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The Gelasian gastropod fauna of Selsoif (Manche, France)

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ABSTRACT
We have little understanding of the evolution of modern marine faunas from the European Atlantic coasts. In NW France very rich Neogene and early Quaternary mollusc assemblages occur that may shed light on the evolution of these modern faunas. Here we describe a Gelasian gastropod assemblage consisting of 76 species-level taxa from Selsoif (Manche, France), recovered from a sand extraction site between 1989-2020 by various collectors. The fauna reflects a range of intertidal to shallow subtidal palaeoenvironments. A few reworked Eocene fossils were also recovered. The extant portion of the Selsoif fauna is dominated by species with a Lusitanian signature, but also contains common species that nowadays have a Boreal-Celtic and Mediterranean signature. Furthermore, the fauna has quite some species in common with Early Pleistocene North Sea Basin faunas and also contains a few endemic species such as *Calliostoma normanensis* n. sp., *Seila quinquecarinata* n. sp., *Alvania selsoifensis* n. sp., *Admete trigostomoides* n. sp. The Selsoif fauna therefore represents a transitional fauna between Neogene and modern marine faunas of the European Atlantic.

KEY WORDS
Quaternary,
Pleistocene,
French Atlantic,
gastropods,
palaeoecology,
biogeography,
new species.

RÉSUMÉ
La faune de gastéropodes gélasiens de Selsoif (Manche, France).
Nous comprenons peu l'évolution des faunes marines modernes des côtes atlantiques européennes. Dans le nord-ouest de la France, nous retrouvons des assemblages de mollusques très riches du Néogène et du début du Quaternaire, qui pourraient éclairer sur l'évolution de ces faunes modernes. Dans cet article, nous décrivons un assemblage de gastéropodes gélasiens composé de 76 taxons de Selsoif (Manche, France). La faune a été collectée par différentes personnes entre 1989 et 2020 sur un site d'extraction de sable. La faune représente des paléoenvironnements intertidal à subtidal peu profond, une très petite fraction de fossiles est remaniée de l'Éocène. La faune du Selsoif est dominée par des espèces à signature lusitanienne. Cependant, la faune contient des espèces ayant d'autres affinités, à savoir des espèces boréoceltiques à arctiques de l'Atlantique nord-est du Pléistocène inférieur, espèces européennes marines tempérées modernes et quelques espèces endémiques tel que *Calliostoma normanensis* n. sp., *Seila quinquecarinata* n. sp., *Alvania selsoifensis* n. sp., *Admete trigostomoides* n. sp. La faune Selsoif représente une faune de transition entre les faunes marines néogènes et modernes de l'Atlantique européen.

MOTS CLÉS
Quaternaire,
Pléistocène,
Atlantique francais,
gastéropodes,
paléocologie,
biogéographie,
espèce nouvelle.

INTRODUCTION

Only very few areas in Atlantic Europe outside the southern North Sea Basin host Early Pleistocene marine fossil assemblages. Within the North Sea Basin, Middle Pleistocene mollusc faunas are almost entirely composed of extant species already showing a modern character (Meijer *et al.* 2021; Wesselingh *et al.* 2023). These 'modern' assemblages differ importantly from Pliocene-Early Pleistocene assemblages (*e.g.* Marquet 2001; Van Dingenen *et al.* 2015; Landau *et al.* 2020c; Preece *et al.* 2020). The lack of known Early Pleistocene faunas from the European Atlantic hinders our understanding of the evolution of the modern Atlantic marine biota. A well preserved Early Pleistocene fauna from Selsoif in Normandy (France) may enable us to fill this gap.

From the temperate Atlantic region very rich late Miocene and early Pliocene faunas are known, especially from the lower Loire region and adjacent Brittany (*e.g.*, Brébion 1964; Lauriat-Rage 1982; Landau *et al.* 2020c). However, these Neogene faunas bear very little resemblance to the modern coastal Atlantic faunas in terms of species and associations. Late Pliocene-Pleistocene faunas are known from the Channel region including faunas from the Wexford Gravels from southern Ireland (MacMillan 1964), and the St. Erth Beds of Cornwall (Harmer 1925; Mitchell *et al.* 1973). However, these faunas have not been fully documented. The Pliocene-Early Pleistocene deposits from the Cotentin were described by Pareyn (1987) and Dugué *et al.* (2000, 2007, 2009, 2012). Previously, they were classified as 'upper Redonian' (a regional French stage covering Tortonian to Gelasian marine intervals mostly centred around the lower Loire and Rennes region: Lauriat-Rage 1986; Van Dingenen *et al.* 2015). However, Landau *et al.* (2020c) found that the Pleistocene faunas that they termed Redonian assemblage IV have very little in common with the Tortonian-Zanclean Redonian I-III assemblages.

In this study, we examined a particularly rich gastropod fauna recovered by different collectors during the past 40 years from a sand and gravel extraction site at Selsoif, located in Cotentin, France. Based on pollen analyses, the Selsoif fauna has been assigned an Early Pleistocene age (Pareyn 1987), and only a few species have been treated previously in taxonomic revisions (Marquet 2001; Van Dingenen *et al.* 2015; Hoeksema *et al.* 2020). We present a complete taxonomic review of the gastropod assemblage in order to characterise the palaeoenvironmental settings of the Selsoif locality and improve our insights into the evolution of modern European temperate Atlantic coastal faunas.

MATERIAL AND METHODS

The material used in this study was collected from a gravel and sand extraction site near Selsoif, municipality Saint-Sauveur-le-Vicomte, dept. Manche, France (Figs 1, 2). At the site, named Sablière du Grand Marais (49°21'20"N, 1°30'34"W), fossiliferous sands and gravels were dredged from 28-50 m water depth according to labels written by Arie W. Janssen. Shells were collected by handpicking and sieving of residues; details of sieving procedures are lacking. The collections were made by A.C. Janse (1995 and 1996), A.W. Janssen (1989) and W. Groeneveld (1995 and 1996). Complementary samples have been provided by S. Mermuys, collected at the same place in 2020 and an unsorted sample collected in 1995 by L. Vaessen.

We use the ecoregions defined by Spalding *et al.* (2007) but for brevity use the term "boreo-arctic ecoregion" for their Northern European Sea and Arctic ecoregions. Ecoregions used in this work from south to north are Mediterranean-Moroccan, French-Iberian (formerly Lusitanian), Boreal-celtic and Boreal-arctic (Fig. 3). For discussion on biogeographic terminology see Sacchetti *et al.* (2023: 103).

The material used in this study is housed at Naturalis, collection Cainozoic Mollusca (indicated by RGM numbers), Collection of Stef Mermuys, Lansingerland (indicated by SM numbers) and in the Muséum national d'Histoire naturelle (MNHN), Paris, France (indicated by MNHN numbers). All species are briefly characterized, with longer discussions devoted to critical species and those that are new. We have restricted synonymy to major taxonomic sources and those most relevant to fossil assemblages. The nomenclature follows WoRMS, 2023 with deviations discussed below.

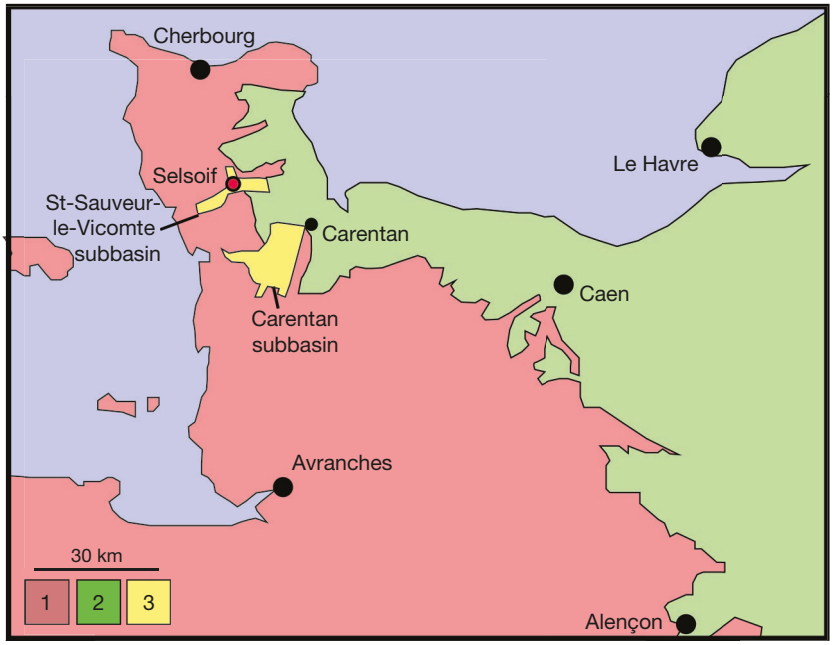


FIG. 1. — Simplified geological map of the Normandy region (after Dugué *et al.* 2000 and Pareyn 1987) showing the location of Selsoif: **1**, Precambrian-Palaeozoic basement; **2**, Permo-Mesozoic Paris Basin fill; **3**, Neogene-Quaternary subbasins.

FIG. 2. — Aerial photographs of the extraction site (La Sablière du Grand-Marais) with the spoil heaps visible in centre: **A**, photographie IGN, Mission C90SAA0491_1990_F1211- 1411_0037, cliché no. 37, 28/04/1990; **B**, photographie IGN, Mission CP12000422_059_12385, cliché n°12385, 26/07/2012. Width of lake in the centre *c.* 400 m.

GEOLOGICAL SETTING

The Cotentin region is located at the transition of the Palaeozoic Armorican Massif in the west and the Paris Basin in the east (Dugué *et al.* 2000: fig. 1). The region contains a number of small sediment-filled grabens (Baize *et al.* 1998) resulting from Alpine orogenesis creating fault and deformation in the Channel region. The basin fill occurred during three transgressive intervals (middle Eocene, Miocene and Plio-Pleistocene) and is dominated by marine deposits. The three phases are separated by periods of non-deposition and erosion signifying emergent phases (Paleocene, middle Oligocene to Early Miocene and Middle Miocene to Early Pliocene: Dugué *et al.* 2007). Most successions are found in the subsurface, outcrops are rare. The Cenozoic stratigraphic sequence was studied after a drilling campaign in the 1980s and discussed by various authors (e.g., Pareyn 1987; Dugué *et al.* 2007; 2012; Baize *et al.* 1998). Subdivision and correlations with other NW European formations were proposed based on different faunal groups (Lauriat-Rage 1982 for bivalves; Kasimi 1986 for ostracods and Le Calvez 1987 for foraminiferans). Further age constraints were provided by palynology (Pareyn 1987). The Cotentin Basin is separated into two large subbasins, the east-west oriented Saint-Sauveur-le-Vicomte subbasin in the north, and the north-south oriented Carentan subbasin in the south (Pareyn 1987). Selsoif is located in the centre of the Saint-Sauveur-le-Vicomte subbasin. The entire Pliocene-Pleistocene sequence contains six formations that represent a transition of marine to fluvial dominated settings (Dugué *et al.* 2012). Exact age estimates for the formations are scarce and uncertain. The oldest formation is the Late Pliocene Grès Coquillier de Marchésieux (thickness of around 70 m), which represents deep marine settings. It is known only from the subsurface

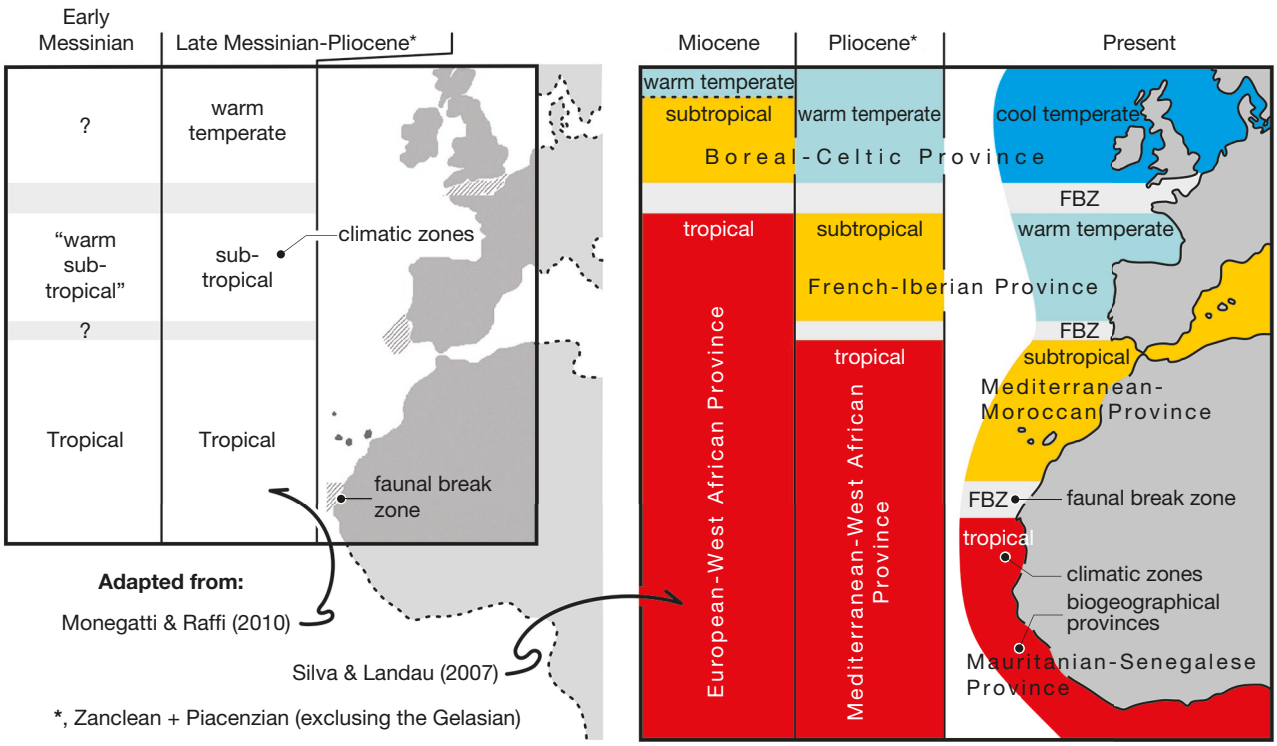


FIG. 3. — Simplified biographic map of South-West of Europe (after Landau *et al.* 2011).

around Marchésieux (Dugué *et al.* 2000) in the southern subbasin. The overlying Marne du Bosq d'Aubigny (thickness of around 55 m) is a fossil-rich marly unit whose age is estimated between 2.75 and 2.4 Ma (Van Dingenen *et al.* 2015; Landau *et al.* 2020c). Intercalated shell intervals, the so-called Falun de Bohon (maximum thickness of 50 m), are present around Saint Georges de Bohon forming the top of the Marne du Bosq d'Aubigny. In the region of Saint-Sauveur-le-Vicomte, the marly and shelly intervals appear intermixed (Baize *et al.* 1998). The overlying Marnes the Saint Nicolas de Pierrepont Formation (maximum thickness 40 m) is only known from boreholes (Dugué *et al.* 2000). That unit has a large extension ranging from Saint-Sauveur le Vicomte in the north to the south part of the Cotentin Basin (Baize *et al.* 1998). Overlying is the Sables de Saint Vigor Formation (maximum thickness 30 m) that is present throughout the Cotentin Basin and lacks fossils, making it difficult to determine its age. It has been referred to as the lowermost Pleistocene unit (Dugué *et al.* 2000). Locally, the upper part of the Sables de Saint-Vigor is eroded, and channels are filled with so-called puddingstone and covered by fluviatile deposits of the Sables de la Lande de Millière Formation (Dugué *et al.* 2000). After the early Pleistocene, the region became uplifted and (marine) deposition ceased.

The sequence contains two transgressive-regressive cycles covering the Pliocene-Pleistocene transition. The oldest maximum transgression occurred during deposition of the Grès Coquillier de Marchésieux during the Late Pliocene. The second transgressive maximum was reached at the transition of the Marnes de Saint-Nicolas-de-Pierrepont Formation and the Sables de Saint Vigor Formation (Dugué *et al.* 2009). The fossiliferous intervals of Selsoif are part of the Saint-Sauveur-de-Pierrepont Formation of Pareyn (1987) that was subsequently renamed as Saint-Nicolas de Pierrepont Formation (Dugué *et al.* 2000). The stratigraphic age of the Selsoif succession is not well constrained. Pareyn (1987) correlated it with Tiglian-C based on palynological analyses of Clet-Pellerin (1983). The Tiglian is a regional Gelasian stage defined for the southern North Sea Basin mostly based on pollen analysis. However, the original Tiglian pollen zones likely represent a number of recurring glacial-interglacial successions whose attribution to marine isotope stages (MIS stages) is not resolved (Westerhoff *et al.* 2020; see Discussion). However, the Selsoif association is of a Gelasian age.

ABBREVIATIONS

WG	W. Groeneveld;
ACJ	A. C. Janse;
AWJ	A. W. Janssen;
LV	L. M. B. Vaessen;
SM	S. Mermuys;
MNHN.F	MuséumnNational d'Histoire naturelle, paleontology collection
RGM	Naturalis Biodiversity Center, paleontology collection.

RESULTS

The gastropod fauna of Selsoif is composed of 76 gastropod taxa (Table 1) representing mostly a shallow marine warm temperate fauna.

TABLE 1. — Gastropod species, ecological and biogeographic affinity of the Selsoif fauna. References: **1**, Alf *et al.* 2020; **2**, Anistratenko *et al.* 2011; **3**, Bensettiti *et al.* 2004; **4**, Borg *et al.* 1998; **5**, Bouchet & Warén 1993; **6**, Çinar *et al.* 2012; **7**, Crocetta & Spanu 2008; **8**, De Bruyne *et al.* 2013; **9**, Feare 1970; **10**, Funder *et al.* 2002; **11**, Hoffman & Freiwald 2020; **12**, Høisæter 2014; **13**, Landau *et al.* 2017; **14**, MarLIN: https://www.marlin.ac.uk [assessed 12-2022]; **15**, Nekhaev *et al.* 2014; **16**, Öztürk *et al.* 2014; **17**, Peacock 1993; **18**, Petović *et al.* 2017; **19**, Rubio *et al.* 1998; **20**, Schander 1995; **21**, Warén 1993; **22**, Wilke & van Aartsen 1998; **23**, WoRMS: https://www.marinespecies.org [assessed 12-2023]; **24**, Rubio *et al.* 1998; **25**, Landau & Micali 2021.

Species	Zone	biogeographic affinity
Patella rustica Linnaeus, 1758	intertidal, rocky substrate, euhaline-polyhaline[1, 3, 16, 18]	celtic – mediterranean[1]
Patella vulgata Linnaeus, 1758	intertidal, rocky substrate, euhaline-polyhaline[1, 3, 16, 18]	celtic – mediterranean[1]
Tectura virginea (Müller, 1776)	intertidal – shallow subtidal, hard substrate, euhaline-polyhaline[1, 15, 16]	boreal – mediterranean[1]
Diodora graeca (Defrance, 1820)	intertidal – shallow subtidal, mixed substrate, euhaline-upper mesohaline[1, 16, 17, 18]	celtic – mediterranean[1]
Emarginula fissura (Linnaeus, 1758)	intertidal – deep subtidal, hard substrate, euhaline[1, 14, 17, 18]	celtic – mediterranean[1]
Jujubinus exasperatus (Pennant, 1777)	intertidal – mid subtidal, mixed substrate, euhaline-polyhaline[1, 6, 16, 18]	arctic – mediterranean[1]
Jujubinus montagui (Wood, 1828)	intertidal – shallow subtidal, mixed substrate, euhaline-polyhaline[1, 16, 18]	celtic – mediterranean[1]
Steromphala cineraria (Linnaeus, 1758)	intertidal, hard substrate, euhaline-upper mesohaline[1, 8, 10, 15]	arctic – mediterranean[1]
Steromphala tumida (Montagu, 1803)	shallow subtidal to mid continental slope, gravel bottoms, euhaline[1]	boreal – mediterranean[1]
Calliostoma normanensis n. sp.	extinct	extinct
Dikoleps cutleriana (Clark, 1849)	intertidal[19]	celtic – mediterranean[13, 19]
Moelleria jansseni Hoeksema, Rijken & Simons, 2020	extinct	extinct
Tricolia pullus picta (da Costa, 1778)	intertidal – shallow subtidal on seagrass, euhaline-lower mesohaline[1, 2, 16, 18]	celtic – mediterranean[1]
Petaloconchus intortus (Lamarck, 1818)	extinct	extinct
Bittium rubanocinctum Glibert, 1958	extinct	extinct
Bittium jadertinum (Brusina, 1865)	intertidal – shallow subtidal, mixed substrate[1]	boreal – mediterranean[1]
Haustator incrassata (Sowerby, 1814)	extinct	extinct
Marshallora cf. *adversa* (Montagu, 1803)	intertidal, mixed substrate, euhaline-upper mesohaline[1, 6, 16, 17, 18]	arctic – mediterranean[1]
Monophorus indet.	indeterminate	indeterminate
Seila selsoifensis Marquet, 2001	extinct	extinct
Seila quinquecarinata n. sp.	extinct	extinct
Cerithiopsis indet.	indeterminate	indeterminate
Boreoscala similis (Sowerby, 1813)	extinct	extinct
Lacuna crassior (Montagu, 1803)	shallow – mid subtidal, hard substrate[1]	boreal – lusitanian[1]
Lacuna pallidula (da Costa, 1778)	intertidal – mid subtidal, euhaline-upper mesohaline[1, 15, 17]	boreal – lusitanian[1]
Lacuna parva (da Costa, 1778)	intertidal – shallow subtidal, soft substrate, upper mesohaline[1, 10]	arctic – lusitanian[1]
Lacuna cf. *vincta* (Montagu, 1803)	shallow subtidal, soft substrate, euhaline-lower mesohaline[1, 8, 10, 15]	boreal – celtic[1]
Littorina obtusata (Linnaeus, 1758)	lower-middle intertidal between large algae and hard substrate, euhaline[15]	boreal – lusitanian[1]
Littorina littorea (Linnaeus, 1758)	supralittoral – intertidal, mixed substrate, euhaline-lower mesohaline[1, 8, 10, 15]	arctic – lusitanian[1]
Alvania cf. *cancellata* (da Costa, 1778)	intertidal - mid subtidal, mixed substrate, euhaline-polyhaline[1, 16, 18]	celtic – mediterranean[1]
Alvania selsoifensis n. sp.	extinct	extinct
Alvania sp. 1	indeterminate	indeterminate
Manzonia crassa (Kanmacher, 1798)	shallow subtidal, mixed substrate, euhaline-polyhaline[1, 6, 16]	boreal – mediterranean[1]
Onoba semicostata (Montagu, 1803)	intertidal – bathyal, euhaline-polyhaline[1, 8, 10, 15]	boreal – mediterranean[1]
Pusillina aff. *inconspicua* (Alder, 1844)	indeterminate	indeterminate
Rissoa curticostata Wood, 1848	extinct	extinct
Rissoa parva (da Costa, 1778)	shallow – mid subtidal, mixed substrate incl. seagrass, euhaline-lower mesohaline[1, 2, 10, 15, 16, 18]	boreal – mediterranean[1]
Ecrobia cf. *ventrosa* (Montagu, 1803)	coastal-estuarine, soft substrate, euhaline-upper mesohaline[1, 8, 16]	boreal – mediterranean[1]
Peringia ulvae (Pennant, 1777)	intertidal-shallow subtidal, soft substrate, euhaline-lower mesohaline[1, 8, 10, 15, 16, 18]	boreal – mediterranean[1]
Caecum glabrum (Montagu, 1803)	mid subtidal – bathyal, soft substrate, euhaline[1, 8, 10]	celtic – mediterranean[1]
Tornus subcarinatus (Montagu, 1803)	intertidal – shallow subtidal, soft substrate, euhaline-polyhaline[1, 8, 16]	boreal – mediterranean[1]
Calyptraea chinensis s.l. (Linnaeus, 1758)	intertidal – mid subtidal, mixed substrate, euhaline-upper mesohaline[1, 6, 8, 16, 18]	celtic – mediterranean[1]
Crepidula gibbosa Defrance, 1818	intertidal – shallow subtidal, hard substrate, euhaline	mediterranean
Capulus ungaricus (Linnaeus, 1758)	shallow subtidal – upper continental slope, hard substrate, euhaline-polyhaline[1, 16, 17, 18]	arctic – mediterranean[1]
Aclis minor (Brown, 1827)	shallow – mid subtidal, soft substrate, polyhaline[1, 16]	boreal – mediterranean[1]
Alcis walleri Jeffreys, 1867	mid subtidal – bathyal[11]	arctic – mediterranean[11]
Melanella alba (da Costa, 1778)	shallow – mid subtidal, soft substrate, euhaline[1, 18]	boreal – mediterranean[1]
Velutina aff. *velutina* (Müller, 1776)	indeterminate	indeterminate
Trivia coccinelloides (Sowerby, 1822)	extinct	extinct
Erato exmaugeriae Sacco, 1894	extinct	extinct
Cryptonatica sp.	intertidal – upper continental slope	indeterminate
Euspira catena (da Costa, 1778)	intertidal – mid subtidal, soft substrate, euhaline[1, 8, 18]	celtic – mediterranean[1]

Table 1. — Continuation.

Species	Zone	biogeographic affinity
Buccinum undatum Linnaeus, 1758	mid subtidal – bathyal, mixed substrate, euhaline-upper mesohaline[1, 8, 10, 15]	boreal – mediterranean[1]
Neptunea inversa Harmer, 1918	extinct	extinct
Tritia incrassata (Strøm, 1768)	intertidal - shallow subtidal, mixed substrate, euhaline-upper mesohaline[1, 6, 8, 16, 18]	boreal – mediterranean[1]
Tritia reticulata (Linnaeus, 1758)	intertidal – shallow subtidal, mixed substrate, euhaline-lower mesohaline[1, 2, 6, 8, 10, 16, 18]	boreal – mediterranean[1]
Nucella lapillus (Linnaeus, 1758)	intertidal – shallow subtidal, rocky substrate, euhaline-polyhaline[1, 8, 9, 10, 15]	boreal – mediterranean[1]
Ocenebra cf. *erinaceus* (Linnaeus, 1758)	intertidal – mid subtidal, mixed substrate, euhaline-upper mesohaline[1, 8, 16, 18]	celtic – mediterranean[1]
Mangelia sp.	indeterminate	indeterminate
Propebela aff. *turricula* (Montagu, 1803)	indeterminate	indeterminate
Cyrillia linearis (Montagu, 1803)	intertidal – shallow subtidal, soft substrate, euhaline[1, 6, 16]	boreal – mediterranean[1]
Admete trigostomoides n. sp.	indeterminate	indeterminate
Graphis albida (Kanmacher, 1798)	shallow subtidal, euhaline[1, 16]	boreal – mediterranean[1]
Retusa obtusa (Montagu, 1803)	shallow – deep subtidal, euhaline-lower mesohaline[1, 8, 10]	arctic – mediterranean[1]
Haminoea sp.	indeterminate	indeterminate
Longchaeus cf. *plicosus* (Bronn, 1838)	extinct	extinct
Odostomia unidentata (Montagu, 1803)	shallow – subtidal, parasite, polyhaline-euhaline[16]	celtic – mediterranean[1]
Odostomiinae indet.	indeterminate	indeterminate
Ondina divisa (Adams, 1797)	parasite, euhaline[8, 15, 23]	boreal – lusitanian[20]
Ondina cf. *micropeas* (Boettger, 1902)	extinct	extinct
Menestho derivata (Wood, 1879)	extinct	extinct
Spiralina alpinoligustica (Sacco, 1892)	parasite[23]	mediterranean[25]
Chemnitzia ?*lactea*	indeterminate	indeterminate
Turbonilla indet.	indeterminate	indeterminate
Chrysallida indet.	indeterminate	indeterminate
"*Ellobium*" *pyramidale* (Sowerby, 1822)	supralittoral[23]	extinct

SYSTEMATIC PALAEONTOLOGY

Family PATELLIDAE Rafinesque, 1815
Genus *Patella* Linnaeus, 1758

Patella rustica Linnaeus, 1758
(Fig. 4A1, A2)

Patella rustica Linnaeus, 1758: 783.

MATERIAL AND DIMENSIONS. — Maximum height 9.1 mm, diameter 28.2 mm. — RGM.1364897 (2), leg. WG; RGM.1364961 (5), leg. ACJ; RGM.1365058 (18), leg. AWJ; RGM.1365190 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Low patelliform shell; apex placed two-thirds distance from anterior margin. Sculpture of about 34 low, narrow, scabrous primary ribs with single secondary intercalated in interspaces. Edge finely crenulated.

DISTRIBUTION. — Fossils records are scarce. Pliocene (indeterminate): Calabria and Modena, Italy (Bucquoy *et al.* 1886: 471). — **Early Pleistocene**: Atlantic, Selsoif, France (this paper). — **Middle/Late Pleistocene**: Italy (Buccheri *et al.* 2014). Today this species occurs in the Atlantic south of Bay of Biscay, Strait of Gibraltar, to the coast of North Africa, including the Macaronesian Islands (Zegaoula *et al.* 2016), and into the Mediterranean Sea from Spain (Gofas *et al.* 2011) to the Aegean Sea (Öztürk *et al.* 2014). It inhabits upper midlittoral rocky environments (Bensettiti *et al.* 2004: 112). *Patella rustica* lives highest on the shore of all extant co-occurring European *Patella* species: just at the high tide line, generally on rocks in exposed zones with strong splash. Even at localities where the species is common, empty shells are rarely found between the rocks or on adjoining beaches. Therefore, it is surprising to find it well represented at Selsoif.

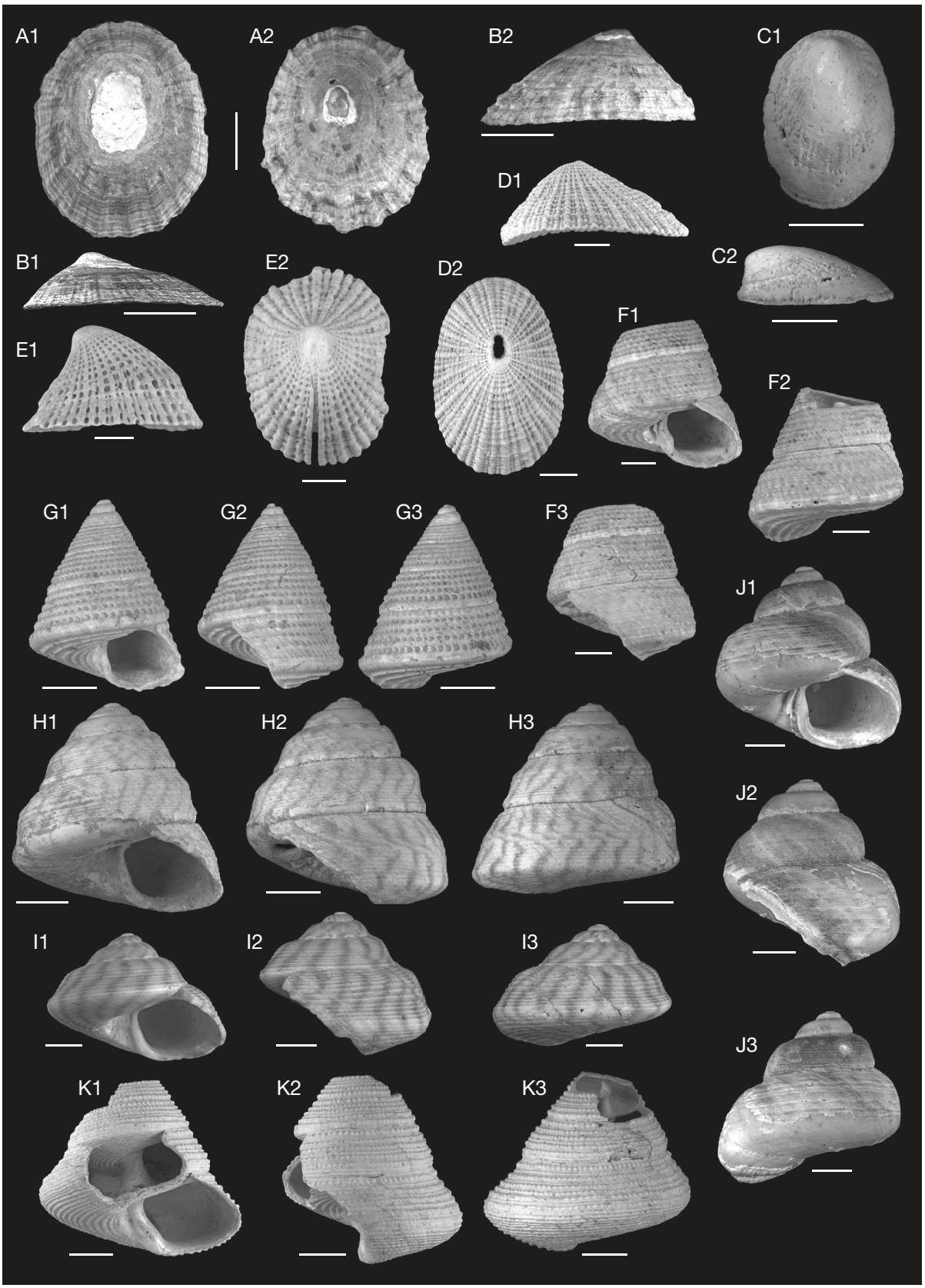
REMARKS

Separation of *Patella* species based on the shell alone is problematic (Côrte-Real *et al.* 1996). The specimens from Selsoif probably represent *P. rustica* Linnaeus, 1758. This species has been considered conspecific or a separate species from *P. piperata* Gould, 1846 although soft tissue and molecular data suggest separation at species/subspecies level (Côrte-Real *et al.* 1996). *Patella rustica* can also be confused with *P. depressa* Pennant, 1777, but that species tends to be more pointed posteriorly, have coarser, more irregular ribs and a less scabrous surface.

Patella vulgata Linnaeus, 1758
(Fig. 4B1, B2)

Patella rustica Linnaeus, 1758: 782.

FIG. 4. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation: **A**, *Patella rustica* Linnaeus, 1758, RGM.1365190, leg. AWJ, H = 7.6 mm; **B**, *Patella vulgata* Linnaeus, 1758, RGM.1310830, leg. AWJ, L = 15.14 mm; **C**, *Tectura virginea* (Müller, 1776), RGM.1365189, leg. ACJ, L = 4.9 mm; **D**, *Diodora graeca* (Defrance, 1820), RGM.1365174, leg. AWJ,



L = 15.04 mm; **E**, *Emarginula fissura* (Linnaeus, 1758), RGM.1365175, leg. WG, L = 4.6 mm; **F**, *Jujubinus exasperatus* (Pennant, 1777), RGM.1365178, leg ACJ, L = 3.5 mm; **G**, *Jujubinus montagui* (Wood, 1828), RGM.1365179, leg. AWJ, L = 4.3 mm; **H**, *Steromphala cineraria* (Linnaeus, 1758), RGM.1365177, leg. ACJ, L = 8.4 mm; **I**, *Steromphala cineraria* (Linnaeus, 1758), RGM.1310831, leg. AWJ, L = 3.6 mm; **J**, *Steromphala tumida* (Montagu, 1803), RGM.1310832, leg. SM, L = 4.6 mm; **K**, *Calliostoma normanensis* n. sp. (**holotype)**, MNHN.F.A91315, leg. AWJ, L = 8 mm. Scale bars: A, C, D, H, K, 2mm; B, 5 mm; E-G, I, J, 1 mm.

Patella vulgata – Harmer 1921: 780, pl. 62, figs 780, 781. — Wesselingh & Pouwer 2011: 129, fig. 1.

MATERIAL AND DIMENSIONS. — Maximum diameter 15.1 mm. — RGM.1310830 (1), leg AWJ; RGM.1315059 (1), leg AWJ.

SPECIES CHARACTERISATION. — Intermediate-high patelliform shell; apex placed two-thirds distance from anterior margin. Largest width at one-thirds distance from anterior margin. Sculpture of about 28 robust primary ribs that can develop slightly irregular knobs, with low secondary ribs and very fine but irregularly developed and spaced tertiary ribs. Edge coarsely wavy, corresponding mostly to primary ribs.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper). — **Upper Pleistocene**: Channel region, Portland and Selsey (Harmer 1921). — **Upper Pleistocene-Holocene**: Netherlands (Wesselingh & Pouwer 2011). — **Present-day**: NE Atlantic coast from Norway to Gibraltar. Rarely reported from western Mediterranean.

REMARKS

As discussed above, identification of fresh Patellidae can be challenging, even more so for fossils, as characteristics such as colouration are generally not preserved. In this case, growth series of the four abundant NE Atlantic species were used for comparison. Most abundant is *Patella rustica* Linnaeus, 1758, which is characterised by a relatively flat shell with fine sculpture of alternating coarser and finer ribs, crossed by growth-lines forming an elongated reticulate sculpture. A few specimens represent *Patella vulgata* Linnaeus, 1758, at this locality characterised by a rugose sculpture, with more prominent and robust broad primary ribs that contain irregular knobs.

Family LOTTIIDAE Gray, 1840
Genus *Tectura* Gray, 1847

Tectura virginea (Müller, 1776)
(Fig. 4C1, C2)

Patella virginea Müller, 1776: 43.

Acmaea virginea – Harmer 1925: 975, pl. 65, fig. 31.

Acmaea (*Tectura*) *virginea* – Landau *et al.* 2003: 8, pl. 5, fig. 3.

Tectura virginea – Chirli & Linse 2011: 26, pl. 1, fig. 4. — Landau *et al.* 2017: 79, pl. 2, figs 1-2.

For more, see synonymy list in Landau *et al.* (2003; 2017)

MATERIAL AND DIMENSIONS. — Maximum height 8.4 mm, width 2.9 mm. — RGM.1364898 (15), leg. WG; RGM.1364962 (236), leg. ACJ; RGM.1365189 (1), leg. ACJ; RGM.1365060 (54), leg. AWJ.

SPECIES CHARACTERISATION. — Shell patelliform, elongate-ovate in profile, apex placed just posterior to centre to close to posterior margin; surface smooth, ribbing suggested in figured specimen due to erosion of surface.

DISTRIBUTION. — **Middle Miocene**: Atlantic of Loire Basin, France (Glibert 1949). — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2017). — **Lower Pliocene**: Coralline Crag, England (Harmer 1925); central Mediterranean, Italy, (Chirli 2004), Tunisia (Fekih 1975). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1925); Atlantic, Mondego Basin, Portugal (Silva 2001); western Mediterranean, Estepona Basin, S. Spain (Landau *et al.* 2003); central Mediterranean, Italy (Sacco 1896a). — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper); central Mediterranean, Italy (Cerulli-Irelli 1916; Ruggieri & Greco 1965; Taviani *et al.* 1998); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Upper Pleistocene**: NSB, Netherlands (Wesselingh & Pouwer 2011); Atlantic, England (Harmer 1925); western Mediterranean, Balearic Islands (Cuerda Barceló 1987). — **Holocene**: NSB (Strand Petersen 2004). Today this species occurs in the Atlantic, from northern Scandinavia to Cape Verde Islands at 0-100 m depth attached to hard substrates (Poppe & Goto 1991) and in the Mediterranean (Giannuzzi-Savelli *et al.* 1994) from the Spain (Gofas *et al.* 2011) coast to the Aegean Sea (Öztürk *et al.* 2014).

REMARKS

This species is extremely variable in height and profile and displays few distinct shell characters. Colour pattern is not preserved in the Selsoif material. For further discussion see Landau *et al.* (2003, 2017).

Family FISSURELLIDAE Fleming, 1822
Genus *Diodora* Gray, 1821

Diodora graeca (Defrance, 1820)
(Fig. 4D1, D2)

Patella graeca Linnaeus, 1758: 784.

Diodora graeca – Landau *et al.* 2003: 26, pl. 4, fig. 4; 2017: 80, pl. 3, figs 1-4. — Chirli & Linse 2011: 35, pl. 4, fig. 5. — Ceulemans *et al.* 2016: 54, pl. 1, figs 5, 6. — Chirli & Forli 2017: 24, fig. 5a.

For more, see synonymy list in Landau *et al.* (2003, 2017) and Ceulemans *et al.* (2016).

MATERIAL AND DIMENSIONS. — Maximum height 23.5 mm, diameter 11.9 mm. — RGM.1364899 (3), leg. WG; RGM.1364964 (7), leg. ACJ; RGM.1365061 (24), leg. AWJ; RGM.1365174 (1), leg. AWJ; RGM.1365062 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Patelliform shell with ovate profile; apical perforation two-third distance from anterior margin; sculpture of primary to tertiary ribs differentiated to a variable degree.

DISTRIBUTION. — **Middle Miocene**: Paratethys (Strausz 1966; Bałuk 1975). — **Upper Miocene**: NW France (Ceulemans *et al.* 2016); Proto-Mediterranean (Sacco 1896a). — **Lower Pliocene**: NW France (Ceulemans *et al.* 2016), Coralline Crag, England (Harmer 1923), Belgium (Marquet & Landau 2006); central Mediterranean (Chirli 2004). — **Upper Pliocene**: Red, Crag, England (Harmer 1923); western and central Mediterranean (Landau *et al.* 2003; Malatesta 1974; Caprotti 1976; Cavallo & Repetto 1992); France (Chirli & Richard 2008). — **Lower Pleistocene**: NW France (Brébion 1964), Selsoif (this paper); central Mediterranean (Cerulli-Irelli 1916; Malatesta 1960; Chirli & Forli 2017); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Upper Pleistocene**: England (Harmer 1923), Netherlands (Wesselingh & Pouwer 2011); western Mediterranean, Balearic Islands (Cuerda Barceló 1987). Today this species occurs from the Atlantic British Isles to Canaries, Mediterranean and Black Sea on rocky shores under stones and rocks, especially where a little silt occurs, living near sponges, on which it feeds (Poppe & Goto 1991).

REMARKS
This species is highly variable in height and the differentiation between the primary to tertiary ribs (see discussion in Ceulemans *et al.* 2016: 55). Some of the Selsoif specimens have weaker primaries than seen in some Mediterranean fossil material.

Genus *Emarginula* Lamarck, 1801

Emarginula fissura (Linnaeus, 1758)
(Fig. 4E1, E2)

Patella fissura Linnaeus, 1758 : 78

Emarginula fissura – Harmer 1923: 776, pl. 62, fig. 7. — Wesselingh & Pouwer 2011: 135, fig. 12. — Chirli & Linse 2011 : 31, pl. 1, fig. 2. — Ceulemans *et al.* 2016: 57, pl. 2, fig. 2. — Brunetti & Cresti 2018: 30, fig. 19.

Emarginula fissura var. *depressa* – Harmer 1923: 777, pl. 62, fig. 8.

For more, see synonymy list in Ceulemans *et al.* (2016).

MATERIAL AND DIMENSIONS. — Maximum height 8.3 mm, diameter 11.7 mm. — RGM.1364900 (2), leg. WG; RGM.1364901 (5), leg. WG; RGM.1365175 (1), leg. WG, RGM.1364965 (13), leg. ACJ; RGM.1365376 (1), leg. ACJ; RGM.1364966 (73), leg. ACJ; RGM.1364967 (28), leg. ACJ; RGM.1365063 (13), leg. AWJ; RGM.1365064 (13), leg. AWJ; RGM.1365065 (22), leg. AWJ; RGM.1365176 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Elevated conical shell; apex placed about two thirds distance from anterior margin, sculpture of alternating primary and secondary ribs, slightly weaker concentric cords forming fine reticulated surface pattern; selenizone narrow, slit extending to one-third shell height.

DISTRIBUTION. — **Middle Miocene**: Loire Basin, France (Glibert 1949). — **Upper Miocene**: NW France (Brébion 1964; not confirmed by Landau *et al.* 2017). — **Lower and Upper Pliocene**: NSB, England (Wood 1848; Harmer 1923), Belgium (Marquet 1998), The Netherlands (Beets 1946); Atlantic, NW France (Ceulemans *et al.* 2016), Portugal (Silva 1990, 2001); western and central Mediterranean (Fekih 1975; Piani 1984; Cavallo & Repetto 1992; Landau *et al.* 2003, 2011; Brunetti & Cresti 2018). — **Lower Pleistocene**: Atlantic, NW France (Brébion 1964), Selsoif, France (this paper); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Pleistocene** (indeterminate): central Mediterranean, Italy (Sacco 1896a; Cerulli-Irelli 1916). Today it occurs along the European Atlantic coasts from Scandinavia to the Mediterranean, at a depth between 0 and 700 m (Piani 1984).

REMARKS
For discussion on the shell variability and comparison with congeners see Ceulemans *et al.* (2016: 57).

Family TROCHIDAE Rafinesque, 1815
Genus *Jujubinus* Monterosato, 1884

Jujubinus exasperatus (Pennant, 1777)
(Fig. 4F1-F3)

Trochus exasperatus Pennant, 1777: 126.

Trochus (*Calliostoma*) *exasperatus* – Harmer 1923: 723, pl. 58, fig. 18.

Jujubinus (*Jujubinus*) *exasperatus* – Cuerda Barceló 1987: 185, pl. 15, figs 11, 12.

Jujubinus exasperatus – Landau *et al.* 2003 : 42, pl. 9, fig. 6. — Chirli 2004: 78, pl. 32, figs 10-12, pl. 33, figs 1-4. — Chirli & Linse 2011: 39, pl. 6, fig. 1. — Chirli & Forli 2017: fig. 6b.

Jujubinus aff. *exasperatus* – Landau *et al.* 2017 97, pl. 21, figs 1-4.

For more, see synonymy list in Landau *et al.* (2003).

MATERIAL AND DIMENSIONS. — Maximum height 9.4 mm, width 7.3 mm. RGM.1364903 (36), leg. WG; RGM.1364969 (48), leg. ACJ; RGM.1365178 (1), leg. ACJ; RGM.1365067 (60+) leg. AWJ.

SPECIES CHARACTERISATION. — Shell trochiform; protoconch severely worn or not preserved. Teleoconch of six flat-sided whorls separated by superficial suture; sculpture of five spiral cords, abapical one broader, stronger, placed just above the suture; fine lamellar ribs visible in cord interspaces giving them a pitted appearance; base flattened bearing six concentric cords; aperture subquadrate; columella short, slightly oblique bearing subobsolete fold.

DISTRIBUTION. — **?Upper Miocene**: NW France (Brébion 1964; conspecificity uncertain; Landau *et al.* 2017). — **Pliocene**: Italy (Brunetti & Vecchi 2005). — **Upper Pliocene**. Western Mediterranean, S. Spain (Landau *et al.* 2003). — **Lower Pleistocene**: Atlantic, southern England (Harmer 1923), Selsoif, France (this paper); central Mediterranean, Italy (Chirli & Forli 2017); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Upper Pleistocene**: Atlantic, Santa Maria Island, Azores (Callapez & Ferreira 2000); western Mediterranean, Balearic Islands (Cuerda Barceló 1987). Today, this species occurs in the Atlantic from the west coast of Scotland to the Canary Islands and Azores (Fretter & Graham 1977; Hernández *et al.* 2011), Mediterranean Sea (Manousis 2021) and Aegean Sea (Öztürk *et al.* 2014).

REMARKS
Jujubinus exasperatus (Pennant, 1777) is a highly variable species that is best distinguish from other *Jujubinus* species by regular spiral cords with a stronger abapical cord.

Jujubinus montagui (Wood, 1828)
(Fig. 4G1-G3)

Trochus montagui W. Wood, 1828: pl. 6, fig. 43.

Jujubinus montagui – Caprotti 1976: pl. 7, fig. 10. — Graham 1988: 120, fig. 39. — Poppe & Goto 1991: 83, pl. 8, fig. 9. — Landau *et al.* 2003: 44, pl. 10, fig. 1. — Chirli 2004: 81, pl. 33, figs 9-16. — Pouwer & Wesselingh 2012: 159, figs 27-29.

Jujubinus (*Jujubinus*) *montagui* – Cavallo & Repetto 1992: 42, fig. 37.

MATERIAL AND DIMENSIONS. — Maximum height 7.0 mm (incomplete), width 7.2 mm. — RGM.1365068 (1), leg. AWJ; RGM.1365179 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Shell trochiform; protoconch and early teleoconch whorls not preserved; last two whorls weakly convex, separated by moderately deeply impressed suture; sculpture of seven to eight irregular, flattened spiral cords; axial sculpture of fine, close-set axial growth lamellae present only in the interspaces; base flattened bearing seven concentric cords; columella short, oblique, curved, bearing stout columellar fold delimiting siphonal fasciole.

DISTRIBUTION. — **Lower Pliocene**: central Mediterranean, Italy (Chirli 2004). — **Upper Pliocene**: western Mediterranean, Estepona Basin, Spain (Landau *et al.* 2003); central Mediterranean, Italy (Caprotti 1976; Cavallo & Repetto 1992). — **Upper Pleistocene**: southern North Sea Basin (Pouwer & Wesselingh 2012). — **Present-day**: Atlantic, Orkneys south into the western Mediterranean, 5-200 m deep, mainly on gravel bottoms (Poppe & Goto 1991).

Genus *Steromphala* Gray, 1847

Steromphala cineraria (Linnaeus, 1758) (Fig. 4H1-H3, I1-I3)

Trochus cinerarius Linnaeus, 1758: 758.

?*non Trochus cinerarius* – Wood 1848: 131, pl. 14, fig. 7.

Trochus (*Gibbula*) *cinerarius* – Harmer 1923: 731 (*partim*, not pl. 58, figs 25, 26) (Upper Pleistocene records only).

Gibbula cineraria – Pouwer & Wesselingh 2012: 151, figs 1-3. — Alf *et al.* 2020*:* 70, pl. 50.

Steromphala cineraria – Affenzeller *et al.* 2017: 804, fig. 5.

MATERIAL AND DIMENSIONS. — Maximum height 12.7 mm, width 12.4 mm. — RGM.1364902 (64), leg. WG; RGM.1364968 (125), leg. ACJ; RGM.1365177 (1), leg. ACJ; RGM.1310831 (1), leg. ACJ; RGM.1365066 (146), leg. AWJ.

SPECIES CHARACTERISATION. — Shell low trochiform; five weakly shouldered teleoconch whorls separated by narrowly impressed suture; sculpture of numerous, fine, irregular spiral cords; axial sculpture reduced to prosocline growth-lines; base depressed bearing numerous concentric cords; umbilicus well developed, moderately narrow and deep; columella short, straight, oblique; colour pattern of red-orange zigzag flammules preserved in all specimens.

DISTRIBUTION. — (**Late Pliocene-Early Pleistocene**: NSB and Irish Sea [Wood 1848; Harmer 1923] likely based on misidentifications [Pouwer & Wesselingh 2012]). **Lower Pleistocene**: Atlantic, Selsoif, France (this paper). **Upper Pleistocene**: British Isles (Harmer 1923). — **Holocene**: NSB (Strand Petersen 2004). Today this species is predominantly found in cooler waters in the NSB and along the European Atlantic coasts North Norway, Iceland to Gibraltar (Fretter & Graham 1977) and adjacent western Mediterranean (Giannuzzi-Savelli *et al.* 1994). Records south of Gibraltar in the Atlantic and into the Mediterranean, such as south Manousis (2021), need to be confirmed.

REMARKS

Based on molecular data, this species is now placed in the genus *Steromphala* Gray, 1847 (Affenzeller *et al.* 2017). Most specimens from Selsoif are small and depressed (Fig. 4I1-I3). One large, gerontic specimen (Fig. 4H1-H3) is taller spired, with more strongly shouldered whorls, the shoulder marked by two slightly strengthened cords. In general, the Selsoif specimens have slightly more shouldered whorls than extant specimens, but we consider them conspecific.

Steromphala tumida (Montagu, 1803) (Fig. 4J1-J3)

Trochus tumidus Montagu, 1803: 280, pl. 10, fig. 4.

Trochus (*Gibbula*) *tumidus* – Harmer 1923: 733 (*partim*, pl. 59, fig. 11, not pl. 59, fig. 10) (Upper Pleistocene-Recent records only).

Gibbula tumida – Pouwer & Wesselingh 2012: 152, fig. 4 (*non Gibbula tumida* Símonarson & Eiríksson *in* Eiríksson & Símonarson, 2021).

MATERIAL AND DIMENSIONS. — Height 4.8 mm. — RGM.1310832 (1), leg. SM; n.n. (8), leg. SM.

SPECIES CHARACTERISATION. — This small *Steromphala* species is characterised by rounded shoulders, fine and slightly irregular spiral ribbing, very strong prosocline growth-lines, a subquadrate aperture with a slight chink on the columella.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper). — **Late Pleistocene**: Channel region, Selsey, west coast of Scotland, Largo bay, Belfast, Livorno (Italy) and Christiana Fjord and Trondhjem in Norway (Harmer 1923). — **Recent**: Iceland and northern Norway to Gibraltar (Pouwer & Wesselingh 2012; Harmer 1923).

Family CALLIOSTOMATIDAE Thiele, 1924
Genus *Calliostoma* Swainson, 1840

Calliostoma normanensis n. sp. (Figs 4K1-K3; 5A1-A3)

urn:lsid:zoobank.org:act:662E6CB4-0935-4328-8183-A0419A765952

TYPE MATERIAL. — **Holotype**: MNHN.F.A91315, height 12.8 mm (incomplete), width 14.7 mm, leg. AWJ.
Paratypes: paratype 1, RGM.1365210, height 8.2, width 8.7 mm (juvenile), leg. WG; paratype 2, RGM.1365270, height 12.7 mm (incomplete), width 13.4 mm, leg. WG; paratype 3, RGM.1364926, height 9.1 mm (incomplete), width 10.9 mm, leg. ACJ; **paratype 4** RGM.1364963, height 10.9 mm (incomplete), width 13.7 mm, leg. AWJ.

DIAGNOSIS. — Trochoid shell with broad, evenly conical spire, flattened base, imperforate, spiral sculpture of four finely beaded primary cords with secondary threads intercalated, 13 weakly beaded cords on base, columella strongly oblique.

ETYMOLOGY. — Named after the Region of Normandy in which the type locality is situated.

TYPE LOCALITY. — Selsoif, Saint-Sauveur-le-Vicomte, Manche department, NW France.

STRATUM TYPICUS. — Gelasian, Early Pleistocene.

OTHER MATERIAL EXAMINED. — Maximum height approx. 17 mm (incomplete), width 16.4 mm. — RGM.1364904 (11 juveniles), leg. WG; RGM.1364970, (27 juveniles + one incomplete adult), leg. ACJ; RGM.1365069 (22 incomplete adults and fragments), leg. AWJ.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper).

DESCRIPTION

Shell medium sized, trochiform; protoconch not preserved; five teleoconch whorls preserved, initially flat-sided, later whorls slightly swollen just above suture, separated by superficial suture; sculpture on first teleoconch whorl of

four finely beaded spiral cords; on second whorl, single secondary spiral intercalated between adapical spiral and second primary cord, strengthening abapically to become almost equal in strength to primaries on later adult whorls. On penultimate whorl secondaries appear between the second and third primaries and between the fourth and the suture. Axial sculpture reduce to weak prosocline growthlines. Last whorl 47% of total height; slightly inflated and strongly rounded at periphery; on last whorl single secondary intercalated in all interspaces, some secondaries almost equal in strength to primaries. Base depressed, imperforate, bearing 13 weakly beaded concentric cords, widening and strengthening toward columella. Aperture subquadrate, 35% of total shell height; outer lip simple, strongly prosocline in profile, roundly angled at base. Columella strongly inclined abaxially, slightly thickened, parietal callus absent.

Comparison

The Selsoif material has sculpture similar to that of *Calliostoma subexavatum* (Wood, 1848) described from the Upper Pliocene Red Crag of England but differs in being lower spired (although one of the specimens figured by Harmer 1923: pl. 57, fig. 15 is similar in profile to the material at hand), and in not having the abapical cord developed into a well-defined and inflated suprasutural band. In some specimens from Selsoif there is a slight tendency for the abapical cord to form a narrow band, but far less prominent than that seen in the Red Crag specimens, or the ones illustrated by Lauriat-Rage *et al.* (1989: pl. 8, figs 5, 6) from the Lower Pliocene of La Limouzinière (NW France). Several similar *Calliostoma* species occur in the Pliocene NSB that share similarities with the Selsoif material. *Calliostoma simile* (Sowerby, 1818) differs in having only beads on the adapical cord on later adult whorls and has weaker spiral sculpture on the base, that is obsolete in some specimens. *Calliostoma multigranus* (Wood, 1848) is probably the most similar with four beaded primary spirals on early whorls, but that species has a narrower apical angle, and a fifth primary appearing at the suture on the second teleoconch whorl, and secondaries are only intercalated on the last whorl. Moreover, the last whorl is less inflated at the periphery, the base is less depressed and there are fewer, smoother concentric cords over the base. *Calliostoma noduliferens* (Wood, 1848) differs in having five beaded primary cords per whorl. The modern European *Calliostoma zizyphinum* (Linnaeus, 1758) is similar in profile, but the cords tend to become smooth on latter whorls, the abapical cord placed just above the suture is usually strengthened, and cords at the periphery and the base are smooth. *Calliostoma conulus* (Linnaeus, 1758) is larger with a narrower apical angle and a taller spire and even smoother sculpture on later teleoconch whorls. *Calliostoma granulatum* (Born, 1778) is larger shelled with a cyrtoconoid spire, more sharply angled at the base, the cords are more finely beaded, and the abapical cord placed just above the suture is usually strengthened.

Family Skeneidae Clark, 1851
Genus *Dikoleps* Hoisaeter, 1968

Dikoleps cutleriana (Clark, 1849)
(Fig. 5B1-B3)

Skenea cutleriana Clark, 1849: 424.

Dikoleps cutleriana – Ceulemans *et al.* 2016: 73, pl. 10, fig. 1. — Landau *et al.* 2017: 142, pl. 66, fig. 1.

For more, see synonymy list in Ceulemans *et al.* (2016).

Material and dimensions. — Maximum height 5.4 mm, width 3.9 mm. — RGM.1365319 (47), leg. AWJ; RGM.1365303 (1), leg. AWJ; RGM.1365300 (2), leg. AWJ; RGM.1365301 (29), leg. AWJ; RGM.1365302 (15), leg. AWJ.

Species characterisation. — Small depressed skeneimorph shell; protoconch of one smooth whorl; teleoconch of two whorls separated by deep suture; sculpture of fine spiral cords that continues inside the deep umbilicus.

Distribution. — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2017). — **Lower Pliocene**: NSB, Luchtbal Member, Belgium (Marquet & Landau 2006); Atlantic, NW France (Ceulemans *et al.* 2016). — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper). Today this species is present from the Atlantic SW England (Fretter & Graham 1977) to southwards into the Mediterranean, Corsica (Van Aartsen *et al.* 1984).

Remarks

There is some variation in shape in the specimen from Selsoif, some slightly more depressed than others and in some specimens the last portion of the last whorl is slightly disjunct. *Dikoleps marianae* Rubio, Dantart & Luque, 1998, from the Mediterranean Sea resembles *D. cutleriana* in having the teleoconch covered in fine spirals, even finer than those of *D. cutleriana* (40 vs 30; *fide* Rubio *et al.* 2004: 131) but the protoconch is rugose rather than smooth.

Family Colloniidae Cossmann, 1917
Genus *Moelleria* Jeffreys, 1865

Moelleria jansseni Hoeksema, Rijken & Simons, 2020
(Fig. 5C1, C2)

Moelleria jansseni Hoeksema, Rijken & Simons, 2020: 6, figs 1-2.

Material and dimensions. — Maximum height 0.61 mm, width 0.96 mm. — **Holotype:** RGM.1362824, height 0.6 mm, width 0.96 mm, leg. AWJ. — **Paratypes**: paratype 1, RGM.1362825, height 0.61 mm, width 0.95 mm, leg. AWJ; paratype 2, RGM.1362630 (8), leg. AWJ.

Original description. — "Shell very small, wider than high, rather solid, opaque, depressed skeneiform, up to 2.25 whorls protoconch included. Suture deep, canaliculate. Protoconch paucispiral, ¾ whorls, smooth, D about 0.30 mm. Protoconch-teleoconch border delimited by shallow groove. Aperture prosocline and circular. Peristome sharp, simple, almost flat, continuous. Umbilicus

open, deep, bordered by sharp peri-umbilical edge (Figs 1c, 1e, 2c, 2e). Teleoconch sculptured with ripple-like, prosocline, straight to sigmoid, flat-topped, partly dichotomous axial ribs, 40-50 on last whorl, broader than interspaces; the branched rib-parts at the periphery coalesce adapically at a short distance from the penultimate whorl and abapically on the base. Body whorl depressed, convex, weakly angled at shoulder (Hoeksema *et al.* 2020: figs 1d, 2d) and in two spirals around the peri-umbilical edge (Hoeksema *et al.* 2020: figs 1e, 2e). Dimensions: H up to 0.65 mm, W up to 1.00 mm." (Hoeksema *et al.* 2020: 6).

Remarks

This species is known only from Selsoif. For full discussion see Hoeksema *et al.* (2020: 6).

Distribution. — **Lower Pleistocene**: Atlantic, endemic to Selsoif (Hoeksema *et al.* 2020).

Family Phasianellidae Swainson, 1840
Genus *Tricolia* Risso, 1826

Tricolia pullus picta (da Costa, 1778)
(Fig. 5D1-D3)

Turbo pictus da Costa, 1778: 103, pl. 8, figs 1, 3.

Tricolia pullus s.l. – Landau *et al.* 2017: 153, pl. 77, figs 1-6.

For more, see synonymy list in Landau *et al.* (2017).

Material and dimensions. — Height 2.3 mm (incomplete), width 2.0 mm. — RGM.1365082 (1), leg. AWJ.

Species characterisation. — Shell turbiniform, only last whorl showing a flattened profile to the upper half, rounded periphery, bearing reddish zigzag colour pattern interrupted by two rows of white blotches the upper placed below the suture, the lower mid-whorl.

Distribution (of subspecies *T. pullus picta*). — **Upper Pliocene**: Atlantic, St Erth, England (Harmer 1925), Selsoif, NW France (this paper). Today it is present from the western coasts of British Isles (absent in Scandinavia and North Sea) south to Gibraltar (Fretter & Graham 1977). Further south it is replaced by the subspecies *T. pullus canarica* Nordsieck, 1973 in the Canary Islands & Madeira (Hernández *et al.* 2011). It lives in rocky pools, 0-35 m depth, common on red weeds (Fretter & Graham 1977).

Remarks

Two subspecies occur today. *Tricolia pullus pullus* (Linnaeus, 1958), present in the Mediterranean to the Strait of Gibraltar, is characterised by its rounded last whorl and spotted colour pattern. The Atlantic *T. pullus picta* (da Costa, 1778) ranging from the British Isles to Morocco has a flattened base of the last whorl and predominantly zigzag pattern that is especially prominent on the base. The material at hand consists of a single fragment of a last whorl that agrees with the present-day Atlantic form. In their work on the Tortonian Upper Miocene of NW France, Landau *et al.* (2017: 153) noted that all forms occurred together in those assemblages and postulated that these subspecies may not have separated at the time. The material from Selsoif is scant, but suggest the Atlantic form had split by at least the Gelasian.

Family Vermetidae Rafinesque, 1815
Genus *Petaloconchus* Lea, 1843

Petaloconchus intortus (Lamarck, 1818)
(Fig. 5E)

Serpula intorta Lamarck, 1818: 365.

Petaloconchus intortus – Van Dingenen *et al.* 2016: 65, pl. 5, fig. 15. — Landau *et al.* 2018: 246, pl. 74, fig. 1.

Material and dimensions. — Maximum height 4.0 mm, width 8.2 mm. — RGM.1364906 (10), leg. WG; RGM.1364971 (17), leg. ACJ; RGM.1365071 (100+), leg. AWJ; RGM.1365216 (1), leg. AWJ.

Species characterisation. — Irregularly coiled gastropod with round cross-section; surface details worn in all material and protoconch lacking.

Distribution. — **Lower Miocene**: Proto-Mediterranean, Italy (Sacco 1896b). — **Lower-Middle Miocene**: NSB, Belgium (Glibert 1952), Germany (Anderson 1964; Moths 1989), Netherlands (Janssen 1984). Middle Miocene: Atlantic, Aquitaine Basin, (Cossmann & Peyrot 1924; Lozouet *et al.* 2001), Loire Basin, France (Glibert 1949); Paratethys, Poland (Friedberg 1914; Bałuk 1970, 1975), Austria (Hörnes 1856; Tejkal *et al.* 1967; Schultz 1998), Bulgaria (Kojumdgieva & Strachimirov 1960), Hungary (Strausz 1966), Romania (Moisescu 1955; Stancu & Andreescu 1968); Proto-Mediterranean, Karaman Basin, Turkey (Erünal-Erentoz 1958; Landau *et al.* 2013). — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2018); Proto-Mediterranean, Italy (Sacco 1896b), Tunisia (Stchepinsky 1938). — **Lower Pliocene**: NSB, England (Wood 1848; Harmer 1918), Belgium (Glibert 1958; Marquet 1998); Atlantic, NW France (Van Dingenen *et al.* 2016), Spain (González-Delgado 1986; Landau *et al.* 2011), Morocco (Lecointre 1952); western Mediterranean, NE Spain, (Martinell & Domènech 1984; Solsona 1998), France (Fontannes 1879); central Mediterranean, Italy (Sacco 1896b; Palla 1967; Caprotti 1974; Anfossi *et al.* 1983; Baroncelli 2001); Tunisia (Fekih 1975). — **Lower-Upper Pliocene**: Atlantic, Mondego Basin, Portugal (Zbyszewski 1959; Silva 2001); western Mediterranean, Spain (Landau *et al.* 2004); central Mediterranean, Italy (Malatesta 1974; Cavallo & Repetto 1992). — **Upper Pliocene-Pleistocene**: NW France (Brébion 1964). — **Lower Pleistocene**: Atlantic, Selsoif (this paper); central Mediterranean, Italy (Cerulli-Irelli 1912; Taviani *et al.* 1998).

Remarks

Specific identity is difficult to establish due to lack of protoconch in the studied material. Here tentatively assigned to *Petaloconchus intortus* (Lamarck, 1818), a common species in fossil faunas from North West Europe. The modern species *Petaloconchus glomeratus* (Linnaeus, 1758) is similar to *P. intortus* except for the protoconch, absent in the specimens from Selsoif. For further discussion see Landau *et al.* (2018: 246).

Family Cerithiidae Fleming, 1822
Genus *Bittium* Gray, 1847

Bittium rubanocinctum Glibert, 1958
(Fig. 5F1-F3)

Bittium rubanocinctum Glibert, 1958: 7, pl. 2, figs 3a-c.

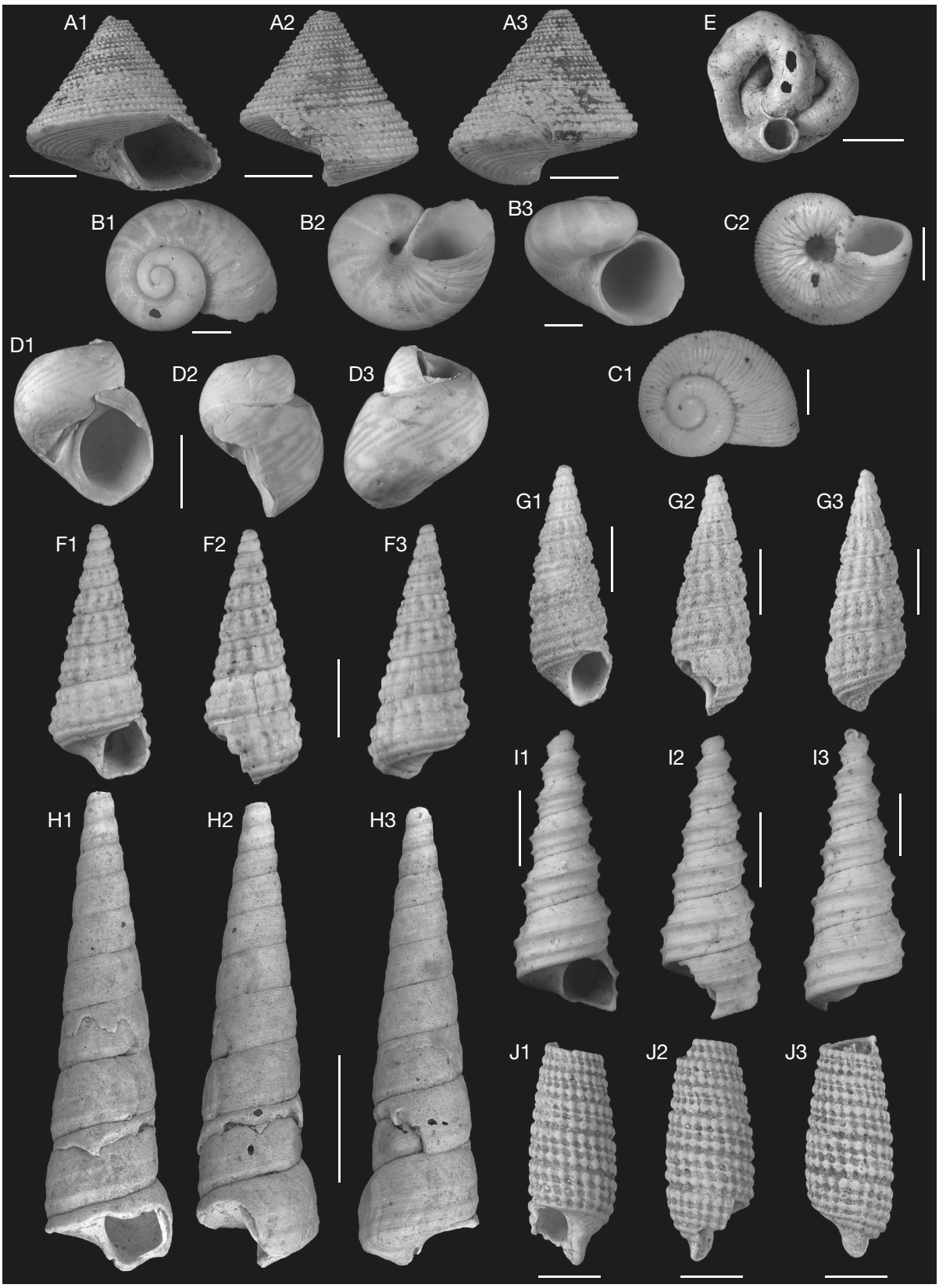


Fig. 5. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Calliostoma normanensis* n. sp. (**paratype 1**), RGM.1365210, leg. WG, L = 5.2 mm; **B**, *Dikoleps cutleriana* (Clark, 1849) RGM.1365303, leg AWJ, H = 700 µm; **C**, *Moelleria jansseni* Hoeksema, Rijken & Simons, 2020 (**holotype)**, RGM.1362824, H = 580 µm; **D**, *Tricolia pullus picta* (da Costa, 1778), RGM.1365082, leg AWJ, H = 2.3 mm; **E**, *Petaloconchus intortus* (Lamarck, 1818), RGM.1365216, leg AWJ, H = 5.1 mm; **F**, *Bittium rubanocinctum* Glibert, 1958, RGM.1365268, leg ACJ, H = 3.3 mm; **G**, *Bittium jadertinum* (Brusina, 1865), RGM.1365269, leg AWJ, H = 3.7 mm; **H**, *Haustator incrassata* (Sowerby, 1814), RGM.1365285, leg AWJ, H = 18.3 mm; **I**, *Haustator incrassata* (Sowerby, 1814), RGM.1365217, leg WG, H = 3.75 mm; **J**, *Marshallora* cf. *adversa* (Montagu, 1803), RGM.1365280, leg AWJ, H = 3.7 mm. Scale bars: A, E, 2 mm; B, C, 200 µm; D, F, G, I, J, 1 mm; H, 5 mm.

MATERIAL AND DIMENSIONS. — Maximum height 6.1 mm, width 1.8 mm. — RGM.1364907 (2), leg. WG; RGM.1364972 (46), leg. ACJ; RGM.1365268 (1), leg. ACJ; RGM.1365072 (70), leg. AWJ; RGM.1365284 (1), leg. AWJ; RGM.1365375 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Robust turriform shell with pronounced suture. Broad paucispiral protoconch of two smooth whorls. Teleoconch whorls with three spirals cords and slightly prosocline axials ribs forming low tubercles at intersections.

DISTRIBUTION. — **Lower Pliocene**: NSB, Kattendijk Formation, Belgium (Glibert 1958), Oosterhout Formation, the Netherlands (RGM collections). — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper).

REMARKS

The Selsoif specimens have more robust axials and lower tubercles that make it slightly different from the specimens illustrated by Glibert (1958) that tend to have finer ribs and less pronounced knobs. Otherwise, the number and organisation of the ribs and cords of the Early Pliocene North Sea Basin (NSB) specimens and the Selsoif material are identical. The geographical and temporal distribution gap between the NSB Early Pliocene and French Gelasian occurrences is remarkable. A *Bittium* species illustrated by Harmer (1916: pl. 41, fig. 4) as *B. reticulatum trinodosa* (Etheridge & Bell) from St Erth also has three prominent spirals. However, the spirals and axials are very regularly spaced and form an evenly reticulated surface pattern. The synonymisation of *B. rubanocinctum* with *B. neerlandicum* (Beets) by Wesselingh *et al.* (2012: 42) is not substantiated.

Bittium jadertinum (Brusina, 1865)
(Fig. 5G1-G3)

Cerithium jadertinum Brusina, 1865: 16.

Bittium jadertinum – Landau *et al.* 2004: 10, pl. 2, fig. 1. — Wesselingh *et al.* 2012: 39, figs 6-9. — Chirli & Forli 2017: 43, fig. 12f.

For more, see synonymy list in Landau *et al.* (2004).

MATERIAL AND DIMENSIONS. — Maximum height 3.8 mm, width 1.3 mm. — RGM.1365269 (1), leg. AWJ; RGM.1365073 (3), leg. AWJ.

SPECIES CHARACTERISATION. — Robust *Bittium* with a very slightly convex whorl profile; four regularly spaced spirals are intersected at regular distances by orthocline to very slightly prosocyrth axial ribs of similar strength with regular knobs on the intersections; six spirals on the shells base.

DISTRIBUTION. — **Upper Pliocene**: western Mediterranean, S. Spain (Landau *et al.* 2004). — **Lower Pleistocene**: Selsoif, NW France (this paper); central Mediterranean, Italy (Chirli & Forli 2017). — **Middle Pleistocene**: NSB, the Netherlands (Wesselingh *et al.* 2023). — **Upper Pleistocene**: NSB, the Netherlands (RGM collections); western Mediterranean, Balearic Islands (Cuerda Barceló 1987). Today it occurs from the North Sea to North Africa, and into the Mediterranean (Poppe & Goto 1991)

REMARKS

Currently WoRMS (2023) considers *B. jadertinum* a synonym of *Bittium reticulatum* (da Costa, 1778). The basis for their synonymy is unclear, as Verduin (1982) is given as the most recent authority in which that author clearly accepted *B. jadertinum* as a valid species. As summarised by Landau *et al.* (2004), the main differences between the two species are that *B. jadertinum* has four equidistant spiral cords and no varices, except possibly on the last 1.5 whorls, whereas *B. reticulatum* has spiral 1 and 2 closer-set and numerous varices along all teleoconch whorls. Both have a multispiral protoconch with a small nucleus. Within large Late Pleistocene samples from the southern North Sea, we are able to separate the *reticulatum* and *jadertinum* morphotypes (Wesselingh *et al.* 2012; 2023). The species *B. pingue* Landau *et al.*, 2018, from Assemblage I of Renauleau, NW France, has similar rib architecture but is much smaller and has a wider apical angle.

Family TURRITELLIDAE Lovén, 1847
Genus *Haustator* Montfort, 1810

Haustator incrassata (Sowerby, 1814)
(Fig. 5H1-H3, I1-I3)

Turritella incrassata Sowerby, 1814: 111, pl. 51, fig. 6.

Turritella (*Haustator*) *incrassata* – Harmer 1925: 446, pl. 42, figs 1-3, 5-7, pl. 43 fig. 16.

Haustator incrassata – Van Dingenen *et al.* 2016: 117, pl. 3, fig. 1.

Turritella incrassata – Moerdijk *et al.* 2018: 27, figs 6-8.

For more, see synonymy list in Van Dingenen *et al.* (2016).

MATERIAL AND DIMENSIONS. — Maximum height 42.4 mm, width 11.5 mm. — RGM.1365074 (700+) leg. AWJ; RGM.1365285 (1), leg AWJ, RGM.1310833 (1), leg. AWJ; RGM.1364908 (140+) leg. WG; RGM.1364974 (200+) leg. ACJ; RGM.1365085 (4), leg WG.

SPECIES CHARACTERISATION. — Medium sized *Turritella* species; protoconch paucispiral of about 1.5 smooth whorls; teleoconch of about 12 whorls with tricostate sculpture, primaries starting in order C-B-A (terminology following Harzhauser & Landau 2019), B and C stronger resulting in bicarinate early whorl profile. Numerous fine and irregular threads appear from fifth whorl onwards. Abapically primary cords flatten and broaden giving whorls a flattened appearance. Base moderately convex, with about five irregular, widely spaced spiral cords, with secondary cords of variable strength intercalated. Lateral sinus on adapical half whorl, steep around ~38° angle and simple abapical inflection. Basal sinus shallow, almost absent, opisthocyrt. Aperture subquadrate, higher than wider.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag Formation, England (Wood 1848; Harmer 1918); Atlantic, NW France (Van Dingenen *et al.* 2016). — **Upper Pliocene**: NSB, Red Crag Formation, England (Wood 1848; Harmer 1918); Oorderen and Kruisschans Members, Belgium (Marquet 1997, 1998), Oosterhout Formation, The Netherlands (Moerdijk *et al.* 2018). — **Upper Pliocene**: Atlantic, St Erth, England (Harmer 1918), Selsoif, NW France (this paper).

REMARKS

Marwick (1957) highlighted the importance in the order of appearance of the cords on the neanic whorls and used a lettering system for the spiral cords in which B was the medial

primary, D the peribasal primary generally involved with the suture, A was the first to appear adapical to B and C the first to appear abapical to B, between B and d (Marwick 1957: 148), and the shape of the lateral and basal sinuses. Subsequently, this work has been neglected by almost all European workers. More recently, Harzhauser & Landau (2019) applied Marwick's model and proposed generic attributions for European fossil turritellids from the Paratethys. Following the diagnostic generic characters proposed in that work, the Selsoif specimens are readily attributed to *Haustator* de Montfort, 1810. These characters are order of appearance of primary spiral cords C-B-A, and lateral sinus with inflection points.

Based on the whorl profile and adult sculpture we attribute these specimens to *H. incrassata* (Sowerby, 1814). This species is highly variable in the development and strength of the spiral sculpture, which has led to the creation of many synonyms. Compared to specimens from other Pliocene sites such as Le Pigeon Blanc (NW France) (Van Dingenen *et al.* 2016) or from the Pliocene Coralline and Red Crag Formations of eastern England, and Pliocene units from Belgium and the Netherlands (Harmer 1925; Marquet 1998; Moerdijk *et al.* 2018), the Selsoif specimens tend to be straight-ided to slightly concave with fine slightly irregular spiral cordlets. The relative smoothness of the later whorls is reminiscent of the endemic Early Pliocene NSB *Haustator vanderfeeni* (Brakman, 1937). The order of appearance of the primary cords places that species also in *Haustator*, however, it has even flatter whorls separated by a more superficial suture, and the whorl profile between the primary cords is concave. Pleistocene records for the Netherlands (*e.g.*, Van Regteren Altena *et al.* 1955) are not supported by *in situ* findings (FW pers. observation) and are not included in the distribution.

Family Triphoridae Gray, 1847
Genus *Marshallora* Bouchet, 1985

Marshallora cf. ***adversa*** (Montagu, 1803)
(Fig. 5J1-J3)

cf. *Murex adversus* Montagu, 1803: 271.

cf. *Triforis perversa* var. *adversa* – Harmer 1918: 425, pl. 41 fig. 25.

cf. *Mashallora* cf. *adversa* – Van Dingenen *et al.* 2016: 162, pl. 14 figs 7, 8.

Material and dimensions. — Maximum height 5.8 mm (incomplete), width 3.2 mm. — RGM.1364975 (3), leg. ACJ; RGM.1365280 (1), leg. AWJ.

Species characterisation. — Apex lacking on all material. Overall shell is slightly spindle shaped. Adult whorls separated by superficial suture; sculpture of three spiral ribs, middle rib slightly stronger than other ribs; numerous weak, prosocline ribs, with rounded tubercles developed at intersections; on last whorl the fourth basal rib is smooth to slightly knobbed and a fifth rib in one specimen is smooth reminiscent of a recent Canarian Island morph of this species (H. Bakker, pers. comm.). The Selsoif specimens are large for this species.

Distribution. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). Today *Marshallora adversa* is distributed in the NE Atlantic from Scandinavia to the Canaries and in the entire Mediterranean (Bouchet 1985).

Remarks

The three extant West European species *Marshallora adversa* (Montagu, 1803), *Cheirodonta pallescens* (Jeffreys, 1867) and *Similiphora similior* (Bouchet & Guillemot, 1978) are almost indistinguishable on shell characters alone (Marquet 1996). The protoconch and position of appearance of the cords on early whorls is required to make a definitive attribution.

Genus *Monophorus* Grillo, 1877

Monophorus indet.
(Fig. 6A1-A3)

Material and dimensions. — Height 3.7 mm (incomplete) mm, width 1.5 mm. — RGM.1365279 (1), leg. AWJ.

Species characterisation. — We only have one damaged specimen lacking protoconch. The earliest whorl preserved has two primary spiral cords, S1 and S3 with large tubercles developed at intersections with narrow axial ribs; the profile between the two spiral cords is concave. S2 appears between S1 and S2, strengthening on later whorls, of almost equal strength on last whorl. The overall shape and tardive S2 fits well in the genus *Monophorus*, but the damaged specimen cannot be attributed to any species (H. Bakker, pers. comm.)

Distribution. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

Family Cerithiopsidae H. Adams & A. Adams, 1853
Genus *Seila* A. Adams, 1861

Seila selsoifensis Marquet, 2001
(Fig. 6B1-B4)

Seila (*S.*) *selsoifensis* Marquet, 2001: 196, pl. 2, figs 5-6.

Material and dimensions. — Maximum height 4.2 mm, width 1.5 mm. **Paratypes** RGM.394128 (2), leg. AWJ. Other material: RGM.1364909 (1), leg. WG; RGM.1364978 (90+) leg. ACJ; RGM.1365180 (1), leg. ACJ; RGM.1365075 (100+) leg. AWJ.

Original description. — "Shell small, turriculate, rather broad, with an apical angle of more than 25°, consisting of eight whorls. Protoconch paucispiral, large (broader than first teleoconch whorl), smooth, very tumid, consisting of only one whorl. Teleoconch whorls tumid for genus. Sculpture starting with axial ribs and two abapical spirals. Third, adapical spiral starting one whorl later and always remaining weaker than both other spirals. Spiral ribs about as broad as intercostal areas. Axial ribs strong, clearly delimited, about as broad as the intercostal spaces, widely spaced, 24 to 30 in number on the middle whorls. Suture deep. Shell base smooth, convex, without additional spirals; aperture nearly square; siphonal canal rather long for genus". (Marquet 2001: 196).

Distribution. — **Lower Pleistocene**: Atlantic, endemic to Selsoif, NW France (Marquet 2001).

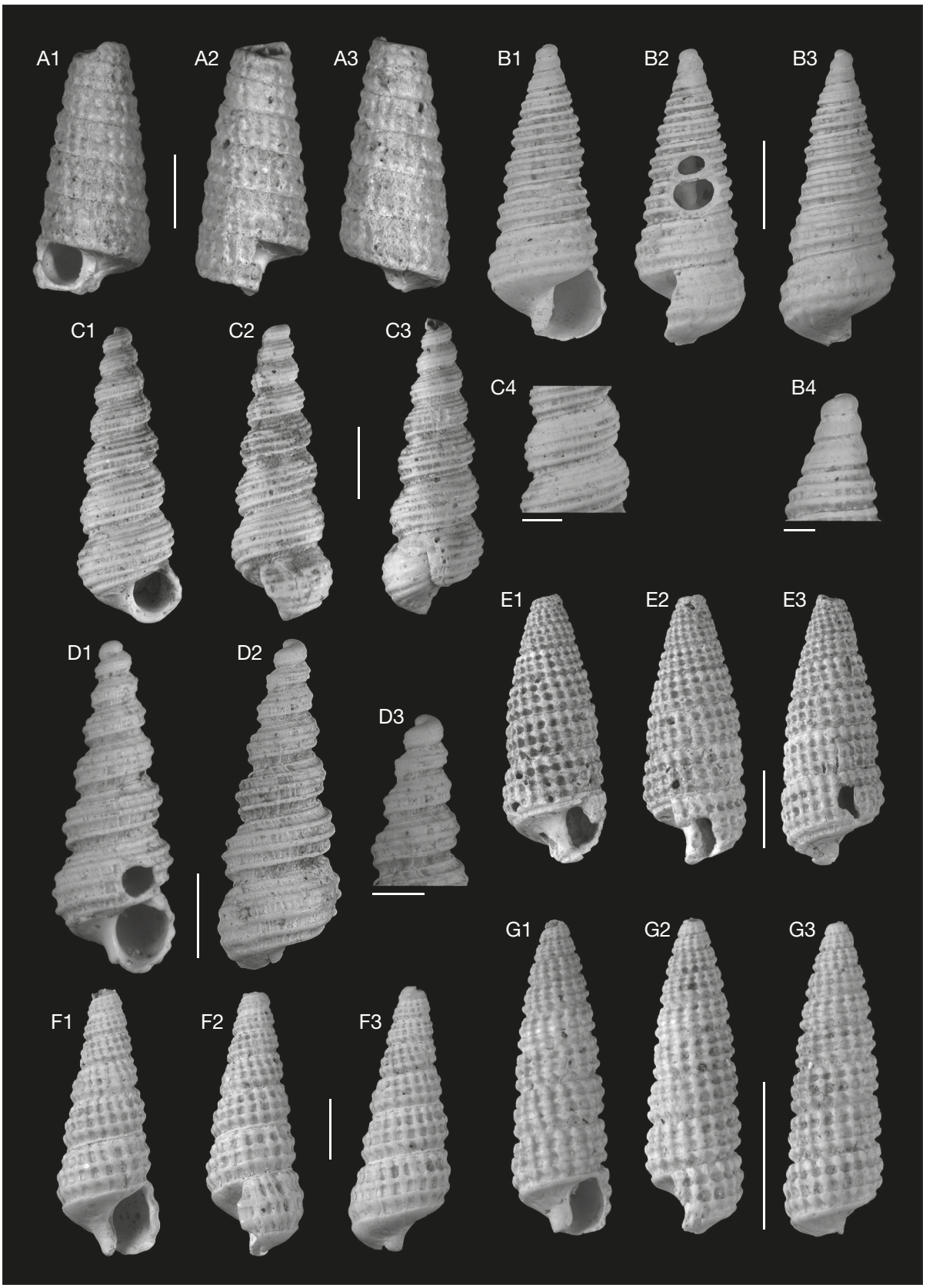


Fig. 6. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Monophorus indet*. , RGM.1365279, leg AWJ, H = 17.19 mm; **B**, *Seila selsoifensis* Marquet 2001, RGM.1365180, leg ACJ, H = 3.4 mm; **C**, *Seila quinquecarinata* n. sp. (**holotype)**, MNHN.F.A91316, leg AWJ, H = 4.2 mm; **D**, *Seila quinquecarinata* n. sp. (**paratype)**, RGM.1365312, leg AWJ, H = 3.9 mm; **E**, *Cerithiopsis* sp., RGM.1365306, leg ACJ, H = 3.5 mm; **F**, *Cerithiopsis* indet., RGM.1365309, leg ACJ, H = 2.8 mm; **G**, *Cerithiopsis* indet., RGM.1365212, leg ACJ, H = 2.15 mm. Scale bars: A1-A3, 5 mm; B1-B3, C1-C3, D1, D2, E1-E3, G1-G3, 1 mm; B4, 200 µm; F1-F3, C4, D3, 500 µm.

Remarks

This endemic species is quite unlike its European Atlantic and NSB congeners in being much squatter and having a wider apical angle. For full discussion see Marquet (2001: 196).

Seila quinquecarinata n. sp.
(Fig. 6C1-C4, D1-D3)

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Type material. — **Holotype**: MNHN.F.A91316, height 8.1 mm (incomplete), width 2.7 mm, leg. AWJ. — **Paratypes**: paratype 1, RGM.1365312, height 3.9 mm (incomplete), width 1.5 mm, leg. AWJ; paratype 2, RGM.1364992, height 4.8 mm (incomplete), leg. AWJ; paratype 3, RGM.1365010, height 5.5 mm (incomplete), leg. AWJ.

Other material. — Maximum height 8.1 mm (incomplete), width 2.7 mm. — RGM.1365119 (26 fragments), leg. AWJ; RGM.1365015 (14 fragments), leg. ACJ; RGM.1364931 (1), leg. WG.

Etymology. — Named reflecting the spiral sculpture consisting of five cords on later adult whorls.

Type locality. — Selsoif, Saint-Sauveur-le-Vicomte, Manche department, NW France.

Stratum typicus. — Gelasian, Early Pleistocene

Diagnosis. — Small *Seila* species with paucispiral protoconch of one rounded whorl, strongly convex teleoconch whorls with five spiral cords on later adult whorls.

Distribution. — **Lower Pleistocene**: Atlantic, endemic to Selsoif, NW France (this paper).

Description

Shell small, turritelliform. Protoconch paucispiral, consisting of one convex whorl with raised nucleus. Teleoconch of at least seven strongly convex whorls separated by moderately impressed linear suture. Sculpture on first teleoconch whorl of three elevated cords, adapical cord placed on subsutural ramp weakest, middle cord delimiting shoulder strongest, abapical cord slightly weaker than mid-cord. Abapically, upper cord strengthens, so that on third teleoconch whorl three strong primary cords, mid-cord still slightly stronger forming whorl periphery, fourth cord appears on subsutural ramp. On fourth whorl a fifth primary cord appears on subsutural ramp; later whorls with five primary spiral cords, upper two slightly weaker than lower three. Fine, elevated axial lamellae present in spiral interspaces. Last whorl short, strongly convex, with six cords above the level of the insertion of the outer lip plus weak peribasal cord; base smooth. Aperture small, rounded, outer lip simple, oblique in profile.

Remarks

The late Neogene of NW France is proving fertile hunting ground for endemic *Seila* species (Marquet 2001; Landau *et al.* 2018). *Seila quinquecarinata* n. sp. is the second *Seila* species endemic to the Sesoif assemblage. It is immediately separated from all its European Neogene congeners in having five spiral cords on later adult whorls. All the *Seila* species discussed by Marquet (2001) and Landau *et al.* (2018) have the more usual number of three spiral cords on all adult whorls. It is also separated from all the present-day Atlantic species discussed by Rolán & Fernandes (1990) that have multispiral protoconchs. It is also unusual in having strongly convex whorls. Most *Seila* species have relatively flat-sided whorls. The shell is somewhat reminiscent of a *Mathilda* species, but these are immediately separated by their heterostrophic protoconch.

Genus *Cerithiopsis* Forbes & Hanley, 1850

Cerithiopsis indet.
(Fig. 6E1-E3, F1-F3, G1-G3)

Material and dimensions. — Height 4.6 mm (incomplete), width 1.7 mm. — RGM.1365212 (1), leg. ACJ; RGM.1365310 (9), leg. ACJ; RGM.1365307 (1), leg. ACJ; RGM.1365306 (1), leg. ACJ; RGM.1365308 (2), leg. ACJ; RGM.1364977 (23), leg. ACJ; RGM.1365309 (1), leg. ACJ; RGM.1365311 (1), leg. ACJ; RGM. 1365313 (1) leg. unknown, RGM.1365078 (c. 135) leg AWJ, RGM.961903 (26), leg. AWJ; RGM.961908 (7), leg. unknown.

Distribution. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

Remarks

Cerithiopsidae can only be reliably identified using protoconch characteristics. The absence of protoconch in all our specimens make it impossible to make a definitive identification. The illustrated specimens show some of the morphological variability encountered in the *Cerithiopsis* specimens at hand.

Family Epitoniidae Berry, 1910
Genus *Boreoscala* Kobelt, 1902

Boreoscala similis (J. de C. Sowerby, 1813)
(Fig. 7A1-A3, B1-B3)

Scalaria similis J. de C. Sowerby, 1813: 49, pl. 16, two upper figures.

non Scalaria similis G.B. Sowerby II, 1844: 94, pl. 34, fig. 90 [synyonym of *Epitonium jomardi* (Audouin, 1826)] (*non* J. de C. Sowerby, 1813).

Scalaria groenlandica – Wood 1848 (*partim*): 90, pl. 8, fig. 11 (fossil specimens only)[*non Boreoscala greenlandica* (Perry, 1811]).

Scala (*Boreoscala*) *similis* – Harmer 1925: 549, pl. 47, figs 18-22.

Epitonium similis – Wesselingh *et al.* 2012: 174, fig. 18.

Material and dimensions. — Maximum height 35.4 mm, width 13.7 mm. — RGM.1364910 (24), leg. WG; RGM.1365181 (1), leg. WG; RGM.1364911 (1), leg. WG; RGM.1364979 (34), ACJ.

Species characterisation. — Robust epitoniid with variable convex to subconvex whorl profile and a characteristic spiral ornamentation of low broad ribs. The whorl profile, number and strength of the ribs, including a basal rib, are very variable.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag Formation, England (Harmer 1925). — **Upper Pliocene**: NSB, Red Crag Formation, England (Wood 1848; Harmer 1925), Netherlands (Wesselingh *et al.* 2012). — **Lower Pleistocene**: NSB, England (Harmer 1925); Atlantic, Selsoif, NW France (this paper).

REMARKS

Boreoscala similis (J. de C. Sowerby, 1813) from Late Pliocene warm temperate and temperate assemblages of the North Sea Basin is closely similar to *B. greenlandica* (Perry, 1811), an arctic to subarctic-boreal, almost circumpolar species, living today. It differs in having a somewhat thicker shell, with stronger ribs and a more convex whorl profile then *B. greenlandica*. Extant specimens of the latter are very variable but have generally thinner axial ribs and less impressed sutures, resulting in less convex whorls. The material from Selsoif is closer to *B. similis*, with a few specimens having less convex whorls and approximating to *B. greenlandica*. These differences are clearly illustrated by Wesselingh *et al.* (2012: compare fig. 17 vs fig. 18).

It is tempting to suggest that *B. greenlandica* evolved from *B. similis* as a colder water adapted species. However, this is unlikely, as the specimen illustrated as *B. greenlandica* by Símonarson *et al.* (2021: pl. 7.8, fig. 6) from the Late Pliocene-Early Pleistocene of Iceland is clearly that species with its shallow suture and weakly convex whorls. Durham & MacNeil (1967) suggested that *B. greenlandica* was most probably of Pacific origin.

It is also possible that the two represent extreme forms of a single species, and that the differences seen are ecophenotypic. Despite the variability seen in both species, Pliocene specimens in the RGM collections could relatively easily be ascribed to *B. similis*, and extant specimens to *B. greenlandica*. In view of this, we maintain the two species separate, and consider the Selsoif material to belong to *B. similis*.

Family LITTORINIDAE Children, 1834
Genus *Lacuna* Turton, 1827

Lacuna crassior (Montagu, 1803)
(Fig. 7C1-C3)

Turbo crassior Montagu, 1803: 309, pl. 20, fig. 1.

Lacuna crassior – Harmer 1921: 667, pl. 53, figs 27-29. — Fretter & Graham 1980: 247, fig. 198. — Moerdijk & Janse 2015: 22, fig. 9.

MATERIAL AND DIMENSIONS. — Maximum height 10.2 mm (incomplete), width 6.3 mm. — RGM.1365195 (1), leg. WG; RGM.1364912 (2), leg. WG; RGM.1365173 (1), leg. ACJ; RGM.1365096 (17), leg. AWJ.

SPECIES CHARACTERISATION. — Smooth, medium-sized shell. Protoconch damaged or lacking in almost all specimens, but in a few specimens the first whorl is flat and not clearly separated from the teleoconch. Teleoconch of four round whorls. Aperture typically circa 40% of shell height. Umbilicus reduced to narrow slit.

DISTRIBUTION. — **Lower Pleistocene**: NSB, England (Harmer 1921); Atlantic, Selsoif, NW France (this paper). — **Holocene**: England (Harmer 1921), West Greenland (Símonarson 1981). Beached occurrences of this species likely of a Late Pleistocene age are known from The Netherlands (Moerdijk & Janse 2015). Today this species occurs from Greenland, Arctic Canada to the British Isles and Normandy (Fretter & Graham 1980; Backeljau *et al.* 1984). The species has been reported living on or near the fleshy bryozoan *Alcyonidium* from between the low water tide line to 90 m water depth in areas with stones, rocks and shells dispersed in soft substratum (Graham 1988).

Lacuna pallidula (da Costa, 1778)
(Fig. 7D1-D3)

Cochlea pallidula da Costa, 1778: 51, pl. 4, figs 4, 5.

Lacuna pallidula – Harmer 1921: 665, pl. 53, fig. 25. — Fretter & Graham 1980: 250, figs 201-202. — Strand Petersen 2004: 29, fig. 7. — Moerdijk & Janse 2015: 23, fig. 11.

MATERIAL AND DIMENSIONS. — Maximum height 4.7 mm, width 5.1 mm. RGM.1364981 (20), leg. ACJ; RGM.1365182 (1), leg. AWJ; RGM.1364913 (2), leg. WG; RGM.1365081 (51), leg. AWJ.

SPECIES CHARACTERISATION. — Small, round shell. Three smooth teleoconch whorls; spire almost flat; last whorl 92% of the total height. Prosocline growthlines. Aperture round; moderately extent columella fold on an open umbilicus.

DISTRIBUTION. — **Lower Pleistocene**: Scotland and Ireland (Harmer 1921); Atlantic, Selsoif, NW France (this paper). — **Holocene**: NSB (Strand Petersen 2004). Today this is predominantly a northern species extending from south of the Arctic Circle on the American coast from Greenland to Connecticut (Gould 1840; Trott 2004), in the eastern Atlantic the distribution extends from the White Sea (Vortsepneva *et al.* 2023), North Sea (Dumoulin 1989), British Isles (Fretter & Graham 1980; Guiry & Guiry 2011), France (Müller 2004) into northern Spain (Rolán 1983). The species is associated with *Fucus serratus* (Smith 1973).

Lacuna parva (da Costa, 1778)
(Fig. 7E1-E3)

Cochlea parva da Costa, 1778: 85.

Turbo puteolus Turton, 1819: 193, figs 90, 91.

Lacuna puteolus – Harmer 1921: 666, pl. 53, fig. 26.

Lacuna parva – Fretter & Graham 1980: 248, figs 199-200. — Moerdijk & Janse 2015: 22, fig. 10.

MATERIAL AND DIMENSIONS. — Maximum height 3.5 mm, width 3.4 mm RGM.1364980 (4), leg. ACJ; RGM.1365183 (1), leg. ACJ.

SPECIES CHARACTERISATION. — Small ovate shell. Three smooth, round teleoconch whorls. Last whorl is 77% of total shell. Aperture round with a thick peristome, columella expanded and flattened abapically. Broad umbilical chink.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). — **Lower and Upper Pleistocene**: England and Ireland (Harmer 1921). — **Upper Pleistocene**: Netherlands (Wolf 2001). — **Holocene**: NSB (Strand Petersen 2004). Today predominantly a northern species extending from south of the Arctic Circle on the American coast to Cape Cod, in the eastern Atlantic British Isles, Norway, Sweden (Fretter & Graham 1980), North Sea of Belgium (Backeljau 1986). The species is associated with algae such as *Fucus* below the low water tide line (e.g., Ockelmann & Nielsen 1981).

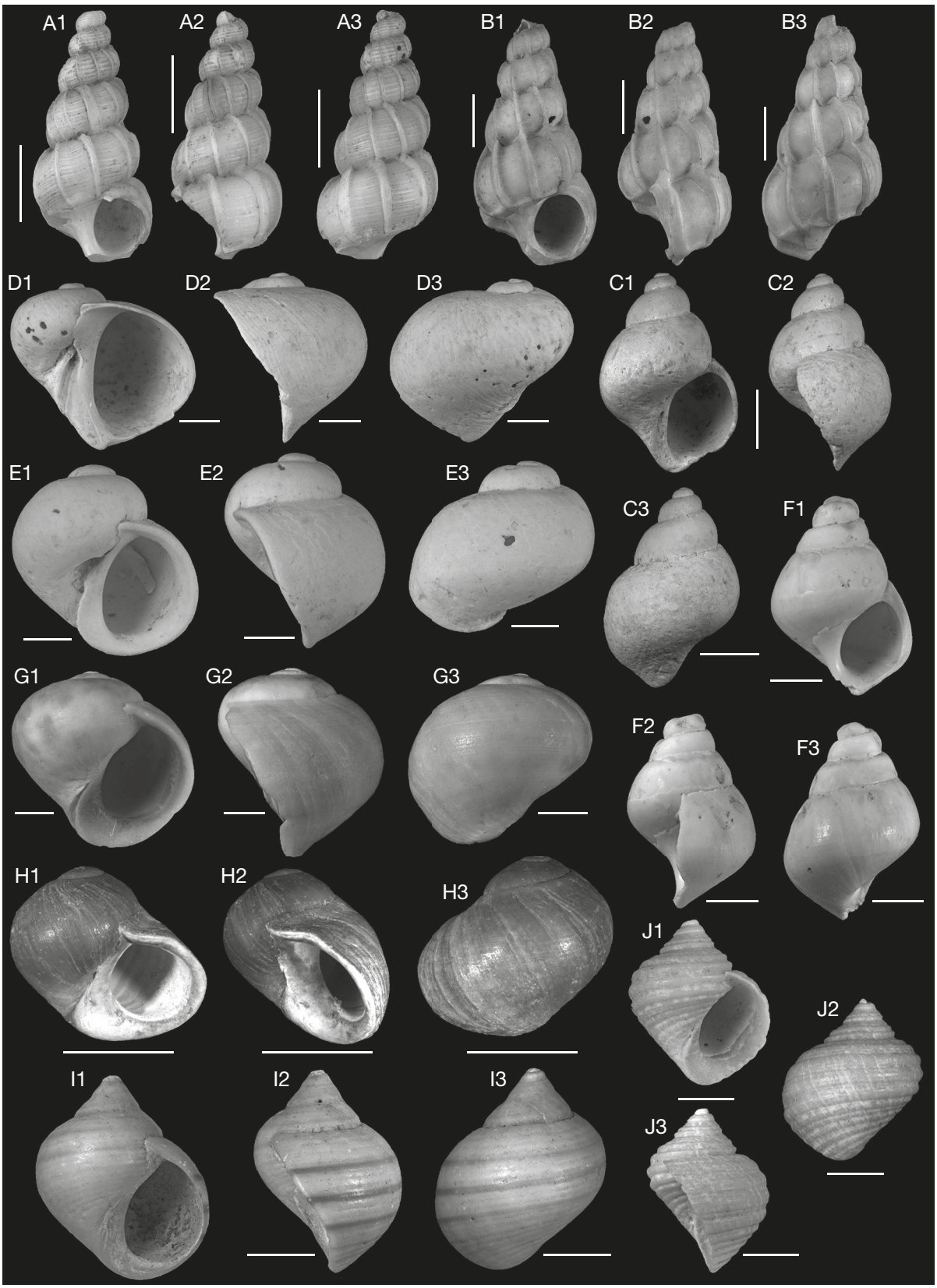

Fig. 7. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Boreoscala similis* (J. de C. Sowerby, 1813), RGM.1365181, leg WG, H = 6.5 mm; **B**, *Boreoscala similis* (J. de C. Sowerby, 1813), RGM.1364911, leg WG, H = 9.3 mm; **C**, *Lacuna crassior* (Montagu, 1803), RGM.1365195, leg WG, H = 3.5 mm; **D**, *Lacuna pallidula* (da Costa, 1778), RGM.1365182, leg AWJ, H = 2.1 mm; **E**, *Lacuna parva* (da Costa, 1778), RGM.1365183, leg ACJ, H = 2 mm; **F**, *Lacuna* cf. *vincta* (Montagu, 1803), RGM.1364982, leg ACJ, H = 1.9 mm; **G**, *Littorina obtusata* (Linnaeus, 1758), RGM.1365211, leg ACJ, H = 2.3 mm; **H**, *Littorina obtusata* (Linnaeus, 1758), RGM.1310829, leg WG, H = 8.4 mm; **I**, *Littorina littorea* (Linnaeus, 1758), RGM.1365070, leg AWJ, H = 6 mm; **J**, *Littorina littorea* (Linnaeus, 1758), RGM.1365202A, leg AWJ, H = 3.02 mm. Scale bars: A, B, 2 mm; C, J, 1 mm; D-G, 500 µm; H, 5 mm; I, 2 mm.

Lacuna cf. ***vincta*** (Montagu, 1803)
(Fig. 7F1-F3)

cf. *Turbo vinctus* Montagu, 1803: 307.

cf. *Lacuna divaricata* – Harmer 1921: 668, pl. 53, fig. 30.

MATERIAL AND DIMENSIONS. — Maximum height 2.7 mm (incomplete), width 2.1 mm. — RGM.1364982 (1), leg. ACJ; RGM.1365184 (2), leg. ACJ.

SPECIES CHARACTERISATION. — Small, ovate-conical shell with subobsolete spiral threads. Four teleoconch flat whorls. Last whorl is 59% of the total height. Prosocline growth-lines. Ovate aperture, with open umbilicus.

DISTRIBUTION. — Selsoif, NW France (this paper). Today *L. vincta* is found in boreal regions of western and eastern Atlantic Ocean with its southern distribution recorded in Brittany (Smith 1973) where it is common on algae such as *Fucus*.

REMARKS
We have only badly damaged material, whose attribution is uncertain. Nevertheless, the flat-sided whorl profile and subobsolete spiral threads suggest it concerns this species.

Genus *Littorina* Férussac, 1822

Littorina obtusata (Linnaeus, 1758)
(Fig. 7G1-G3, H1-H3)

Turbo obtusatus Linnaeus, 1758: 761.

Littorina obtusata – Harmer 1921 (*partim*): 661, pl. 52, figs 27-28 (*non* fig. 29, that corresponds to *Littorina littorea* (Linnaeus, 1758)).

Littorina (*Neritrema*) *obtusata* – Reid 1996: 196, pl. 53, figs 3-5, 76-81.

Littorina obtusata – Moerdijk & Janse 2015: 21, figs 4, 5.

For more, see synonymy list in Reid (1996).

MATERIAL AND DIMENSIONS. — Maximum height 8.4 mm, width 9.3 mm. RGM.1365211 (1), leg. ACJ; RGM.1364983 (6), leg. ACJ; RGM.1365076 (7), leg. WG., RGM.1310829 (1), leg. WG; RGM.1365087 (3), leg AWJ, RGM. 1365286 (24) leg. WG; RGM.1365086 (c. 90) leg. AWJ; RGM.1405527 (46), leg ACJ.

CHARACTERISATION. — Relatively small (H = 6 mm) thick shelled, robust, often smooth and shiny *Littorina*; The Selsoif specimens are somewhat pointed, higher spired compared to modern specimens (*viz.* Reid 1996); aperture rounded with particularly thickened abapical margin; well preserved specimens bear very fine, slightly irregular spiral grooves. The ratio between the height of the lower apertural lip and the height of the outerlip ranges between 0.20 and 0.29, which is within the range of *Littorina obtusata* (Reid, 1996); *Littorina fabalis* has a ratio over 0.29.

DISTRIBUTION. — The published fossil distribution of *L. obtusata* may not be entirely correct as previous authors had difficulties in distinguishing the species from *L. fabalis* (see Reid 1996). The Early Pleistocene North Sea Basin records (Norwich Crag Formation & Bridlington Beds: Harmer 1921) are based on misidentifications (Reid 1996). The record from Selsoif, NW France (this paper) is possibly the oldest fossil occurrence. The species is common in Late Pleistocene deposits in the entire northern Atlantic region (Reid 1996). — **Present-day**: western North Atlantic New-Foundland to NewYork and unconfirmed records from Hudson Bay; eastern North Atlantic from White Sea and Iceland in the north to southern Portugal in the south (Reid 1996).

REMARKS
Today in western Europe two closely resembling *Littorina* species, *L. fabalis* (Turton, 1825) and *L. obtusata* (Linnaeus, 1758) occur that can be best distinguished by soft anatomy and ecological differences (Reid 1996), as well as allozyme differences. Reid however provided a morphological character that leads to 95% success in the separation of the species, *viz*. the ratio between basal lip height versus the aperture height. The dated phylogenies of Reid (1996) indicate they are sister species that evolved from a common ancestor around 2 Ma, broadly contemporary with the Selsoif material.

Littorina littorea (Linnaeus, 1758)
(Fig. 7I1-I3, J1-J3)

Turbo littoreus Linnaeus, 1758: 761.

Littorina littorea – Wood 1848: 118, pl. 10, figs 14a-k. — Harmer 1920: 645, pl. 52, figs 1-8. — Van Regteren Altena *et al.* 1954: 61, fig. 29. — Moerdijk & Janse 2015: 20, figs 1-2.

Littorina (*Littorina*) *littorea* – Reid 1996: 95, figs 3, 5, 6B, 32-38.

non Littorina littorea – Gladenkov *et al.* 1980 (*partim*): 65, pl. 13, figs 8-9.

non Littorina littorea – Gladenkov *et al.* 1980 (*partim*), p. 65, pl. 13, figs 10-11 (that corresponds to *Littorina islandica* Reid, 1996).

MATERIAL AND DIMENSIONS. — Maximum height 25.3 mm (incomplete), width 22.6 mm. RGM.1365202 (100+) leg. AWJ; RGM.1365070 (1), leg. AWJ; RGM.1364984 (37), leg. ACJ; RGM.1365088 (82), leg. AWJ; RGM.1365086 (56), leg. WG; RGM.1364914 (28), WG.

SPECIES CHARACTERISATION. — Globular to ellipsoid, thick shell. Short spire with a pointed apex. Juveniles have strong spiral ribs that become obsolete early on the teleoconch. On some specimens the last whorl has at least three brown or red spiral lines. Even though the strength and location of disappearance of spiral ribs is somewhat variable, the overall shape is very distinct.

DISTRIBUTION. — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1920; Reid 1996). — **Lower Pleistocene**: NSB, England (Harmer 1920), Netherlands (Van Regteren Altena *et al.* 1954; Moerdijk & Janse 2015); Atlantic, Iceland (not in Icelandic modern fauna) (Reid 1996), Selsoif, NW France (this paper). — **Middle Pleistocene**: Channel region England (Preece & Bates 1999). — **Upper Pleistocene**: NSB, England (Harmer 1920). Recent distribution in the western Atlantic from Newfoundland to Chesapeake Bay in the western Atlantic (Reid 1996), in the eastern Atlantic from the White Sea southwards, occasionally as far as southern Portugal. The lack of fossil occurrences in the western Atlantic allows the possibility that the species was introduced there by e.g., Vikings (Reid 1996).

Family Rissoidae Gray, 1847
Genus *Alvania* Risso, 1826

Alvania cf. ***cancellata*** (da Costa, 1778)
(Fig. 8A1-A3)

cf. *Turbo cancellatus* da Costa, 1778: 104, pl. 8, figs 6, 8.

Material and dimensions. — Maximum height 2.6 mm, width 1.6 mm. — RGM.1364986 (1), leg. ACJ; RGM.1310338 (1), leg ACJ.

Species characterisation. — Shell small, rissoiform. Protoconch not preserved. Three teleoconch whorls preserved. Sculpture of three spiral cords on spire whorls, and 13 orthocline ribs forming coarsely reticulated sculpture. Last whorl bearing six spiral cords. Aperture round, peristome complete, thickened, outer lip thickened.

Distribution. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). *Alvania cancellata* is known from the Upper Pliocene Atlantic of the Mondego Basin, Portugal, and was widespread in the Pliocene Mediterranean. Raad *et al.* (2013) reported occasional findings from the Upper Pleistocene NSB of the Netherlands. Today it is distributed from the British Isles south into the Mediterranean (Landau *et al.* 2004).

Remark
Due to the scarcity and poor preservation of the material at hand, identification is uncertain. It is clearly separated from the other two congeners present in the assemblage by the shape and the number of spiral cords.

Alvania selsoifensis n. sp.
(Fig. 8B1-B3)

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Type material. — **Holotype**: RGM.1365286, height 1.4 mm, width 0.9 mm, leg. ACJ.

Etymology. — Named after the type locality of Selsoif.

Type locality. — Selsoif, Saint-Sauveur-le-Vicomte, Manche department, NW France.

Stratum typicus. — Gelasian, Early Pleistocene.

Diagnosis. — *Alvania* species of the *A. dictyophora*-complex with biangular whorls, deeply impressed suture, two elevated primary cords on spire whorls, three above the insertion of the outer lip on the last whorl, three further strong cords over base, axial sculpture 12-13 sharp ribs that weaken over base, base somewhat depressed.

Distribution. — **Lower Pleistocene**: Atlantic, endemic to Selsoif, NW France (this paper).

Description
Shell small, rissoiform. Protoconch of two smooth whorls (surface sculpture may be abraded). Three teleoconch whorls; sculpture on spire whorls of two elevated spiral cords; axial sculpture of 12-13 narrow, elevated, widely spaced, orthocline ribs forming coarsely reticulated pattern. Whorl profile sharply angled at the cords. Last whorl 60% of total height, single secondary develops on second half of last whorl, profile sharply angular at shoulder and peripheral cord, peribasal cord prominent with two further cords of equal strength over base, axials weakening over base: base somewhat depressed. Aperture 35% of total height, ovate; outer lip thickened by varix, peristome complete; columella thickened in abapical portion.

Remarks
Alvania selsoifensis n. sp. is a very distinctive *Alvania* species and merits formal description. Unfortunately, all other specimens are too incomplete to nominate as paratype material. *Alvania selsoifensis* n. sp. might belong to the *A. dictyophora*-complex of Amati & Smriglio (2016) characterised by having relatively coarsely reticulated surface sculpture with two cords on the spire whorls, although all the species included in the complex by those authors are endemic to the Pliocene to present-day of Italy. The Selsoif species differs from *A. dictyophora* (Philippi, 1844) and *A. desabatae* Amati & Smriglio, 2016 in having a deeper suture making the whorls more angular, and only three cords above the insertion of the outer lip on the last whorl as opposed to four in *A. dictyophora*. It is more closely similar to *A. clathrella* (Seguenza, 1903), a Pleistocene to extant species from Italy, in having two primary cords on spire whorls and widely spaced axials forming a reticulated pattern. However, the Selsoif species differs in having a deeper suture, fewer axials on the spire whorls resulting in a slightly denser reticulated pattern and the cords over the base are thinner and the reticulation stronger, whereas in the Selsoif species the cords over the base are stronger and broader and the axials weaker giving the base a strongly corded rather than reticulated appearance. *Alvania bicingulata* (G. Seguenza, 1876) from the Pliocene of Sicily differs in having a more superficial suture, a more rounded last whorl, and, like *A. clathrella* has reticulated sculpture on the base. The last species included in the group by Amati & Smriglio (2016), *A. tenuicostata* (G. Seguenza, 1876), another fossil species from the Pliocene of Sicily is far more elongate with weaker sculpture.

If we review species with similar shell characters outside the Mediterranean, *A. milleti* Landau, Ceulemans & Van Dingenen, 2018 from the Atlantic Tortonian Upper Miocene of NW France could also be included, but like *A. clathrella* this species has a more superficial suture, and the base is less depressed and reticulated.

Alvania sp. 1
(Fig. 8C1-C3)

Material and dimensions. — Maximum height 1.3 mm, width 0.8 mm. — RGM.1364985 (8), leg. ACJ; RGM.1365091 (107), leg. AWJ; RGM.1365090 (1), leg. AWJ; RGM.1365089 (10), leg. AWJ; RGM.1364987 (2), leg. ACJ.

Species characterisation. — Shell small, rissoiform. Protoconch of two smooth whorls. Three teleoconch whorls; spire whorls sculpture of four spiral cords; axial sculpture of around 16 broad orthocline ribs forming a reticulated pattern. Last whorl develops one secondary cord between suture and first cords. Base somewhat depressed, with four spiral cords; axial ribs stop at peribasal cord.

Distribution. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

Remark

The material at hand is too worn to identify with certainty. In profile and sculpture, it is similar to several Italian Pliocene species such as *Alvania lanciae* (Calcara, 1845) and *A. thalia* (De Stefani & Pantanelli, 1878), which both have more numerous cords on the base,

Genus *Manzonia* Brusina, 1870

Manzonia crassa (Kanmacher, 1798)
(Fig. 8D1-D3)

Turbo crassus Kanmacher 1798: 638, fig. 20.

Manzonia (*Manzonia*) *costata* – Cuerda Barceló 1987: 202, pl. 16, fig. 18.

Manzonia crassa – Chirli & Linse 2011: 83, pl. 24, fig. 4. — Van Dingenen *et al.* 2016: 140, pl. 10, fig. 2. — Landau *et al.* 2018: 274, pl. 103, fig. 1.

For more, see synonymy list in Van Dingenen *et al.* (2016) and Landau *et al.* (2018).

Material and dimensions. — Maximum height 1.7 mm, width 1.0 mm. RGM.1364988 (4), leg. ACJ; RGM.1365201 (1), leg. ACJ; RGM.1365093 (16), leg. AWJ.

Species characterisation. — Shell small, rissoiform. Protoconch not preserved. Four strongly convex teleoconch whorls separated by deeply impressed suture; sculpture of numerous, regular, flattened spiral cords; about ten high, widely spaced, sinuous, prosocline axial ribs. Ribs stop abruptly at strong, elevated peribasal cord; base narrow, deeply concave forming wide groove between peribasal cord and peristome. Aperture ovate, outer lip strongly thickened by rounded labial varix, peristome complete.

Distribution. — **Middle Miocene**: Atlantic, Loire Basin, France (de Morgan 1915; Cossmann 1918; Glibert 1949); Paratethys, Austria (Kowalke & Harzhauser 2004), Hungary (Strausz 1966), Poland (Friedberg 1923; Bałuk 1975), Romania (Kowalke & Harzhauser 2004); Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al.* 2013). — **Upper Miocene**: Atlantic, NW France (Calas 1949; Landau *et al.* 2018); Proto-Mediterranean, Italy (Sacco 1895; Venzo & Pelosio 1963). — **Lower Pliocene**: Atlantic of NW France (Van Dingenen *et al.* 2016); central Mediterranean, Italy (Chirli 2006), Tunisia (Fekih 1975). — **Upper Pliocene**: Atlantic, Portugal (Silva 2001); western Mediterranean, Spain (Landau *et al.* 2004); central Mediterranean, Italy (Sacco 1895; Malatesta 1974; Cavallo & Repetto 1992; Sosso & dell'Angelo 2010; Tabanelli *et al.* 2011). — **Lower Pleistocene**: NSB, British Isles (Harmer 1918); Atlantic, Selsoif, NW France (this paper); western Mediterranean of France (Glibert 1962); central Mediterranean, Italy (Cerulli-Irelli 1914; Buccheri 1970); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Upper Pleistocene**: NSB, the Netherlands (Van Regteren Altena *et al.* 1954; Raad *et al.* 2013); western Mediterranean, Balearic Islands (Cuerda Barceló 1987). Today this species occurs in the northeastern Atlantic from Norway southwards to Morocco, entire Mediterranean, from extreme low tide line to 50 m depth, often on sandy bottoms, but also under stones and in weeds (Poppe & Goto 1991).

Remarks

For discussion on fossil populations, see Landau *et al.* (2013: 74) and Van Dingenen *et al.* (2016: 140).

Genus *Onoba* H. Adams & A. Adams, 1852

Onoba semicostata (Montagu, 1803)
(Fig. 8E1-E3)

Turbo semicostatus Montagu, 1803: 326, pl. 21, fig. 5.

Rissoa striata – Wood 1848: 100, pl. 11, fig. 1.

Onoba striata – Harmer 1920: 641, pl. 51, fig. 42.

Cingula (*Cingula*) *semicostata semicostata* – Van Regteren Altena *et al.* 1954: 12, pl. 4, fig. 35b. — A.W. Janssen 1967: 128, pl. 4, fig. 7.

Onoba semicostata – Marquet 1997: 16, pl. 3, fig. 5. — Wienrich 2001: 408, pl. 66, fig. 9. — Raad *et al.* 2013: 52, fig. 19. — Símonarson & Eiríksson *in* Eiríksson & Símonarson 2021: 264, pl. 7.3, fig. 5.

Material and dimensions. — Maximum height 1.9 mm, width 0.8 mm. — RGM.1364989 (27), leg. ACJ; RGM.1365197 (1), leg. ACJ; RGM.1365095 (800+), leg. AWJ.

Species characterisation. — Shell small, rissoiform. Smooth protoconch of 1.5 whorl; five round teleoconch whorls separated by deep suture. Adult sculpture consist of axial ribs marked on the upper whorls and numerous fine crowded spiral cords covering the entire whorl. Ovate aperture; rounded, thickened outer lip.

Distribution. — **Middle Miocene**: NSB, Germany (Janssen 1967; Wienrich 2001). — **Lower Pliocene**: Coralline Crag, England (Wood 1848; Harmer 1920) and Belgium (Marquet 1997). — **Upper Pliocene**: NSB, Belgium (Marquet 1997). — **Pliocene to Lower Pleistocene**: Iceland (Eiriksson & Símonarson 2021). — **Lower Pleistocene**: Atlantic, England (Harmer 1920; Norton 1967); Selsoif, NW France (this paper). — **Pliocene and Pleistocene** (indeterminate): NSB, Netherlands (Van Regteren Altena *et al.* 1954; Raad *et al.* 2013). — **Holocene**: NSB (Strand Petersen 2004). Today this species is present in the Atlantic from Iceland (Warén 1996), Norway (Høisæter 2009), Kola Peninsula, Russia (Golikov & Kussakin 1978; Nekhaev *et al.* 2014), British Isles (Fretter & Graham 1978), Madeira (Ávila *et al.* 2012), southwards to the Alboran Sea in the Mediterranean (Templado & Rolán 1986). Shells collected in the central Mediterranean are probably Late Pleistocene glacial fossils (Amati & Nofroni 2015). Abundant under rocks and among algae, from the intertidal to 1000 m depth.

Remark

Onoba semicostata (Montagu, 1803) is primarily a cooler water species that occurs today in the Mediterranean in the Alboran Sea in upwelling zones.

Genus *Pusillina* Monterosato, 1884

Pusillina aff. ***inconspicua*** (Alder, 1844)
(Fig. 8F1-F3)

Material and dimensions. — Maximum height 1.3 mm, width 0.8 mm. — RGM.1365258 (1), leg. ACJ; RGM.1365125 (5), leg. AWJ; RGM.1365097 (62), leg. AWJ; RGM.1405528 (2), leg. ACJ; RGM.794506 (1), leg. AWJ.

Species characterisation. — Small rather high-spired rissoiform shell. Protoconch not preserved. Five convex teleoconch whorls separated by a deep suture. Sculpture variable mostly smooth but with some specimens consisting of numerous sinuous, opisthocline ribs strengthening towards abapical suture. Base rounded, smooth. Aperture ovate, angled at anal sinus.

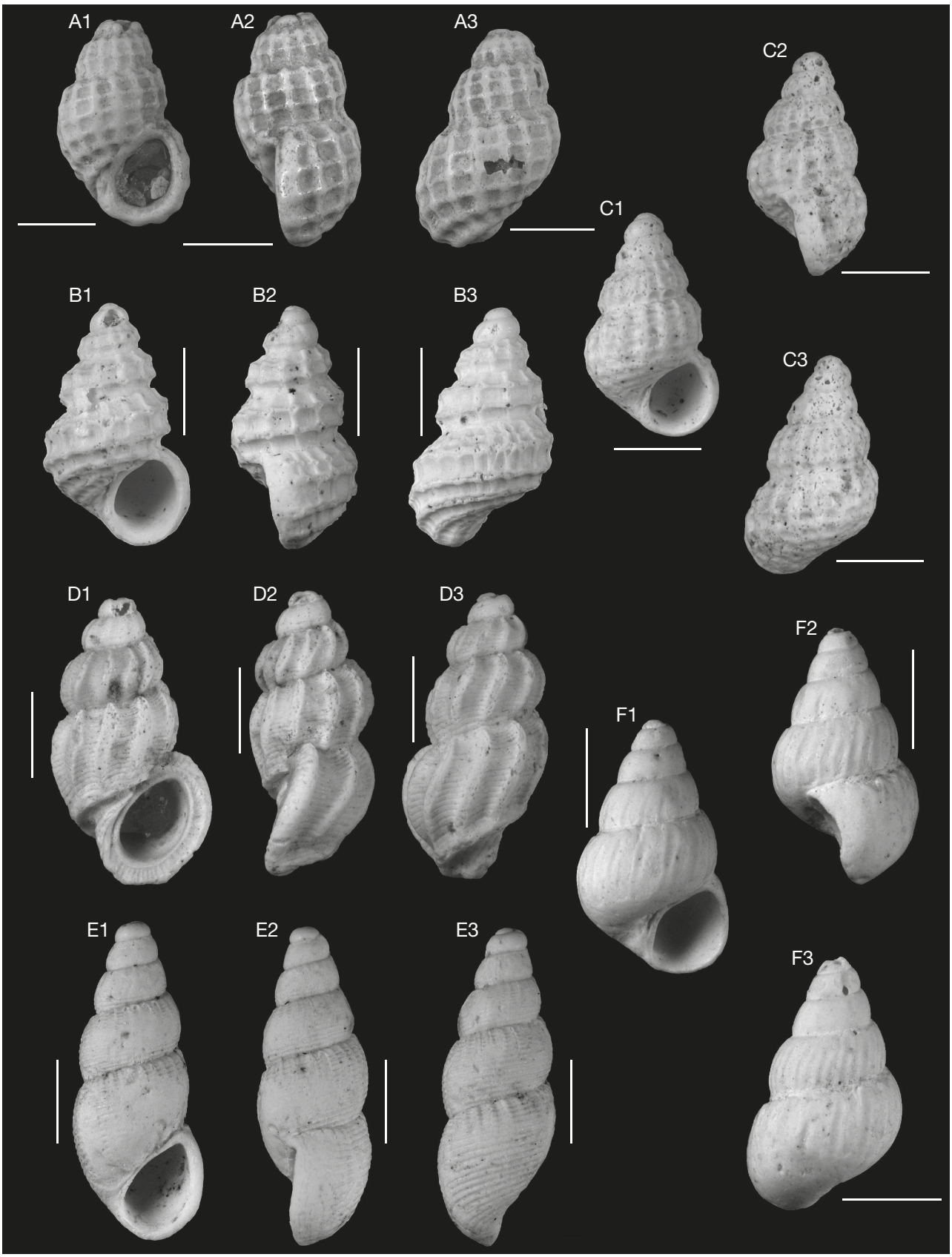

Fig. 8. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Alvania* cf. *cancellata* (da Costa, 1778), RGM.1364986, leg ACJ, H = 2.64 mm; **B**, *Alvania selsoifensis* n. sp. **(holotype)**, RGM.1365286, leg ACJ, H = 1.28 mm; **C**, *Alvania* sp. 1, RGM.1365090, leg AWJ, H = 1.39 mm; **D**, *Manzonia crassa* (Kanmacher, 1798), RGM.1365201, leg ACJ, H = 1.68 mm; **E**, *Onoba semicostata* (Montagu, 1803), RGM.1365197, ACJ, H = 1.9 mm; **F**, *Pusillina* aff. *inconspicua* (Alder, 1844), RGM.1365258, leg ACJ, H = 1.3 mm. Scale bars: A, 1 mm; B-F, 500 µm.

REMARK
The overall characters resemble those of *Pusillina inconspicua* (Alder, 1844) but the specimens studied from Selsoif are consistently taller. Possibly this represents a new species, but the poor preservation and lack of protoconch preclude a formal description.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

Genus *Rissoa* Desmarest, 1814

Rissoa curticostata Wood, 1848
(Fig. 9A1-A3)

Rissoa curticostata Wood, 1848: 102. — Raad *et al.* 2013 : 55, fig. 26.

Rissoa semicostata – Wood 1848: 102, pl. 11, fig. 10 (*non* Montagu, 1803). — Harmer 1920: 634, pl. 51, fig. 16 (not fig. 17).

Rissoa (*Turboella*) *curticostata* – Van Regteren Altena *et al.* 1954: 13, pl. 4, fig. 41. — Marquet 1997: 15, pl. 2, fig. 4.

MATERIAL AND DIMENSIONS. — Maximum height 1.6 mm, width 1.0 mm. — RGM.1364990 (273), leg. ACJ; RGM.1365196 (1), leg. AWJ; RGM.1365092 (66), leg. AWJ; RGM.1364915 (4), leg. WG.

SPECIES CHARACTERISATION. — Small broad rissoiform shell. Three, flattened protoconch whorls. Four teleoconch whorls. Sculpture of around 16 strong, orthocline ribs covering numerous spiral ribs. Base covered by five weak spiral cords. Umbilicus closed; aperture ovate, thick, denticulate outer lip.

DISTRIBUTION. — **Upper Pliocene**: NSB, Red Crag, England (Harmer 1920), Belgium (Marquet 1997). — **Pliocene to Lower Pleistocene** (indeterminate): Netherlands (Van Regteren Altena *et al.* 1954; Raad *et al.* 2013). — **Lower Pleistocene**: NSB, England (Wood 1848; Harmer 1920); Atlantic, Selsoif, NW France (this paper).

REMARKS
Wood (1848: 102) figured this species under the name *Rissoa semicostata* Woodward but stressed that it was not the same species as *R. semicostata* Montagu, 1803 and in his discussion proposed the name *R. curticostata* for the Crag species. Harmer (1920: 634) argued that Woodward's name was available because Montagu's species was a junior subjective synonym of *R. striata* J. Adams, 1797. However, J. Adams's name is an unavailable basionym.

Rissoa parva (da Costa, 1778)
(Fig. 9B1-B3)

Turbo parvus da Costa, 1778: 132, fig. 4.

Rissoa parva – Harmer 1920: 630, pl. 51, figs 11, 12. — Símonarson *et al.* 1998: 31, figs 12d, 15. — Raad *et al.* 2013: 57, figs 31-32.

Rissoa (*Turboella*) *parva* – Van Regteren Altena *et al.* 1954: 13, pl. 4, fig. 42.

Turboella (*Turboella*) *parva* – Cuerda Barceló 1987: 208, pl. 16, fig. 26.

MATERIAL AND DIMENSIONS. — Maximum height 2.4 mm, width 1.1 mm. — RGM.1364991 (89), leg. ACJ; RGM.1365260 (1), leg. ACJ; RGM.1365035 (7), leg. AWJ; RGM.1365094 (60), leg. AWJ.

SPECIES CHARACTERISATION. — Small elongated rissoiform shell. Up to six convex teleoconch whorls. Sculpture only on the three last whorls of around eight axial ribs separated by wider interspace. Base smooth. Aperture pyriform; columella oblique; imperforate.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag, England (Harmer 1920). — **Lower and Upper Pleistocene**: British Isles (Harmer 1920). — **Lower Pleistocene**: Atlantic, Greenland (Símonarson *et al.* 1998), Selsoif, NW France (this paper). — **Upper Pleistocene to Holocene**: Netherlands (Van Regteren Altena *et al.* 1954; Raad *et al.* 2013). — **Holocene**: NSB (Harmer 1920; Strand Petersen 2004). Today, this species is present along the entire European Atlantic coast, Norway (Christie *et al.* 2003), North Sea (Ziegelmeier 1966; de Bruyne 1991), entire Mediterranean and into the Aegean (Öztürk *et al.* 2014) and Black Sea (Öztürk *et al.* 2014).

REMARK
This species shows large morphological variations in the shape, size and whorl profile, as well as ornamentation (from smooth to strongly ribbed on the three last whorls).

Family HYDROBIIDAE Stimpson, 1865
Genus *Ecrobia* W. Stimpson, 1865

Ecrobia cf. ***ventrosa*** (Montagu, 1803)
(Fig. 9C1-C3)

cf. *Turbo ventrosus* Montagu, 1803: 317, pl. 12, fig. 13.

cf. ?*Peringia ulvae* – Harmer 1922: 873, pl. 65, fig. 27.

cf. *Hydrobia ventrosa* – Fretter & Graham 1978: 125, fig. 114.

cf. *Ecrobia ventrosa* – Hoeksema & Raad 2015: 25, fig. 2.

cf. *Ecrobia* cf. *ventrosa* – Símonarson & Eiríksson *in* Eiriksson & Símonarson 2021: 256, pl. 7.2, fig. 8.

MATERIAL AND DIMENSIONS. — Maximum height 1.5 mm, width 0.8 mm. — RGM.1365261 (1), leg. ACJ.

SPECIES CHARACTERISATION. — Thin shelled hydrobiid with marked convex whorl profile and relatively deep suture; aperture rounded. The specimen at hand suffers from corrosion of the outer shell layer, hence its uncertain attribution.

DISTRIBUTION. — **Lower Pliocene**: Iceland (Símonarson *et al.* 2021). — **Upper Pliocene**: NSB, Red Crag, England (Hoeksema & Raad 2015). — **Lower Pleistocene**: Maassluis Formation, Netherlands (RGM collection); Atlantic, Selsoif, NW France (this paper). — **Pleistocene and Holocene** (indeterminate): NSB, Netherlands (Hoeksema & Raad 2015). Today it occurs along the European coasts from Norway and the Baltic to the Mediterranean and Black Sea (Fretter & Graham 1978).

Genus *Peringia* Paladilhe, 1874

Peringia ulvae (Pennant, 1777)
(Fig. 9D1-D3)

Turbo ulvae Pennant, 1777: 132, pl. 86, fig. 120.

Paludestrina ulvae – Wood 1848: 71, pl. 4, fig. 23.

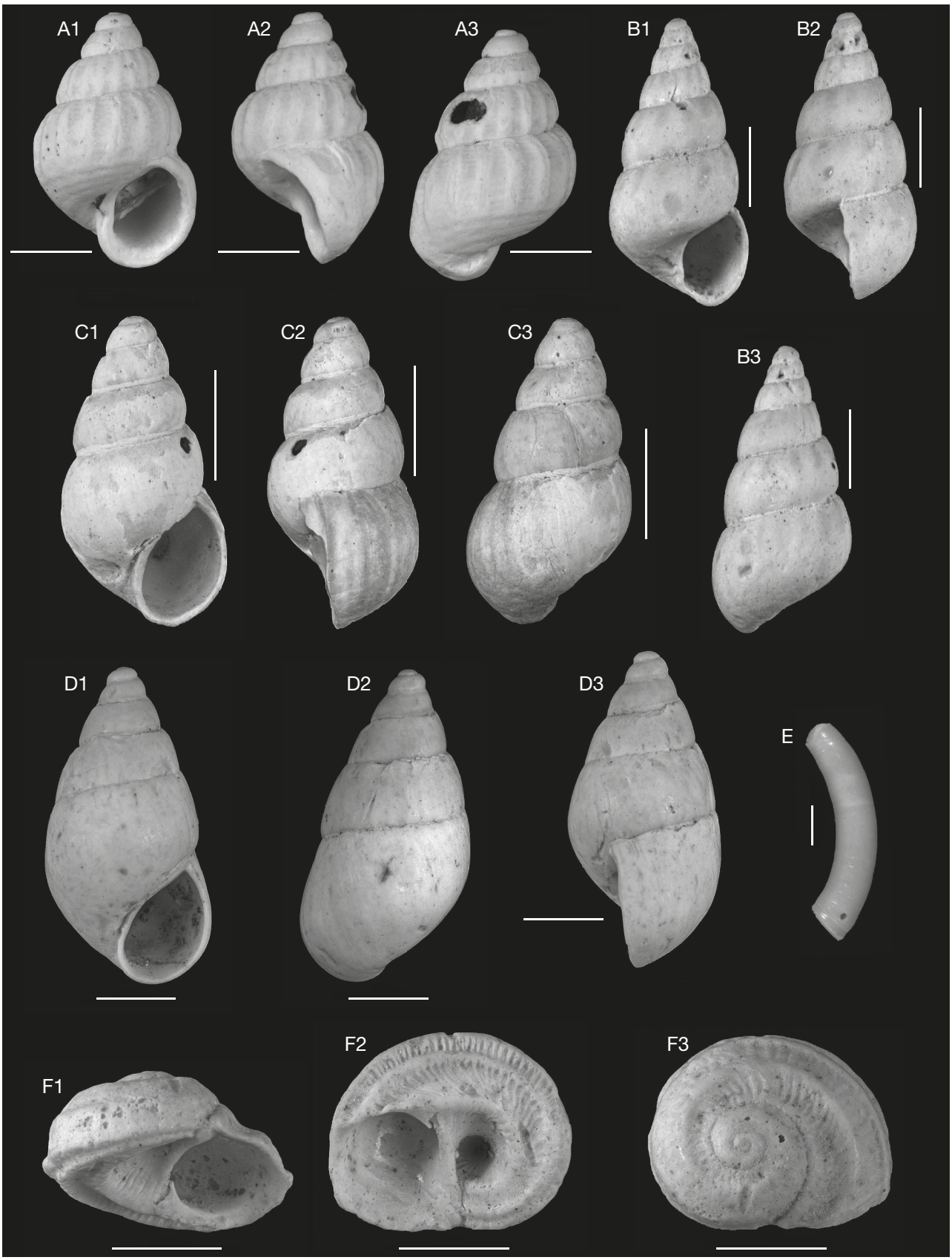

Fig. 9. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Rissoa curticostata* Wood, 1848 , RGM.1365196, leg AWJ, H = 1.58 mm; **B**, *Rissoa parva* (da Costa, 1778), RGM.1365260, leg ACJ, H = 1.83 mm; **C**, *Ecrobia* cf. *ventrosa* (Montagu, 1803), RGM.1365261, leg ACJ, H = 1.4 mm; **D**, *Peringia ulvae* (Pennant, 1777), RGM.1365198, leg ACJ, H = 2 mm; **E**, *Caecum glabrum* (Montagu, 1803), RGM.1365191, leg AWJ, H = 1 mm; **F**, *Tornus subcarinatus* (Montagu, 1803), RGM.1405531, leg ACJ, H = 2.26 mm. Scale bars: A-D, 500 µm; E, 200 µm; F, 1 mm.

Peringia ulvae – Harmer 1925: 873, pl. 65, fig. 27. — Fretter & Graham 1978: 122, fig. 113. — Hoeksema & Raad 2015: 25, fig. 1.

Hydrobia ulvae – Van Regteren Altena *et al.* 1954: 12, pl. 3, fig. 32. — Símonarson & Eiríksson *in* Eiriksson & Símonarson 2021: 255, pl. 7.2, fig. 7.

MATERIAL AND DIMENSIONS. — Maximum height 2.1 mm, width 1.1 mm. — RGM.1364993 (10), leg. ACJ; RGM.1365198 (1), leg. ACJ; RGM.1365202 (200+), leg. AWJ.

SPECIES CHARACTERISATION. — Smooth, solid, fusiform shell with regularly conical spire. Five flat teleoconch whorls separated by shallow suture. High base; pyriform aperture.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848), Iceland (Símonarson *et al.* 2021). — **Upper Pliocene**: NSB, Red Crag, England (Harmer 1925; Norton 1967). — **Lower Pleistocene**: Atlantic, England (Harmer 1925), Selsoif, NW France (this paper). — **Upper Pleistocene to Holocene**: NSB, England (Harmer 1925), Netherlands (Van Regteren Altena *et al.* 1954; Hoeksema & Raad 2015). Today, this species occurs in the eastern Atlantic from northern Norway (Bank & Neubert 2020), along the coast of Europe to Senegal (Fretter & Graham 1978), it enters the Mediterranean and extends into the Aegean Sea (Öztürk *et al.* 2014) and Baltic Sea (Kedra 2010).

Family CAECIDAE Gray, 1850
Genus *Caecum* J. Fleming, 1813

Caecum glabrum (Montagu, 1803)
(Fig. 9E)

Dentalium glabrum Montagu, 1803: 197.

Caecum glabrum – Van Dingenen *et al.* 2016: pl. 11, fig. 5.

For more, see synonymy list in Van Dingenen *et al.* (2016).

MATERIAL AND DIMENSIONS. — Maximum length 1.1 mm. — RGM.1365099 (52), leg. AWJ; RGM.1365191 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Small, elongate, smooth shell. Dome-shaped apical septum.

DISTRIBUTION. — **Middle Miocene**: Loire Basin, France (Glibert 1949). — **Lower Pliocene**: Atlantic, NW France (Van Dingenen *et al.* 2016); NSB, Coralline Crag, England (Wood 1848; Harmer 1923). — **Upper Pliocene**: NSB, Red Crag, England (Harmer 1923); Oorderen Sands, Belgium (Marquet 1997). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper); central Mediterranean, Italy (Cerulli-Irelli 1912). — **Pleistocene** (indeterminate): Atlantic, British Isles (Harmer 1923); NSB, The Netherlands (Van Regteren Altena *et al.* 1955). — **Holocene**: NSB (Strand Petersen 2004). Today this species occurs at the Atlantic coasts of Europe from British Isles to the Bay of Biscay (Fretter & Graham 1978). Mediterranean records are not *C. glabrum*, but *C. subannulatum* de Folin, 1870 or *C. auriculatum* de Folin, 1868; Van Aartsen 1977: 11).

Family TORNIDAE Sacco, 1896
Genus *Tornus* W. Turton & Kingston, 1830

Tornus subcarinatus (Montagu, 1803)
(Fig. 9F1-F3)

Helix subcarinata Montagu, 1803: 438, pl. 7, fig. 9.

Tornus subcarinatus – Van Dingenen *et al.* 2016: 149, pl. 11, fig. 9, pl. 12, fig. 3. — Landau *et al.* 2018: 303, pl. 131, fig. 1.

For more, see synonymy list in Van Dingenen *et al.* (2016) and Landau *et al.* (2018).

MATERIAL AND DIMENSIONS. — Maximum height 0.8 mm, width 1.2 mm. — RGM.1364994 (19), leg. ACJ; RGM.1365009 (93), leg. AWJ; RGM.1365299 (1), leg. AWJ; RGM.1405531 (1), leg. ACJ.

SPECIES CHARACTERISATION. — Small, depressed, subcircular shell. Protoconch of 2.5 smooth whorls; three teleoconch whorls with carinate shoulder, mid-whorl and peribasal cords, sinuous ribs on dorsum and venter; base flattened, bearing two further elevated cords, the medial periumbilical cord delimiting wide, deep umbilicus with ribs extending within; aperture wide, rounded, strongly oblique in profile.

DISTRIBUTION. — **Middle Miocene**: Atlantic, Loire Basin, France (Glibert 1949). — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2018). — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1923; Atlantic, NW France (Van Dingenen *et al.* 2016); central Mediterranean, Italy (Chirli 2006). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1923). — **Upper Pliocene-Pleistocene**: Atlantic, NW France (Cossmann 1918; Brébion 1964). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). — **Upper Pleistocene**: NSB, The Netherlands (Van Regteren Altena *et al.* 1954); Atlantic, British Isles (Harmer 1923). Today this species is present in the Atlantic coasts of Europe from British Isles to Tarifa (Fretter & Graham 1978).

REMARK

Van Dingenen *et al.* (2016:149) highlighted the problem with the *Tornus subcarinatus* (Montagu, 1803) species concept as accepted at present, in which specimens with paucispiral and multispiral protoconchs are considered conspecific. They concluded that there were two species: an Atlantic species *T. subcarinatus*, with a multispiral protoconch of about 2.1-2.25 whorls, with a small nucleus (counting including first half whorl: Rolán & Rubio 2002: figs 5, 6; Van Aartsen *et al.* 1998: fig. 7), and a Mediterranean species that is at present unnamed with a paucispiral protoconch of 1.25-1.4 whorls, with a larger nucleus (Rolán & Rubio 2002: figs 13, 14; Van Aartsen *et al.* 1998: fig. 7). With a protoconch of 2.5 whorls the specimens from Selsoif are typical of the Atlantic species *T. subcarinatus*.

Family CALYPTRAEIDAE Lamarck, 1809
Genus *Calyptraea* Lamarck, 1799

Calyptraea chinensis *s.l.* (Linnaeus, 1758)
(Fig. 10A)

Patella chinensis Linnaeus, 1758: 1257.

Calyptraea chinensis – Landau *et al.* 2013: 95, pl. 9, fig. 7, pl. 61, fig. 6. — Chirli & Forli 2017: 52, fig. 15a. — Landau *et al.* 2018: 316, pl. 147, fig. 1. — Sacchetti *et al.* 2023: 51, pl. 3, fig. F.

Calyptraea cf. *chinensis* – Símonarson & Eiríksson *in* Eiríksson & Símonarson 2021: 267, pl. 7.4, fig. 1.

For more, see synonymy list in Landau *et al.* (2013, 2018).

MATERIAL AND DIMENSIONS. — Maximum height 4.8 mm, diameter 11.4 mm. — RGM.1364916 (2), leg. WG; RGM.1364995 (127), leg. ACJ; RGM.1365194 (1), leg. ACJ; RGM.1365100 (2), leg. AWJ; RGM.1405530 (18), leg. WG.

SPECIES CHARACTERISATION. — Relatively large, smooth, strongly depressed conical shell. Apex subcentral, consisting of only protoconch whorl. Aperture entire venter, septum with sinuous border extending from mid-shell to outer edge.

DISTRIBUTION. — **Lower Miocene**: Paratethys, Austria (Schaffer 1912); Proto-Mediterranean: Italy (Sacco 1896b). — **Lower-Middle Miocene**: NSB: Belgium (Glibert 1952), Germany (Anderson 1964), the Netherlands (Janssen 1984). — **Middle Miocene**: Atlantic, Aquitaine Basin, France (Cossmann & Peyrot 1919), Loire Basin, France (Glibert 1949); Paratethys, Poland (Friedberg 1923; Bałuk 1975), Austria (Hörnes 1856; Schultz 1998), Bulgaria (Kojumdgieva & Strachimirov 1960), Hungary (Strausz 1966), Ukraine (Zelinskaya *et al.* 1968), eastern Paratethys (Iljina 1993); Proto-Mediterranean, NE Spain (Solsona 1998), Karaman Basin, Turkey (Fischer 1866; Landau *et al.* 2013). — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2020a), Portugal (Glibert 1963), SW Spain (Cárdenas *et al.* 2019); Proto-Mediterranean, Italy (Sacco 1896b; Venzo & Pelosio 1963; Boschele *et al.* 2021). — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1921), Belgium (Glibert 1958; Marquet 1998), Iceland (Eiríksson & Símonarson 2021), Atlantic, Santa Maria Island, Azores (Sacchetti *et al.* 2023); NW France (Van Dingenen *et al.* 2016), SW Spain (González-Delgado 1988; Landau *et al.* 2011; Brunetti 2022), Morocco (Lecointre 1952); NE Spain (Martinell 1979), Roussillon Basin, France (Fontannes 1879); central Mediterranean, Italy (Sacco 1896b; Palla 1967; Caprotti 1974; Brunetti & Cresti 2018), Tunisia (Fekih 1975). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1921), Belgium (Glibert 1958; Marquet 1998); Atlantic, Pombal Basin, Portugal (Silva 2001), Morocco (Lecointre 1952); western Mediterranean, S. Spain (Landau *et al.* 2004); central Mediterranean, Italy (Malatesta 1974; Chirli 1988; Cavallo & Repetto 1992). — **Upper Pliocene-Pleistocene**: NW France (Brébion 1964). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). — **Pleistocene**: Atlantic, British Isles (Glibert 1963), Morocco (Lecointre 1952); central Mediterranean, Italy (Cerulli-Irelli 1912; Taviani *et al.* 1998; Brunetti & Vecchi 2015; Chirli & Forli 2017), Sicily (Glibert 1963); eastern Mediterranean (Chirli & Linse 2011). Today this species occurs in the NE Atlantic, British Isles to Zaire, Madeira and Canaries, Mediterranean and Black Sea (Poppe & Goto 1991).

REMARKS

As discussed by Landau *et al.* (2004, 2013, 2020a), this species has an extremely variable shell in both profile profile; tall conical to almost flat, and sculpture; smooth or bearing small spines. The size and position of the protoconch varies between populations and it is possible that it represents a species complex rather than a single taxon (B. Landau & R. Pouwer pers. obs.).

Genus *Crepidula* Lamarck, 1799

Crepidula gibbosa Defrance, 1818
(Fig. 10B1, B2)

Crepidula gibbosa Defrance, 1818: 397. — Chirli & Forli 2017: 53, fig. 15c. — Landau *et al.* 2018: 317, pl. 148, fig. 1.

MATERIAL AND DIMENSIONS. — Maximum height 3.5 mm, diameter 12.3 mm. — RGM.1364917 (1), leg. WG; RGM.1364996 (2), leg. ACJ; RGM.1365101 (62), leg. AWJ; RGM.1365185 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Thick, low, smooth, convex shell. Aperture ovate. Concave, shallow septum covering almost 2/3 of the aperture.

DISTRIBUTION. — **Middle Miocene**: Atlantic, Aquitaine Basin, France (Cossmann & Peyrot 1919), Loire Basin, France (Glibert 1949); Paratethys, Austria (Hörnes 1856), Poland (Bałuk 1975), Hungary (Strausz 1966); Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al.* 2013). — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2018); Proto-Mediterranean, Italy (Sacco 1896b). — **Lower Pliocene**: Atlantic, NW France (Van Dingenen *et al.* 2016); SW Spain (González-Delgado 1988; Landau *et al.* 2011). — **Upper Pliocene**: Atlantic, Morocco (Lecointre 1952); western Mediterranean, S Spain (Landau *et al.* 2004); central Mediterranean, Italy (Chirli 1988; Cavallo & Repetto 1992). — **Upper Pliocene-Pleistocene**: NW France (Glibert 1963). — **Lower Pleistocene**, Atlantic, Selsoif, NW France (this paper); central Mediterranean (Chirli & Forli 2017). Today, this species occurs in the Mediterranean Sea, below low tide line, often attached to other molluscs (Poppe & Goto 1991).

REMARKS

Our assignment of *Crepidula* to *C. gibbosa* does not conform to its treatment in WoRMS and follows arguments provided in Landau *et al.* (2004: 74). In our opinion the taxonomy of European *Crepidula* is not resolved and requires in-depth studies that are beyond the scope of this paper.

Family CAPULIDAE J. Fleming, 1822
Genus *Capulus* Montfort, 1810

Capulus ungaricus (Linnaeus, 1758)
(Fig. 10C1, C2)

Patella ungarica Linnaeus, 1758: 782.

Capulus (*Capulus*) *hungaricus* [*sic*] – Domènech & Martinell 1982: 50, fig. 15.

Capulus ungaricus – Landau *et al.* 2011: 14, pl. 4, fig. 7. — Chirli & Linse 2011: 63, pl. 14, fig. 5. — Van Dingenen *et al.* 2016: 123, pl. 4, fig. 4. — Chirli & Forli 2017: 54, fig. 15d.

For more, see synonymy list in Landau *et al.* (2011) and Van Dingenen *et al.* (2016).

MATERIAL AND DIMENSIONS. — Maximum height 25.2 mm, width 11.9 mm (incomplete). — RGM.1364918 (4), leg. WG; RGM.1364997 (18), leg. ACJ; RGM.1365102 (57), leg. AWJ; RGM.1365200 (1), leg. AWJ; RGM.1364998 (1), leg. ACJ.

SPECIES CHARACTERISATION. — Medium sized capuliform shell with ovate aperture, convex elevated in profile with coiled, recurved apex displaced slightly to the right overhanging posterior margin. Protoconch of just under two smooth whorls with small nucleus, rapidly expanding last whorl sculpture of fine axial ribs. U-shaped internal muscle scar.

DISTRIBUTION. — **Middle Miocene**: Paratethys, Poland (Bałuk 1975), Vienna (Hörnes 1856); Proto-Mediterranean, Italy (Sacco 1896b); Atlantic, Aquitaine Basin, France (Cossmann & Peyrot 1919), Loire Basin, France (Glibert 1949). — **Upper Miocene**: Proto-Mediterranean, Italy (Sacco 1896b). — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1916), Kattendijk Formation, Belgium (Glibert 1958; Marquet 1998); Atlantic, NW France (Van Dingenen *et al.* 2016), SW Spain (Landau *et al.* 2011);

central Mediterranean, Italy (Chirli 2008). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1916), Oorderen Sands, Belgium (Glibert 1958; Marquet 1998); Atlantic, Portugal (Zbyszewski 1959; Silva 2001); western Mediterranean, S Spain (Landau *et al.* 2004), France (Chirli & Richard 2008); central Mediterranean, Italy (Sacco 1896b; Cavallo & Repetto 1992). — **Upper Pliocene-Pleistocene**: NW France (Brébion 1964). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper); central Mediterranean, Italy (Cerulli-Irelli 1914; Brambilla & Galli 1988; Di Geronimo & La Perna 1997; Chirli & Forli 2017); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Upper Pleistocene**: western Mediterranean, Spain (Domènech & Martinell 1982). Today this species occurs in the Atlantic from Iceland to West Africa and North America to Florida, Mediterranean. It is not present in the North Sea (Fretter & Graham 1981). It inhabits in the sublittoral zone to 850 m depth, attached to stones and shells (Poppe & Goto 1991)

Remarks

The Selsoif specimens have a protoconch of about two whorls, similar to that illustrated by Fretter & Graham (1981: fig. 225). For further discussion see Van Dingenen *et al.* (2016).

Family Eulimidae Philippi, 1853

Genus *Aclis* Lovén, 1846

Aclis minor (Brown, 1827)
(Fig. 10D1-D3)

Turritella minor Brown, 1827: pl. 57, figs 57-58.

Aclis minor – Van Regteren Altena *et al.* 1955: 33, fig. 77. — Menkhorst & Wesselingh 2018: 42, figs 13, 14. — Landau & Mulder 2022: 161, figs 10a-c.

For more, see synonymy list in Landau & Mulder (2022).

Material and dimensions. — Maximum height 1.8 mm (incomplete), width 0.6 mm. — RGM.1365077 (11), leg. AWJ; RGM.1365257 (1), leg. AWJ.

Species characterisation. — Small, turriform shell with narrow apical angle. Protoconch absent in all specimens. About six convex teleoconch whorls separated by narrowly impressed suture. Three spiral cords on early whorls, a fourth one appearing above the suture on later whorls; aperture ovate.

Distribution. — **Upper Miocene**: NSB, Denmark (Rasmussen 1968; Schnetler 2005), Germany (Moths 1989). — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1842, 1848; Harmer 1925); central Mediterranean, Italy (Chirli 2009; Brunetti & Cresti 2018). — **Upper Pliocene**: western Mediterranean, S Spain (Landau *et al.* 2006; Landau & Mulder 2022). — **Lower Pleistocene**: NSB, England, Ireland (Harmer 1925); Atlantic, Selsoif, NW France (this paper); central Mediterranean, Italy (Cerulli-Irelli 1914); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Pleistocene** (indeterminate): NSB, Netherlands (Van Regteren Altena *et al.* 1955; Menkhorst & Wesselingh 2018). — **Holocene**: NSB (Strand Petersen 2004). Today this species is present in the Atlantic, from the British Isles (Guiry & Guiry 2011) to Madeira (Segers *et al.* 2009) and in the Mediterranean Sea from Spain (Peñas *et al.* 2009) to the Aegean Sea (Öztürk *et al.* 2014), at depths of 2-250 m, on calcareous algae, sandy, or muddy bottoms (Albanesi *et al.* 1981).

Aclis walleri Jeffreys, 1867
(Fig. 10E1-E3)

Aclis walleri Jeffreys, 1867: 105. — Harmer 1925: 869, pl. 65, fig. 25. — Van Regteren Altena *et al.* 1955: 21, fig. 78. — Menkhorst & Wesselingh 2018: 43, fig. 15.

Alvania ascaris – Wood 1848: 99, pl. 12, fig. 11 [*non Aclis ascaris* (Turton, 1819)].

Material and dimensions. — Maximum height 2.4 mm, width 1.1 mm. — RGM.1365001 (1), leg. ACJ.

Species characterisation. — Small, smooth, turriform shell with relatively broad apical angle. Protoconch missing. Up to six low, convex teleoconch whorls separated by deep suture; smooth, somewhat flattened base; aperture incomplete.

Distribution. — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1925). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). — **Upper Pleistocene**: NSB, Netherlands (Van Regteren Altena *et al.* 1955; Menkhorst & Wesselingh 2018). Today this species occurs from Iceland to Spain (Bouchet & Warén 1986), Azores (Hoffman & Freiwald 2020).

Genus *Melanella* Bowdich, 1822

Melanella alba (da Costa, 1778)
(Fig. 10F1-F3)

Strombiformis albus da Costa, 1778: 116.

Melanella alba – Landau *et al.* 2018: 313, pl. 143, figs 1-3. — Menkhorst & Wesselingh 2018: 38, fig. 1.

For more, see synonymy list in Landau *et al.* (2018).

Material and dimensions. — Maximum height 11.7 mm, width 3.7 mm. — RGM.1364919 (112), leg. WG; RGM.1365000 (67), leg. ACJ; RGM.1365103 (*c.* 50), leg. AWJ; RGM.1365318 (1), leg. AWJ.

Species characterisation. — Relatively large, slender, elongate shell, slightly curved with smooth polished surface without magnification, finely reticulated sculpture under magnification. Nine flat teleoconch whorls separated by a shallow suture. Base flat; columellar lip short, thickened, almost straight to inclined; aperture pyriform.

Distribution. — **Middle Miocene**: NSB, Netherlands (Janssen 1984). — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2018). — **Lower Pliocene**: Atlantic, NW France (Van Dingenen *et al.* 2016); NSB, Coralline Crag, England (Harmer 1920), Kattendijk Formation, Belgium (Marquet 1998). — **Upper Pliocene**: NSB, Red Crag, England (Harmer 1920), Atlantic, Portugal (Landau *et al.* 2006); western Mediterranean, S Spain (Landau *et al.* 2006). — **Pliocene** (unspecified): NSB, the Netherlands (Van Regteren Altena *et al.* 1955; Menkhorst & Wesselingh 2018); Atlantic, St Erth, England (Harmer 1920), Selsoif NW France (this paper). — **Holocene:** NSB (Strand Petersen 2004). Today this species is present in the Atlantic, from Norway and rare into the Mediterranean (Fretter & Graham 1982).

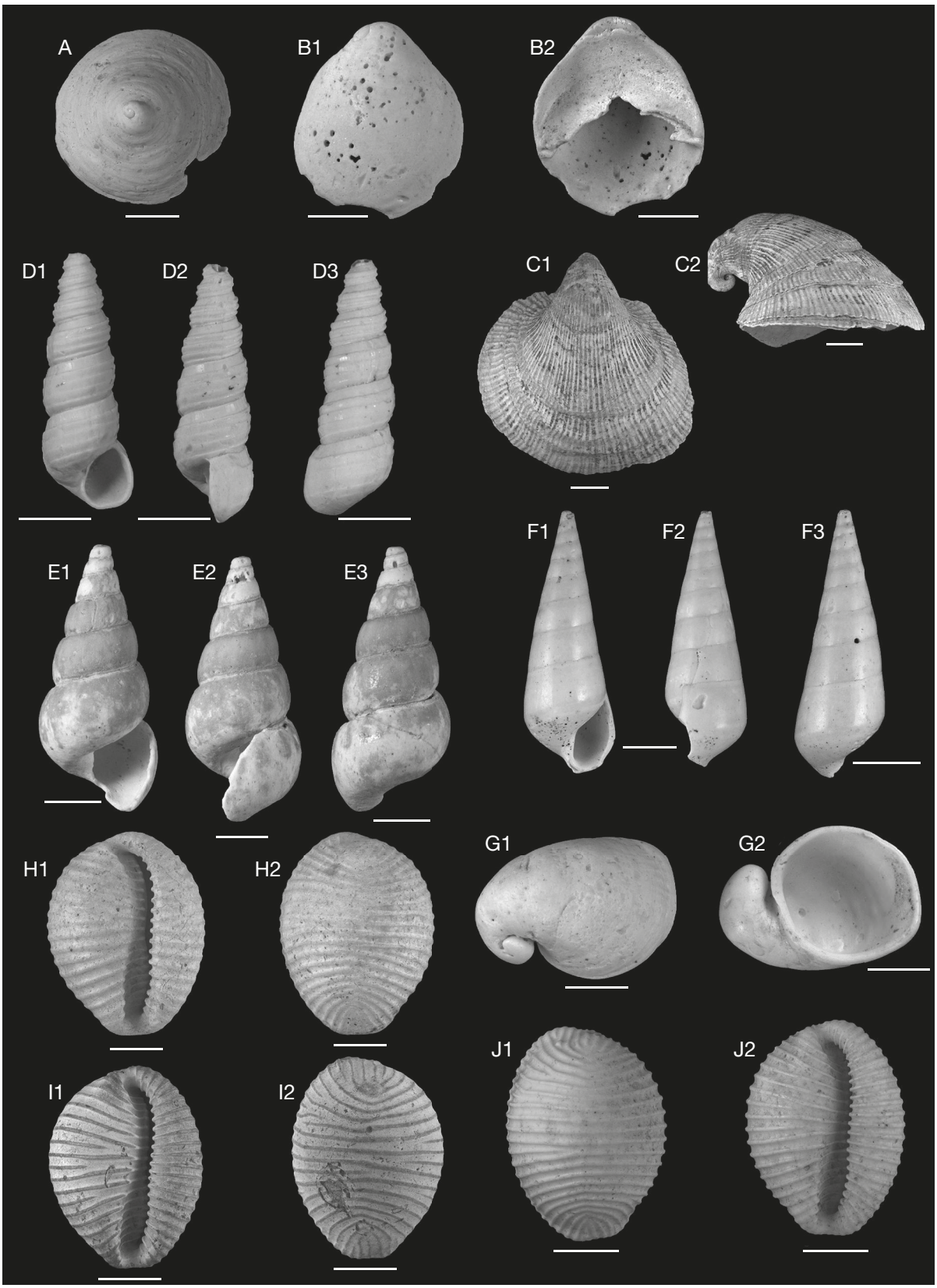

Fig. 10. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Calyptraea chinensis s.l.* (Linnaeus, 1758), RGM.1365194, leg ACJ, H = 3.2 mm; **B**, *Crepidula gibbosa* Defrance, 1818, RGM.1365185, leg AWJ, H = 3.3 mm; **C**, *Capulus ungaricus* (Linnaeus, 1758), RGM.1365200, leg AWJ, H = 12 mm; **D**, *Aclis minor* (Brown, 1827), RGM.1365257, leg AWJ, H = 1.79 mm; **E**, *Aclis walleri* Jeffreys, 1867, RGM.1365001, leg ACJ, H = 2.33 mm; **F**, *Melanella alba* (da Costa, 1778), RGM.1365318, leg AWJ, H = 5.96 mm; **G**, *Velutina* aff. *velutina* (Müller, 1776), RGM.1365186, leg AWJ, H = 3.27 mm; **H**, *Trivia coccinelloides* (J. de C. Sowerby, 1822), RGM.1365272, leg WG, H = 7.7 mm; **I**, *Trivia coccinelloides* (J. de C. Sowerby, 1822), RGM.1365271, leg WG, H = 6.38 mm; **J**, *Trivia coccinelloides* (J. de C. Sowerby, 1822), RGM.1365203, leg WG, H = 6.7 mm. Scale bars: A, B, G, 1 mm; C, F, H-J, 2 mm; D, E, 500 µm.

Family VELUTINIDAE Gray, 1840
Genus *Velutina* J. Fleming, 1820

Velutina* aff. *velutina (Müller, 1776)
(Fig. 10G1-G3)

aff. *Bulla velutina* Müller, 1776: 242.

aff. *Velutina laevigata* – Wood 1848: 152, pl. 19, figs 8 a-b. — Harmer 1923: 760, pl. 60, fig. 26.

aff. *Velutina velutina* – Van Regteren Altena *et al.* 1965: 26, pl. 10 fig. 99. — Símonarson & Eiríksson *in* Eiríksson & Símonarson 2021: 269, pl. 7.4, fig. 2. — Van Nieulande *et al.* 2022: 16, fig. 1.

MATERIAL AND DIMENSIONS. — Maximum height 3.5 mm, width 4.5 mm. — RGM.1364920 (1), leg. WG; RGM.1365002 (4), leg. ACJ; RGM.1365186 (1), leg. AWJ; RGM.1365104 (93), leg. AWJ; RGM.1365206 (2), leg. AWJ.

SPECIES CHARACTERISATION. — Capuliform shell with paucispiral protoconch and rapidly expanding last whorl resulting in large circular aperture, disjunct last whorl.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper).

REMARKS

The specimens from Selsoif differ from *Velutina velutina* (Müller, 1776), in being thicker shelled and in having a narrower last whorl that is disjunct. The aperture is large and ovate, with the margin erect on the medial side, reminiscent of that seen in a *Capulus* species.

Disjunct last whorls occur in numerous gastropod groups as a variable feature, often associated with gerontic individuals. This does not seem to be the case with the Selsoif species, as most of the specimens are juvenile and both the disjunct whorl and the thicker shell are constant characters.

Wood (1848) described *Velutina virgata* from the Lower Pliocene Coralline Crag of England, said to differ from *V. velutina* in the form of the less ovate aperture and the less curved outer lip making the spire slightly more elevated. We have not seen this species, but the specimen illustrated by Wood (1848: pl. 29, fig. 1) and Harmer (1923: pl. 60, fig. 27) has quite a different profile and shape of the aperture from the Selsoif specimens. *Vetulina plicatilis* (Müller, 1776), another Atlantic circumboreal species extending in Europe southwards to northern Spain differs in having a much larger expanded aperture.

We are unsure if these Selsoif specimens represent an unknown *Vetulina* species. However, due to the unusually small size of the specimens for the genus and worn preservation, we hesitate to erect a new species.

Family TRIVIIDAE Troschel, 1863
Genus *Trivia* Gray, 1837

Trivia coccinelloides (J. de C. Sowerby, 1822)
(Fig. 10H1, H2, I1, I2, J1, J2)

Cypraea coccinelloides J. Sowerby, 1822: 107, pl. 378, fig. 1.

Trivia coccinelloides – Fehse & Landau 2003: 87, fig. 1/1a-c. — Landau *et al.* 2011: 17, pl. 6, fig. 8. — Van Dingenen *et al.* 2016: 123, pl. 4, fig. 5. — Van Nieulande *et al.* 2022: 20, figs 18-22.

For more, see synonymy list in Fehse & Landau (2003).

MATERIAL AND DIMENSIONS. — Maximum height 12.4 mm, width 9.1 mm. — RGM.1365271 (1), leg. WG; RGM.1365272 (1), leg. WG; RGM.1365003 (42), leg. ACJ; RGM.1365322 (17), leg. AWJ; RGM.1365203 (1), leg. WG; RGM.1365320 (4), leg. WG; RGM.1365274 (8), leg. ACJ; RGM.1365275 (3), leg. AWJ; RGM.1365321 (3), leg. AWJ; RGM.1365057 (20), leg. WG; RGM.1365323 (18), leg. AWJ; RGM.1365105 (239), leg. AWJ.

SPECIES CHARACTERISATION. — Aperture well to the right of the ventral mid-line, the fossula not delimited from the columella and the inner border of the columella; fossula not covered by outer lip when seen in ventral view.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1920); Atlantic, NW France (Van Dingenen *et al.* 2016); S Spain (Landau *et al.* 2011). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1920), Lillo Formation, Belgium (Glibert 1958; Marquet 1998); Atlantic, Portugal (Silva 2001); western Mediterranean, Spain (Fehse & Landau 2003); central Mediterranean, Italy (Sacco 1894). — **Upper Pliocene-Pleistocene**: NW France (Brébion 1964). — **Lower Pleistocene**: Atlantic, Selsoif, France (this paper).

REMARKS

The species varies slightly in the development of the dorsal hump, and in the number of dorsal ribs and labial teeth. This same variability is seen in the Selsoif material, where this species is abundant. We consider this to be the only *Trivia* species present in the Selsoif assemblage. For further discussion see Van Dingenen *et al.* (2016: 123) and Van Nieulande *et al.* (2022: 20).

Family ERATOIDAE Gill, 1871
Genus *Erato* Risso, 1826

Erato exmaugeriae Sacco, 1894
(Fig. 11A1-A3)

Erato exmaugeriae Sacco, 1894: 60. — Fehse & Landau 2002: 97, figs 26, 28. — Van Nieulande *et al.* 2022: 22, figs 33-34.

Erato maugeriae – Wood 1848: 19, pl. 2, fig. 11 (*non* J.E Gray, 1832). — Harmer 1920: 512, pl. 45, fig. 2.

Erata (*Eratopsis*) *exmaugeriae* – Beets 1946: 65, pl. 3, figs 21-23.

Erato pernana – Van Regteren Altena *et al.* 1956: 85, pl. 10, fig. 100.

Erata (*Eratopsis*) *pernana exmaugeriae* – Glibert 1958: 26, pl. 2, fig. 24.

Erata (*Eratopsis*) *pernana* – Marquet 1997: 75, pl. 2, fig. 9.

MATERIAL AND DIMENSIONS. — Maximum height 5.2 mm, width 3.6 mm. — RGM.1365106 (2), leg. AWJ; RGM.1365287 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Shell small, squat, smooth, relatively low spire, outer lip thickened, finely denticulate at inner edge, single terminal fold, two strong anterior columellar denticles, three or four posterior columellar denticles weakening adapically.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1920). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1920), Belgium (Glibert 1958; Marquet 1997). — P**liocene-Lower Pleistocene** (indeterminate): NSB, Netherlands (Beets 1946; Van Regteren Altena *et al.* 1956; Van Nieulande *et al.* 2022). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

REMARKS

The specimens from Selsoif agree with those illustrated by Van Nieulande *et al.* (2022: figs 33-34).

Family NATICIDAE Guilding, 1834
Genus *Cryptonatica* Dall, 1892

Cryptonatica sp.
(Fig. 11B1-B3)

MATERIAL AND DIMENSIONS. — Maximum height 9.2 mm, width 8.3 mm. — RGM.1364921 (188), leg. WG; RGM.1365004 (200+), leg. ACJ; RGM.1365218 (1), leg. AWJ; RGM.1310339 (1), leg. AWJ; RGM.1365107 (500+), leg. AWJ; RGM.1365265 (1 damaged operculum), leg. AWJ.

SPECIES CHARACTERISATION. — Globular smooth shell. Three squared teleoconch whorls separated by deep suture. Base covered by a large collumelar lip. Large umbilicus, closed by a thick columellar callus.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

REMARKS

At present, two closely similar extant *Cryptonatica* species are recognised; *Cryptonatica affinis*, a cold water species present in shallow water of the Arctic Sea, Greenland, Island and Norway, but occurring rarely further southwards into the Bay of Biscay at greater depths, and therefore in colder waters, and *C. operculata* (Jeffreys, 1885), a warmer water species extending from the Bay of Biscay to North Africa, where it occurs in shallow water settings. The species were differentiated by Bouchet & Warén (1993) based on protoconch diameter. The diameter of the first half whorl of the warm water *C. operculata* is larger (0.6-0.7 mm) than that of the cold water *C. affinis* (below 0.5 mm). Specimens from Selsoif are intermediate, having a first half whorl diameter of 0.56 mm (based on 8 specimens).

Material from the Naturalis collections was re-examined (RP). Five specimens from northern Norway and Nova Zembla gave a first half whorl diameter of 0.44 to 0.48 mm (mean 0.46), agreeing with Bouchet & Warén's *C. affinis* measurements of <0.5 mm given for that species. Three specimens from northern Scotland had a mean first half whorl of 0.22 mm (0.20-0.23), less than half the size of *C. affinis*, and similar in size to specimens in the Naturalis collection from Mauritania wrongly identified as *C. operculata*.

It is therefore likely that this group is composed of a species complex of more than two species. Detailed morphometric and genetic work is needed to clarify the taxonomic status of the Recent species, which is beyond the scope of this work. We also prefer not to erect a new taxon based on the Selsoif fossil specimens.

Genus *Euspira* Agassiz, 1837

Euspira catena (da Costa, 1778)
(Fig. 11C1-C3)

Cochlea catena da Costa, 1778: 83.

Natica (*Lunatia*) *catena* – Harmer 1921: 681, pl. 54, figs 1-3.

Euspira catena – Marquet 1997: 76, pl. 2, fig. 11. — Pouwer & Rijken 2022: 31, figs 3-4.

For more, see synonymy list in Marquet (1997).

MATERIAL AND DIMENSIONS. — Maximum height 26.2 mm (incomplete), width 28.5 mm. — RGM.1365192 (10), leg. WG; RGM.1365193 (6), leg. ACJ; RGM.1365108 (29), leg. AWJ; RGM.1365219 (1), leg. AWJ; RGM.1365273 (2), leg. WG; RGM.1365220 (1), leg. WG; RGM.1365282 (11), leg. ACJ; RGM.1365288 (43), leg. AWJ.

SPECIES CHARACTERISATION. — Smooth naticiform shell, with low spire; protoconch consisting of 1.75-2.0 whorls; four convex teleoconch whorls separated by deep suture; last whorl 78% of the total height; aperture large, funicle and inner furrow absent, umbilicus open, with spiral sculpture within.

DISTRIBUTION. — **Lower Pliocene**: NSB, Belgium (Marquet 1997; Marquet & Landau 2006). — **Upper Pliocene**: NSB, Belgium (Marquet 1997), Red Crag, England (Harmer 1921). — **Lower Pleistocene**: Atlantic, England (Harmer 1921), Sesoif, NW France (this paper). — **Upper Pleistocene**: NSB, Eemian, Netherlands (Spaink 1958), Atlantic, England, Scotland, Ireland (Harmer 1921). — **Holocene**: Netherlands (Pouwer & Rijken 2022). Today this species occurs from North Sea (Pouwer & Rijken 2022) to the Mediterranean Sea (Fretter & Graham 1981). We cannot confirm Fretter & Graham's Mediterranean records and note that Pedriali & Robba (2009) did not record it from the Mediterranean Pliocene.

REMARKS

In their excellent review of the Italian Pliocene Poliniceinae, Pedriali & Robba (2009) characterised *Euspira catena* (da Costa, 1778) and *E. helicina* (Brocchi, 1814), which had often been confused in the past. *Euspira helicina* has a subobsolete funicle, a moderately deep to deep inner furrow of variable width and no inner spiral sculpture. *Euspira catena* lacks a funicle and the inner furrow but has spiral sculpture within the umbilicus (Pedriali & Robba 2009: 383, table 1). They also differ in the size of their protoconchs. *Euspira helicina* has a protoconch consisting of 2.5-2.75 whorls, whereas *E. catena* has a smaller protoconch consisting of 1.75-2.0 whorls.

Family BUCCINIDAE Rafinesque, 1815
Genus *Buccinum* Linnaeus, 1758

Buccinum undatum Linnaeus, 1758
(Fig. 11D1-D3)

Buccinum undatum Linnaeus, 1758: 740. — Wood 1848: 35, pl. 3, fig. 12a-b. — Harmer 1914: 90, pl. 6, figs 1-10, pl. 7, figs 1-6, pl. 8, figs 1-2, pl. 10, fig. 13. — Domènech & Martinell 1982: 52, fig. 16. — Marquet 1997: 91, pl. 7, fig. 6. — Wesselingh *et al.* 2014: 194, fig. 1. — Símonarson & Eiríksson *in* Eiríksson & Símonarson 2021: 277, pl. 7.5, fig. 2.

For more, see synonymy list in Marquet (1997) and Símonarson *et al.* (2021).

MATERIAL AND DIMENSIONS. — Maximum height 32.1 mm, width 18.7 mm. — RGM.1364922 (2), leg. WG; RGM.1365005 (3), leg. ACJ; RGM.1365109 (11), leg. AWJ; RGM.1365187 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Shell large, relatively fragile, broadly fusiform; protoconch not preserved; teleoconch of four strongly convex whorls separated by impressed linear suture; sculpture of weak spirals cords with secondaries variably developed; sinuous axial ribs variably developed on early whorls weakening abapically, obsolete on last 1-2 whorls; aperture large, ovate; outer lip weakly thickened by varix, sinuous in profile; columella twisted at fasciole, columella and parietal callus moderately expanded over base, variably thickened.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1848; Harmer 1914). — **Upper Pliocene**: NSB, Belgium (Marquet 1997), Red Crag, England (Wood 1848; Harmer 1914). — **Lower Pleistocene**: Atlantic, Iceland (Eiriksson & Símonarson 2021), Atlantic, West Greenland (Símonarson 1981), Selsoif, NW France (this paper). — **Upper Pleistocene**: western Mediterranean, Spain (Domènech & Martinell 1982); central Mediterranean, Italy (Malatesta & Zarlenga 1986), Baltic (Funder *et al.* 2002). — **Holocene**: NSB (Strand Petersen 2004). Today, this species is present in the North Atlantic, from Greenland and New Jersey on the western side and Iceland to the Bay of Biscay (Fretter & Graham 1984). Occurs in every kind of habitat, but prefers soft bottoms, lowest tide line to 1200 m depth.

REMARKS

Although highly variable, it cannot be confused with any other species. The Selsoif specimens are mostly incomplete but ascribed to the species without doubt. This is a boreal species.

Genus *Neptunea* Röding, 1798

Neptunea inversa Harmer, 1918
(Fig. 11E1-E3)

Neptunea contraria var. *informis* Harmer, 1918 (*partim*): 367, pl. 36, figs 30-31 [not pl. 16, fig. 6, that corresponds to *Neptunea contraria* (Linnaeus, 1771) forma *informis* Harmer, 1914] (*non* Harmer, 1914).

Neptunea antiqua (Linnaeus) var. *inversa* Harmer, 1918 (*partim*): 368, pl. 36, fig. 26 [not fig. 28, that corresponds to *Neptunea contraria* (Linnaeus, 1771)].

Neptunea inversa – Vervoenen *et al.* 2014: 31, figs 24-26. — Wesselingh *et al.* 2014: 196, fig. 10. — Preece *et al.* 2020: fig. 7e.

MATERIAL AND DIMENSIONS. — Maximum height 50.2 mm, width 31.9 mm (incomplete). — RGM.1364923 (18), leg. WG; RGM.1365006 (26), leg. ACJ; RGM.1365188 (1), leg. ACJ; RGM.1310340 (1), leg. ACJ; RGM.1365110 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Relatively small, **s**inistral *Neptunea* species with flat whorl profile and shallow suture. Shell smooth or with low spiral cords separated by faint spiral grooves; thickened axial growthlines on the bigger specimens. Aperture elongate with an open siphonal canal. Juveniles are common in the studied material with a prominent protoconch.

DISTRIBUTION. — **Lower Pleistocene**: NSB, Norwich Crag and Weybourne Crag, England (Harmer 1918; Preece *et al.* 2020); Atlantic, Selsoif, NW France (Vervoenen *et al.* 2014). — **Lower-Middle Pleistocene**: Channel region, England (Vervoenen *et al.* 2014). — **Middle Pleistocene**: Irish Sea (Harmer 1918). — **Pleistocene** (indeterminate): Netherlands (Vervoenen *et al.* 2014).

REMARKS

Neptunea inversa Harmer, 1918 differs from *N. contraria* (Linnaeus, 1771) in being smaller, lower spired, with less convex whorls separated by a shallower suture. It is a marker species for early-middle Pleistocene assemblages of the southern North Sea Basin, Channel and Irish Sea (Vervoenen *et al.* 2014). Those authors noted than the specimen from Selsoif has slightly more convex whorls than usual for specimens of *N. inversa* from Early and Middle Pleistocene localities (not Late Pleistocene; *lapsus*). Adult specimens are uncommon in Selsoif where the species is represented by hundreds of juveniles. However, one of the specimens illustrated (Pl. 6, fig. 9) has a low spire and very flat whorls in keeping with the species.

Family NASSARIIDAE Iredale, 1916

Genus *Tritia* Risso, 1826

REMARK

Based on molecular phylogenetics, all European Neogene nassariids belong in the genus *Tritia* Risso, 1826 (Galindo *et al.* 2016).

Tritia incrassata (Strøm, 1768)
(Fig. 11F1-F3)

Tritonium incrassatum Strøm, 1768: 369, pl. 16, fig. 25.

Nassa incrassata – Harmer 1914: 88, pl. 5, figs 25, 26.

Nassa (*Hima*) *incrassata* – Harmer 1918: 324, pl. 34, figs 8-10.

Hinia (*Tritonella*) *incrassata* – Brébion 1964: 464, pl. 11, figs 32, 33 [corresponds to *Nassarius pacaudi* Van Dingenen, Ceulemans, Landau & Silva, 2015]. — Cuerda Barceló 1987: 297, pl. 27, fig. 2 (*lapsus*, figs 22, 23). *non Hinia* (*Tritonella*) *incrassata* Müller, 1776.

Nassarius incrassatus – Landau *et al.* 2009: 33, pl. 6, figs 10-12. — Rijken & Pouwer 2014: 49, fig. 19. — Van Dingenen *et al.* 2015: 94, pl. 7, fig. 1.

For more, see synonymy list in Landau *et al.* (2009) and Van Dingenen *et al.* (2015).

MATERIAL AND DIMENSIONS. — Maximum height 11.5 mm, width 6.7 mm. — RGM.1364924 (299), leg. WG; RGM.1365209 (1), leg. WG; RGM.1365008 (178), leg. ACJ; RGM.1365296 (1), leg. AWJ; RGM.1008174 (1), leg. AWJ; RGM.1008175 (100+), leg. AWJ.

SPECIES CHARACTERISATION. — Shell fusiform, with rounded whorls, separated by deeply impressed, undulating suture. Sculpture of 11-15 rounded, undulating axial ribs, overrun by seven spiral cords per whorl. Outer lip strongly thickened by varix, bearing about seven irregular denticles within. Columella moderately expanded, bearing numerous rugae and tubercles, strong parietal tubercle. Siphonal fasciole broad, separated from base by broad groove.

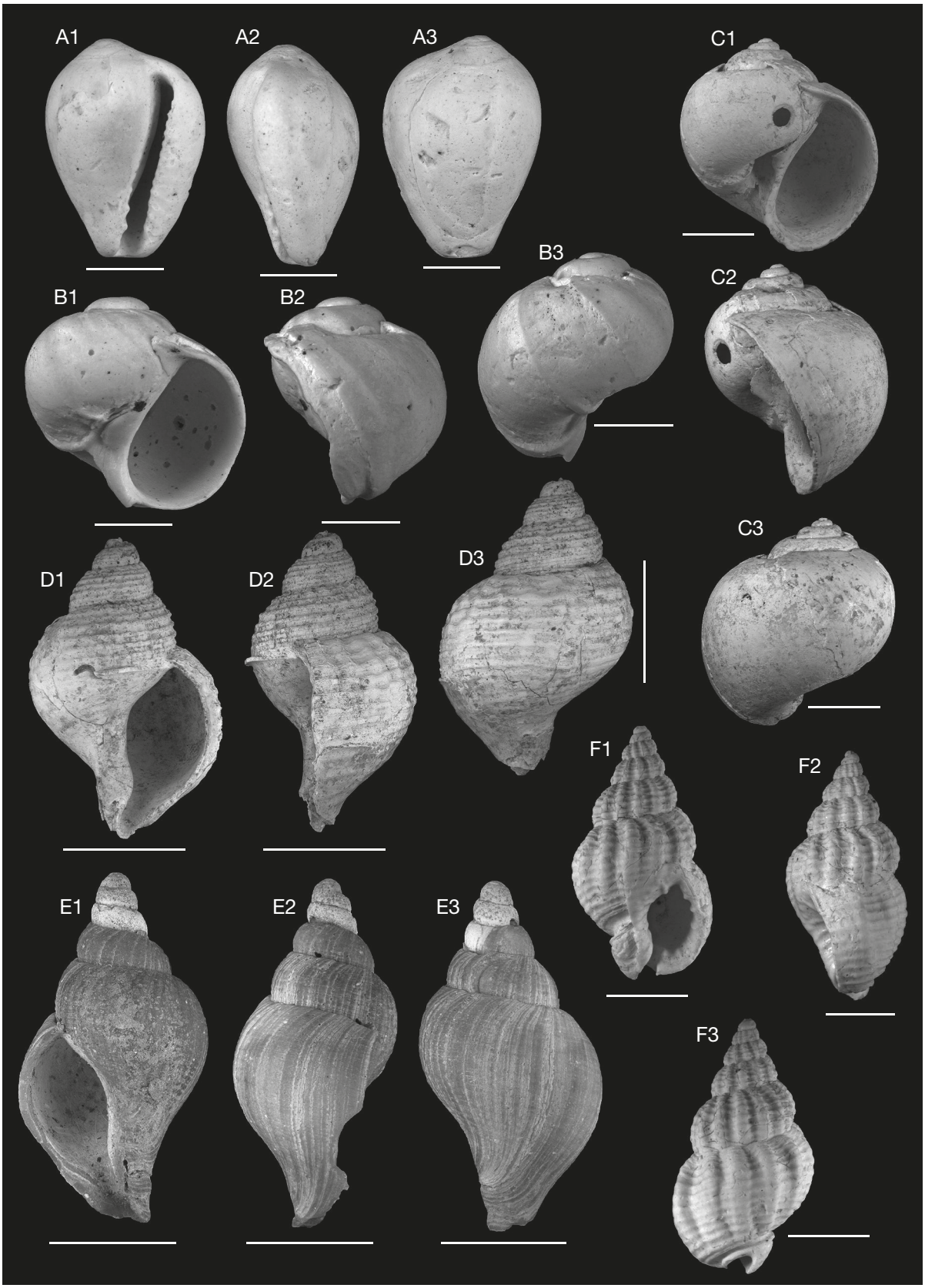

Fig. 11. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Erato exmaugeriae* Sacco, 1894, RGM.1365287, leg AWJ, H = 2.9 mm; **B**, *Cryptonatica* sp., RGM.1365218, leg AWJ, H = 1.37 mm; **C**, *Euspira catena* (da Costa, 1778), RGM.1365219, leg AWJ, H = 5.48 mm; **D**, *Buccinum undatum* Linnaeus, 1758, RGM.1365187, leg AWJ, H = 12 mm; **E**, *Neptunea inversa* Harmer, 1918, RGM.1365188, leg ACJ, H = 13.7 mm; **F**, *Tritia incrassata* (Strøm, 1768), RGM.1365209, leg WG, H = 6.2 mm. Scale bars: A, 1 mm; B, 500 µm; C, F, 2 mm; D, E, 5 mm.

DISTRIBUTION. — **Lower Pliocene**: ?central Mediterranean, Italy (Chirli 2000; needs confirmation). — **Upper Pliocene**: NSB, Red Crag, England (Harmer 1914, 1918); western Mediterranean, S Spain (Landau *et al.* 2009). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (Van Dingenen *et al.* 2015), Sicily (NHMW coll.). — **Middle Pleistocene**: Wexford Gravels, Irish Sea (Harmer 1918); Netherlands (Rijken & Pouwer 2014). — **Upper Pleistocene**: western Mediterranean, Balearic Islands (Cuerda Barceló 1987). Today it is distributed in the eastern Atlantic from Iceland, Northern Norway to the Mediterranean, Canaries (Poppe & Goto 1991), intertidal to 200 m.

REMARKS
For discussion see Landau *et al.* (2009: 34) and Van Dingenen *et al.* (2015: 94). This is one of the most abundant molluscs in the Selsoif assemblage.

Tritia reticulata (Linnaeus, 1758)
(Fig. 12A1-A3)

Buccinum reticulatum Linnaeus, 1758: 740.

Nassa (*Hinia*) *reticulata* – Harmer 1925: 318, pl. 34, figs 1, 2.

Hinia (*Hinia*) *reticulata* – Cuerda Barceló 1987: 295, pl. 27, fig. 19.

Nassarius reticulatus – Landau *et al.* 2009: 29, pl. 5, figs 15-18, pl. 6, fig. 1, pl. 17, fig. 5. — Chirli & Linse 2011: 160, pl. 54, fig. 3. — Rijken & Pouwer 2014: 54, fig. 35. — Van Dingenen *et al.* 2015: pl. 8, fig. 1.

For more, see synonymy list in Landau *et al.* (2009) and Van Dingenen *et al.* (2015).

MATERIAL AND DIMENSIONS. — Maximum height 24.3 mm, width 12.3 mm. — RGM.1364925 (2), leg. WG; RGM.1365204 (1), leg. ACJ; RGM.1365007 (4), leg. ACJ; RGM.1310337 (1), leg. AWJ; RGM.1365111 (40), leg. AWJ.

SPECIES CHARACTERISATION. — Shell solid, bucciniform, with elevated conical spire. Protoconch not preserved. Teleoconch of five weakly convex whorls, separated by a shallowly impressed suture. Sculpture of low axial ribs overrun by strap-like cords swollen over the intersection giving surface reticulated appearance. Aperture pyriform; outer lip thickened by varix, denticulated within; columella bearing two folds abapically and parietal fold adapically; columellar callus thickened; parietal callus extended over venter forming parietal shield.

DISTRIBUTION. — **Lower Pliocene**: Atlantic, SE Spain (González-Delgado 1989; Landau *et al.* 2011); western Mediterranean, NE Spain (Gili 1991), SE France (Fontannes 1879, Cossmann 1901); central Mediterranean, Italy (Bellardi 1882; Chirli 2000), Tunisia (Fekih 1975). — **Upper Pliocene**: Atlantic, Portugal (Zbyszewski 1959; Gili *et al.* 1995; Silva 2001); western Mediterranean, S Spain (Landau *et al.* 2009); central Mediterranean, Italy (Bellardi 1882; Malatesta 1974). — **Upper Pliocene-Lower Pleistocene**: Atlantic, NW France (Van Dingenen *et al.* 2015). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (Van Dingenen *et al.* 2015); central Mediterranean, Italy (Cerulli-Irelli 1911); eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Middle Pleistocene**: Atlantic, Wexford Gravels, Irish Sea (Harmer 1916). — **Pleistocene** (indeterminate): Netherlands (Rijken & Pouwer 2014). — **Upper Pleistocene**: western Mediterranean, Balearic Islands (Cuerda Barceló 1987). — **Holocene**: NSB (Strand Petersen 2004). Today, it occurs in the Atlantic and western Mediterranean (Rolán & Luque 1994).

REMARKS
Within the *Tritia reticulata* species group (of Landau *et al.* 2009), *T. nitida* (Jeffreys, 1867) differs in having a paucispiral protoconch of less than two whorls, *T. reticulata* has 2.75-3.25 whorls. Moreover, *T. nitida* has a slightly gradate spire, fewer axial ribs and stronger and more regular dentition within the outer lip. Specimens from Selsoif show the same variability in axial sculpture as seen in other populations. For further discussion see Landau *et al.* (2009: 30).

Family MURICIDAE Rafinesque, 1815
Genus *Nucella* Röding, 1798

Nucella lapillus (Linnaeus, 1758)
(Fig. 12B1-B3, C1-C3, D1-D2)

Buccinum lapillus Linnaeus, 1758: 39.

Purpura lapillus – Wood 1848: 36, pl. 4, figs 6a-h. — Harmer 1914: 117, pl. 11, figs 1-5, 7-12, 14-17, 19-23.

Thais (*Polytropa*) *lapillus vulgaris* – Van Regteren Altena *et al.* 1956: 88, pl. 11, fig. 114b.

Nucella lapillus – Fretter & Graham 1984: 444, figs 314-315. — Raad *et al* 2021: 19, figs 25-29.

MATERIAL AND DIMENSIONS. — Maximum height 54.2 mm, width 33.8 mm. — RGM.1364927 (250+), leg. WG; RGM.1365011 (230+), leg. ACJ; RGM.1365290 (1), leg. ACJ; RGM.1365267 (1), leg. AWJ; RGM.1365114 (500+), leg. AWJ; RGM.1365115 (500+), leg. AWJ; RGM.1405529 (1), leg. R. van Slageren.

SPECIES CHARACTERISATION. — Shell solid broadly fusiform; protoconch paucispiral of about 1.5 smooth whorls with large, elevated nucleus. Teleoconch of about three whorls; spire whorls convex, first whorl bearing two primary cords with secondaries intercalated on second whorl; last whorl inflated, with numerous scabrous spiral cords of roughly alternating strength, shoulder and peribasal cords usually slightly stronger; aperture ovate; outer lip not thickened by varix, with internally bevelled edge, with denticles strongly developed to absent; columella thickened abapically, detached, forming medial border of umbilical chink.

DISTRIBUTION. — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848; Harmer 1914). — **Pliocene and Pleistocene** (indeterminate): NSB, Netherlands (Van Regteren Altena *et al.* 1956; Raad *et al* 2021). — **Lower Pleistocene**: NSB, England (Wood 1848; Harmer 1914), Atlantic: Selsoif, NW France (this paper). — **Middle Pleistocene**: Channel region England (Preece & Bates 1999). — **Holocene**: NSB (Strand Petersen 2004). Today this species is widely in the northern Atlantic, in the west from Greenland to Connecticut, in the east from Iceland to the Strait of Gibraltar (Fretter & Graham 1984). It inhabits rocky shores to depth of 30-40 m. it lives between 0 and 19°C isotherms (Moore 1936).

REMARKS
Nucella lapillus (Linnaeus, 1758) is an exceptionally variable species both in the fossil record (Wood 1848; Harmer 1914) and in extant faunas (Berry & Crothers 1974; Rolán *et al.* 2004; *inter alia*). Some papers have associated these morphs with particular habitats (Rolán *et al.* 2004) and or presence/absence of predators (Crothers 1983 and others), whereas others have found no association (Berry & Crothers 1974; Crothers 2008).

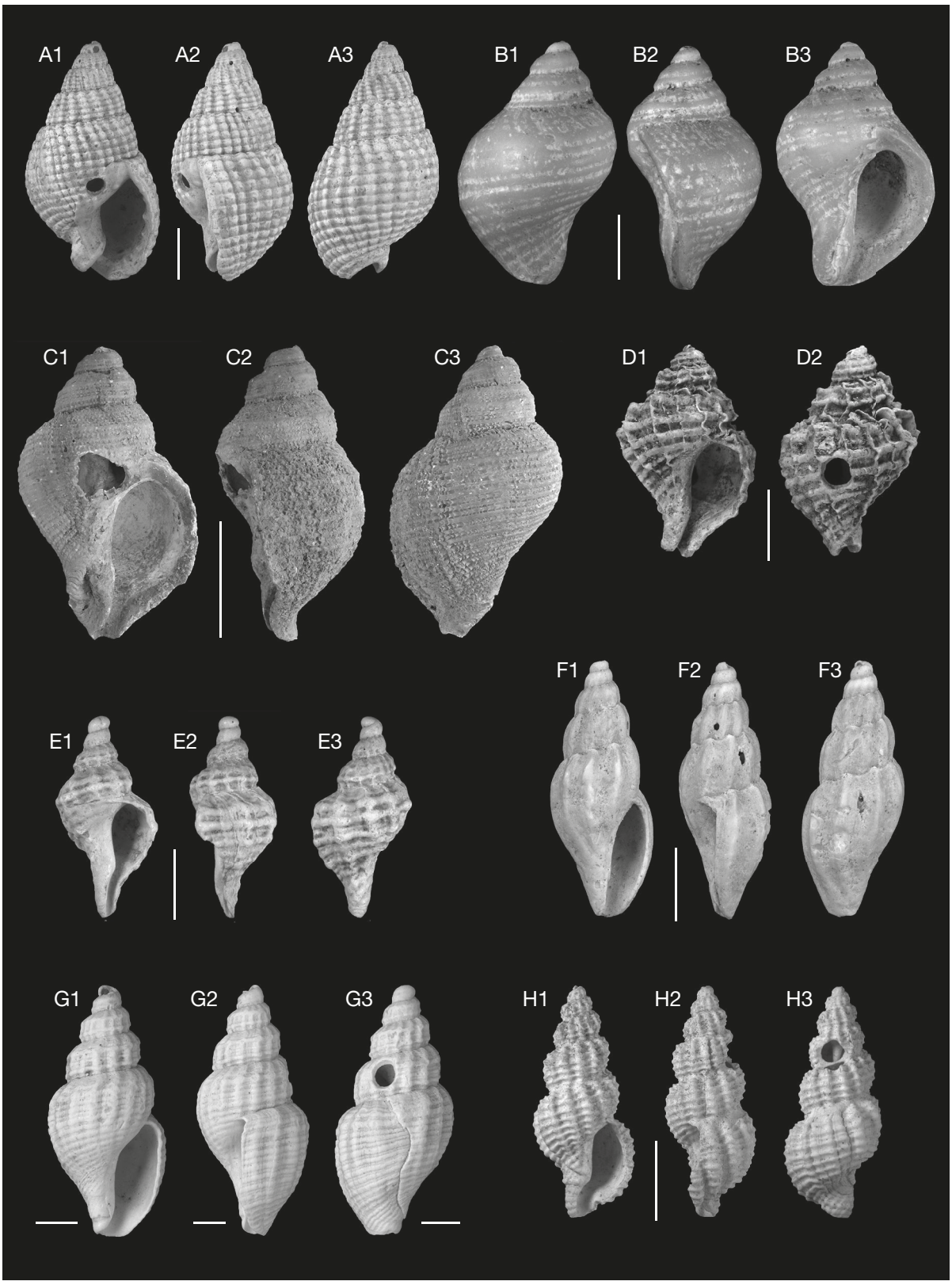

Fig. 12. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Tritia reticulata* (Linnaeus, 1758), RGM.1310337, leg AWJ, H = 9.34 mm; **B**, *Nucella lapillus* (Linnaeus, 1758), RGM.1365267, leg AWJ, H = 7.3 mm; **C**, *Nucella lapillus* (Linnaeus, 1758), RGM.1365290, leg ACJ, H = 5.07 mm; **D**, *Nucella lapillus* (Linnaeus, 1758) RGM.1405529, leg R. van Slageren, H = 15.1 mm; **E**, *Ocenebra* cf. *erinaceus* (Linnaeus, 1758), RGM.1364928, leg WG, H = 5.74 mm; **F**, *Mangelia* sp., RGM.1365293, leg ACJ, H = 3.5 mm; **G**, *Propebela* aff. *turricula* (Montagu, 1803), RGM.1365291, leg AWJ, H = 4.14 mm; **H**, *Cyrillia linearis* (Montagu, 1803), RGM.1365215, leg ACJ, H = 5.8 mm. Scale bars: A-C, E, H, 2 mm; D, 5 mm; F, G, 1 mm.

In the Selsoif material, the larger adult specimens usually have spiral cords (Fig. 4C), smaller but fully adult specimens judging by the thickness of their shell are smoother (Fig. 4B). The inner lip can be smooth or bear coarse denticles. Some of the juvenile specimens have an imbricated surface with raised lamellae, similar to the juvenile specimen illustrated by Fretter & Graham (1984: fig. 315) as *N. lapillus* var. *imbricata* (Fig. 4D).

Similar variability has been described for the size of the protoconch ranging from 800-1400 µm (Rolán *et al.* 2004) to 500-700 µm (Fretter & Graham 1984). A large number of juveniles are present in the Selsoif material with their protoconch preserved (npw = 1.25-1.5, dp = 740-1000 µm, hp = 730-1030 µm, n = 340-600 µm, p1 = 580-910 µm). These measurements fall between those given above for the recent populations, although the size variation of the nucleus in the Selsoif material is much greater than that reported by Rolán *et al.* (2004: table 1). This is a good example of the variability in protoconch size for species with paucispiral protoconchs.

Genus *Ocenebra* Gray, 1847

Ocenebra cf. ***erinaceus*** (Linnaeus, 1758)
(Fig. 12E1-E3)

cf. *Murex erinaceus* Linnaeus, 1758: 753.

cf. *Ocinebra erinacea* – Harmer 1914: 124, pl. 12, figs 12-14.

cf. *Ocenebra erinaceus* – Landau *et al.* 2003 26, pl. 7, figs 1-4. — Raad *et al.* 2021: 12, figs 1-2.

For more, see synonymy list in Landau *et al.* (2003).

MATERIAL AND DIMENSIONS. — Maximum height 9.0 mm, width 4.3 mm. — RGM.1364928 (1), leg. WG.

SPECIES CHARACTERISATION. — Small biconic shell. Two smooth protoconch whorls with large bulbous first whorl. Three convex teleoconch whorls separated by an impressed suture. Sculpture on spire whorls of two spiral cords and around ten ribs. Last whorl with six primary cords, shoulder cord appears on second half of last whorl and secondaries intercalated in interspaces; long, narrow siphonal canal.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). The oldest stratigraphic record of *Ocenebra erinaceus* is from Atlantic Pliocene deposits of the Guadalquivir Basin, Spain (Landau *et al.* 2007, 2011) and western (Martinell & Marquina 1981) and central Mediterranean (Chirli 2000). — In the Upper Pliocene it is present in the Mondego Basin of Portugal (Silva 2001) and is widespread in the Mediterranean. Today it occurs from the southern British Isles to the Azores, Madeira, and Canary Islands and entire Mediterranean (Houart 2001).

REMARK
We attribute the specimen with some hesitation to *Ocenebra erinaceus* (Linnaeus, 1758); it is represented by a single juvenile specimen that differs from the many juveniles of *Nucella lapillus* (Linnaeus, 1758) in having a larger, more elevated protoconch with a more bulbous first whorl, the teleoconch is more slender and the axial sculpture stronger than in *N. lapillus*. This single juvenile could represent *Ocenebra erinaceus* (Linnaeus, 1758), but further specimens would be required to confirm its identity.

Family MANGELIIDAE Fischer, 1883
Genus *Mangelia* Risso, 1826

Mangelia sp.
(Fig. 12F1-F3)

MATERIAL AND DIMENSIONS. — Maximum height 3.6 mm, width 1.4 mm. — RGM.1365116 (6), leg. AWJ; RGM.1365293 (1), leg. ACJ; RGM.1365292 (5), leg. ACJ.

SPECIES CHARACTERISATION. — Shell small, slender fusiform. Protoconch not preserved. Teleoconch of 4.5 convex, weakly shouldered whorls bearing ten elevated, opisthocline ribs, about half width of their interspaces. No sign of spiral sculpture; possibly abraded. Last whorl elongate, weakly shouldered, moderately constricted at base. Aperture elongate, outer lip incomplete. Columella weakly excavated, siphonal canal moderately long, open, wide.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

REMARK
All specimens are too incomplete and abraded to offer further identification.

Genus *Propebela* Iredale, 1918

Propebela aff. ***turricula*** (Montagu, 1803)
(Fig. 12G1-G3)

MATERIAL AND DIMENSIONS. — Maximum height 10.7 mm, width 4.4 mm. — RGM.1365012 (90+), leg. ACJ; RGM.1365294 (21), leg. ACJ; RGM.1364929 (31), leg. WG; RGM.1365291 (1), leg. AWJ; RGM.1365117 (115), leg. AWJ.

SPECIES CHARACTERISATION. — Small fusiform shell. Two smooth protoconch whorls. Three quadrate teleoconch whorls separated by well-defined swallow suture. Sculpture consists of two spiral cords conferring the quadrate aspect of the whorls; and around 15 opisthocline axial ribs. Last whorl is covered by numerous spiral cords and ribs, continuing on the base. Well developed columelar lip. Elliptical aperture, with a short, widely open siphonal canal.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif (this paper).

REMARKS
Even though *Propebela turricula* has a wide morphological variability particularly in material from the Quaternary of the NSB (Raad *et al.* 2016), the elongate-shaped specimens with well pronounced ribbing from Selsoif appear to fall outside the range of variation. Further study is required to establish whether this might represent a new species.

Family RAPHITOMIDAE Bellardi, 1875
Genus *Cyrillia* Kobelt, 1905

Cyrillia linearis (Montagu, 1803)
(Fig. 12H1-H3)

Murex linearis Montagu, 1803: 261, pl. 9, fig. 4.

Clathurella linearis – Harmer 1915: 237, pl. 28, figs 26-29.

Raphitoma (*Cirillia* [*sic*]) *linearis* – Cuerda Barceló 1987: 325, pl. 30, figs 6, 7.

Cyrillia linearis – Landau *et al.* 2022:170, pl. 10, figs 1-3.

For more, see synonymy list in Landau *et al.* (2022).

MATERIAL AND DIMENSIONS. — Maximum height 9.4 mm, width 3.6 mm. — RGM.1364930 (17), leg. WG; RGM.1365013 (43), leg. ACJ; RGM.1365215 (1), leg. ACJ; RGM.1365118 (50), leg. AWJ; RGM.1365215 (1), leg. ACJ.

SPECIES CHARACTERISATION. — Small, fusiform shell. Protoconch not preserved. Five convex teleoconch whorls separated by weakly marked suture. Sculpture consists of 12 orthocline to prosocline, broad, round ribs and two spiral cords running over the ribs on the first teleoconch whorl, the third appears below the suture and the fourth above the suture on second whorl. Third whorl has 5 spiral cords. Last whorl with six spiral cords, continuing until the columella. Aperture ovate, extended by a broad, twisted siphonal canal.

DISTRIBUTION. — **Upper Miocene**: Atlantic, southwestern Spain (Cárdenas *et al.* 2019); central Proto-Mediterranean, Italy (Montanaro 1937: Venzo & Pelosio 1963). — **Lower Pliocene**: NSB, Coralline Crag, England (S.V. Wood 1848; Harmer 1915); Atlantic, Guadalquivir Basin, S. Spain (González-Delgado 1993); central Mediterranean, Italy (Chirli 1997; Brunetti & Cresti 2018). — **Upper Pliocene**: NSB, Red Crag, England (S.V. Wood 1848; Harmer 1915); western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez 2002; Landau *et al.* 2022); central Mediterranean (Bellardi 1877; Cavallo & Repetto 1992). — **Lower Pleistocene**: central Mediterranean, Italy (Cerulli-Irelli 1914). — **Middle Pleistocene**: eastern Mediterranean, Rhodes Island (Chirli & Linse 2011). — **Pleistocene** (indeterminate): Atlantic, England (Harmer 1915, 1918). — **Upper Pleistocene**: western Mediterranean, Balearic Islands (Cuerda Barceló 1987). Holocene: NSB (Strand Petersen 2004). — **Present-day**: Atlantic: Norway (Høisæter 2016), Scotland (E.H. Smith 1967), British Isles (Fretter & Graham 1984; Graham 1988), Galicia (Oliver *et al.* 2022), south to Portugal (Nobre 1931) and Canary Islands (Nordsieck & García-Talavera 1979); western Mediterranean (Bucquoy *et al.* 1882), central Mediterranean (Bogi *et al.* 1980; Cachia *et al.* 2001). Today it is occurs in the Atlantic from Norway (Høisæter 2016), Scotland (Smith 1967) and British Isles (Fretter & Graham 1984; Graham 1988) to Galicia (Oliver *et al.* 2022), south to Portugal (Nobre 1931) and Canary Islands (Nordsieck & García-Talavera 1979) and in the western Mediterranean (Bucquoy *et al.* 1882) and central Mediterranean (Bogi *et al.* 1980; Cachia *et al.* 2001).

REMARK

For discussion see Landau *et al.* (2022).

Family CANCELLARIIDAE Forbes & Hanley, 1851
Genus *Admete* Möller, 1842

Admete trigostomoides n. sp.
(Fig. 13A1-A3, B1-B3)

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TYPE MATERIAL. — **Holotype**: MNHN.F.A91318, height 5.4 mm, width 2.9 mm, leg. SM. — **Paratypes**: paratype 1, RGM.1310836, height 5.9 mm, width 3.3 mm, leg. SM; paratype 2, RGM.1365263, height 8.7 mm, width 5.2 mm, leg. AWJ.

OTHER MATERIAL EXAMINED. — Maximum height 8.7, width 5.2. — RGM.1365014 (1), leg. ACJ.

ETYMOLOGY. — Name reflecting the close resemblance to members of the cancellariid genus *Trigonostoma*.

TYPE LOCALITY. — Selsoif, Saint-Sauveur-le-Vicomte, Manche department, NW France.

STRATUM TYPICUS. — Gelasian, Early Pleistocene

DIAGNOSIS. — Medium sized *Admete* species, protoconch of 1.5 whorls, teleoconch of four depressed barrel-shaped whorls, subsutural platform canaliculate, sculpture of narrow spiral cords, axials restricted to weak tubercules over cords, last whorl bearing 12 cords, narrow umbilical chink, three subequal columellar folds, columellar callus thickened, parietal callus not developed.

INTRASPECIFIC VARIABILITY. — The Selsoif specimens are relatively consistent in profile and sculpture, although in some the subsutural ramp is slightly slanted giving the profile a more typically *Admete*-like appearance. The width and concavity of the subsutural ramp is somewhat variable. In one specimen, a further cord runs on the subsutural platform just medial to the shoulder cord on the last two whorls and a fine secondary spiral is intercalated between the second and third primary cords. The subobsolete axial sculpture in this same specimen is slightly stronger, forming poorly defined axial ribs. The small size of the specimens and the unthickened outer lip suggests that they may not represent fully grown adults.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, endemic to Selsoif (this paper).

DESCRIPTION

Shell small and relatively thin for genus, with moderate height scalate spire. Protoconch paucispiral, dome-shaped, about 1.5 whorls, surface abraded. Teleoconch of four low, barrel-shaped, strongly tabulate whorls, separated by narrowly impressed, linear suture: subsutural platform broad, increasingly concave and canaliculate abapically, delimited by elevated shoulder cord. Sculpture on early teleconch whorls of three narrow spiral cords, with fourth appearing just above suture. On penultimate whorl single secondary cord intercalated between shoulder cord and mid cord. Axial sculpture subobsolete, represented mainly by indistinct tubercles over cords, and crowded slightly prosocline growth-lines. Last whorl 70% of total height with relatively broad, shallowly canaliculate subsutural platform, sharply angled at shoulder cord, weakly constricted at base, sculptured of four weakly tubercular cords above level of insertion of outer lip, about eight further smooth cords below, becoming closer-spaced over siphonal fasciole; base not delimited; siphonal fasciole weakly developed, slightly rounded with very narrow umbilical chink medially. Aperture 50% of total height, subquadrangular, outer lip not thickened, sharply angled at shoulder; anal sinus lacking, siphonal canal moderately short, open, bent adaxially. Columella excavated in upper third, straight below, twisted at fasciole, bearing three columellar folds of subequal strength, becoming increasingly oblique abapically. Columellar callus thickened, sharply delimited medially by umbilical chink, parietal callus not developed.

COMPARISONS

The strongly scalate spire and deeply canaliculate suture are reminiscent of members of the cancellariid genus *Trigonostoma* Blainville, 1827. However, species placed in that group are usually larger and thicker-shelled, have stronger axial sculpture and

a broad, deep umbilicus. Moreover, the presence of *Trigonostoma* was highlighted by Landau *et al.* (2011: table 1) as a thermophilic marker, which has its maximum diversity in tropical assemblages and does not occur in waters that are colder than subtropical.

Placement in the temperate to cold water genus *Admete* Möller, 1842 is more likely. Members of that genus are medium-sized, thin-shelled, and show similar sculpture and apertural characters to that seen in the new species. *Admete trigostomoides* n. sp. is similar to some forms of the extremely variable Pliocene to present-day *A. viridula* (Fabricius, 1780) that occurs at northern latitudes on both sides of the Atlantic, most notably the form described as *A. contabulata* Friele, 1879, which is considered a synonym (see Bouchet & Warén 1985: fig. 684). However, in that form the broad, sloping subsutural ramp is not as flat, and never canaliculate as seen in the French species. Moreover, despite the reasonably wide variation seen in Selsoif discussed above, all specimens have the subsutural ramp flat, or almost so, and none approximate to the more usual rounded whorl profile of *A. viridula*. The *contabulata* form was also recorded by Harmer (1920: 524, pl. 49, fig. 10) from the Lower Pleistocene of NE England. The figured specimen has a far steeper subsutural ramp than *A. trigostomoides* n. sp.

Genus *Graphis* Jeffreys, 1867

Graphis albida (Kanmacher, 1798)
(Fig. 13C)

Turbo albidus Kanmacher 1798: 637, pl. 14, fig. 17.

Graphis albida – Landau & Micali 2021: 207, pl. 5, fig. 1.

For more, see synonymy list in Landau & Micali (2021).

MATERIAL AND DIMENSIONS. — Maximum height 0.5 mm, width 0.2 mm. — RGM.1365080 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Small, thin turriform shell. Protoconch and early teleoconch whorls not preserved. Three convex teleoconch whorls, swollen in abapical half. Sculpture of sinuous axial ribs and fine spiral cords in visible in axial interspaces.

DISTRIBUTION. — **Lower Pliocene**: central Mediterranean, Italy (Chirli & Bogi 2002; Chirli 2013). — **Upper Pliocene**: Atlantic, Mondego Basin, Portugal (Landau & Micali 2021); western Mediterranean, Estepona Basin, S. Spain (Landau & Micali 2021). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). Today this species occurs in the eastern Atlantic of south Norway, British Isles (Fretter & Graham 1982), North Sea (Raven 2020) to Canaries (Hernández *et al.* 2011), Madeira and Selvagens Islands (Segers *et al.* 2009), Cape Verde Islands, West Africa (Rolán 2005) and Mediterranean, Italy (Giannuzzi-Savelli *et al.* 2014).

Family RETUSIDAE Thiele, 1925
Genus *Retusa* T. Brown, 1827

Retusa obtusa (Montagu, 1803)
(Fig. 13D1-D3)

Bulla obtusa Montagu, 1803: 223.

Utriculus obtusus – Harmer 1923: 797, pl. 63, fig. 4.

Retusa alba – Van Regteren Altena *et al.* 1965: 26, pl. 21, fig. 205. — Ceulemans *et al.* 2018: 122, pl. 7, fig. 9.

For more, see synonymy list in Ceulemans *et al.* (2018).

MATERIAL AND DIMENSIONS. — Maximum height 1.7 mm, width 0.8 mm. — RGM.1365120 (20), leg. AWJ; RGM.1365121 (1), leg. AWJ; RGM.1365017 (3), leg. ACJ.

SPECIES CHARACTERISATION. — Shell small, subcylindrical with low spire. Two to three teleoconch whorls separated by deeply impressed suture. Surface smooth. Aperture elongate expanded abapically.

DISTRIBUTION. — **Lower Pliocene**: NSB, England (Harmer 1923); Atlantic, NW France (Ceulemans *et al.* 2018). — **Upper Pliocene**: NSB, Red Crag, England (Wood 1848). — **Upper Pliocene-Pleistocene**: NSB, Holland (Van Regetren Altena *et al.* 1955). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper). — **Middle Pleistocene**: Atlantic, Irish Sea (Harmer 1923). Today, this species occurs in the Atlantic from Greenland, Iceland to Scandinavia, Nova Scotia to Aleutian Islands, British Isles (Thompson 1988).

REMARKS
Retusa obtusa is variable in shape and size with a more or less elevated apex (Ceulemans *et al.* 2018). As noted by those authors, this species is rarely reported in the fossil literature. It is predominantly a cooler water species with the most southern record being that of the Lower Pliocene of Le Pigeon Blanc (NW France).

Family HAMINOEIDAE Pilsbry, 1895
Genus *Haminoea* W. Turton & Kingston, 1830

Haminoea sp.
(Fig. 13E)

Bulla navicula – da Costa 1778: 36.

MATERIAL AND DIMENSIONS. — Fragment of apex. — RGM.1365018 (1), leg. ACJ., W of incomplete fragment 3.5 mm.

SPECIES CHARACTERISATION. — Apical fragment.

REMARKS
This single fragment probably represents a *Haminoea* sp. but is too fragmentary for further identification.

Family PYRAMIDELLIDAE Gray, 1840
Genus *Longchaeus* Mörch, 1875

Longchaeus cf. ***plicosus*** (Bronn, 1838)
(Fig. 13F1-F3)

cf. *Pyramidella plicosa* Bronn, 1838: 1026, pl. 40, fig. 24.

cf. *Longchaeus plicosus* – Landau & Micali 2021: 211, pl. 8, figs 5-8.

For more, see synonymy list in Landau & Micali (2021).

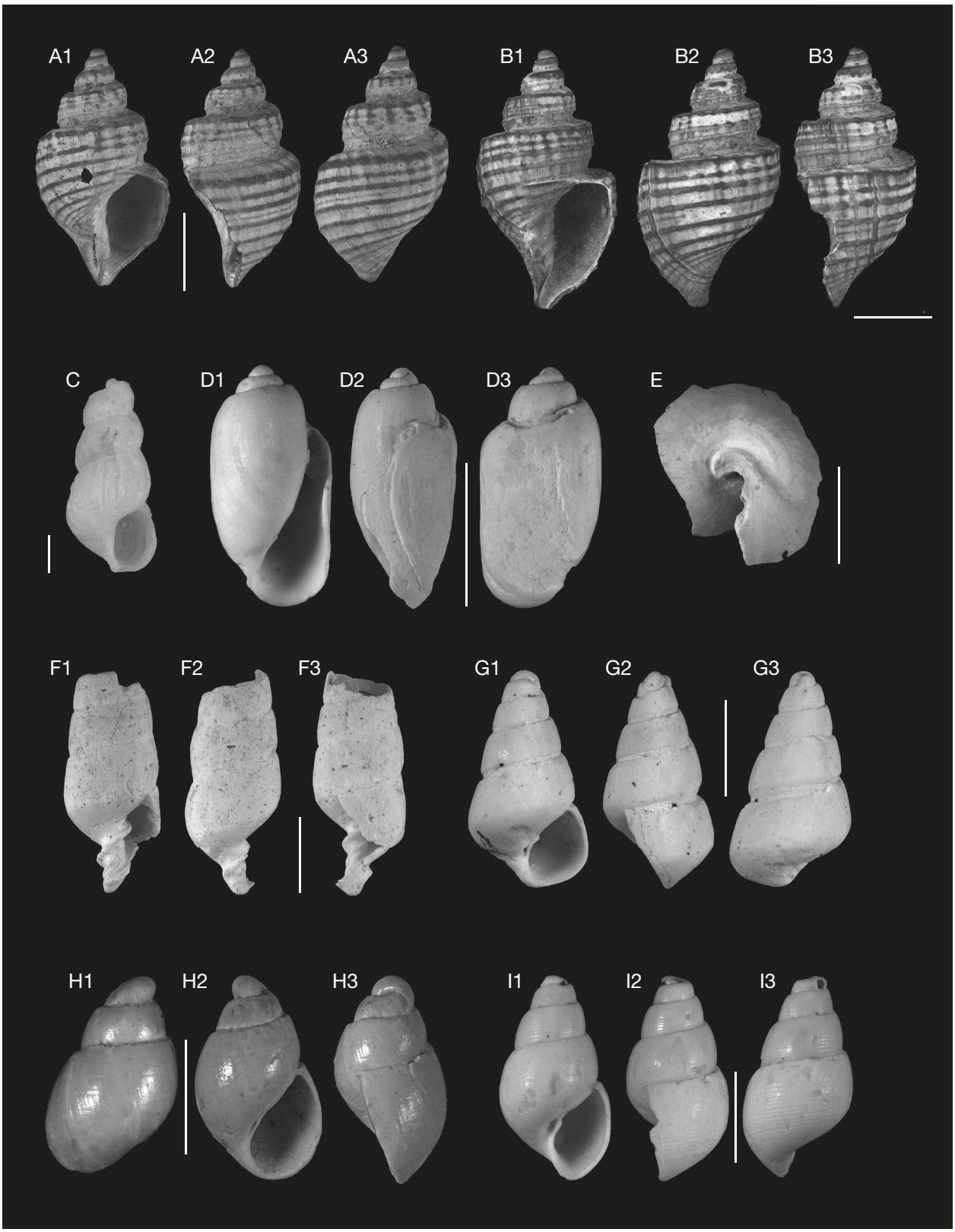

Fig. 13. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Admete trigostomoides* n. sp. (**holotype)**: MNHN.F.A91318, leg SM, H = 6.12 mm; **B**, *Admete trigostomoides* n. sp. (**paratype)**, RGM.1310836 leg. SM, H = 5.7 mm; **C**, *Graphis albida* (Kanmacher, 1798), RGM.1365080, leg AWJ, H = 519 µm; **D**, *Retusa obtusa* (Montagu, 1803), RGM.1365121, leg AWJ, H = 1.69 mm; **E**, *Haminoea* sp., RGM.13650018, leg ACJ, W = 3.49 mm; **F**, *Longchaeus* cf. *plicosus* (Bronn, 1838), RGM.1365276, leg AWJ, H = 2.96 mm; **G**, *Odostomia unidentata* (Montagu, 1803), RGM.1365214, leg AWJ, H = 1.14 mm; **H**, *Odostomiinae* indet., RGM.1365199, leg AWJ, H = 0.9 mm; **I**, *Ondina divisa* (J. Adams, 1797), RGM.1365266, leg AWJ, H = 1.13 mm. Scale bars: A, B, E, 2 mm; C, 100 µm; D, F, 1 mm; G, H, I, 500 µm.

MATERIAL AND DIMENSIONS. — Maximum height 2.9 mm (incomplete), width 1.3 mm. — RGM.1365276 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Three smooth, weakly convex abraded adult whorls preserved. Aperture broken. Columella marked by three folds; abapical two folds weaker.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

REMARKS

This fragment is unusual in having columellar folds suggesting placement in the genus *Longchaeus*, and the whorl outline suggesting *Eulimella*. Unfortunately, it is represented by a single poorly preserved specimen.

Genus *Odostomia* J. Fleming, 1813

Odostomia unidentata (Montagu, 1803)
(Fig. 13G1-G3)

Turbo unidentatus Montagu, 1803: 324.

Odostomia unidentata – Landau & Micali 2021: 242, pl. 46, figs 1-3.

For more, see synonymy list in Landau & Micali (2021).

MATERIAL AND DIMENSIONS. — Maximum height 1.1 mm, width 0.6 mm. — RGM.1365020 (2), leg. ACJ; RGM.1365214 (1), leg. AWJ; RGM.1365122 (50+), leg. AWJ.

SPECIES CHARACTERISATION. — Small shell with tall conical spire, type A2 helicoid protoconch (Landau *et al.*, 2020a), almost flat-sided teleoconch whorls, last whorl angular at the periphery, prosocline growth-lines and well developed columellar fold.

DISTRIBUTION. — **Middle Miocene**: Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.* 2013). — **Upper Miocene**: Atlantic (Tortonian and Messinian), NW France (Landau *et al.* 2020a). — **Lower Pliocene**: NSB, Coralline Crag, England (Harmer 1923); western Mediterranean, Tunisia (Fekih 1969); central Mediterranean, Italy (Sacco 1892; Crovato & Micali 1992b; Guioli *et al.* 2009; Chirli & Micali 2011). — **Upper Pliocene**: Atlantic, St Erth, England (Harmer 1923), NSB, Red Crag, England (Harmer 1923), Kruisschans and Oorderen Sands, Belgium (Marquet 1993, 1998); Atlantic, Mondego Basin, Portugal (Landau & Micali 2021); western Mediterranean, Estepona Basin, S. Spain (Peñas & Rolán 1999; Landau & Micali 2021); central Mediterranean, Italy (Sacco 1892; ?Cavallo & Repetto 1992; Ferrero *et al.* 1998). — **Upper Pliocene-Pleistocene**: NSB, Netherlands (Van Regteren Altena *et al.* 1964). — **Lower Pleistocene**: Selsoif, NW France (this paper); central Mediterranean, Italy (Cerulli-Irelli 1914; Gianolla *et al.* 2010; Brunetti 2011); eastern Mediterranean, Rhodes (Chirli & Linse 2011). — **Upper Pleistocene**: Ireland (Harmer 1923). — **Present-day**: eastern Atlantic from North Iceland, Norway to British Isles (Nordsieck 1972; Høisæter 2014), North Sea (Raven 2020), northwestern Spain (Trigo *et al.* 2018), Azores, Madeira and Selvagens Islands (Segers *et al.* 2009), south to Canaries (Hernández *et al.* 2011), West Africa, Cape Verde Islands to Angola (Peñas *et al.* 2009, 2014), into western Mediterranean (Bucquoy *et al.* 1882; Peñas *et al.* 1996), central Mediterranean (Cachia *et al.* 2001; Giannuzzi-Savelli *et al.* 2014), eastern Mediterranean (Öztürk *et al.* 2013).

Odostomiinae indet.
(Fig. 13H1-H3)

MATERIAL AND DIMENSIONS. — Maximum height 2.2 mm, width 1.4 mm. — RGM.1365098 (10), leg. AWJ; RGM.1365199 (1), leg. AWJ; RGM.794508 (*c.* 250), leg. AWJ; RGM.961907 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Thick, smooth, ovate shell. Protoconch heterostrophic. Two teleoconch whorls separated by a deep suture. Pyriform aperture with small fold deep within columella.

REMARKS

This species is unusual in being extremely small and thick-shelled. The protoconch is clearly heterostrophic and there is a small columellar fold deep within the aperture seen only in tangential view. We are unsure where to place this species and leave it in open nomenclature.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif (this paper).

Genus *Ondina* de Folin, 1870

Ondina divisa (J. Adams, 1797)
(Fig. 13I1-I3)

Turbo divisus J. Adams, 1797: 254.

Turbo insculptus Montagu, 1808: 129.

Odostomia insculpta – Wood 1872: 62, pl. 4, fig. 18.

Odostomia (*Ondina*) *insculpta* – Harmer 1923: 839, pl. 64, fig. 20.

Evalea divisa – Graham 1988: 566, fig. 244.

Ondina divisa – Marquet 1997: 108, pl. 10, fig. 3.

MATERIAL AND DIMENSIONS. — Maximum height 1.1 mm, width 0.6 mm. — RGM.1365021 (1), leg. ACJ; RGM.1365266 (1), leg. AWJ; RGM.794507 (19), leg. AWJ; RGM.961906 (1), leg. AWJ; RGM.1365022 (1), leg.ACJ, RGM.1365123 (6), leg. AWJ.

SPECIES CHARACTERISATION. — Elongate-ovoid shell, strongly intorted type C protoconch (Landau *et al.* 2020a), teleoconch of three moderately convex whorls, separated by deeply impressed suture, opisthocline to orthocline growth-lines, sinuous towards adapical suture, fine spirals cover entire whorl, last whorl inflated, regularly convex, narrow umbilical chink. Aperture pyriform, columella bearing weak fold mid-aperture.

DISTRIBUTION. — **Lower Pliocene**: NSB, Coralline Crag, England (Wood 1872); Kattendijk Formation, Belgium (Marquet 1997). — **Late Pliocene**: St Erth, Atlantic, England (Harmer 1923), Selsoif, NW France (this paper). Today this species occurs in northern Europe from North Norway to the Bay of Biscay (Fretter *et al.* 1986).

REMARKS

The specimens from Selsoif differ slightly from modern ones in having the spiral sculpture extending along the entire whorl surface, whereas in extant specimens it is restricted to the abapical portion of the whorl.

Ondina cf. ***micropeas*** (Boettger, 1902)
(Fig. 14A1-A3)

cf. *Odostomia* (*Ondina*) *micropeas* Boettger, 1902: 100.

cf. *Macrostomia micropeas* – Zilch 1934: 237, pl. 11, fig. 12.

Ondina cf. *micropeas* – Landau *et al.* 2020c: 298, pl. 22, figs 1-3. — Landau & Micali 2021: 298, pl. 22, figs 1-3.

Material and dimensions. — Maximum height 2.1 mm, width 0.9 mm. — RGM.1365019 (4), leg. ACJ; RGM.1365213 (1), leg. ACJ.

Species characterisation. — Small, solid shell. Protoconch not preserved. Five teleoconch whorls, spire telescopic, whorls weakly convex, surface appears smooth (abraded). Outer lip prosocline in profile and arched. Small columellar fold. Narrow umbilical chink.

Distribution. — **Upper Miocene**: Atlantic, NW France (Landau *et al.* 2020a). — **Upper Pliocene**: western Mediterranean, Estepona Basin, Spain (Landau & Micali 2021). — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

Remarks

This seems to be the same species as that recorded by Landau *et al.* (2020a) from the Upper Miocene of NW France and Landau & Micali (2021) from the Upper Pliocene Estepona Basin of Spain as *Ondina* cf. *micropeas* (Boettger, 1902). Unfortunately, the Pliocene specimens from Estepona and the Selsoif material do not have their protoconchs preserved enabling comparison with the Assemblage I material from NW France. Nevertheless, they share the relatively solid shell, telescopic spire, small columellar fold and narrow umbilical chink.

Genus *Menestho* Möller, 1842

Menestho derivata (Wood, 1879)
(Fig. 14B1-B3)

Odostomia derivata Wood, 1879: 39, unnumbered text-fig. p. 40.

Menestho derivata – Harmer 1920: 583, p. 583, pl. 50, fig. 4.

Material and dimensions. — Maximum height 1.6 mm, width 0.8 mm. — RGM.1365207 (1), leg. AWJ.

Species characterisation. — Shell fusiform. Protoconch type C. Teleoconch of 3.5 convex whorls separated by narrowly impressed suture. Sculpture consist of numerous spiral cords, broader than their interspaces, six on first teleoconch whorl, 18 on last whorl. Last whorl 70% of the total height. Aperture pyriform; outer lip not complete; columella without fold.

Distribution. — **Lower Pleistocene**: NSB, England (Wood 1879; Harmer 1920); Atlantic, Selsoif, NW France (this paper).

Remarks

We tentatively ascribe the specimen to *Menestho derivata* (Wood, 1879), described from the Lower Pleistocene Bramerton Crag (= Norwich Crag) of England. It is similar in sculpture to two extant northern European species: *Menestho albula* (Fabricius, 1780) and *M. truncatula* Odhner, 1915, but both of these species are squatter with more convex whorls.

Genus *Spiralina* Chaster, 1901

Spiralina alpinoligustica (Sacco, 1892)
(Fig. 14C1-C3)

Pyrgulina turbonilloides var. *alpinoligustica* Sacco, 1892: 67, pl. 1, fig. 110.

Spiralina alpinoligustica – Landau & Micali 2021: pl. 84, figs 1-6.

For more, see synonymy list in Landau & Micali (2021).

Material and dimensions. — Maximum height 1.2 mm, width 0.6 mm. — RGM.1365024 (5), leg. ACJ; RGM.1365126 (450+), leg. AWJ; RGM.1365205 (1), leg. AWJ.

Species characterisation. — Small turriform shell. Flat protoconch of one whorl. Teleoconch of 5 flat-sided whorls separated by canaliculated suture with 20 orthocline, axial ribs stopping at adapical cord. Base marked by weakened spiral cord. High, pyriform aperture with one tooth on the inner lip, at the level of a small umbilicus.

Distribution. — First occurences in the Upper Miocene from the Atlantic, NW France (Landau *et al.* 2020a). In the Lower Pliocene, only present in the Mediterranean of Italy (Sacco 1892; Ferrero Mortara *et al.* 1984; Crovato & Micali 1992a; Bogi & Chirli 2004; Chirli & Micali 2011). This species occurs in the Upper Pliocene from the Mediterranean of Estepona Basin, Spain (Landau & Micali 2021), Italy (Crovato & Micali 1992b; Ragaini & Bernieri 2007). Present in the Lower Pleistocene from the Mediterranean of Italy (Crovato & Micali 1992a) and Rhodes (Chirli & Linse 2011). Last fossil occurence in the Upper Pleistocene from Mediterranean, Italy (Crovato & Micali 1992a). Today this species occurs in the Atlantic from northwestern Spain (Trigo *et al.* 2018), south Portugal, Canaries (Hernández *et al.* 2011) to West Africa (Peñas & Rolán 1998; Van Aartsen *et al.* 2000; Peñas *et al.* 2014), and in the Mediterranean (Peñas *et al.* 1996; Giannuzzi-Savelli *et al.* 2014; Micali & Palazzi 1992; Öztürk *et al.* 2011) to the Black Sea (Nordsieck 1972; Wilke & Van Aartsen 1998).

Genus *Chemnitzia* d'Orbigny, 1840

Chemnitzia ?lactea (Linnaeus, 1758)
(Fig. 14D1-D3)

Material and dimensions. — Maximum height 4.3 mm (incomplete), width 1.5 mm. — RGM.1364932 (1), leg. WG; RGM.1365023 (68), leg. ACJ; RGM.794509 (*c.* 95), leg. AWJ.

Species characterisation. — Fragment consisting of last 4.5 whorls, sculptured by broad, curved, opisthocline ribs, wider than their interspaces, stopping abruptly at suprasutural cord and at base.

Distribution. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

Remarks

The character of the spiral sculpture stopping abruptly at a suprasutural cord on the later spire whorls and at the base on the last whorl allows attribution to the genus *Chemnitzia* d'Orbigny, 1840 (see Landau & Micali 2021: 284). The material resembles the modern highly variable *Chemnitzia lactea*, but the general worn appearance and the lack of preserved protoconch make attribution uncertain.

Genus *Turbonilla* Rosso, 1826

Turbonilla indet.
(Fig. 14E1-E3)

MATERIAL AND DIMENSIONS. — Maximum height 1.3 mm, width 0.6 mm. — RGM.1365304 (1) leg. AWJ; RGM.1365305 (1), leg. AWJ; RGM.1365223 (4), leg. AWJ.

SPECIES CHARACTERISATION. — Small, relatively broad turriform shell. Protoconch absent. Last 4.5 teleoconch whorls preserved, whorls rather flat-sided, first two whorls surface abraded, last two whorls with very broad opisthocline ribs separated by narrow interspaces. Pyriform aperture angled at top of straight columella. Subobsolete columellar fold.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, Selsoif, NW France (this paper).

REMARKS
The species from Selsoif has a similar outline to that of *Turbonilla pumila* G. Seguenza, 1876, but with broader ribs and flatter whorls but further identification is not possible.

Genus indet.

Chrysallida indet.
(Fig. 14F1-F3)

MATERIAL AND DIMENSIONS. — Height 1 mm, width 0,52 mm. — RGM.1365029 (1), leg. AWJ; RGM.1365324 (1), leg AWJ, RGM.1310835 (1), leg. AWJ; RGM.1364976 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Small turriform shell. Protoconch heterostrophic. Three convex teleoconch whorls separated by a weakly impressed suture. Sculpture of two spiral cords on spire whorls, with numerous lamellar axial riblets in spiral interspaces. Last whorl with three spiral cords, abapical cord delimiting base, cords broaden and weaken abapically, base rounded, riblets weaken on last whorl, subobsolete. Aperture pyriform, no columellar fold.

DISTRIBUTION. — **Lower Pleistocene**: Atlantic, endemic to Selsoif (this paper).

REMARKS
This single specimen has very distinctive sculpture of strong spirals and riblets in the interspaces. It might represent an *Iolaea* A. Adams, 1868 species, but members of that genus usually have three spiral cords on all teleoconch whorls.

Family ELLOBIIDAE Pfeiffer, 1854
Genus indet.

"***Ellobium*" *pyramidale*** (J. de C. Sowerby, 1822)
(Fig. 14G1-G3)

Auricula pyramidalis J. de C. Sowerby, 1822: 109, pl. 379, fig. 12.

Ellobium pyramidale – Ceulemans *et al.* 2018: 140, pl. 9, figs 3-5.

For more, see synonymy list in Ceulemans *et al.* (2018).

MATERIAL AND DIMENSIONS. — Maximum height 23.5 mm, width 13.2 mm. — RGM.1364933 (7), leg. WG; RGM.1365025 (11), leg. ACJ; RGM.1365127 (15), leg. AWJ; RGM.1365208 (1), leg. AWJ.

SPECIES CHARACTERISATION. — Shell medium sized, globular, teleoconch composed of about eight smooth whorls, except for subsutural cord (abraded in most specimens); spire whorls flat-sided, last whorl inflated, aperture elongate-ovate with two narrow columellar teeth, narrow, deep umbilicus.

DISTRIBUTION. — **Lower Pliocene**: NSB, Red Crag, England (Harmer 1923); Atlantic, NW France (Ceulemans *et al.* 2018). — **Upper Pliocene**: Atlantic, St Erth, England (Harmer 1923); NSB, Red Crag, England (Wood 1848; Harmer 1923), Oorderen Sands, Belgium (Marquet 1997). — **Pliocene** (indeterminate): NSB, Netherlands (Van Regteren Altena *et al.* 1964). — **Upper Pliocene-Pleistocene**: Atlantic, NW France (Brébion 1964). — **Lower Pleistocene**: Selsoif, NW France (this paper).

REMARK
This is the only terrestrial pulmonate gastropod in the Selsoif fauna. Ellobiids typically live in supratidal habitats. This species has usually been placed in the genus *Ellobium* Röding, 1798 but Harzhauser *et al.* (2023) showed that *Ellobium* is an Indo-Pacific genus that disappeared from the European faunas around the Oligocene/Miocene boundary. Therefore, attribution to a more appropriate genus is required but that is beyond the scope of this work.

DISCUSSION

The gastropod fauna of Selsoif contains 76 species-level taxa (Table 1). Abundant species are *Haustator incrassata*, *Nucella lapillus* and *Spiralina alpinoligustica*. Other very common species are *Tectura virginea*, *Steromphala cineraria*, *Littorina littorea* and *Rissoa curticostata*. The Selsoif fauna represents shallow marine settings with present-day ranges of most species centred around shallow subtidal to intertidal habitats. Typical intertidal to supratidal groups include *Patella, Littorina, Nucella* and "*Ellobium*". Many of the common taxa such as the rissoids, *Lacuna, Littorina obtusata* and *Bittium* are known to graze or live on seagrass, seaweed and/or red algae in the photic zone. The single species that represents strict brackish or euryhaline settings (*Ecrobia* cf. *ventrosa*) is known from a single specimen; all other taxa occur in euhaline and or polyhaline salinities. Six species are known only from the Selsoif fauna, *viz*. *Calliostoma normanensis* n. sp., *Seila selsoifensis* Marquet, 2001, *Seila quinquecarinata* n. sp., *Alvania selsoifensis* n. sp., *Admete trigostomoides* n. sp. and *Moelleria jansseni* Hoeksema, Rijken & Simons, 2020. *Velutina* aff. *velutina* and *Cryptonatica* sp. may also represent new species, although we are hesitant to formally describe them based on the material at hand. A further 17 species are extinct. A small number of worn specimens are present in the assemblage that are derived from Eocene deposits known to occur in the subsurface in the region These derived shells include *Nerita* s. lat., *Bittium* cf. *cancellatum*, *Hipponix* indet. and an indeterminate cerithid.

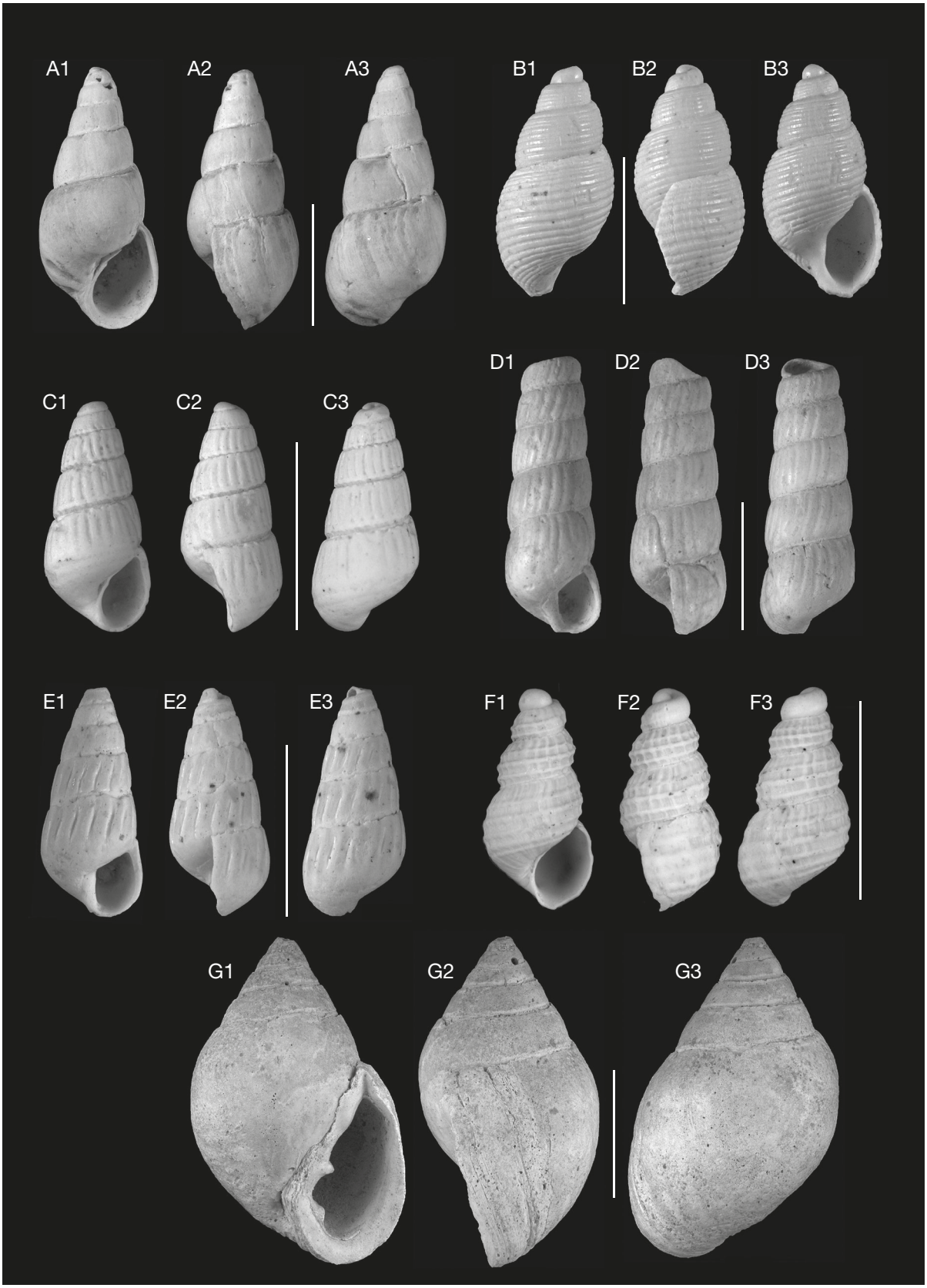

Fig. 14. — Gastropods from Selsoif. All illustrated specimens are collected from the Sablière du Grand Marais, Selsoif, France and come from the Early Pleistocene Saint-Nicolas de Pierrepont Formation (continuation): **A**, *Ondina* cf. *micropeas* (Boettger, 1902), RGM.1365213, leg ACJ, H = 2.13 mm; **B**, *Menestho derivata* (Wood, 1879), RGM.1365207, leg AWJ, H = 1.56 mm; **C**, *Spiralina alpinoligustica* (Sacco, 1892), RGM.1365205, leg AWJ, H = 1.23 mm; **D**, *Chemnitzia* ?*lactea* (Linnaeus, 1758), RGM.1364932, leg WG, H = 4.39 mm; **E**, *Turbonilla* indet., RGM.1365305, leg AWJ, H = 1.32 mm; **F**, *Chrysallida* indet., RGM.1365324, leg AWJ, H = 1.12 mm; **G**, "*Ellobium*" *pyramidale* (J. de C. Sowerby, 1822), RGM.1365208, leg AWJ, H = 13 mm. Scale bars: A-C, E, F, 1 mm; D, 2 mm; G, 5mm.

The studied fauna contains a number of groups with very different biogeographic affinities (Table 1). The vast majority of the fauna consists of extant species, all of which live in the Boreoceltic, Franco-Iberian to Mediterranean realm. This component has a distinct modern littoral character and includes species such as *Patella rustica*, *Steromphala cineraria*, *Jujubinus exasperates* and *Tritia* spp. A smaller component, including taxa such as *Lacuna* spp., has a distinct boreal distribution with their modern southern distribution limits typically in the northern Gulf of Biscay. The fauna contains common species such as *Littorina*, *Nucella* and *Boreoscala* species that are thought to be descendants of Pacific immigrant species (Vermeij 1991) that reached the Atlantic during the Pliocene.

The Selsoif fauna is predominantly a modern East Atlantic littoral fauna, but with some transitional components. The fauna has almost no species in common with the Tortonian-Zanclean faunas from the lower Loire and Brittany region of Assemblages I-III (of Van Dingenen *et al.* 2015; commonly referred to as the Redonian). Their Assemblage IV (Upper Pliocene-Pleistocene) may share more species in common with that of Selsoif but is at present too poorly known to be certain (BL personal observation). Although the Selsoif assemblage has previously been associated with the 'Redonian' (e.g., Marquet 2001), the latter term is now restricted to Miocene-Pliocene associations in the Ligerian Gulf (see Landau *et al.* 2020b) and should not be applied to Selsoif.

There are some species in common with the latest Pliocene St Erth Beds from Cornwall and the Bosq d'Aubigny fauna from the Cotentin, but both faunas represent different, calmer depositional settings. Furthermore, both the St Erth and the Bosq d'Aubigny faunas require revision and further description to enable meaningful comparisons with the Selsoif fauna. The Selsoif fauna has several species in common with Late Pliocene and especially Early Pleistocene faunas from the North Sea Basin. Species in common with the Early Pleistocene Norwich and Weybourne Crag Formations of eastern England and the Dutch Maassluis Formation are *Littorina littorea*, *Rissoa curticostata, Nucella lapillus, Buccinum undatum* and *Peringia ulvae* (Slupik *et al.* 2007; Preece *et al.* 2020). *Neptunea inversa* is known from the "Tiglian" Weybourne Crag Formation of eastern England.

Remarkably, three extinct species are present in the Selsoif fauna that were known previously only from North Sea Basin Pliocene, viz. *Bittium rubanocinctum*, *Haustator tricarinata* and *Boreoscala similis*. These possibly represent relict species. The larger part of the Selsoif fauna consists of extant species known from the eastern temperate Atlantic. Several of the common species in this category are known from Middle-Late Pleistocene interglacial deposits from the North Sea Basin (Meijer *et al.* 2021; Wesselingh *et al.* 2023) and the south coast of England. (Harmer 1917). It concerns common species such as *Diodora graeca, Steromphala cineraria, Bittium jadertinum, Tritia reticulata* and *T. incrassata*. These species are unknown from Early Pleistocene deposits of NW Europe other then Selsoif and underline the transitional nature of the Selsoif fauna between Early Pleistocene and modern eastern Atlantic faunas.

CONCLUSIONS

The Gelasian gastropod fauna from Selsoif (Cotentin, France) represents a diverse marine littoral fauna that is dominated by extant species but also contains a few endemics and some Pliocene relict species. The biogeographical affinity of the fauna is one that is typical of the southern part of the Boreo-Celtic and northern part of the French-Iberian province but the overall assemblage differs from Late Quaternary/modern assemblages in the region in terms of species composition. The Selsoif fauna therefore forms a transition between Pliocene and modern faunas in the temperate East Atlantic domain and shows that the modern nature of molluscan faunas already existed in the Early Pleistocene.

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