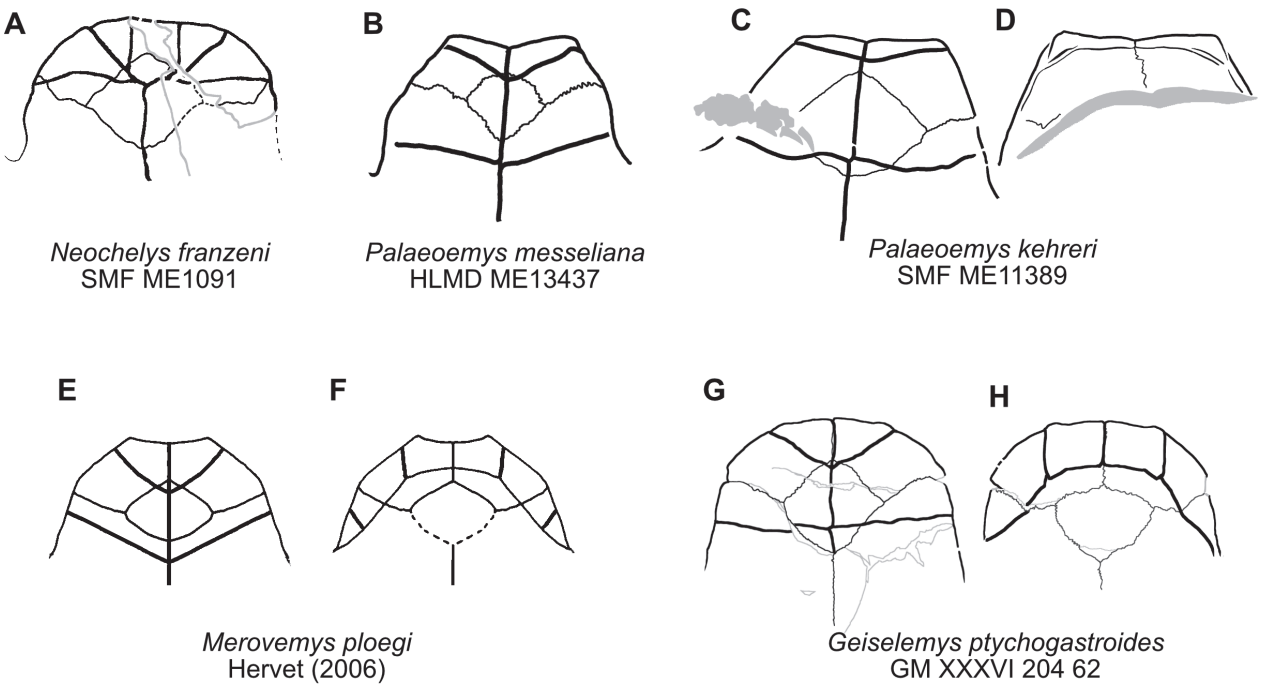


**Figure 2.** Anterior plastral lobes of select turtle taxa from the Eocene of western Europe. The pleurodire *Neochelys franzeni* (SMF ME1091, Messel Pit, Middle Eocene) in ventral aspect (**A**), based on Cadena (2015). The geoemydid *Palaeoemys* "*messeliana*" (HLMD ME13437, Messel Pit, Middle Eocene) in ventral aspect (**B**). The geoemydid *Palaeoemys* "*kehreri*" (SMF ME11389, Messel Pit, Middle Eocene) in ventral (**C**) and visceral (**D**) aspect. Hervet's (2006) reconstruction of the "ptychogasterid" *Merovemys ploegi* (northern France, Early Eocene) in ventral (**E**) and visceral (**F**) aspect. The "ptychogastrid" *Geiselemys ptychogastroides* (GM XXVI-204/62, Geiseltal, Middle Eocene) in ventral (**G**) and visceral (**H**) aspect. Grey lines and shading represent breakage lines or regions covered by other structures.

SMF ME-3495 differs markedly from the Messel geoemydid morphs *Palaeoemys messeliana* and *P. kehreri* (Fig. 2B–D) as described in a recent paper (Ascarrunz et al. 2021). The new specimen's gular scutes are longer than wide, clearly lap onto the entoplastron, and form a sinuous sulcus with the humeral. This contrasts the gulars of both *P. messeliana* and *P. kehreri*, which are broader than long, do not lap or barely onto the entoplastron, and form a straight sulcus with the humeral. The overall shape of the gulars in SMF ME-3495 makes the gular tubercles more distinct than in *P. messeliana* and *P. kehreri*. Lastly, while SMF ME-3495 displays a distinct epiplastral lip on the visceral side of anterior plastral lobe, this character is incipient to absent in *P. kehreri* (SMF-ME 3774 and SMF-ME 11389, Fig. 2D). The relevant area cannot be observed in *P. messeliana*.

The distinct epiplastral lip with lateral swellings and gular tubercles of SMF ME-3495 are consistent with the diagnosis of the putative clade "Ptychogasteridae" De Stefano, 1903 (Hervet 2004b, 2006). Among Eocene "ptychogasterids", SMF ME-3495 stands out by the presence of a markedly sinuous gulo-humeral sulcus, but the shape and dimensions of the epiplastral lip are within the range of variation of the group without clearly matching any particular figured specimen (Hervet 2004b, 2006; Schäfer 2012; Bourque 2022). The two spatially and temporally closest named "ptychogasterids" are *Merovemys ploegi* Hervet, 2006 from the Early Eocene (Ypresian, MP 7; Fig. 2E, F) of France (Hervet 2006) and *Geiselemys ptychogastroides* (Hummel, 1935) from the Middle Eocene of Geiseltal (Lutetian, MP 11–13; Fig. 2G, H). SMF ME-3495 somewhat bridges the morphological gap between *Merovemys ploegi* and *Geiselemys ptychogastroides* by having a more expanded anterior plastral lobe with widely spaced gular tubercles, unlike *Merovemys ploegi*, but not yet having achieved the extremely long epiplastral lip, as seen in *Geiselemys ptychogastroides*. Still, the erection of a new species for SMF ME-3495 is unwarranted on the basis of the scant material, also given that, as figured by Schäfer (2012), "ptychogasterids" display extensive intraspecific variation of the epiplastral lip character complex in particular, likely also during ontogeny. Thus, we tentatively identify SMF ME-3495 as an indeterminate "ptychogasterid". Given the great amount of interspecific variability that is apparent to the development of the gular scutes among geoemydids in general and the Messel geoemydids in particular (Ascarrunz et al. 2021), combined with the poor preservation of many Messel turtles, we cannot rule out that this taxon is known from other specimens, but until the epiplastral lip of additional specimens with unclear characters favoring identity as *Palaeoemys kehreri* or *P. messeliana* have been exposed, either mechanically or radiographically, SMF ME-3495 is the only specimen available from Messel with likely "ptychogasterid" affinities. The taxonomy of "Ptychogasteridae" itself remains an open problem.

## Biogeography and paleoecology

A comparison of the rich Messel Pit turtle fauna to roughly coeval faunas in France and Germany suggest a strong taxonomic bias at this site. More than 250 individuals held in the three largest collections (HLMD, IRSBN, and SMF) document a dominance of the carettochelyid *Allaeochelys crassesculpta* (N ≈ 100) and the geoemydid *Palaeoemys kehreri*/*messeliana* (N ≈ 100), followed by the less common trionychid *Palaeoamyda messeliana* (N ≈ 40) and the rare pleurodire *Neochelys franzeni* (N ≈ 6). The notable absence of terrestrially adapted tortoises, which are common across France and Germany at that time (Lapparent de Broin 2001), suggests a strong bias towards aquatic turtles at Messel. Prior to this publication, possible "ptychogasterids" were unknown for Messel.

There is evidence that at least some "ptychogasterids" were terrestrial. In Geiseltal, *G. ptychogastroides* is most commonly found in localities called "Trichter" (funnels). These are holes in the forest floor, a kind of doline that is filled up with vertebrate remains. True aquatic turtles (e.g., trionychids) are never found there, but tortoises and *G. ptychogastroides* are common (Krumbiegel 1962; Krumbiegel et al. 1983). An interpretation of SMF ME-3495 as a terrestrial "ptychogasterid" would account for its unusual preservation as an isolated anterior plastral lobe, in contrast to a complete skeleton, as this suggests transport from the outside into Messel lake. Although some extant tortoises and terrestrial geoemydids live in mountainous terrain today (e.g., *Geoemyda spengleri*, *Manouria impressa*; Ernst and Barbour 1989), their absence from Messel may suggest that they did not live in the volcanic slopes that likely surrounded the Messel lake, but rather favored flat terrain beyond this volcanic Maar lake.

Alternatively, a preference for an aquatic habitat would be consistent with the presence of bone corrosion lesions on SMF ME-3495, as they strongly resemble shell disease lesions common in continental aquatic taxa (J.-P. Zonneveld, pers. comm.; Zonneveld and Bartels 2023). The "shell diseases" characteristic of terrestrial turtle taxa are cutaneous dyskeratosis and necrotizing scute disease, both of which primarily cause lesions on the epidermis with minimal effect on bone (Zonneveld and Bartels 2023). Even if SMF ME-3495 is indeed a "ptychogasterid", it is not certain that all "ptychogasterids" must have been terrestrial. Unlike the clade of tortoises (Testudinidae), which is uniformly terrestrial, the geoemydid clades *Cuora*, *Heosemys*, *Rhinoclemmys*, and *Melanochelys* all contain both aquatic and terrestrial species.

## Pathology and preservation

Other hard-shelled turtles from Messel are similarly affected by shell bone lesions, although none of them quite replicate the features of the large lesion on the humeral scute of SMF ME-3495, which has well-defined boundaries, lighter coloration, and is uniformly corroded. In most other specimens that display pitting and bone corrosion, when large patches (relative to scute size) of bone corrosion occur, the necrosis tends to be deeper and very irregular, and the color is not different from the rest of the bone (e.g. *N. franzeni* SMF-ME 1267, *Palaeoemys kehreri* HLMD-ME 7229 and HLMD-ME 8877). Shell lesions with lighter coloration do occur in the *P. messeliana* specimen HLMD-ME 10477 and, possibly, in the *P. messeliana* specimen HLMD-ME 9051, albeit the lesion borders are not well-defined. That the precise lesion of SMF ME-3495 is not replicated in other specimens is perhaps not surprising, as pathologies can have different susceptibilities and manifestations in different species.

The cream-orange colored coat on the visceral aspect of the specimen is circumscribed to the surface of the plastron that walled the body cavity. It is interesting that changes in coloration correspond to areas that were never protected by scutes on the visceral side, and to the lesion surface on the ventral side, where the scute either had necrosed or flaked off. In other Messel turtles, similar coloration is not observed on exposed visceral surfaces of the plastra, or even on preserved internal organs (Gaßner et al. 2001). The taphonomic significance of the coloration patterns is not immediately clear, but it could be a reflection of different depositional conditions, perhaps due to behavior, habitat, or some other factors.

# Conclusions

SMF ME-3495 displays a unique combination of characters that may well be indicative of a currently unrecognized species with affinities to "ptychogasterid" geoemydids. Yet, these characters are largely quantitative and known to present high variation. On the basis of the present material, a diagnosis is unlikely to be robust enough to warrant the erection of a new species. Nonetheless, the other turtle species hitherto described for the Eocene of Messel are sufficiently well characterized to recognize SMF ME-3495 as distinct.

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