FOSSIL PUPILLOIDEA LAND SNAILS FROM THE BORGLOON FORMATION (EARLY OLIGOCENE, BELGIUM)

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Abstract *Pupilloidea is a diverse group of land snails, most of which are of minute size. Because of that, Paleogene pupilloid fossils are often overlooked and scarcely studied, partly because of a historical collection bias against small-sized fossils and partly due to the preservation bias against their fragile shells. The Borgloon Formation in Belgium (Rupelian, Early Oligocene), despite well-studied, still lacks proper identifications for most of its pupilloid snails. Herein, we present a reassessment and taxonomic account of the fossil Pupilloidea from the Borgloon Formation. Four species were identified in the material:* Pupoides gerardae *(Karnekamp, 1990) comb. nov. (Pupillidae),* Gastrocopta didymodus *(Sandberger, 1858) (Gastrocoptidae),* Vallonia sandbergeri *(Deshayes, 1863) (Valloniidae), and* Vertigo ovatula *(Sandberger, 1875) (Vertiginidae).*

Key words *Atuatuca Formation, Gastrocoptidae, micro-CT, Pupillidae, Rupelian, Tongeren Group, Stylommatophora, Valloniidae, Vertiginidae.*

INTRODUCTION

Pupilloidea is a worldwide-distributed superfamily of land snails, typically of minute size and, as the name suggests, bearing pupoid shells, although some families contain larger animals or have lineages bearing discoid shells. Pupilloids are common and widespread in the Central and Western European fossil record, being much more frequently found in Neogene sediments, with records getting sparser in the Oligocene and further back in the Paleogene (e.g., Wenz, 1923; Preece, 1982; Pacaud & Le Renard, 1995; Salvador *et al.*, 2016a). Pupilloid snails from the older Cenozoic epochs are often overlooked and scarcely studied, partly because of the historical collection bias against small-sized fossils and partly due to the preservation bias against their fragile shells.

The Borgloon Formation in Belgium (Rupelian, Early Oligocene) is somewhat of an exception. Its molluscan fauna has been recently and thoroughly described (Marquet *et al.*, 2008; Janssen & Lenaerts, 2019), but even so the identity of most of its pupilloid snails remained an open question, with the majority bearing only a generic name and the tag 'sp.'. Therefore, herein we present a reassessment and taxonomic account of the fossil Pupilloidea from the Borgloon Formation.

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GEOLOGICAL SETTING

The deposits of the Early Oligocene in Belgium, the so-called Tongeren Group, are divided in three formations; from bottom to top: Zelzate Formation, Sint-Huibrechts-Hern Formation, and Borgloon Formation (Laga *et al.*, 2001). While the first two include predominantly sediments deposited in a marine environment, Borgloon Formation includes continental coastal environments. Borgloon Formation is well-developed towards eastern Belgium in Flemish Brabant (Vlaams-Brabant) and Limburg, especially in the municipalities of Tienen and Boutersem (Brabant) and in the area between Borgloon and Kleine Spouwen (near Tongeren, Limburg) (Laga, 1988). Mammalian fossils indicate the Borgloon Formation dates from the earliest Rupelian (King *et al.*, 2016).

The name Borgloon Formation ("Formatie van Borgloon" in Dutch) was introduced by Laga (1988) without type locality or type section. Laga (1988) presented type sections only for each member of the formation, but none is situated in Borgloon. The Formation's members are: Henis Member and Alden Biesen Member in Limburg, and Boutersem Member (including Hoogbutsel Bed and Kerkom Bed) in Brabant (Laga, 1988). Furthermore, the name Borgloon Formation replaced, without proper explanation, the older name Atuatuca Formation (Janssen *et al.*, 1976), which represented the

same stratigraphical sequence in the Tongeren area (known as "Atuatuca Tungrorum" by the Romans) and counted with descriptions of its type locality and section, along a detailed stratigraphical profile (Janssen & Lenaerts, 2019). A proposal to reconsider the name of the formation was advanced to the National Commission for Stratigraphy Geological Survey of Belgium (Janssen & Lenaerts, 2019).

The members of the Borgloon Formation consist in a system of coastal-continental lagoon deposits (Laga *et al.*, 2001; Marquet *et al.* 2008; King *et al.*, 2016). In the area near Boutersem, where the remains of terrestrial vertebrates have been found, islands or near coast marshlands might have occurred. Tidal influences with influx of euhaline water and freshwater from the mainland created a euryhaline environment with species tolerating considerable changes in salinity (Marquet *et al.* 2008). These outcrops yielded vast amounts of molluscan fossils, among which was found a small quantity of freshwater species and an even smaller amount of land snails (Marquet *et al.* 2008). The latter seem to be restricted to the clayey/marly deposits. It is not fully clear whether the terrestrial snails were carried to the near-coast environment by freshwater streams or if they were living on offshore islands that were flooded when see levels rose.

Terrestrial snails have been found in the following seven outcrops of the Borgloon Formation (Cadée *et al.*, 1976): **(1)** Vertebrate horizon, Boutersem Member (European land mammal age MP 21); Hoogbutsel near Boutersem municipality, Flemish Brabant (lat 50.842770, long 4.851880). A thin layer (ca. 10cm) of clay overlying the Neerrepen Sands with numerous euryhaline molluscan fossils (Glibert & de Heinzelin, 1952). Most work conducted there by Belgian researchers failed to find land snails, although the Dutch "Werkgroep voor Tertiaire en Kwartaire Geologie" recovered *Vallonia* sp. and *Vertigo* sp. in the early 1970's. **(2)** A similar vertebrate horizon to (1) was found in Hoeleden (Kortenaken municipality, Flemish Brabant), with a somewhat richer molluscan fauna including a few specimens of *Vallonia* sp. and *Vertigo* sp. (Glibert & de Heinzelin, 1954b). **(3)** Alden Biesen Member; Hulsberg, Borgloon municipality, Limburg (lat 50.803808, long 5.326165). From the several boreholes drilled in Hulsberg (Kruissink *et al.*, 1978), one sample from mid-Alden Biesen Member contained the land snails *Carychium* sp. and *Gastrocopta* sp. **(4)** Alden Biesen Member; Nachtegaalstraat, former Kleine Spouwen municipality (now Bilzen), Limburg (lat 50.836410, long 5.548390). Thin clayey layer (ca. 10cm) forming the top of the Alden Biesen Member and containing a well-preserved euryhaline molluscan fauna, with freshwater and a few land snails, including all the Pupillidae species discussed herein. **(5)** Base of the Berg Sands ("Zone à *Callista kickxi* (Nyst, 1836)"; Glibert & de Heinzelin, 1954b), Bilzen Formation. Keistraat, hamlet of Berg, former Kleine Spouwen municipality (now Bilzen), Limburg (lat 50.847790, long 5.548890). This is the type locality of the Berg Sands, containing marine mollusks. However, the base of the Sands has eroded the underlying the Alden Biesen Member and reworked some of its contents, including its mollusks. A few reworked specimens of *Vertigo* sp. were found in this outcrop. The distance from outcrop (4), also in Kleine Spouwen, is ca. 1.5km. **(6)** Alden Biesen Sands, Alden Biesen Member; Alden Biesen Castle Park, former Rijkhoven municipality (now Bilzen), Limburg (lat 50.840552, long 5.529177). The type locality of Alden Biesen Sands is situated in this locality (at the former entrance of the Estate), but no land snails were recovered from its 2 m-thick shell bed. Instead, land snails (*Vallonia* sp. and *Vertigo* sp.) were found in in a shell bed 300m away from it, about 1.5m deep. For more information on these outcrops, please refer to the full account by Marquet *et al.* (2008). **(7)** Alden Biesen Member; construction pit at Driekruisenstraat, Tongeren municipality (lat 50.789728, long 5.464075). This was a temporary outcrop exposed during a building excavation, consisting of 5m of visible Alden Biesen Member, more clayey than (and with thin layers of sand) outcrops of Kleine Spouwen and Alden Biesen. Well-preserved euryhaline mollusks were found, including species that are otherwise rare in the Member. Two freshwater species were found, alongside rare terrestrial *Vertigo* sp.

MATERIAL AND METHODS

The specimens studied herein are deposited in the collections of the Naturalis Biodiversity Center (RGM; Leiden, The Netherlands) and the Royal Belgian Institute of Natural Science (RBINS; Brussels, Belgium). The material is largely the same studied by Marquet *et al.* (2008), with a few

additions. There were some errors and mix-ups of register numbers in the work of Marquet *et al.* (2008), so here we provide the correct numbers for the lots.

Selected specimens were imaged using the x-ray micro-computed tomography technique to better visualize and analyze their apertural barriers and internal structures. Micro-CT scans were performed at the RBINS using the XRE UniTOM system (TESCAN XRE, Ghent, Belgium). No filter was used. Each sample was previously glued on the tip of a sharpened carbon stick with water-soluble fish glue in order to immobilize it during the scanning process. All samples were scanned using the microfocus mode at a voltage of 85 kV and an exposure of 2000 ms. Other parameters were adapted depending on specimen size and the voxel size to reach (voxel size range: 1.5µm to 5µm). A summary of the parameters used for each sample can be seen in Table 1. The resulting projections were reconstructed using the XRE Reconstruction software to get a stack of 2D TIF images. Then segmentation, visualization and analysis were performed using the Dragonfly software v. 4.5.0.711 (ORS, 2016). We exported 3D models as STL files and uploaded them to the SketchFab platform for 3D rendering. Transparency was applied to some models to display internal structures.

Interactive 3D models of the RBINS collections are freely available online on SketchFab (https://sketchfab.com/naturalsciences). For some specimens, we also provide a version of the model with the sediment inside the shell digitally excluded and/or a model with a transparent shell, in order to better visualize the internal structures. The models can also be seen on the RBINS virtualcollections website (http://virtualcollections.naturalsciences.be/) by searching for their RBINS registration number.

Systematic classification follows Bouchet *et al.* (2017). For simplicity, the entries in the cresonymies given below are restricted only to those works dealing with the Borgloon Formation.

SYSTEMATICS

SUPERFAMILY PUPILLOIDEA
FAMILY PUPILLIDAE
Genus *Pupoides* L. Pfeiffer, 1854
Pupoides gerardae (Karnekamp, 1990) comb. nov.
(Fig. 1A–D)

Microstele gerardae Karnekamp, 1990: 113, pl. 1; Marquet *et al.*, 2008: 71, text-fig. 12, pl. 20, fig. 3; Kronenberg, 2009: 18, pl. 2, fig. 17.

Material analyzed RBINS 07220, RBINS 07221, RBINS 07222; Borgloon Formation: Alden Biesen Member (outcrop Kleine Spouwen, Bilzen).

Discussion. This species was originally described as *Microstele gerardae* from the Early Oligocene (Rupelian) Atuatuca Formation, retrieved from a temporary exposure near Spouwen, Bilzen, Belgium (Karnekamp, 1990). The present material from the Borgloon Formation, although fragmentary, compares very well with the material from the type locality (holotype RGM 229794), as already pointed out by Marquet *et al.* (2008).

However, the classification of this species in *Microstele* Boettger, 1886 is contentious, based on superficial similarity with Recent *M. muscerda* (Benson, 1853) from Sri Lanka and India (Raheem *et al.*, 2014). The latter species has a much narrower shell, with a deeper suture, and differently-placed and additional apertural dentition (Raheem *et al.*, 2014). The difference is even more accentuated in comparison to other species of *Microstele*, in particular to the type species *M. noltei* (Boettger, 1886) from southern Africa (Zilch, 1959; Verdcourt, 1968; van Bruggen, 1970; van Bruggen & Rolán, 2003).

The present species bears a much closer resemblance and correspondence of structures to the genus *Pupoides*: the more conical shell profile, with a broader body whorl; the shallower suture and less convex whorls; and especially the presence of the parietal tooth and its positioning near the insertion of the peristome (Fig. 1C; Zilch, 1959). The present fossils are especially akin to *P. coenopictus* (Hutton, 1834), a Recent species that ranges from Africa to Southeast Asia (Raheem *et al.*, 2014). As such, herein we propose the new combination *Pupoides gerardae* (Karnekamp, 1990).

The same reasoning might be valid for other supposed Central and Western European fossil *Microstele*, such as *M. wenzi* (Fischer, 1920) and *M. mariae* (Morgan, 1920) from the Miocene of Germany and France, respectively. In fact, Fischer (1920) had originally described the former species as *Pupoides wenzi*, so a revision of those fossils is necessary.

Pupoides, as currently understood, is distributed worldwide except for Europe (Schileyko,

Table 1 Micro-CT scan parameters for each sample.

Sample	Scanning time (min)	Filter	Focus mode	Tube voltage (kV)	Power (W)	Imaging mode	Expo (ms)	Voxel Size (µm)	Number of averages	Projection number
RBINS 7216: *Vallonia sandbergeri*	54	No	microfocus	85	3	HW2SW1	2000	2,5	1	1500
RBINS 7218: *Vertigo ovatula*	38	No	microfocus	85	3	HW2SW2	2000	5	1	1000
RBINS 7219: *Vertigo ovatula*	42	No	microfocus	85	3	HW2SW2	2000	5	1	1103
RBINS 7220: *Pupoides gerardae*	89	No	microfocus	85	5	HW2SW1	3000	1,5	1	1600
RBINS 7221: *Pupoides gerardae*	40	No	microfocus	85	5	HW2SW2	2000	4	1	1000
RBINS 7222: *Pupoides gerardae*	43	No	microfocus	85	5	HW2 SW2	2000	4,5	1	1100
RBINS 7223: *Gastrocopta didymodus*	43	No	microfocus	85	5	HW2SW2	2000	4	1	1100

1998); its type species is *P. nitidulus* (L. Pfeiffer, 1839), from Cuba. There are several subgenera proposed (Schileyko, 1998), but the group likely represents a polyphyletic assemblage pending revision. In any event, the genus is distributed through tropical and subtropical areas today (Schileyko, 1998), which might be interpreted as indicative of warmer climates during the Early Oligocene in the area covered by the Borgloon Formation (Karnekamp, 1990; Rasser *et al.*, 2019).

FAMILY GASTROCOPTIDAE
Genus *Gastrocopta* Wollaston, 1878
Gastrocopta didymodus (Sandberger, 1858)
(Fig. 1E)

Gastrocopta (*Sinalbinula*) sp.: Marquet *et al.*, 2008: 72, pl. 21, fig. 1.

Material analyzed RBINS 07223, RGM.607305 (erroneously numbered RGM 550-113-114 in Marquet *et al.*, 2008 and assigned to figure 2a–b; it is instead likely the specimen from fig. 1c–e); Borgloon Formation: Alden Biesen Member (outcrops Kleine Spouwen and Alden Biesen Castle, Bilzen).

Discussion The present specimens can be identified by: a slender and cylindrical shell (in line with a select group of European fossil *Gastrocopta* spp.; Stworzewicz & Prisyazhnyuk, 2006; Stworzewicz *et al.*, 2013); a strong and straight columellar lamella; the three palatal teeth diminishing in size towards the adapical region of aperture; a faint basal tooth; and the shape of the anguloparietal lamella (only slightly bifid, with the angular portion being only a faint protrusion). This set of conchological features allow the identification as *G. didymodus* (Sandberger, 1858), a species originally described and only known from the Late Oligocene (Chattian) Landschneckenkalk ("land snail limestone"), in Flörsheim and Hochheim am Main, Germany (Sandberger, 1858), now Hochheim Formation or lower Oppenheim Formation (Salvador *et al.*, 2016a). The present record, therefore, represents an extension in the stratigraphic as well as geographic range of the species.

Despite *G. didymodus* being for a time considered by Sandberger (1875) as synonymous with *G. fissidens* (Sandberger, 1858), further authors later argued that it is in fact a separate taxon

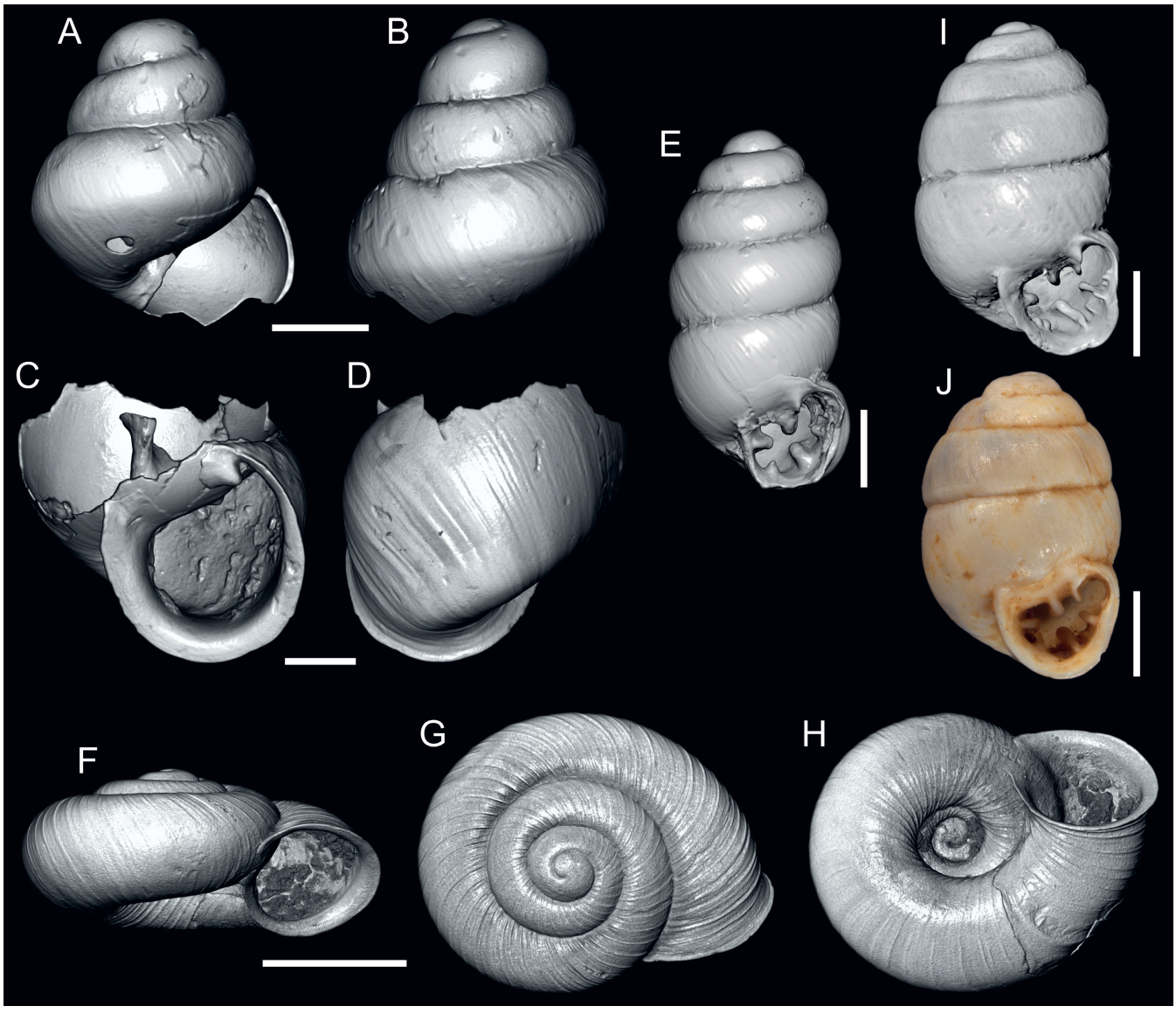

Figure 1 **A–D** *Pupoides gerardae* (Karnekamp, 1990), micro-CT scan images. Scale bars=1mm. **A, B** Fragmentary specimen, spire apex only; RBINS 07221. **C, D** Fragmentary specimen, apertural region only; RBINS 07222. **E** *Gastrocopta didymodus* (Sandberger, 1858), micro-CT scan image. RBINS 07223. Scale bar=0.5mm. **F–H** *Vallonia sandbergeri* (Deshayes, 1863), micro-CT scan image. RBINS 07216. Scale bar=1mm. **I, J** *Vertigo ovatula* (Sandberger, 1875). Scale bars=1mm. **I** Micro-CT scan image. RBINS 07218. **J** Photograph (auto-montage). RGM.550109.

(Boettger, 1889; Fischer & Wenz, 1914; Wenz, 1921). While the species is generally referred to the subgenus *Sinalbinula* Pilsbry, 1916 (Pilsbry, 1917; Wenz, 1923), we refrain from a subgeneric classification, since, as discussed by Manganelli & Giusti (2000), they likely do not represent natural groupings as presently defined.

There are no *Gastrocopta* living in Europe today, so their use for any paleoecological interpretations is very limited (Rasser *et al.*, 2019); even more so, they occur worldwide from temperate to tropical regions (Zilch, 1959).

FAMILY VALLONIIDAE
Genus *Vallonia* Morse, 1864
Vallonia sandbergeri (Deshayes, 1863)
(Fig. 1F–H)

Helix Sandbergeri Deshayes, 1863: 816, pl. 52, figs. 23–25.
Helix (*Vallonia*) *lepida*: Sandberger, 1875: 375 [in part].
Vallonia sandbergeri: Wenz, 1923: 910 [in part]; Gerber, 1996: 155, textfig. 3z, fig. 58c–e; Marquet *et al.*, 2008: 72, pl. 19, fig. 2.

Helix (*Vallonia* ?) cf. *sandbergeri*: Glibert & de Heizelin, 1954a: 11, pl. 2, fig. 11.
Vallonia cf. *sandbergeri*: Glibert & de Heizelin, 1954b: 376.

Material analyzed RBINS 07216, RGM.550332; Borgloon Formation: Alden Biesen Member (outcrops Kleine Spouwen and Alden Biesen Castle, Bilzen).

Discussion The present fossils can be identified as *V. sandbergeri*, as revised by Gerber (1996). This species is very similar to *V. lepida* (Reuss, 1849), but as remarked by Marquet *et al.* (2008), it can be distinguished by its larger umbilicus, axial sculpture, and a smaller parieto-columellar region of the aperture. Nevertheless, these features can also be observed in *V. lepida*, which is a species widely distributed, from the Netherlands to Eastern Europe and from the Early Oligocene to the Late Miocene (Gerber, 1996). *Vallonia sandbergeri* resembles more closely the Lower Miocene forms from Germany, which also bear a marked axial sculpture (Gerber, 1996). Further revisions of *V. lepida* might still show that it is a species complex.

Besides the Borgloon Formation, *V. sandbergeri* is known from outcrops in the region of Étampes, France (Late Oligocene, Chattian), and other localities in Belgium belonging to the Borgloon Formation (Boutersem Sand Member; Early Oligocene, Rupelian) (Gerber, 1996; Marquet *et al.*, 2008).

FAMILY VERTIGINIDAE
Genus *Vertigo* O.F. Müller, 1774
Vertigo (*Alaea*) *ovatula* (Sandberger, 1875)
(Fig. 1I, J)

Vertigo (*Ptychalaea* ?) cf. *fissidens*: Glibert & de Heizelin, 1954a: 11, pl. 2, fig. 12.
Vertigo (*Ptychalaea*) cf. *fissidens*: Glibert & de Heizelin, 1954b: 376.
Vertigo (*Vertigo*) sp. 1: Marquet *et al.*, 2008: 73, pl. 20, fig. 1.
Vertigo sp. 2: Marquet *et al.*, 2008: 74, pl. 20, fig. 2.

Material analyzed RBINS 07218, RBINS 07219, RGM.550109; Borgloon Formation: Alden Biesen Member (outcrops Kleine Spouwen and Alden Biesen Castle, Bilzen). RGM.510110, RGM.510111, RGM.607304 (erroneously numbered RGM 550–112 in Marquet *et al.*, 2008 and assigned to figure 2c–d; it is instead the specimen from fig. 2a–b); Borgloon Formation: Alden Biesen Member (outcrops Boutersem, Borgloon, and Hulsberg, Limburg). RGM.1362806; Bilzen Formation: Berg Sand Member (outcrop Kleine Spouwen, Bilzen, horizon with *Callista kickxi* (Nyst, 1836)).

Discussion The present specimens can be identified as *V. ovatula* by its aperture shape (more circular when compared to Late Paleogene and Early Neogene congeners) and the presence, shape and position of the six apertural barriers: two strong and parallel parietal teeth, one strong parietal lamella, one faint basal tooth, and two strong palatal teeth (with the basalmost one deeply inserted into the aperture). There is some variation in shell size and shape (from the typical more oval and elongated shells to a rounder shell) and dentition (Fig. 1I, J).

Intraspecific variation in the size and number of apertural barriers is well-reported in vertiginids (e.g., Stworzewicz, 1999; Salvador, 2015, 2016b; Nekola *et al.*, 2018). Even though the overall number of available specimens is small, there is some variation in the present material. Some specimens present a very faint upper palatal tooth and one (RBINS 07218: Fig. 1I) even has a faint nodule between the two strong palatal teeth. Furthermore, one specimen (RGM.607304, representing *Vertigo* sp. 2 *sensu* Marquet *et al.*, 2008: pl. 20, fig. 2a–b) has no parietal teeth whatsoever, but all the other teeth are still present. This latter specimen does not seem to represent a distinct species, being instead just an individual that did not develop the teeth. However, the main and stronger teeth and lamella are important in vertiginid taxonomy (Nekola *et al.*, 2018), and accordingly, the subspecies *V. ovatula mosbachensis* Boettger, 1889, for instance, has as diagnostic feature the lack of one parietal tooth (Boettger, 1889).

There are presently four recognized subspecies (Boettger, 1889; Wenz, 1923; Stworzewicz, 1999) within *V. ovatula*: (1) nominate *V. ovatula ovatula* from the Late Oligocene (Chattian) Landschneckenkalk of Flörsheim and Hochheim am Main (Germany); *V. ovatula hydrobiarum* Boettger, 1889 from the Early Miocene (Aquitanian) Hydrobienschichten ("*Hydrobia* beds", now Wiesbaden Formation) from Wiesbaden (Germany); *V. ovatula mosbachensis* Boettger, 1889, also from the Hydrobienschichten

of Wiesbaden; and *V. ovatula miliiformis* Boettger, 1889 from the Middle Miocene (Burdigalian/Langhian) of the Landschneckenmergel from Frankfurt am Main (Germany). *Vertigo ovatula* is also reported from the Middle Miocene (Burdigalian to Serravallian) of Poland and Ukraine (Stworzewicz, 1999; Höltke *et al.*, 2016); these forms could represent a further subspecies or even a distinct species. The specimens from the Borgloon Formation correspond very well to nominate *V. ovatula*. The present record, thus, is an extension in both stratigraphic and geographic range of the species.

Vertigo ovatula has been traditionally placed in the Northern Hemisphere subgenus *Alaea* Jeffreys, 1838 (*e.g.*, Boettger, 1889; Fischer & Wenz, 1914), although Wenz (1923) placed it in nominate *Vertigo*. Nekola *et al.* (2018) recently published a molecular phylogeny of *Vertigo*, confirming and better defining several subgenus level taxa. However, those authors did not discuss fossil species older than Pleistocene, did not include them in their revised classification, and did not estimate the times when each subgenera possibly appeared. Nevertheless, based on their classification (and the original diagnosis of Jeffreys, 1830), we can propose the species to be allocated within *Alaea* due to the following diagnostic features: dextral ovate-elongated shell, reduced teleoconch striation, thickened parietal callus, modest apertural sinulus, weak palatal depression on outer surface of body whorl, and the number and position of the apertural barriers (see above). Furthermore, *Alaea* has been recovered as a basal branch of *Vertigo* in the mtDNA tree presented by Nekola *et al.* (2018), which is in line with a group that has potentially been around since the Early Oligocene.

Recent *Vertigo* (*Alaea*) spp. live in open to forested wetlands (although some inhabit upland forests and grasslands; Nekola *et al.*, 2018). Given that congeneric land snails tend to share ecological preferences (Rasser *et al.*, 2019), considering *V. ovatula* as a wetland dweller is in line with the paleoenvironmental interpretation of the Borgloon Formation (Marquet *et al.*, 2018).

Remarks Some specimens (RGM.1362806) were found in the Berg Sand Member (Bilzen Formation), which overlies the Alden Biesen Member of the Borgloon Formation and represents a fully marine transgressive environment (Janssen *et al.*, 1976; King *et al.*, 2016). This material is deemed to represent reworked fossils from the Alden Biesen member, given such small land snails would very unlikely be deposited in a marine environment. Furthermore, those fossils have a more whitish color and hardened aspect, which are usual of reworked specimens. Gaemers (1972) also noted that the "Zone of *Callista kickxii*" of the Berg Sand Member had reworked gastropods from the Alden Biesen level. Finally, even though our sample size is small, the reworked specimens are slightly larger than the other specimens, which could be indicative of a taphonomical bias favouring larger shells.

Conclusion

In total, four species of Pupilloidea snails were identified in the available material from the Borgloon Formation: *Pupoides gerardae* (Karnekamp, 1990) comb. nov. (Pupillidae), *Gastrocopta didymodus* (Sandberger, 1858) (Gastrocoptidae), *Vallonia sandbergeri* (Deshayes, 1863) (Valloniidae), and *Vertigo ovatula* (Sandberger, 1875) (Vertiginidae). Micro-CT imaging has proven to be a great tool for studying these minute pupilloid snails, as it allows full visualization of apertural barriers (including inside the shell), which are important characters for species identification.

The terrestrial snail fauna of the Borgloon Formation (Marquet *et al.*, 2008; present work) has more in common with the younger fauna from the Mainz Basin ("Mainzer Becken" in German; ca. 250km southeast of Limburg; Chattian), than it does with the fauna from the Paris Basin to the south (Sandberger, 1858–1863; Fischer & Wenz, 1914; Wenz, 1921; Marquet *et al.*, 2008; present work). The relationship among terrestrial Paleogene faunas in Western Europe is still scarcely investigated when compared to Neogene ones, so this should be an interesting venue for future investigation.

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