Euroscaphella nov. gen. (Gastropoda: Volutidae) in the Neogene of Europe, with the description of a new species: *Euroscaphella namnetensis* nov. sp. from the Mio-Pliocene transition of northwestern France

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The genus *'Scaphella'* as used until now is polyphyletic, and *Euroscaphella* nov. gen. is proposed for the European species, and also for the Paleocene and Eocene New World and Australian species, pending further review. *Euroscaphella namnetensis* nov. sp. is described from the latest Miocene-early Pliocene 'cool' Redonian of department Loire-Atlantique in northwestern France and *Euroscaphella* cf. *miocenica* (Fischer & Tournouër, 1879) is reported from the chronologically slightly younger late Tortonian to early Messinian 'warm Redonian' of Maine-et-Loire, northwestern France.

Key words: Gastropoda, Volutidae, *Euroscaphella*, Redonian, early Pliocene, France, new genus, new species.

Introduction

Landau & Silva (2006a) reviewed the species within the genus *Scaphella* Swainson, 1832 in the Neogene of Europe, followed the history of the genus both in the Old and New World, and discussed the palaeobiogeographical implications of their distribution. The authors traced the history of *Scaphella* in the Atlantic and suggested that the group originated in the Cretaceous/Paleocene Tethys, from a genus such as *Caricella* Conrad, 1835, dispersing during this time to the New World, and thence giving rise in the Neogene to *Scaphella*. They also showed that in the Old World the record of *Scaphella* was uninterrupted from the Paleocene to the late Pliocene, after which the genus disappeared from the eastern Atlantic.
Landau & Silva (2006a) also showed *Scaphella* to be a heterogeneous genus, the European species differing in certain constant shell characters from the New World species. In the original manuscript submitted for review, these constant differences between the Old and New World species led Landau & Silva to consider the Old World species a separate genus. In the manuscript submitted, erection of this new genus was approved by the reviewers, but suppressed by editorial choice, a decision reluctantly accepted by the authors. Fortunately, the present editor decided that introduction of a new taxon is the authors' responsibility, and not a matter of editorial policy.

Since Landau & Silva (2006), new material has come to light. Firstly the European Palaeogene has been shown to be more speciose than previously thought (Pacaud & Meyer, 2014). All these early species conform to the Old World clade of '*Scaphella*' species as defined in Landau & Silva (2006). Secondly new material from the 'Redonian' of northwestern France has become available. The discovery of a further species again reaffirming the differences between the two '*Scaphella*' clades and the more restricted use of genera in recent years to comprise more closely related phylogenetic groups of species (*i.e.* Beu, 2010; Landau *et al*., 2013), have led us to take advantage of the discovery of this new species to erect a new genus for the Old World species.
The French 'Redonian' Scaphellinae are poorly known. This is due in part to their rarity, most specimens are poorly preserved and decalcified, and in part to the nature of the 'Redonian' outcrops, which are scattered geographically, limited in areal extent and only accessible with an excavator. Nevertheless, the presence of '*Scaphella*' in the French 'Redonian' deposits was noted

over a century ago by Dumas (1908), who attributed these shells to the well-known Pliocene North Sea Basin species *Voluta lamberti* J. Sowerby, 1816. In his unpublished thesis describing the French 'Redonian' assemblages, Brébion (1964) and later Brébion *et al*. (1975), recognized the presence of two species in these deposits; *S. lamberti* and *S. miocenica* Fischer & Tournouër, 1879. The most recent reference is that of Lauriat-Rage *et al.* (1989) who figured a specimen from La Marnière as *S. lamberti*.
In this paper we consider the Old World scaphellids distinct from those of the New World at genus level, erecting a new genus taxon for the former, and critically review references to '*Scaphella*' in the 'Redonian' deposits and describe a new species.

Fossil-bearing localities

The material studied was collected by the authors between 2009 and 2014 from two localities: Le Pigeon Blanc (Le Landreau) and La Marnière (La Limouzinière), both in the department Loire-Atlantique in northwestern France.

The fossil bearing deposits can only be accessed by excavation. According to Margerel (1968), the fossiliferous deposits at Le Pigeon Blanc are limited in area and form a relatively thick layer, starting at 2.00 m below surface and no longer fossiliferous at 3.45 m. The layer is highly fossiliferous, the upper part of the layer more clayey, becoming sandier towards the base. Apart from mollusc fossils, the assemblage also contains macrofossils representing bryozoans, echinoids, fish teeth and marine mammal bones.
In the 2011 excavation, the section observed was similar to that reported by Margerel (1968) (Figure 2). The top of the Redonian is partly decalcified, the whole layer consisting of highly fossiliferous clayey sand, with a well-preserved fauna in which bivalves predominate. The base (3.50–3.70 m) is poor in fossils, and concentrated mostly in the pockets between the Gneiss du Landreau.

Additional material from the départments of Vendée and Loire-Atlantique is present in the private collections of Jean-Pierre Cambien, Joël Dugast and the authors. Furthermore we examined material from Saint-Clément-de-la-Place (Le Grand Chauvereau), housed in the Naturalis Biodiversity Center, Leiden, The Netherlands.

The age of the 'Redonian' assemblages has been a subject of much debate. Brébion (1964) and Lauriat-Rage (1981) recognized that these assemblages were not all contemporaneous and recognized three transgressive cycles, dividing the 'Redonian' into a lower 'warm Redonian' and an upper 'cool Redonian'. This stratigraphic model was reconfirmed using strontium isotopic data on mollusk shells, benthic foraminifera and electron spin resonance (ESR) of quartz grains from 'Redonian' deposits by Mercier *et al*. (2000) and Néraudeau *et al*. (2002, 2003). In the Anjou region, the warm Redonian was dated at about 7-6.5 Ma for stratotype I and 6.5-6

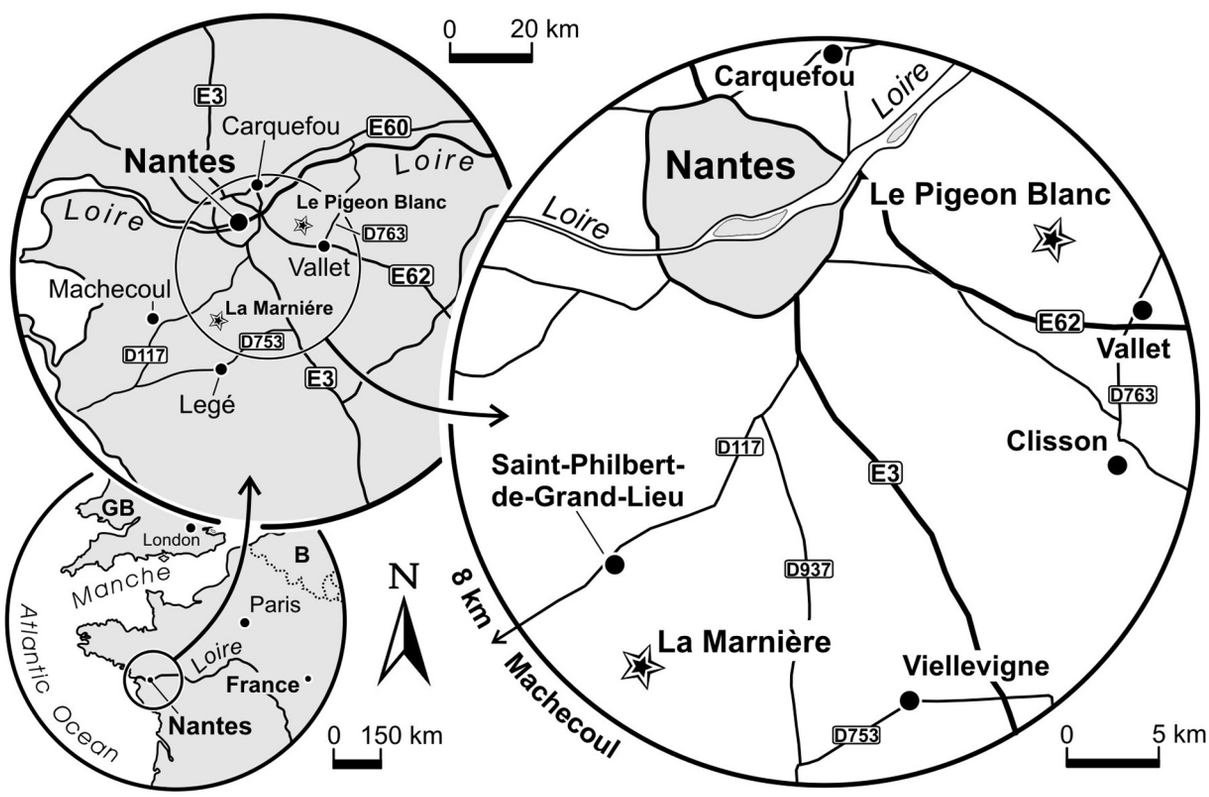

Figure 1. Geographic location of the localities sampled.

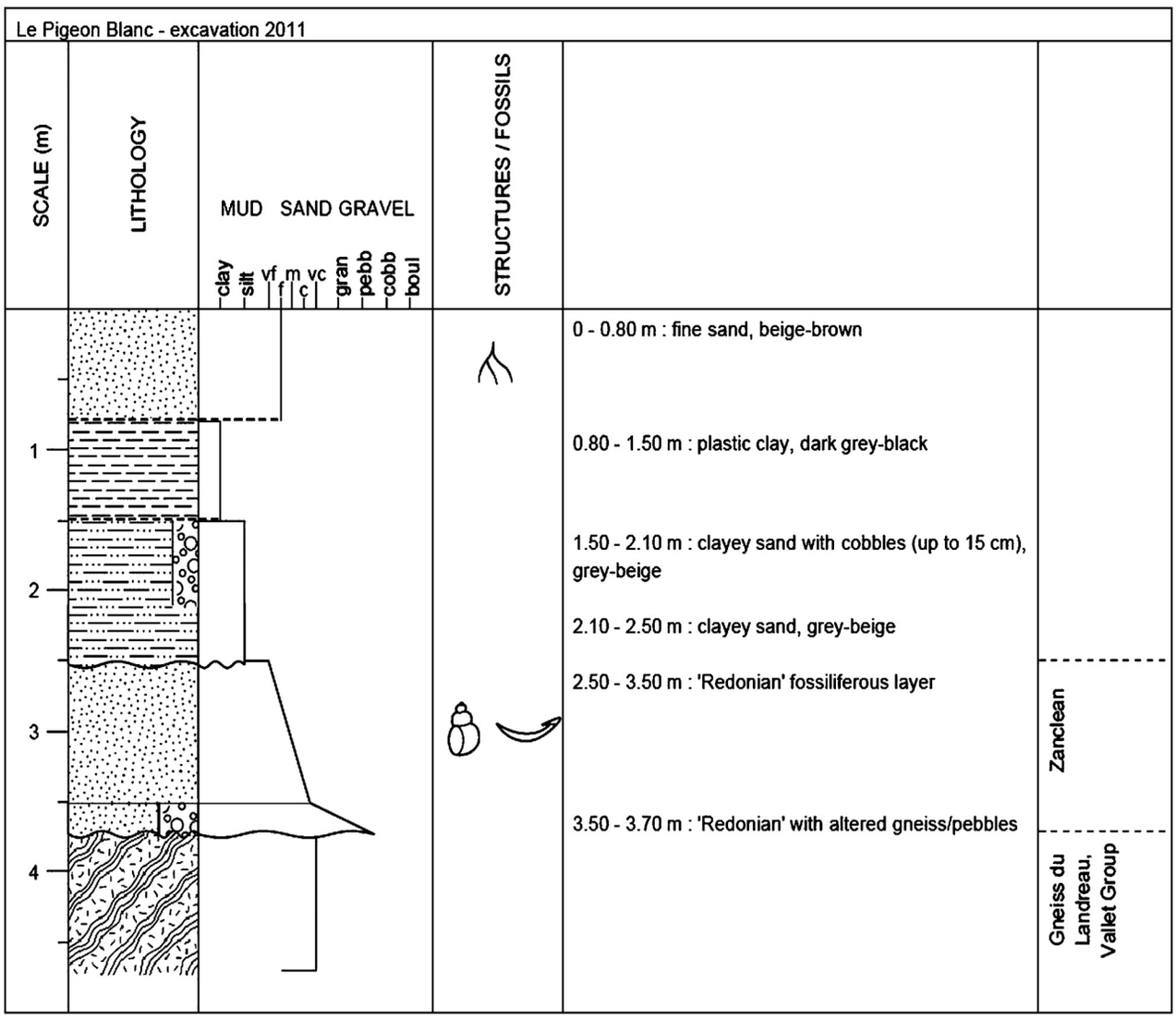

Figure 2. Section taken at 2011 excavation.

Ma for stratotype II, late Tortonian to early Messinian. The cool Redonian, mainly preserved in the departments Vendée and Loire-Atlantique was dated at 6.0-4.6 Ma, late Messinian to early Zanclean. Using this stratigraphic model, the classic localities of Lillion and Apigné in Brittany and Sceaux d'Anjou and Saint-Clément-de-la-Place (Le Grand Chauvereau) in Maine-et-Loire are considered late Tortonian to early Messinian, whereas the localities of La Limouzinière (La Marnière), Le Pigeon Blanc, La Dixmerie, Montaigu, Paluau are late Messinian to early Zanclean. The assemblage found in La Marnière and Le Pigeon Blanc contain *Megacardita striatissima* (Cailliaud *in* Mayer, 1868), which was considered by Lauriat-Rage (1981) and Brault *et al*. (2004) to be a biostratigraphic index species indicating an early Pliocene age.

Almost all the French 'Redonian' '*Scaphella'* material at hand is from 'cool Redonian'. Only the specimen housed in the Naturalis Biodiversity Center in Leiden from Saint-Clément-de-la-Place comes from a 'warm Redonian' assemblage.

Methods and material

The material described here was collected by the authors. Type material was deposited in the Naturhistorisches Museum Wien, Vienna, Austria.

Abbreviations:

NHMW	Naturhistorisches Museum Wien collection (Austria)
FVD	Frank Van Dingenen private collection, Brecht (Belgium)
LC	Luc Ceulemans private collection, Rixensart (Belgium)
RGM	Naturalis Biodiversity Center, Fossil Mollusca collection, Leiden (The Netherlands).

Systematic palaeontology

Family Volutidae Rafinesque, 1815
Subfamily Scaphellinae Gray, 1857
Genus *Euroscaphella* nov. gen.

Type species – *Voluta lamberti* J. Sowerby, 1816, North Sea Basin, Pliocene, England.

Included species – **Old World Paleocene:** *Voluta crenistria* von Koenen, 1885; *Voluta faxensis* Ravn, 1902; *Voluta volginica* Netschaew, 1897; *Scaphella vignyensis* Chavan, 1949; *Voluta crenistria* von Koenen, 1885; *Scaphella baudoni* Deshayes, 1865; *Scaphella volvestrensis* Villatte, 1962; *Scaphella veliocassina* Pacaud & Meyer, 2014. **Eocene:** *Voluta wetherellii* J. de C. Sowerby *in* Wetherell, 1836; *Scaphella honi* Glibert, 1938; **Oligocene:** *Voluta siemssenii* Boll, 1851. **Miocene:** *Voluta bolli* Koch, 1862; *Voluta tarbelliana* Grateloup, 1840; *Voluta miocenica* Fischer & Tournouër, 1879. **Pliocene:** *Voluta lamberti* J. Sowerby, 1816; *Scaphella carlae* Landau & Silva, 2006, *Euroscaphella* sp.
New World Paleocene: ? *Voluta showalter*i Aldrich, 1886; ? *Caricella leana* Dall, 1890.
Australian Eocene: ? *Scaphella (Aurinia) johannae* Darragh, 1988.

Diagnosis – Shell medium to large, fusiform, relatively slender to inflated, protoconch paucispiral, globose to flattened, in some species bearing a small blunt caricella at the apex; spire whorls depressed to elevated, without any trace of axial sculpture, spiral sculpture of subtle, fine, close-set threads. Last whorl large, elongate to inflated, regularly convex in most species, although weakly shouldered in a few. Aperture elongate, relatively large, outer lip simple, columella folds well-developed, elevated and rounded; without siphonal fasciole and probably without colour pattern.

Etymology – The first part of the generic name is derived from Europe, the second part from *Scaphella*, to which these shells have traditionally been assigned. Gender feminine.

Discussion – *Euroscaphella* differs from *Scaphella* (*s.str.*) and its subgenus *Clenchina* Pilsbry & Olsson, 1953 in not having axial sculpture on the early teleoconch whorls, and in having no siphonal fasciole and probably no colour pattern, and from the subgenus *Aurinia* H. Adams & A. Adams, 1853 by again not having axial sculpture or colour pattern and having well-developed columellar folds. Although the number of columellar folds is similar in *Scaphella* and its subgenera to that in *Euroscaphella*, and in both they become more oblique abapically, there is a subtle difference in their shape. The folds in New World *Scaphella* species are highly asymmetrical; the anterior face is much less steep than the posterior face, giving the folds a ratcheted appearance. This is not so in *Euroscaphella*, in which the folds are elevated and symmetrically rounded. This ratchet-like character of the columellar folds of the New World *Scaphella* species is not present in *Caricella* Conrad, 1835, in which the folds are symmetrical and much finer than in *Scaphella*.

Although the absence of colour pattern in fossil shells is not always a reliable guide to the colour of the living shell, fossil *Scaphella* species from the New World are characterized by the persistence of the colour pattern (see Olsson & Petit, 1964; Campbell, 1993; Petuch, 1994). Many shells from the Estepona deposits have the colour pattern preserved and one would have expected some of the strong spotted pattern of *Scaphella* to be seen if present, but none has been observed in the species from Estepona, or in any other European fossil "*Scaphella*" species.
In the list of included species we have placed the New World and Australian Paleocene and Eocene species as they cannot belong to *Scaphella*, if it only evolved from *Caricella* in the early Miocene. Since the origin of these groups is Tethyan, *Euroscaphella* is more appropriate, pending further review of the genus.
Unlike Recent American *Scaphella* species, which are tropical to subtropical, *Euroscaphella* occupied warm temperate to subtropical waters, and possibly extended its range southwards following the cooling of the Atlantic during Miocene and Pliocene time (see Silva & Landau, 2008). Moreover, two of the three more southern deposits where *Euroscaphella* has been found (Mondego and Estepona Basins) reflect areas where there was some degree of upwelling of cooler nutrient-rich waters (Landau *et al*, 2004; Silva *et al*., 2006). *Euroscaphella* possibly managed to survive in the Mediterranean Alboran Sea thanks to the relatively cooler waters caused by upwelling. This ability of a temperate genus to survive in a tropical zone has already been observed in the genus *Amalda* (see Landau & Silva, 2006b). Although still with a thermophilic affinity, *Euroscaphella* is uncommon in all deposits, except in the early Pliocene North Sea Basin, which at the time was the warm-temperate Boreo-Celtic province (see Silva & Landau, 2008). Here it is the most common large gastropod. Even though *Euroscaphella* was widespread and diverse during the early Pliocene, the genus did not survive Pleistocene cooling, and the youngest record is of *E. lamberti* from the late Pliocene Kruisschans Sands of Belgium, where it is rare (Marquet, 1997). Interestingly, *Euroscaphella* did not follow the prevalent trend of southward migration seen in many other gastropod taxa as a result of the late Neogene cooling events (Monegatti & Raffi, 2001; Silva & Landau, 2008), and does not survive off West Africa.

Euroscaphella namnetensis nov. sp.

Plate 1, figs 1-10

1908 *Voluta Lamberti* Sow. – Dumas, p.121.
1964 *Scaphella lamberti* (Sowerby, 1816) – Brébion, p. 517, pl. 13, fig. 2 [not *Euroscaphella lamberti* (J. de C. Sowerby, 1816)].

1989 *Scaphella lamberti* (Sowerby, 1816) – Lauriat-Rage *et al.*, p. 131, pl. 8, fig. 19 [not *Euroscaphella lamberti* (J. de C. Sowerby, 1816)].

Type material – **Holotype** NHMW 2014/0287/0001 (Pl. 1, figs 1-3), length 82.3 mm, width 30.2 mm, protoconch diameter 5.2 mm; **paratype 1** NHMW 2014/0287/0002, length 96.6 mm, width 31.3 mm (incomplete: outer lip damaged); **paratype 2** NHMW 2014/0287/0003, length 84.3 mm, width 27.4 mm (incomplete: outer lip damaged); **paratype 3** NHMW 2014/0287/0004, length 63.3 mm, width 23.6 mm (subadult: outer lip damaged); **paratype 4** NHMW 2014/0287/0005, length 46.9 mm, width 17.4 mm (juvenile).

Type locality – Le Pigeon Blanc, Le Landreau, dep. Loire-Atlantique, France.

Type stratum – 'Cool Redonian', late Messinian-early Zanclean, late Miocene to early Pliocene.

Other material examined – La Marnière: 1 subadult specimen (FVD); Le Pigeon Blanc: 4 adult specimens (FVD), 106 subadult/juvenile specimens (FVD), 13 outer lip fragments (FVD), 32 spire fragments/incomplete specimens (FVD), 3 adult specimens (LC), 45 subadult/juvenile specimens (LC), 1 incomplete specimen (LC). 11 juvenile specimens (NHMW 2014/0287/0006).

Etymology – Named after *Portus Namnetum*, the Roman name for the city of Nantes.

Diagnosis – A relatively small solid *Euroscaphella* species, with a slender fusiform shell, strongly flattened protoconch, short spire, with whorls rapidly increasing in height, a slender, weakly shouldered last whorl, outer lip with well-developed palatal callus and a short siphonal canal.

Description – Shell medium-sized, robust, narrowly fusiform, with a short siphonal canal. Protoconch of 1.5 smooth flattened whorls, with medium-sized nucleus, calcarella blunt, pointed. Junction with teleoconch sharply delimited by a thin scar. Teleoconch of 4-5 whorls, with impressed suture. Spire shorter than aperture, first teleoconch whorl strongly depressed, about 3.5 times wider than tall, the whorls becoming taller abapically. Last whorl about 85% of total height, elongate, slender, slightly shouldered. Sculpture restricted to faint, equally spaced spiral threads, obsolete on the mid-portion of the last whorl. Aperture tall, 73% of total height, narrow. Outer lip not thickened, smooth edged, internally bearing elongated palatal callus thickening abapically, weakly convex in profile. Columella weakly concave, bearing 4 or 5 oblique, elevated columellar folds, becoming increasingly oblique abapically; abapical fold weakest. Columellar callus moderately thickened, flattened; parietal callus very thin to absent, although present as an expanded polish graze over the venter in some specimens (Pl. 1, fig. 4). Siphonal canal short, straight, open. Siphonal fasciole absent.

Comparison – *Euroscaphella namnetensis* nov. sp. is most similar to the slightly older *E. miocenica* from the Middle Miocene Langhian of the Loire Basin, which also has a relatively solid shell and a well-developed palatal callus, but differs in being smaller in size, in having a more slender last whorl, which is less shouldered than in *E. miocenica* and in having the base of the last whorl hardly constricted, and therefore the siphonal fasciole is not well-developed, as it is in *E. miocenica*. The North Sea Basin Pliocene species *E. lamberti* differs in having a much larger and thinner shell, the last whorl is far more inflated in *E. lamberti* and the inner side of the outer lip is not thickened by palatal callus, as it is in *E. namnetensis*. *Euroscaphella lamberti* also differs from most of its congeners in having a sinuous outer lip in profile rather than convex, as in *E. namnetensis* and most other species. *Euroscaphella carlae* from the early Pliocene Zanclean of the Estepona Basin, southern Spain differs from *E. namnetensis* in having a much larger shell, with a much taller spire. As discussed by Landau & Silva (2006), *E. tarbelliana* (Grateloup, 1840) from the Atlantic early and middle Miocene Aquitaine Basin has characters intermediate between those of *E. carlae* and *E. lamberti*. *Euroscaphella tarbelliana* is smaller, narrower and less inflated than *E. lamberti*, but still broader, with a proportionally lower spire than *E. carlae*. The outer lip is convex in profile and not sinuous as in *E. lamberti*, and the aperture intermediate in width between the two. Nevertheless, the overall outline of *E. tarbelliana* is still considerably more inflated than that of *E. carlae*. *Euroscaphella miocenica* differs from *E. tarbelliana* in being thicker-shelled, squatter, and in having a lower spire and a more inflated, more shouldered last whorl. *Euroscaphella tarbelliana* differs from *E. namnetensis* in having a broader shell, with a far more inflated last whorl, in being more constricted at the base and having a longer siphonal canal.

The protoconch of all *Euroscaphella* species is paucispiral, consisiting of about 1.5-2.0 whorls, with a small blunt calcarella at the apex. However, there are differences between the species. *Euroscaphella namnetensis* has relatively small and very flattened protoconch (diameter: min. 4.4 mm - max. 6.0 mm - average 5.1 mm, measurements based on 87 individuals, Fig. 4). *Euroscaphella miocenica* also has a flattened protoconch, but larger (average 7.0 mm). The protoconch of *E. carlae* is also flattened, but much larger (average 9.3 mm) and the protoconch in *E. lamberti* comprises about two whorls, is intermediate in diameter (average 7.3 mm), rounded, and more bulbous than in *E. namnetensis* or *E. carlae*. We have seen few specimens of *E. tarbelliana*, but the protoconch available has a diameter of 6.2 mm, slightly larger than that of *E. namnetensis*.

Distribution – Late Miocene to early Pliocene: 'cool Redonian', late Messinian to early Zanclean, Loire-Atlantique, northwestern France.

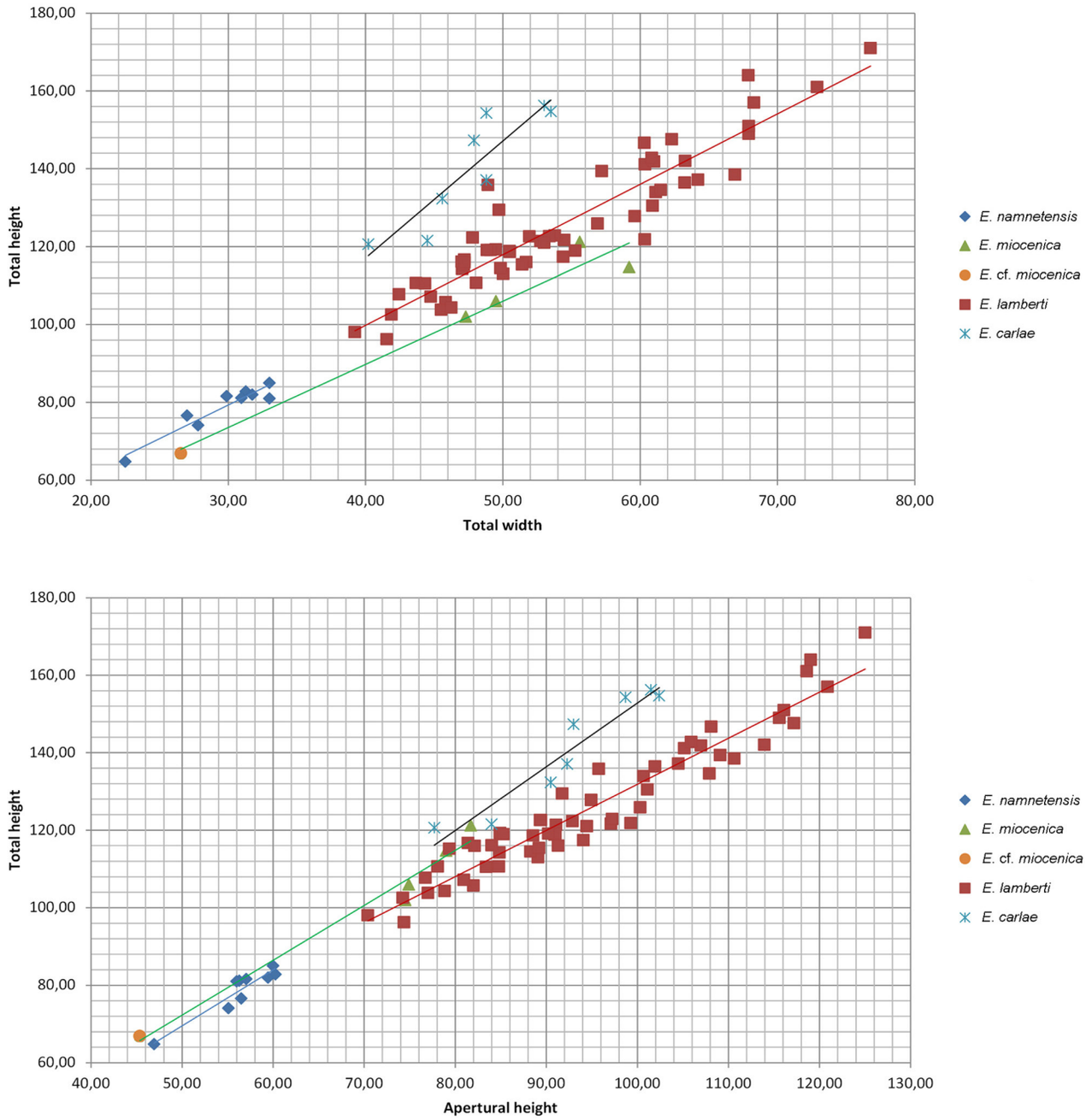

Figure 3. Morphometric comparison of teleoconch between *Euroscaphella namnetensis* nov. sp. and other European Neogene *Euroscaphella*.

Euroscaphella cf. ***miocenica*** (Fischer & Tournouër, 1879)
Plate 1, figs 11-13

cf. 1837 *Voluta lamberti* (*non* Sowerby) – Dujardin, p. 300.
cf. 1879 *Voluta miocenica* Fischer & Tournouër, p. 50.
cf. 1886 *Voluta (Ficula) miocenica* Fischer & Tournouër – Dollfus & Dautzenberg, p. 102.
cf. 1899 *Scaphella (Scaphella) miocenica* Fischer & Tournouër – Cossmann, p. 126, pl. 5, fig. 5.
cf. 1938 *Scaphella miocenica* Fischer & Tournouër – Peyrot, p. 248.
cf. 1952 *Scaphella (Scaphella) miocenica* Fischer & Tournouër – Glibert, p. 365, pl. 11, fig. 10.
cf. 1964 *Scaphella miocenica* [*sic*] Fischer & Tournouër – Brébion, p. 515.
cf. 2006 *Scaphella miocenica* Fischer & Tournouër – Landau & Silva, p. 84, fig. 18, p. 88, figs 35-37.

Material studied – RGM 794 200 (Figs 11-13), length 66.9 mm, width 26.6 mm, Saint-Clément-de-la-Place (Le Grand Chauvereau), Maine-et-Loire, France, 'warm Redonian', late Tortonian to early Messinian, late Miocene.

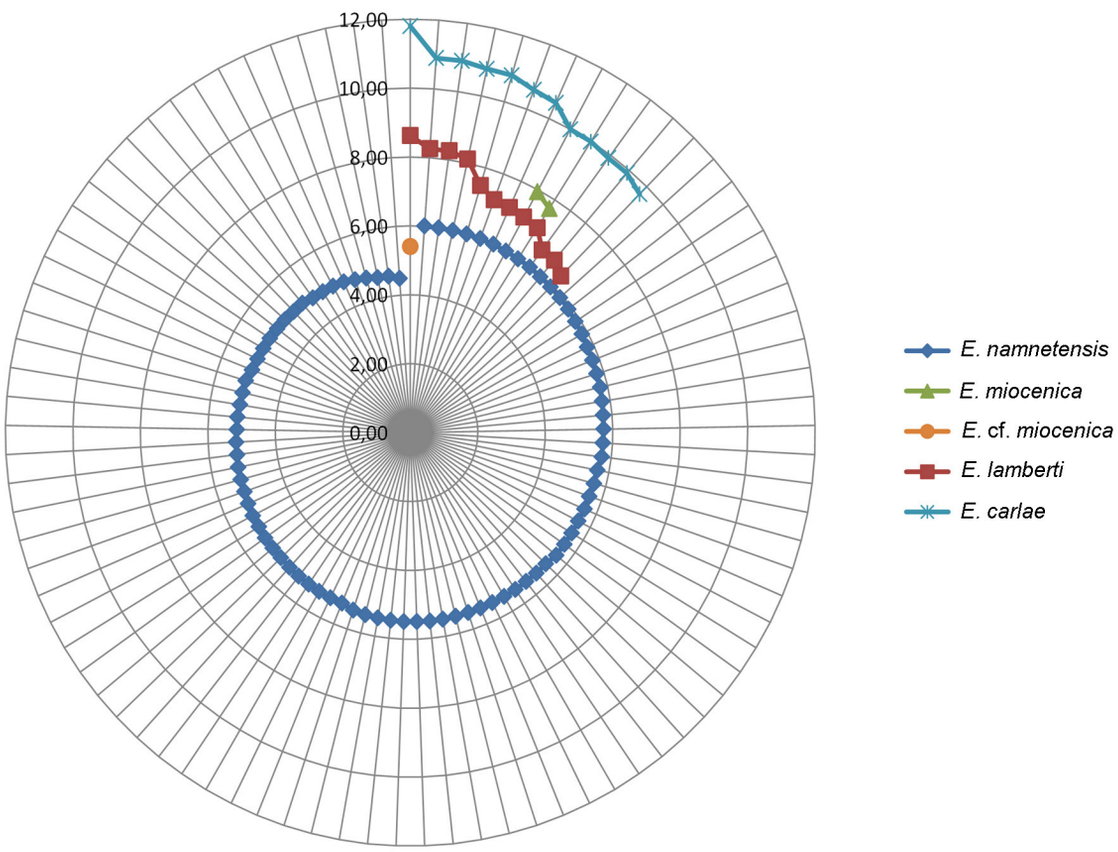

Figure 4. Morphometric comparison of protoconch diameter between *Euroscaphella namnetensis* nov. sp. and other European Neogene *Euroscaphella*. Specimens measured and plotted from largest to smallest clockwise.

Distribution – Late Miocene: 'warm Redonian', late Tortonian to early Messinian, Maine-et-Loire, northwestern France.

Discussion – A single, well-preserved shell is at hand from Saint-Clément-de-la-Place. This is the only complete adult scaphellid shell available from the stratigraphically older 'warm Redonian'. The teleoconch is indistinguishable from that of *Euroscaphella miocenica*, characterized by its solid shell, relatively broad, inflated, strongly shouldered last whorl, which is moderately strongly constricted at the base, in contrast to *E. namnetensis*, which is hardly constricted. However, the French Redonian shell differs from middle Miocene Langhian specimens of *E. miocenica* in being much smaller (66.9 mm height as opposed to about 100 mm in *E. miocenica*) and in having a smaller protoconch, with a diameter of only 5.4 mm as opposed to 7.7-7.9 in *E. miocenica*.
Both *E. miocenica* and *E. namnetensis* have a well-developed palatal callus, whereas all other *Euroscaphella* species have a thin outer lip without any internal callus. It is possible that *E. namnetensis* evolved from *E. miocenica*, as both share a relatively solid shell, the same number of columellar folds, a flattened protoconch and the development of a palatal callus. The specimen from Saint-Clément-de-la-Place shows the teleoconch features of *E. miocenica* and the protoconch size of *E. namnetensis*. This specimen could represent either a 'dwarf' *E. miocenica* or a transitional form between the two species.

Conclusions

The genus *Scaphella* as used previously is polyphyletic, with its centre of distribution around the Tethys. The European species form a distinct stock/clade, *Euroscaphella* nov. gen., which occurs continuously in the European Caenozoic from the Paleocene to the late Pliocene. Early Caenozoic representatives of this group also occur in the New World and Australia, but disappeared before the end of the Eocene. The New World genus *Scaphella* and its subgenera only appeared in the Neogene, and probably evolved in the Tropical Western Atlantic from *Caricella* stock.
As discussed by Landau & Silva (2006), volutids show a direct method of development, which has resulted in many locally distinct populations and often a hazy delineation of the species-group taxa (*i.e.*, Darragh & Ponder, 1998). The same applies to Recent *Scaphella* species in the New World, which explains the enormous discrepancy in the number of species recognized by different authors (four, Weaver & du Pont, 1970; 11, Poppe & Goto, 1992) and *Euroscaphella* in the Old World, the species being restricted both geographically and stratigraphically.

The transitional forms between *E. miocenica* and *E. lamberti* reported by Brébion (1964) from the 'Redonian' of northwestern France are here considered a distinct species, *E. namnetensis*, differing from *E. miocenica* and *E. lamberti* in both protoconch and teleoconch characters. *Euroscaphella namnetensis* is restricted to the 'cool Redonian', late Messinian to early Zanclean assemblages of northwestern France and is far more closely related to the stratigraphically older *E. miocenica* than it is to the younger North Sea Basin *E. lamberti*.

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Plate 1

1-10.*Euroscaphella namnetensis* nov. sp.; 1-3. **Holotype** NHMW 2014/0287/0001, height 82.3 mm, width 30.2 mm; 4-5: height 74.1 mm, width 27.8 mm (LC coll.); 6-7: height 82.8 mm, width 31.3 mm (FVD coll.); 8, subadult, height 76.6 mm, width 27.0 mm (FVD coll.); 9, juvenile, height 39.4 mm, width 14.7 mm (FVD coll.); 10, juvenile, height 37.6 mm, width 14.8 mm (FVD coll.). All from Le Pigeon Blanc, Le Landreau, dep. Loire-Atlantique, France, 'cool Redonian', late Messinian-early Zanclean, late Miocene to early Pliocene.

11-13.*Euroscaphella* cf. *miocenica* (Fischer & Tournouër, 1879), RGM 794 200, height 66.9 mm, width 26.6 mm, Saint-Clément-de-la-Place (Le Grand Chauvereau), Anjou, France, 'warm Redonian', late Tortonian to early Messinian, late Miocene.


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