



Identification of the African–European *Erymnochelys* group (Pleurodira, Podocnemididae) in the Belgian fossil record: first finding of *Eocnochelus eremberti* outside its type locality

Adán Pérez-García¹ and Thierry Smith²

¹Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, Paseo de la Senda del Rey 9, 28040 Madrid, Spain

²Directorate Earth & History of Life, Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Brussels, Belgium

Correspondence to: Adán Pérez-García (paleontologo@gmail.com)

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Abstract. An almost complete plastron, as well as several peripherals and a costal plate of a turtle from the middle Eocene of Saint-Gilles, is presented here. Although this turtle specimen was donated to the Institut royal des Sciences naturelles de Belgique (Brussels, Belgium) more than a century ago, it remained undescribed. Its study allows us to recognize the second pleurodiran in the Belgian fossil record, where, until now, the Eocene *Neochelys* was the only one known. The Belgian material of *Neochelys* is known in lower Eocene (early Ypresian) levels, but the new pleurodiran specimen comes from the middle Eocene (early Lutetian). It is the first partial articulate shell of a pleurodiran turtle recognized in Belgium, and the only member of this clade recognized in this country at specific level. The new specimen is a representative of the so-called *Erymnochelys* group, this lineage being known in Africa from the Upper Cretaceous to the present but in Europe only during the Eocene. It represents the first specimen of *Eocnochelus eremberti* identified outside its type locality, the French region of Saint-Germain-en-Laye (Yvelines, Île-de-France), where only one specimen was found. The plastron of the Belgian individual corresponds to the most complete for this species. Its analysis allows us not only to broaden the range of paleobiogeographical distribution of *Eocnochelus eremberti* but also to improve the knowledge about the anatomy and variability of this taxon.

of them is Bothremydidae, identified in Europe from the Cenomanian (Pérez-García, 2016a). The greatest diversity of this lineage in Europe was achieved during the uppermost Cretaceous (Tong et al., 1998; de Lapparent de Broin, 2001; Gaffney et al., 2006; Pérez-García et al., 2012). The presence of this clade in the Cenozoic record of Europe has recently been confirmed, thanks to the discovery of cranial and postcranial material from the lower Eocene (early Ypresian) of Saint-Papoul (Aude, France) (Pérez-García, 2016b). Whereas the confirmed record of Bothremydidae in the Cenozoic levels of Europe is currently restricted to that finding, the other lineage of the crown Pleurodira that reached Europe was very successful during the Eocene, being represented in several countries (de Broin, 1977; de Lapparent de Broin, 2003; Pérez-García and de Lapparent de Broin, 2013, 2015; Cadena, 2015; Pérez-García et al., 2017; Pérez-García and Chapman, 2017). This lineage is Podocnemididae, with two genera being currently recognized. The most abundant and diverse is *Neochelys* Bergouinioux, 1954, known by nine species (de Lapparent de Broin, 2003; Pérez-García and de Lapparent de Broin, 2013, 2015). *Neochelys* is a genus of freshwater turtles, belonging to Erymnochelyinae. The presence of a second genus of Erymnochelyinae, closely related to the African extant form *Erymnochelys madagascariensis* (Grandidier, 1867), has been recognized in several publications (see de Broin, 1977; Lapparent de Broin in Merle, 2008; Pérez-García and de Lapparent de Broin, 2015). However, it has only recently been named (Pérez-García et al., 2017): it is the littoral form of *Eocnochelus* Pérez-García, Lapparent de Broin and Murelaga, 2017. The middle Eocene (upper middle Lutetian) “*Erymnochelys*” *eremberti* de Broin, 1977, from Saint-Germain-en-Laye (Yvelines, France), was

1 Introduction

Two lineages of the crown Pleurodira have been recognized in the European fossil record, both coming from Africa. One

defined as the type species of *Eocnochelus* (Pérez-García et al., 2017). It is represented by a single specimen, corresponding to a partial skeleton including the articulated skull and lower jaw, the partial carapace and plastron, and some vertebrae and appendicular elements. In addition, two other species of this genus are currently recognized, each of them by a single shell: the lower Eocene (early Ypresian) *Eocnochelus lacombianus* Pérez-García, Lapparent de Broin and Murelaga, 2017, from Jonquières (Aude, France), and the upper Eocene (Priabonian) *Eocnochelus farresi* Pérez-García, Lapparent de Broin and Murelaga, 2017, from Osona (Catalonia, Spain).

Only one representative of Pleurodira has so far been recognized in the Belgian record: *Neochelys*, identified by scarce and disjointed plates from the lowest Eocene (earliest Ypresian) of Dormaal (de Broin, 1977; de Lapparent de Broin, 2003). A specimen found more than a century ago, but remaining unpublished up to now, is studied in this paper. It comes from the middle Eocene (Lutetian) of Saint-Gilles (Brussels, Belgium) (Fig. 1) and is a partial shell, which preserves the almost complete plastron, some peripheral plates and a costal plate. It is identified as a member of Podocnemididae, but it cannot be attributed to *Neochelys*. Its study allows us to recognize the presence of the littoral form *Eocnochelus* in the Belgian record. Its attribution to the middle Eocene *Eocnochelus eremberti* is justified, the knowledge about this poorly represented form being improved.

Institutional abbreviations: IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; NHMUK, Natural History Museum, London, UK; MNHN.ZA AC, Anatomie Comparée, Muséum national d'Histoire naturelle, Paris, France; MNHN.ZR, Zoologie des Reptiles, Muséum national d'Histoire naturelle, Paris, France; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

2 Geographical and geological context

The specimen described herein comes from the E. Delheid collection that had been donated to the Royal Belgian Institute of Natural Sciences (RBINS) on 2 August 1911. This collection bears the general inventory number IG8289 and is represented by fossil remains of mammals, birds, reptiles, crustaceans, mollusk shells, and plants from different fossil localities of the Belgian Tertiary.

The turtle specimen, originally referred to *Emys?*, was found in 1893 in middle Eocene calcareous sands that were temporarily exposed during the construction of a house in Aqueduc Street in Saint-Gilles (now a municipality of Brussels) (Fig. 1). This information was communicated by E. Delheid on 6 May 1893 at the Royal Belgian Malacological Society (Delheid, 1893). Delheid discovered this fossil turtle in the Brussels Sand Formation about 1.25 m below the basal gravel bed of the Laekonian regional stage. The Brussels

Sand Formation (Bruxellian in the old literature; De Geyter et al., 2006) belongs to the upper part of the Zenne Group and is correlated with the NP14 biozone (Steurbaut, 2006), corresponding to the early Lutetian (46 to 48 Ma) (Fig. 1). The matrix that was associated with the specimen also contained a valve of an oyster referred to *Ostrea cymbula* and some buccinoid gastropods referred to *Fusus longaevus*, both taxa being sea forms (Delheid, 1893).

3 Systematic paleontology

Testudines Batsch, 1788

Pan-Pleurodira Joyce, Parham and Gauthier, 2004

Pleurodira Cope, 1864

Pelomedusoides Cope, 1868

Podocnemidoidea Cope, 1868

Podocnemididae Cope, 1868

Erymnochelyinae Broin, 1988

Eocnochelus Pérez-García, Lapparent de Broin and Murelaga, 2017

Eocnochelus eremberti (de Broin, 1977)

Material: IRSNB R356, a partial shell preserving the almost complete plastron articulated with the right partial third to sixth bridge peripherals (Fig. 2a–d), a disjointed left bridge peripheral (Fig. 2e–g), and a disjointed costal plate, probably corresponding to the left fourth costal (Fig. 2h–i) (Collection Delheid, IG 8289).

Locality and horizon: Saint-Gilles (Brussels, Belgium), Bruxellian regional stage, Brussels Sand Formation, early Lutetian, middle Eocene.

Description: The plastron of IRSNB R356 is almost complete, only lacking the right latero-posterior margin of the posterior lobe (Fig. 2a–d). Its maximum length is 39.7 cm. The anterior lobe is subrounded (Fig. 2a–b). The length of this lobe is approximately half of its width. It lacks intergular or gular protrusions. The length of the epiplastral symphysis is a quarter of that of the entoplastron. The entoplastron is rhombic, being slightly wider than long. Although this plate is relatively large, its anterior end does not reach the level of the axillary notches. The hyoplastra are longer than the hypoplastra. A pair of subelliptical mesoplastra is laterally located. These plates are longer than wide. The posterior plastral lobe is wide, being as wide as the anterior. It is longer than the anterior. Its lateral margins are slightly convex. A well-developed anal notch is present. Its total length is about half of its width. The lateral margins are subrounded. Both the pubis and the ischia were sutured

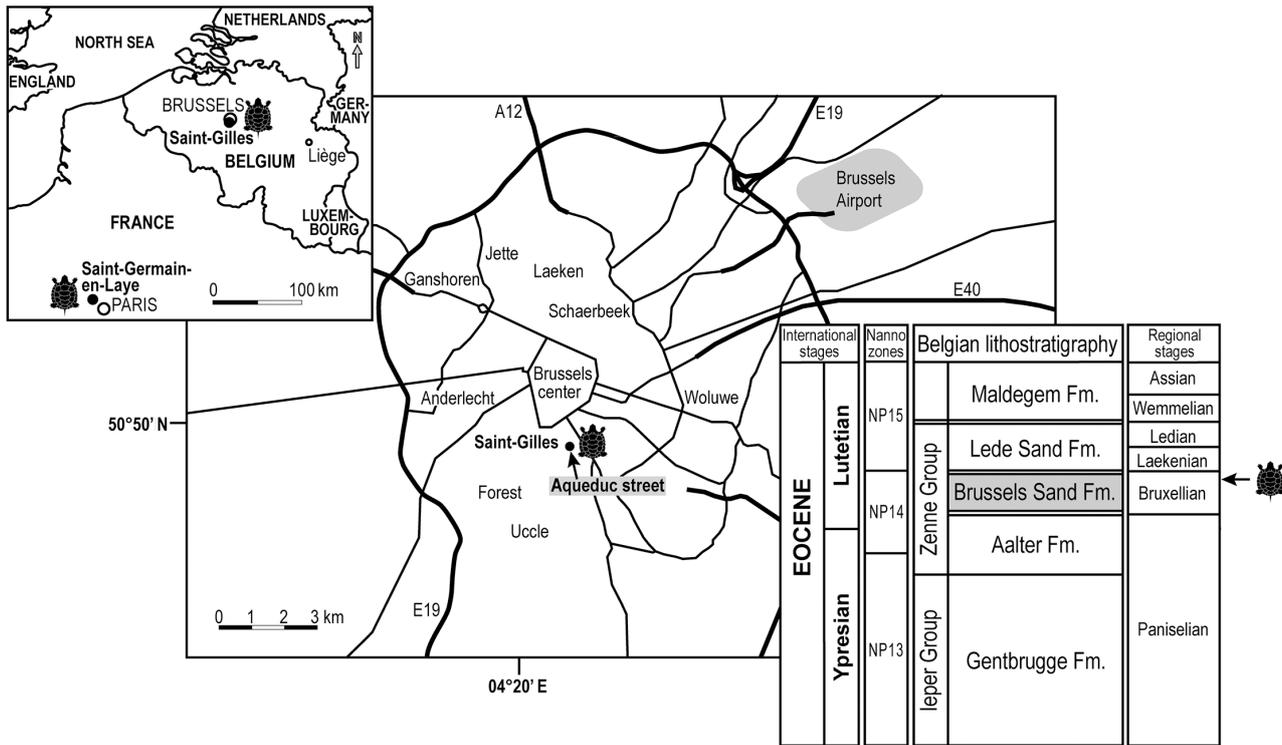


Figure 1. Map of Brussels municipality (Belgium) showing the geographic position of Aqueduc Street in Saint-Gilles where the specimen IRSNB R356 of *Eocnochelus eremberti* studied in this paper was discovered, in the lower Lutetian Brussels Sand Formation (middle Eocene). The position of the holotype of this species, from the upper middle Lutetian of Saint-Germain-en-Laye (Yvelines, France), is also indicated in the first map.

with the plastron (Fig. 2b). The pubic scar is more than twice longer than wide. A well-developed participation of the ischiatic scar in the region of the xiphiplastra located posterior to the anterior margin of the anal notch is present. The posterior branches of the ischiatic scars reach a region close to the anal notch.

IRSNB R356 has a single intergular scute (Fig. 2a). It is longer than wide, reaching the anterior region of the entoplastron. Its maximum width is much smaller than that of each of the gular scutes. The lateral margins are convergent towards the posterior area. The gular scutes contact in the axial plane. This medial length is similar to that of the humerals, both pairs of scutes being the shortest on the sagittal area of the plastron. The sagittal sulcus is slightly sinuous. A moderate overlap of the latero-posterior region of the humerals on the hyoplastra is present, the humero-pectoral sulci traversing the lateral half of the epi-hyoplastral sutures. The postero-lateral margins of the pectorals are in contact with the anterior margins of the mesoplastra. The overlap of the marginal scutes on the lateral region of the mesoplastra is much reduced. The anal scutes are relatively short. In visceral view, the plastral scutes are very narrow (Fig. 2b).

The peripherals of the bridge are relatively high (Fig. 2c–g). At least in this region, the pleuro-marginal sulcus is not close to the sutures between the costal and the peripheral plates

(Fig. 2d–e). The lateral margins of the vertebral scutes are markedly sinuous (Fig. 2h).

4 Discussion

The presence of mesoplastra allows us to exclude the assignment of the specimen presented here to Pan-Cryptodira, this clade being the most abundant and diverse lineage of turtles in the Cenozoic record of Europe (de Lapparent de Broin, 2001; Pérez-García, 2017). IRSNB R356 can be attributed to the sister group of Pan-Cryptodira, i.e., Pan-Pleurodira, due to the presence of a sutured contact between the pelvis and the shell. In addition, it shares with the members of this group the fusion of the intergulars, resulting in a single scute. The only lineage of Pan-Pleurodira identified in the post-Paleocene record of Europe is Pelomedusoides (de Lapparent de Broin, 2001; Pérez-García, 2016b). IRSNB R356 shares with the representatives of this group the presence of reduced mesoplastra, laterally located. The absence of a subtrapezoid anterior plastral lobe is not shared with the only member of Pan-Pleurodira hitherto recorded in the Belgian record: the Eocene podocnemidid *Neochelys* (a member of Erymnochelyinae) (de Broin, 1977; de Lapparent de Broin, 2003; Pérez-García and de Lapparent de

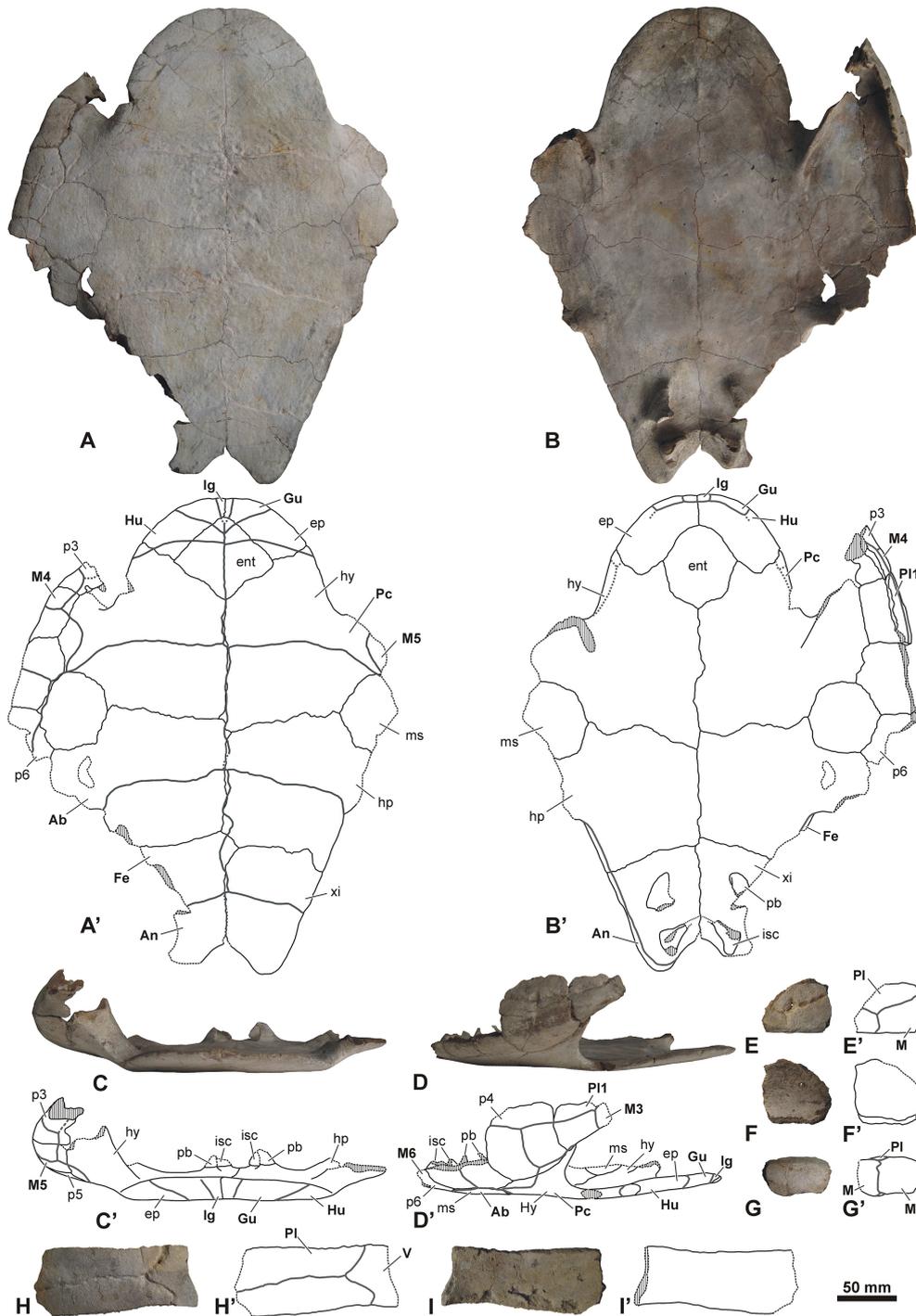


Figure 2. IRSNB R356, specimen of *Eocnochelus eremberti* from the middle Eocene (early Lutetian) of Saint-Gilles (Brussels, Belgium). A–D, plastron and articulated right bridge peripherals, in ventral (A), dorsal (B), anterior (C) and right lateral (D) views. E–G, disjointed left bridge peripheral, in left lateral (E), visceral (F), and ventral (G) views. H–I, disjointed costal plate (probably the left fourth costal), in dorsal (H) and ventral (I) views. Abbreviations for the plates and pelvic scars (in normal font and lowercase): ent, entoplastron; ep, epiplastron; hp, hypoplastron; hy, hyoplastron; isc, ischiatic scar; ms, mesoplastron; p, peripheral; pb, pubic scar; xi, xiphiplastron. Abbreviations for the scutes (in bold): Ab, abdominal; An, anal; Fe, femoral; Gu, gular; Hu, humeral; Ig, intergular; M, marginal; Pc, pectoral; Pl, pleural; V, vertebral. The solid lines represent the edges of the plates. The dashed lines indicate the broken margins. The broken surfaces are indicated by a striped pattern. The scute margins are represented by thicker gray lines.

Broin, 2015). In addition, the new specimen lacks the relatively long intergular scute present in *Neochelys*, which prevents the medial contact of the gulars. The other so far defined European member of Erymnochelyinae is the Eocene *Eocnochelus* (Pérez-García et al., 2017). It not only has a rounded anterior lobe but is also part of a lineage characterized by the presence of a posteromedial contact of the gulars, located posterior to a reduced intergular scute (i.e., the *Erymnochelys* group). Both character states are present in IRSNB R356. The sedimentary environment in which this specimen was found is compatible with that in which the littoral *Eocnochelus* inhabited, but not with that for the freshwater *Neochelys*. Other characters available in the specimen confirm its attribution to *Eocnochelus*, not being shared with those of the other so far defined representatives of the *Erymnochelys* group (all being African freshwater forms, in contrast to the European littoral *Eocnochelus*) (see Pérez-García et al., 2017). Thus, the well-developed participation of the ischiatic scar in the xiphiplastral posterior area is not shared with the extant *Erymnochelys madagascariensis*, the lower Oligocene “*Podocnemis*” *fajumensis* Andrews, 1903, and the lower Miocene “*Podocnemis*” *aegyptiaca* Andrews, 1900. The absence of gular protrusions is not shared with the upper Miocene–Pliocene *Kenyemys williamsi* Wood, 1983 and some “*P.*” *fajumensis* specimens. The presence of a relatively long intergular scute, overlying the most anterior region of the entoplastron, is not shared with *K. williamsi* and *Er. madagascariensis*. The absence of a long overlap of the anal scutes onto the xiphiplastra, being shorter than 2 times the femoral length on the lateral borders of this pair of plates, is not shared with *Er. madagascariensis*, the upper Miocene–Pliocene *Turkanemys pattersoni* Wood, 2003 and *K. williamsi*. The very short dorsal expansion of the plastral scute borders is not shared with “*P.*” *fajumensis*.

The lateral margins of the vertebral scutes of the specimen analyzed here are not substraight as in the case of the lower Eocene *Eocnochelus lacombianus*, but they are markedly sinuous, as in the middle Eocene *Eocnochelus eremberti* and in the upper Eocene *Eocnochelus farresi*. As in *Eo. eremberti* and *Eo. lacombianus*, the epiplastral symphysis is longer than that of *Eo. farresi*, a taxon in which its length is less than one-fifth of that of the entoplastron. The posterior plastral lobe is wider than those of *Eo. lacombianus* and *Eo. farresi*, as in *Eo. eremberti*. The presence of slightly convex lateral margins of the posterior plastral lobe is shared with *Eo. eremberti* and *Eo. farresi*, contrasting with the known concave morphology for *Eo. lacombianus*. The anterior area of these margins are subrounded as in *Eo. eremberti*. The presence of a relatively wide and short anal notch, its total length being approximately about half of its width, is shared with *Eo. eremberti* and *Eo. lacombianus*. This structure is almost as long as wide in *Eo. farresi*. As in *Eo. eremberti*, the pubic scar is relatively long, being more than twice longer than wide. However, that of *Eo. lacombianus* is much wider, its width being approximately half of its length. This char-

acter is not known for *Eo. farresi*. IRSNB R356 lacks posterior branches of the ischiatic scars near the xiphiplastral tips, which is shared with *Eo. eremberti* and *Eo. lacombianus*, but not with *Eo. farresi*. The presence of the anterior border of the intergular scute narrower than that of each gular is only shared with *Eo. eremberti*. *Eocnochelus lacombianus* is characterized by the presence of a short overlap of the latero-posterior region of the humeral scutes on the hyoplastra. The humero-pectoral sulci of *Eo. farresi* are located in the middle region of the epiplastra–hyoplastra sutures, generating a relatively large overlap of the humerals on the hyoplastra. An intermediate situation is known for *Eo. eremberti*, which is shared with the new specimen presented here. Taking into account all these characters considered in the differential diagnoses for the three known *Eocnochelus* species, the specimen analyzed here cannot be attributed to the older species *Eo. lacombianus* (from the lower Eocene), nor to the younger species *Eo. farresi* (from the upper Eocene). Considering all these characters, it is recognized as belonging to *Eo. eremberti*. Moreover, *Eo. eremberti* is the only species of *Eocnochelus* hitherto known for the middle Eocene record.

The maximum length of the plastron analyzed here is significantly longer than that known for *Eo. lacombianus*, i.e., 29.3 cm. It is slightly longer than that of the holotype of *Eo. farresi*, i.e., 38 cm. The holotype of *Eo. eremberti* is the largest known specimen of this genus, the length of its plastron being estimated as close to 50 cm. Several characters subject to intraspecific variability are identified thanks to the finding of this second specimen of *Eo. eremberti*. The posterior plastral lobe of the new specimen of *Eo. eremberti* is slightly wider than that of the holotype of this taxon, relative to the width of the anterior lobe. Thus, the width of both lobes is subequal in the new specimen. The epiplastral symphysis of the new specimen, although being markedly longer relative to the length of the entoplastron than that known for *Eo. farresi*, is shorter than that of the holotype of *Eo. eremberti*. The posterior branches of the ischiatic scars are longer in relation to the width of these scars than in the holotype. Therefore, their distance to the anal notch is less. As Pérez-García et al. (2017) indicated, differences in the overlap of the intergular onto the entoplastron are known for several taxa of the *Erymnochelys* group, such as “*P.*” *fajumensis*, *T. pattersoni*, and *Er. madagascariensis*. Thus, although the intergular contacted the anterior margin of the entoplastron in the holotype of *Eo. eremberti*, a slight overlap on the most anterior area of this plate is identified in the new specimen presented here. Although the lateral margins of the intergular of the holotype of *Eo. eremberti* are subparallel throughout much of its path, they are posteriorly convergent in the new specimen, as in the other known plastra of *Eocnochelus*. The new specimen is the only individual of this genus so far known in which the postero-lateral margins of the pectorals are in contact with the anterior edge of the mesoplastra. Variability in this character can also be observed in other taxa of the *Erymnochelys*

group known by several specimens, as occurs, for example, in the Oligocene “*P.*” *fajumensis*, the distance between the pectorals and the mesoplastra being much greater in SMNS 12647 than in NHMUK R3435, and in the extant *Er. mada-gascariensis*, the contact being present in MNHN.ZA AC 1897-80, but not in MNHN.ZR To.0609-16.

5 Conclusions

Until now, only a single representative of Pan-Pleurodira was recognized in the Belgian fossil record. This is the Eocene freshwater turtle *Neochelys*, corresponding to a member of Podocnemididae belonging to Erymnochelyinae. In Belgium, *Neochelys* was only known by scarce and disjointed plates, from the lower Eocene record. A new turtle specimen, from the middle Eocene levels of Saint-Gilles (Brussels, Belgium), is presented here. It corresponds to the only partial shell of a pleurodiran turtle recognized in the fossil record of Belgium. It can also be attributed to a podocnemidid belonging to Erymnochelyinae. However, and unlike *Neochelys*, it corresponds to a member of the *Erymnochelys* group. This specimen is recognized as attributable to the recently described littoral taxon *Eocnochelus*, the depositional environment of the site where it was found being compatible with that in which this form could have lived. Therefore, it corresponds to the first Belgian evidence of this genus, which had hitherto been recognized in France, Spain, England and, probably, Italy. Three species of *Eocnochelus* are known: the lower Eocene *Eocnochelus lacombianus*, the middle Eocene *Eocnochelus eremberti*, and the upper Eocene *Eocnochelus farresi*. Each of these species was, until now, only recognized by a single specimen, the holotype of *Eo. lacombianus* coming from Jonquières (Aude, France), that of *Eo. eremberti* from Saint-Germain-en-Laye (Yvelines, France), and that of *Eo. farresi* from Osona (Catalonia, Spain). The availability of characters in the new middle Eocene specimen from Saint-Gilles allows its attribution to the synchronous form *Eo. eremberti*. The plastron of the specimen studied here is much more complete than that of the holotype of this taxon. Its study and comparative analysis allow us to recognize intraspecific variability for some characters.

Data availability. The specimen studied here is deposited in the Institut royal des Sciences naturelles de Belgique (Brussels, Belgium).

Competing interests. The authors declare that they have no conflict of interest.

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