


NEWS FROM THE WESTERN FRONT: OCCURRENCE OF *MEDITERRANEA DEPRESSA* (STERKI, 1880) (MOLLUSCA: GASTROPODA: OXYCHILIDAE) IN THE VOSGES AND JURA MOUNTAINS (NORTH-EASTERN FRANCE)

JEAN-MICHEL BICHAIN^{1*}, JULIEN RYELANDT²

¹ Malacologie, Musée d'Histoire naturelle et d'Ethnographie de Colmar, 11 rue Turenne, 68000, Colmar, France (e-mail: jean-michel.bichain@museumcolmar.org);  <https://orcid.org/0000-0003-3849-9364>

² Malacologie, CBNFC-ORI, Conservatoire Botanique National de Franche Comté – Observatoire régional des Invertébrés, France;  <https://orcid.org/0000-0001-6419-8069>

*corresponding author

ABSTRACT: We report here the first record of *Mediterranea depressa* (Sterki, 1880) in the north-eastern quarter of France, in the Vosges and Jura massifs. After the fortuitous discovery of some shells attributed to *M. depressa* in the southern Vosges Mts., an extensive sampling campaign was carried out both in the Vosges and in the Jura Mts. In total, about 20 shells and seven live specimens were found at eight localities, which, according to the present state of our knowledge, represent its north-western range limit. The species was found exclusively under stones of rocky slope screes on siliceous and calcareous substrates. Some of these habitats could be described as Mesovoid Shallow Substratum. It is not clear whether the rarity of the species is an effect of under-sampling or of its small size and unusual habitat or/and to intrinsic rarity due to isolated populations at the distribution limits of the species. The extreme north-eastern quarter of France constitutes an oceanic-continental transition zone where about thirty gastropod species from Central and Eastern Europe are currently documented at the western limit of their ranges.

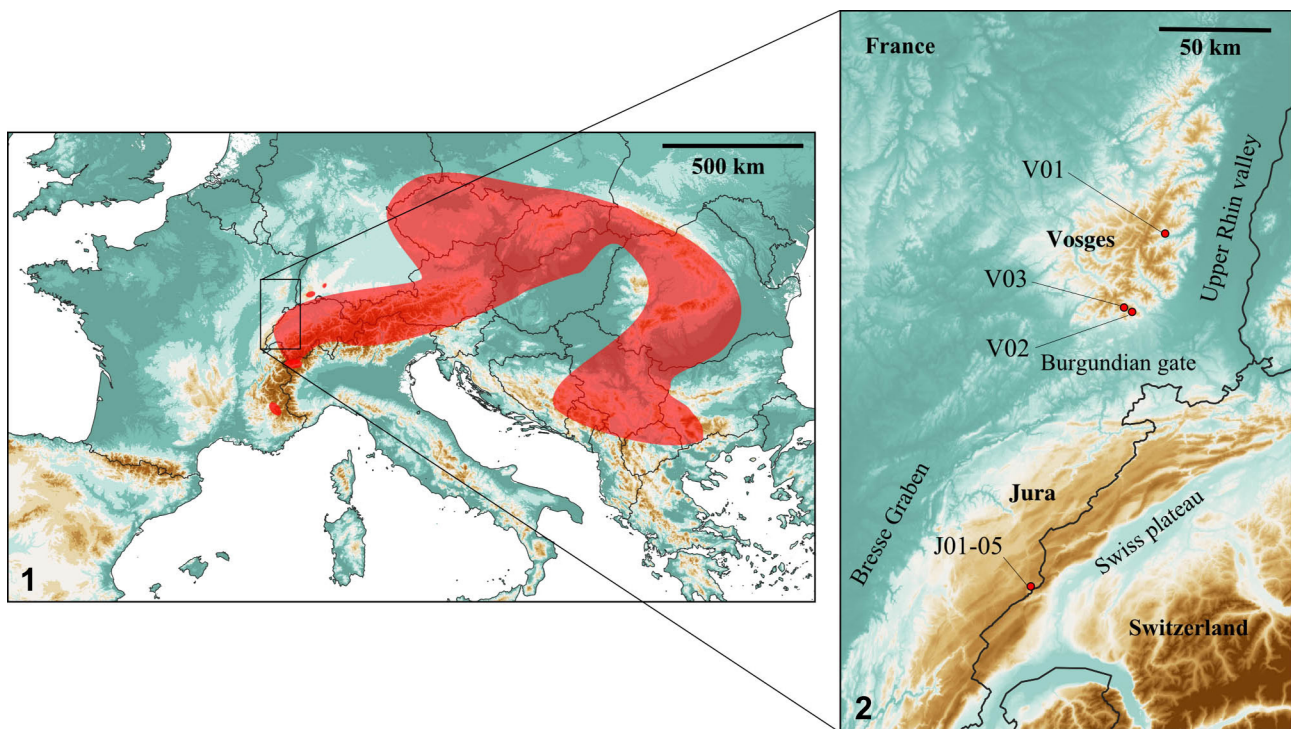
KEY WORDS: Jura; Vosges; slope screes; *Mediterranea depressa*; biogeographic limit; Mesovoid Shallow Substratum

INTRODUCTION

The Flat Gloss snail, *Mediterranea depressa* (Sterki, 1880), is a Carpathian-Alpine species with a wide distribution in Eastern and Central Europe that extends from the eastern border of France to the Romanian Carpathians (Fig. 1). The species reaches the Black Forest in Germany and Poland in the north, and northern Greece at the southern limit of its range. It also occurs in the mountain areas of Albania (FEHÉR & ERŐSS 2009), Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czech and Slovak Republics (HORSÁK et al. 2013), Germany, Hungary, Italy (CIANFANELLI et al. 2005), Liechtenstein, Montenegro, North Macedonia, Serbia, Slovenia and

Switzerland (RÜETSCHI et al. 2012) (for overview see WELTER-SCHULTES 2012 and NEIBER 2017).

According to WELTER-SCHULTES (2012), this species is mainly found in moderately humid and rocky forests, but also in various other habitat types such as open grassy mountain slopes above the tree line or in habitats with scattered shrubs or trees. It also inhabits rocks rich in crevices and colonises retaining walls of dry stones (RÜETSCHI et al. 2012) or ruins of mediaeval castles (JUŘIČKOVÁ & KUČERA 2004). It occurs mainly on calcareous substrates but also tolerates siliceous substrates and reaches elevations of up to 2,600 m in Switzerland and 2,000 m in Italy.



Figs 1–2. *Mediterranea depressa* (Sterki, 1880): 1 – Geographic distribution of *Mediterranea depressa* (Sterki, 1880) after WELTER-SCHULTES (2012) and NEIBER (2017); 2 – sampling sites in north-eastern France (see Material and Methods for details of each locality). Locality V01, Mittlach, Haut-Rhin, alt. 601 m; locality V02, Lamadeleine-Val-des-Anges, Territoire de Belfort, alt. 560 m; locality V03, Riersvescemont, Territoire de Belfort, alt. 675 m; localities J01-05, Jougne, Doubs, alt. from 1,155 m to 1,300 m a.s.l.

The Flat Gloss snail is also reported from subterranean and edaphic environment, in caves (NEGREA 1975, KOCOT-ZALEWSKA & DOMAGAŁA 2020), within superficial subterranean habitats up to 65 cm deep (RENDOŠ et al. 2014) and frequently in mountain scree slope areas (CIANFANELLI et al. 2005). For these reasons, *M. depressa* can be regarded as a species with a tolerance or affinity to subterranean habitats.

The western edge of the Alps in Switzerland, Italy and France currently represents the western limit of the species' distribution. In the Swiss Alps, except the south of Tessin and westernmost Switzerland, the species has been documented from about 130 localities (François CLAUDE 2021, personal communication). CIANFANELLI et al. (2005) recorded it in two isolated localities in the westernmost Italian Alps, one of which is on the border with France.

In France, *M. depressa* was first recorded by FAVRE (1927) from the Haute-Savoie Alps near Cluses.

According to the INPN collaborative database (<https://inpn.mnh.fr>, accessed July 15th, 2021), the species is still poorly documented in France with only eight records, all located in two adjacent valleys in the Alps of Haute-Provence. However, it remains unclear whether its rarity reflects insufficient field research in hypogean habitats or/and the scattered distribution and low density of its populations at the fringes of its range.

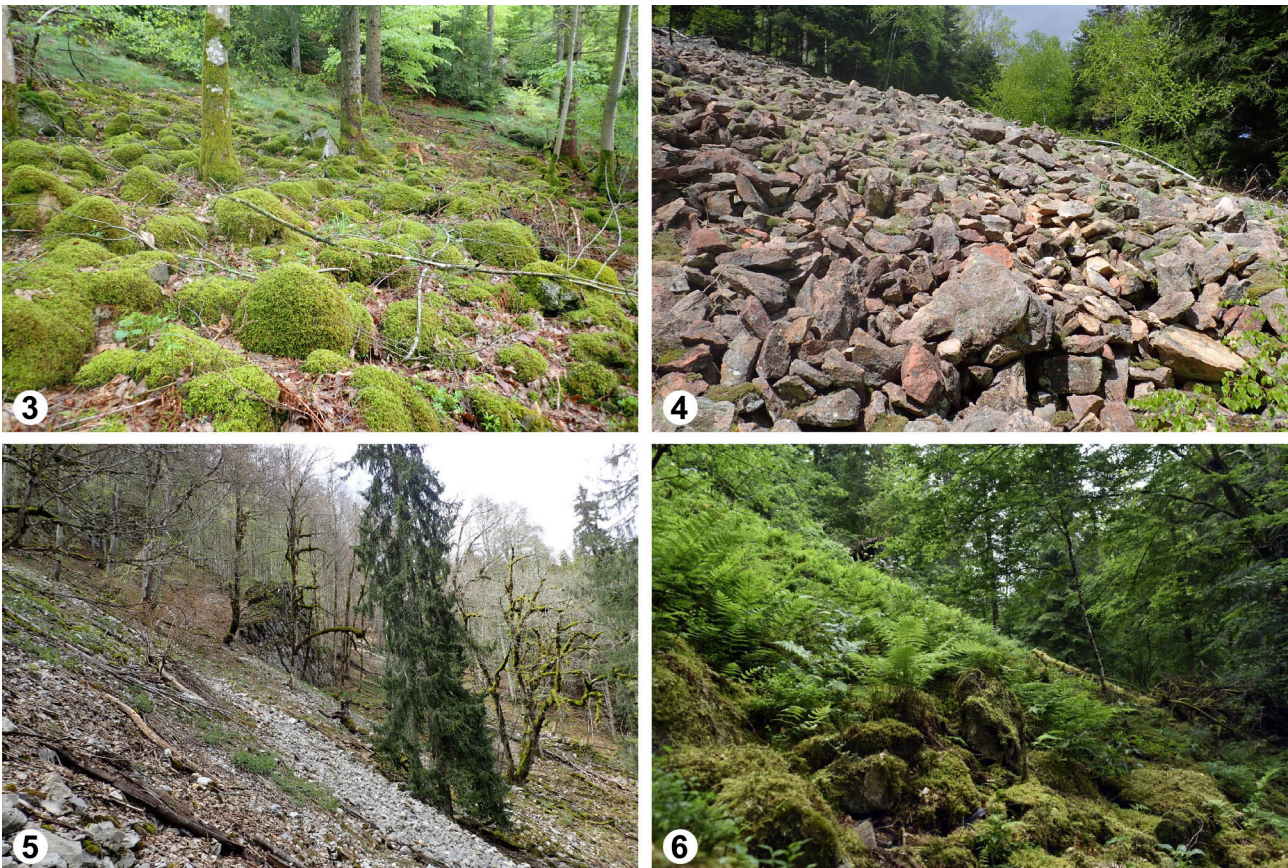
After the fortuitous discovery by one of us (JR) of an empty shell attributable to *M. depressa* in the south of the Vosges Mts. (north-eastern France), an extensive campaign was carried out not only in the Vosges but also in the Jura. The main objectives of this article are (1) to provide diagnostic characters that allow the unambiguous identification of this species and its distinction from other oxychilid species, (2) to provide a description of its habitats, and (3) to present the accompanying gastropod assemblages.

MATERIAL AND METHODS

STUDY AREA AND SAMPLING METHODS

The study area includes the southern Vosges and Jura mountain ranges in north-eastern France (Fig. 2) which are located in the two administrative re-

gions of Grand Est and Bourgogne-Franche-Comté (BICHAIN et al. 2021). The Vosges are a low mountain range (highest point 1,424 m) located near the German border. With the Palatinate Forest on the German side, to the north, they form a single geo-



Figs 3–6. Sampling sites of *Mediterranea depressa* (Sterki, 1880) in the Vosges and Jura mountains: 3 – scattered granitic scree on a gentle slope in a forested landscape, southern Vosges (locality V02, Lamadeleine-Val-des-Anges); 4 – scree dotted with a few fir and birch trees, southern Vosges (locality V03, Riervescemont); 5 – beech-fir forest on limestone scree, Jura (locality J02, Jougne); 6 – granitic scree on a steep slope with a thick and dense moss cover, beech wood, central Vosges (locality V01, Mittlach)

morphological unit of about 8,000 km². The Vosges form a SW–NE-oriented relief and represent the western border of the Upper Rhine Valley, the Black Forest in Germany forming its eastern boundary. The southern and central parts of the massif, also called the High Vosges, are mainly constituted by granites, gneiss, and volcanic rocks (ELLER et al. 1970b, FLÜCK et al. 1991). The northern of the massif is covered by sandstones (ELLER et al. 1970a). The Vosges are located in a transition zone between oceanic and continental climates, with average annual temperature and precipitation at the highest altitudes of about 4 °C and 2,000 mm, respectively.

The Jura can be broadly defined as a folded limestone massif marked by a continental mountain climate with a surface area of 14,000 km² that extends over 340 km from north to south and delimits a long part of the French-Swiss border with the highest point at 1,720 m. At this altitude, the average annual temperature and precipitation are about 1 °C and 1,900 mm, respectively. Shaped like a crescent, 70 km wide at its widest point, it is delimited by the Bresse Graben to the west and the Swiss plateau to the east, the Burgundian gap (also called the Belfort gap) to

the north which separates it from the Vosges massif, and it extends southwards to the Bugey plateau. It is characterised by a multitude of folds and plateaus with a rich karstic network and incised with valleys, as well as numerous depressions sheltering peaty complexes.

In these two areas, sampling was carried out mainly in scree slopes, habitats documented as favourable to *M. depressa* (CIANFANELLI et al. 2005, RENDOŠ et al. 2014). In order to access the interstitial zone, it was often necessary to remove the upper layer of vegetation, soil and litter. Specimens were collected directly by hand. In addition, both live individuals and empty shells of all gastropod species encountered on the surface, or within the excavations, were recorded.

SHELL MEASUREMENTS AND ANATOMY OF THE REPRODUCTIVE SYSTEM

Empty shells of *M. depressa* were mounted on an adhesive support to aid shell orientation and then imaged with a graduated scale using a stereomicroscope connected to a digital camera. Six parameters were recorded on each picture using the ToupView

software version 3.7: height (SH) and width (SW) of the shell, aperture height (AH) and width (AW), umbilicus width (UW) and number of whorls (NW) (see HUANG et al. 2014: fig 1, for details of the measurements performed).

Live juveniles and adults were photographed in the laboratory using a Nikon D700 camera equipped with a 150 mm macro lens. For anatomical studies, animals were drowned in water for about 12 hours and then preserved in a 75% ethanol solution. Bodies were extracted by breaking the shells with round-tip tweezers. All dissections were performed under a stereomicroscope using thin-pointed forceps. Reproductive systems were dissected out and photographed. Line drawings were done by hand from the photographs. The nomenclature used here to describe the different parts of the reproductive system follows CIANFANELLI et al. (2005).

RESULTS

Family Oxychilidae Hesse, 1927 (1879)

Genus *Mediterranea* Clessin, 1880

Mediterranea depressa (Sterki, 1880)

Basionym: *Hyalina depressa* STERKI 1880: 104–105

Previous generic assignments:

Oxychilus depressus: GERMAIN (1931), KERNEY et al. (1999), WELTER-SCHULTES (2012), HORSÁK et al. (2013);

Oxychilus (Morlina) depressus: RIEDEL (1957);

Oxychilus (Riedelius) depressus: HUDEC (1961), RIEDEL (1969), NEGREA (1975);

Mediterranea depressa: FALKNER et al. (2001, 2002), BANK & NEUBERT (2017);

Riedeliconcha depressa: SCHILEYKO (2003), SYSOEV & SCHILEYKO (2009).

Systematics: There is no clear consensus on the taxonomic contours of genera within the Oxychilidae (RIEDEL 1980, 1998), in particular for the former subgenera traditionally included in *Oxychilus* Fitzinger, 1833 (for overview see CIANFANELLI et al. 2005) and ranked as full genera by FALKNER et al. (2001, 2002) and currently adopted in MolluscaBase (www.molluscabase.org, accessed July 15th, 2021). A global revision of the Oxychilidae using integrative taxonomic approaches (DAYRAT 2005) combining morpho-anatomical and molecular characters is necessary to evaluate phylogenetic groupings within the family. A family revision is beyond the scope of this paper and we follow CIANFANELLI et al. (2005) in assigning the nominal species *Hyalina depressa* Sterki, 1880 to the genus *Mediterranea* Clessin, 1880.

The nomenclature of all the taxa cited in this article follows MolluscaBase (www.molluscabase.org, accessed July 15th, 2021).

ABBREVIATIONS

Institutions and collections: MHNEC – Musée d’Histoire naturelle et d’Ethnographie, Colmar (France); CBNFC-ORI – Conservatoire Botanique National de Franche-Comté – Observatoire régional des Invertébrés, Besançon (France); JMBC – J.-M. Bichain collection, Colmar (France)

Anatomical description (text and Fig. 16): BC – bursa copulatrix; DBC – duct of bursa copulatrix; E – epiphallus; FO – free oviduct; P – penis; POS – prostatic portion of spermoviduct; PR – penial retractor; PS – penial sheath; UOS – uterine portion of spermoviduct; V – vagina; VD – vas deferens; VG – vaginal gland.

Material examined:

France, Vosges: **V01** – Mittlach, Haut-Rhin, 48°00'16.35"N, 07°01'00.90"E, alt. 601 m, collector J.-M. BICHAIN, 03/06/2021, 3 empty shells and 3 live specimens (2 adults and 1 juvenile), MHNEC and JMBC; **V02** – Lamadeleine-Val-des-Anges, Territoire de Belfort, 47°44'56.5"N, 06°54'54.5"E, alt. 560 m, collectors J. RYELANDT and J.-M. BICHAIN, 02/06/2020 and 12/05/2021, 4 empty shells, 2 live juveniles, CBNFC-ORI; **V03** – Riervescemont, Territoire de Belfort, 47°45'58.5"N, 06°51'53.6"E, alt. 675 m, collectors J. RYELANDT and J.-M. BICHAIN, 2 empty shells, 2 live juveniles, collection CBNFC-ORI; **Jura: J01** – Jougne, Doubs, 46°43'28.0"N, 06°21'56.8"E, alt. 1,155 m, collector J. RYELANDT, 18/05/2021, 3 empty shells; **J02** – Jougne, Doubs, 46°43'40.8"N, 06°21'35.5"E, alt. 1,300 m, collector J. RYELANDT, 18/05/2021, 2 empty shells; **J03** – Jougne, Doubs, 46°43'27.7"N, 06°21'40.3"E, alt. 1,235 m, collector J. RYELANDT, 18/05/2021, 1 empty shell; **J04** – Jougne, Doubs, 46°44'19.5"N, 06°21'28.0"E, alt. 1,160 m, collector J. RYELANDT, 14/05/2021, 1 empty shell; **J05** – Jougne, Doubs, 46°44'16.3"N, 06°21'24.1"E, alt. 1,200 m, collector J. RYELANDT, 14/05/2021, 5 empty shells.

Habitats: In the Jura Mts (Fig. 2), *M. depressa* was sampled at Jougne in a cold mountain cirque with a north-east exposure at the foot of Mont d’Or, the highest point of the Doubs département. The area is characterised by the presence of cold chimney scree sheltering many plant species with an affinity for subalpine habitats (FERNEZ et al. 2007). Empty shells were collected under rocks at five points (lo-

calities J01 to J05) spread among two large limestone screes, covered by beech-fir forest, between 1,155 and 1,300 m in altitude (Fig. 5). A total of 39 gastropod species were observed (Appendix 1). The list of accompanying species is strongly biased towards the presence of taxa with montane affinities, such as *Cochlodina fimbriata* (Rossmässler, 1835), *Discus ruderatus* (W. Hartmann, 1821), *Ena montana* (Draparnaud, 1801), *Eucobresia diaphana* (Draparnaud, 1805), *Isognomostoma isognomostomos* (Schröter, 1784), *Macularia sylvatica* (Schröter, 1784) or *Trochulus villosus* (Draparnaud, 1805).

In the Vosges Mts. (Fig. 2), empty shells and/or live animals were found at three distinct locations (localities V01 to V03) in beech or beech-fir forests on screes at altitudes between 560 and 675 metres. Two sites (V02 and V03) are situated in deep valleys located in the southern Vosges in the Territoire

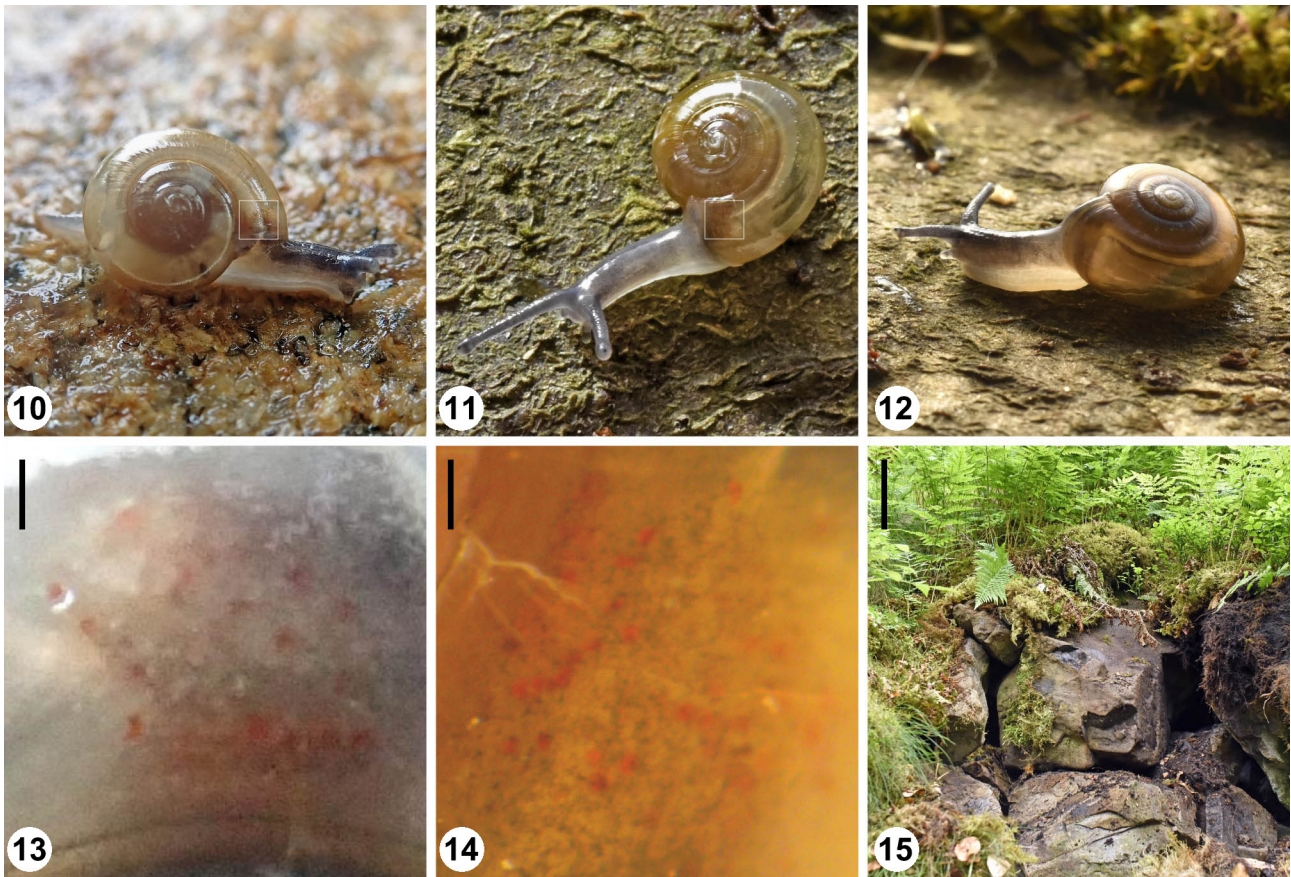
de Belfort département (Figs 3–4) and one (V01) is located at a valley entrance in central Vosges, in the Haut-Rhin département (Fig. 6).

The Rievescemont locality (V03) is a very open landscape, consisting of a scree dotted with a few fir and birch trees (Fig. 4). The Lamadeleine-Val-des-Anges locality (V02) is a small and relatively flat scree with dense leaf-litter between boulders within a beech-fir forest (Fig. 3). A total of 11 gastropod species were observed in this habitat (Appendix 1).

In Mittlach (V01), *M. depressa* was collected in a large and deep granitic scree on a steep slope with sparse beech trees and a dense, continuous, understory mainly composed of mosses and ferns (Figs 6, 15). A total of 13 gastropod species were observed in this habitat (Appendix 1). Only *A. arbustorum*, *I. isognomostomos* and *O. cellarius* were observed syntopical-



Figs 7–9. Shells of *Mediterranea depressa* (Sterki, 1880): 7 – specimen from Lamadeleine-Val-des-Anges (locality V02), southern Vosges (shell diameter = 8.45 mm); 8 – specimen from Jougne (locality J03), Jura (shell diameter = 8.25 mm); 9 – specimen from Jougne (locality J05), Jura (shell diameter = 8.28 mm). Scale bar 4 mm



Figs 10–15. Live specimens and micro-habitat of *Mediterranea depressa* (Sterki, 1880) in the Vosges Mountains: 10 – juvenile specimen from Riervescemont (locality V03, shell diameter = 7.9 mm); 11 – juvenile specimen from Mittlach (locality V01, shell diameter = 5.80 mm); 12 – adult specimen from Mittlach (shell diameter = 8.11 mm); 13 – red dots on the mantle present in the specimen illustrated in Fig. 10; 14 – red dots on the mantle present in the specimen illustrated in Fig. 11; 15 – interstitial rock system where live specimens were sampled at Mittlach. Scale bars 0.2 mm (13–14) and 25 cm (15)

ly with *M. depressa* between the boulders, deep under the vegetation cover.

At all sites in the two massifs, empty shells and live individuals of *M. depressa* were exclusively collected under boulders, adhering to them or in the underlying litter.

Shell morphology and soft body tissue coloration:

Of the total of 21 shells (Figs 7–9), 11 adult ($NW \geq 4$) and unbroken shells were measured. Adult shells are flat, usually white or pale yellowish to brownish yellow, thin and translucent with about 4.0–4.5 weakly convex whorls. The shell sculpture of axial striae is not very pronounced except near the suture, which gives the shell a shiny appearance. The shells reach a diameter of up to 8.7 mm (SW: mean = 7.87 ± 0.75 mm, range 6.29–8.72 mm) and 4 mm in height (SH: mean = 3.72 ± 0.29 mm, range 3.08–4.04 mm). The aperture is up to 4.68 mm in width (AW: mean = 4.15 ± 0.41 mm, range 3.33–4.68 mm) and up to 3.42 mm in height (AH: mean = 3.13 ± 0.22 mm, range 2.67–3.42 mm). The umbilicus is deep, narrow, with a diameter (UW: mean = 0.51 ± 0.09 mm,

range 0.38–0.64 mm) not exceeding one sixth of the aperture width (AW) or about one thirteenth of the shell width (SW).

Two live adults and five juveniles were examined (Figs 10–14). The body of the animal is light blue-grey, slightly darker dorsally and on the head. In juveniles, red mantle glands are visible through the translucent upper side of the body whorl (Figs 13–14). A few red spots may remain in young adults, but most granulations become milky white in adults.

All these characters correspond perfectly with the previous descriptions of the species (GERMAIN 1931, KERNEY et al. 1999, WELTER-SCHULTES 2012, HORSÁK et al. 2013).

Reproductive system: Two adult individuals were examined. The penis (P) has a cylindrical base expanding apically (Fig. 16) and a short, thick epiphallus (E), which extends over about 1/3 of the penis length. The epiphallus is attached laterally along the penis by connective tissue. The penial retractor (PR) and epiphallus are inserted apically on the penis. The distal part of the penis is covered by a sheath (PS)

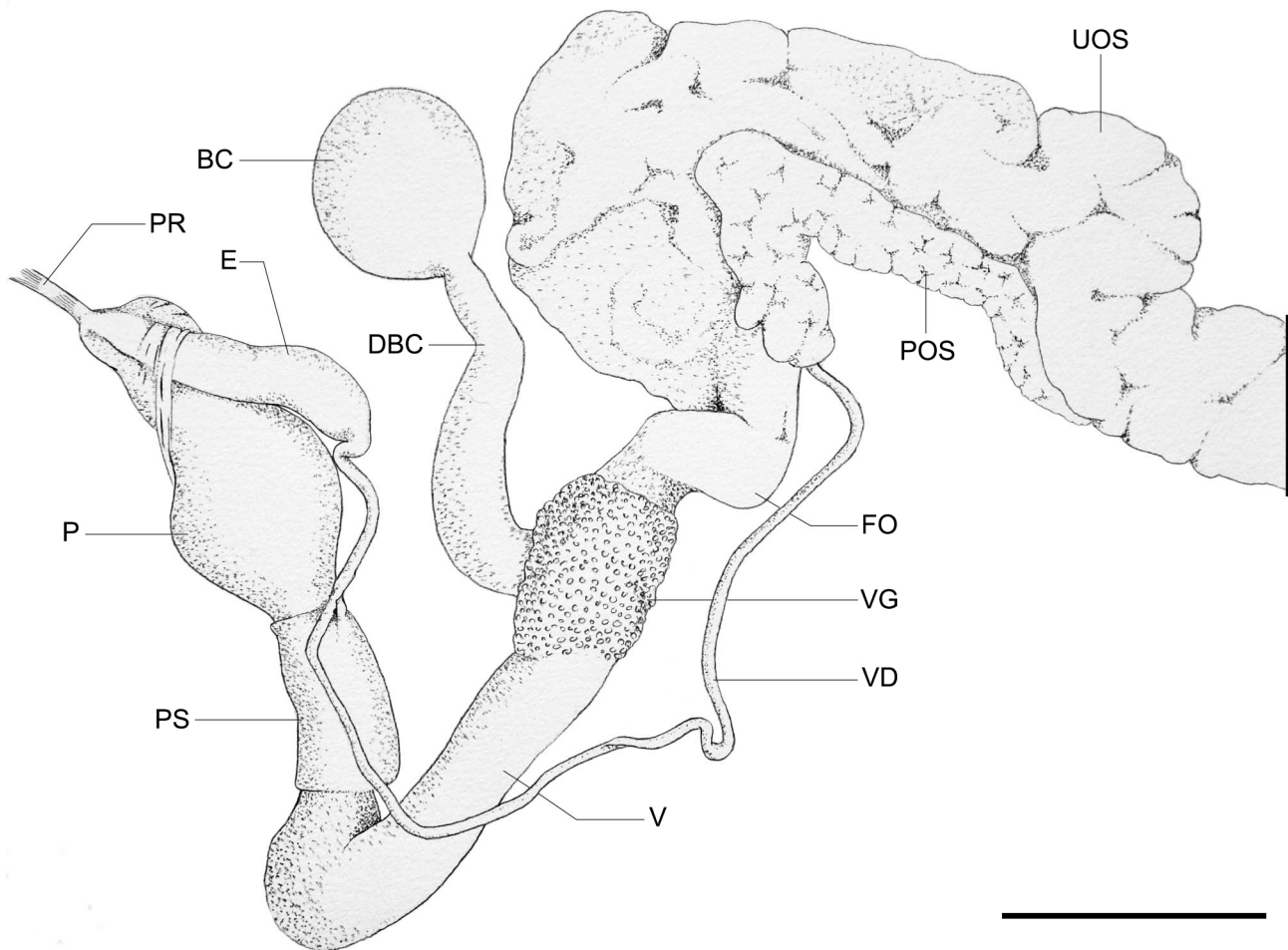


Fig. 16. Distal part of the reproductive system of a specimen of *Mediterranea depressa* (Sterki, 1880) from the Vosges Mountains at Mittlach (locality V01). For lettering see Abbreviations. Scale bar 1 mm

from which adhesions connect to the vas deferens (VD). The internal sculpture of the penis consists of pleats and rows of papillae, some or all with apical thorns (not illustrated here, observed by us on one of the two specimens). However, the apical spines may be missing in sub-adult specimens (CIANFANELLI et al. 2005) and this is probably the case of the second specimen. In addition, the inner wall of the epiphallus shows series of transverse pilasters on one side and a few slender longitudinal pilasters on the other. The perivaginal gland (VG) consists of dense, yellowish

glandular tissue which covers the distal part of the free oviduct (FO) but also part of the vagina (V) at the junction with the insertion of the bursa copulatrix duct (DBC). The bursa copulatrix (BC) is round and, in anatomical position, embedded within the folds of the uterine portion of the spermoviduct (UOS).

All these anatomical characters also match the description of the species given in the literature (RIEDEL 1957: figs 29–31, 1969: figs 12 and 16–19, NEGREA 1975, CIANFANELLI et al. 2005: figs 6 and 9).

DISCUSSION

We report here the first record of *M. depressa* in north-eastern France, in the Vosges and Jura massifs. The live specimens, shells and reproductive anatomy of the specimens we sampled and examined match the diagnostic characters provided for the species (RIEDEL 1957, 1969, NEGREA 1975, KERNEY et al. 1999, CIANFANELLI et al. 2005). The species differs from *Oxychilus cellarius* and *O. navarricus* in having a

much narrower umbilicus and from *Morlina glabra* in having a much lower spire and a smaller adult size. Besides, the shells of *M. depressa* have a translucent white colouration unlike the dark brown shells of these other species, except for *O. cellarius* which is very similar both in shell and body colour. However, whereas atypical specimens of *M. glabra* may have shell morphology or colour resembling those of *M.*

depressa (JULIEN RYELANDT, unpublished data), the characters of the reproductive system can be used to differentiate the two species. *M. depressa* presents a penis distinctly bulging in its apical half, which is not the case in *M. glabra*. In addition, *M. glabra* has a large fold on the inner wall of the penis, absent in *M. depressa*. Furthermore, juvenile *M. depressa* can be distinguished by the presence of red spots on the upper and distal part of the mantle. This pigmentation is clearly visible through the shell at the end of the body whorl. To our knowledge, this character was only reported by CIANFANELLI et al. (2005) and WELTER-SCHULTES (2012) and therefore we cannot state whether it can be used as a reliable diagnostic feature.

As far as we know, the localities described here in north-eastern France represent the westernmost occurrences of the species (WELTER-SCHULTES 2012, NEIBER 2017). Although never recorded before, the presence of the species in this area is not surprising. Indeed, the natural habitats of the Vosges are relatively close to those found further east in the Black Forest mountains (Germany) where the species was already documented (www.bw.mollusca.de, accessed July 15th, 2021). Moreover, its presence on the other side of the border in the Swiss Jura – although very rare and localised (www.cscf.ch, accessed July 15th, 2021) – made its presence very likely on the French side.

Current knowledge of molluscs in north-eastern France is based on nearly 60,000 records for 272 continental species including 144 terrestrial gastropods (BICHAIN et al. 2021). By comparison, Switzerland and Baden-Württemberg, with areas two to three times smaller than that of these two regions of north-eastern France, are documented by approximately 280,000 records (for 293 mollusc species, of which 211 are terrestrial, www.cscf.ch) and 85,000 records (for 266 species, of which 166 are terrestrial, ARBEITSGRUPPE MOLLUSKEN BW 2008), respectively (RÜETSCHI et al. 2012, FRANÇOIS CLAUDE 2021, personal communication). This represents a sampling effort four times less intensive in this part of France than in the neighbouring areas of Switzerland and Germany and may explain why the presence of *M. depressa* has remained unreported until now in north-eastern France.

We only found *M. depressa* in various types of scree and/or boulder fields. These habitats are not strictly classified (MAMMOLA et al. 2016) as Mesovoid Shallow Substratum (MSS, CULVER & PIPAN 2013; originally called Milieu Souterrain Superficiel by JUBERTHIE et al. 1980), but share common characteristics with that category. In general, MSSs are aphotic near-surface habitats (< 10 metres) and consist of air-filled void systems within rocky fragments, usually regarded as suitable for the survival of troglobiont

organisms (MAMMOLA et al. 2016). The MSSs are regarded as intermediate zones between the superficial soil horizons (edaphic area) and the deep subterranean environments, which are represented by caves and deep fissure systems. Some authors disagree with this view and consider MSSs as full-fledged subterranean habitats and not as transitional zones (GIACHINO & VAILATI 2010). In addition to the absence of light, MSSs are characterised by attenuated daily and annual temperature fluctuations, generally higher humidity than at the surface and overall higher allochthonous energy inputs from the surface than in deep subterranean environments (CULVER & PIPAN 2019). The fauna is composed of troglobionts, i.e. organisms that are strictly subterranean, but also of other organisms that can spend their entire life cycle underground. These may actively or accidentally colonise the MSS. Knowledge of molluscs in these habitats remains very patchy because sampling is particularly difficult and provides only a very partial view of the ecology of these species (RENDOŠ et al. 2014).

Moreover, gastropod species diversity and population densities are low in this type of habitat, especially on low pH granitic substratum, where the shells do not remain intact for long. All these elements may explain why *M. depressa* had not been found until now in the Vosges Mts.

In all of our samples in which we detected *M. depressa*, several additional species also considered to have affinities with subterranean environments are present, such as *O. cellarius*, *O. alliarius* or *Vitrea* species.

In north-eastern France, but also in northern Italy (CIANFANELLI et al. 2005), it is interesting to note that *M. depressa* seems to be present only in this type of hypogean habitat, whereas in the centre of its range the species colonises many other epigeous environments (KERNEY et al. 1999, WELTER-SCHULTES 2012, NEIBER 2017).

With *M. depressa*, about 30 other species of terrestrial and freshwater gastropods (hydrobioids and slugs excluded from this count) reach their westernmost limit in north-eastern France (Appendix 2), i.e. nearly 7% of the 445 indigenous gastropod species (hydrobioids and slugs also excluded from this count) listed from the French metropolitan territory, including Corsica. Of these, 14 are restricted to north-eastern France (BICHAIN et al. 2019, 2021; species marked with an asterisk in Appendix 2). This geographical part of France, which includes the Vosges and Jura massifs, belongs to a transition zone between the Atlantic and Continental climates. It therefore represents a physical and biogeographical boundary marking the western limit of the ranges of some central and eastern European snail species.



Additionally, the Vosges and Jura are low-altitude mountains with cold, sub-boreo-alpine climate and several northern and alpine species are present, such as *Causa holosericea* (S. Studer, 1820), *Columella columella* (G. von Martens, 1830), *Discus rudersatus* (W. Hartmann, 1821), *Macularia sylvatica* (Draparnaud, 1801), *Nesovitrea petronella* (L. Pfeiffer, 1853), *Pupilla alpicola* (Charpentier, 1837), *P. sterrii* (Voith, 1840), *Vertigo genesii* (Gredler, 1856) or *V. geyeri* Lindholm, 1925. In the Jura, the presence of these species is best explained by the specific north-east to south-west orientation of the mountain range, which generates strong annual temperature variations (with extremes ranging from -40°C to 35°C in the same location) with a warm southern flow in summer and a cold northern flow in winter (TRAUTSOLT 1969). In addition, erosion and successive glaciations have generated an important karstic network and favoured the emergence of unique habitats and refuges sheltering a suite of relict boreo-alpine species (CASTELLARINI et al. 2007, SCHMITT et al. 2010, BUONCRISTIANI & CAMPY 2011, HAMPE & JUMP 2011), be it among plants or insects. All these factors also allow an alpine malacofauna to maintain itself within these latitudes at a relatively low altitude. The situation is similar in the Vosges, with annual temperatures variations close to those of Reykjavik in Iceland (SELL et al. 1998). However, apart from the limestone foothills located at the eastern part of the massif, the vast majority of the Vosges consists of siliceous rocks such as granite or sandstone, that is, rocks extremely unfavourable for snails. Only about fifty species of terrestrial gastropods have been recorded in the Vosges massif (GEISSERT 1963 and associated litera-

ture), which is poor compared to the calcareous areas of the Jura, for which about 120 species have been recorded (BICHAIN et al. 2021) and where a single site can have up to forty species.

The discovery of *M. depressa* confirms the unique character of these two areas as parts of a biogeographical transition zone but also shows the need to increase sampling efforts in difficult-to-access and therefore poorly-known environments. An extensive field campaign seems necessary to better understand the real distribution of the species in these two regions and the diversity of these habitats, but also to assess potential threats facing populations.

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APPENDIX 1

Species recorded in scree and boulder fields in the Vosges and Jura Mts. (see Material and Methods for details of each locality). Anatomical characters were used to identify *Aegopinella* and *Oxychilus* spp.

	V01	V02	V03	J01	J02	J03	J04	J05
<i>Abida secale</i> (Draparnaud, 1801)						×	×	×
<i>Acanthinula aculeata</i> (O. F. Müller, 1774)	×							
<i>Aegopinella nitens</i> (Michaud, 1831)				×		×	×	×
<i>Aegopinella nitidula</i> (Draparnaud, 1805)		×						
<i>Aegopinella pura</i> (Alder, 1830)	×	×				×	×	×
<i>Arianta arbustorum</i> (Linnaeus, 1758)	×	×			×	×	×	
<i>Cepaea hortensis</i> (O. F. Müller, 1774)	×				×			
<i>Cepaea nemoralis</i> (Linnaeus, 1758)		×						
<i>Chondrina avenacea</i> (Bruguière, 1792)								×
<i>Clausilia bidentata</i> (Strøm, 1765)	×						×	
<i>Clausilia cruciata</i> (S. Studer, 1820)				×				
<i>Clausilia dubia</i> Draparnaud, 1805						×		
<i>Clausilia rugosa parvula</i> A. Férussac, 1807						×		×
<i>Cochlicopa lubrica</i> (O. F. Müller, 1774)						×		
<i>Cochlodina fimbriata</i> (Rossmässler, 1835)				×		×		×
<i>Cochlodina laminata</i> (Montagu, 1803)						×		×
<i>Cochlostoma septemspirale</i> (Razoumowsky, 1789)				×	×	×		×
<i>Discus rotundatus</i> (O. F. Müller, 1774)	×	×		×	×	×		×
<i>Discus ruderatus</i> (W. Hartmann, 1821)						×		×
<i>Edentiella edentula</i> (Draparnaud, 1805)		×		×			×	
<i>Ena montana</i> (Draparnaud, 1801)	×			×	×			
<i>Eucobresia diaphana</i> (Draparnaud, 1805)		×		×		×	×	
<i>Euconulus fulvus</i> (O. F. Müller, 1774)				×	×	×		×
<i>Helicigona lapicida</i> (Linnaeus, 1758)	×	×	×			×	×	×
<i>Helicodonta obvolvata</i> (O. F. Müller, 1774)	×	×		×	×	×	×	×
<i>Helix pomatia</i> Linnaeus, 1758		×		×				
<i>Isognomostoma isognomostomos</i> (Schröter, 1784)	×	×	×	×	×	×	×	×
<i>Macrogastra plicatula</i> (Draparnaud, 1801)					×	×	×	×
<i>Macrogastra ventricosa</i> (Draparnaud, 1801)				×		×		
<i>Macularia sylvatica</i> (Draparnaud, 1801)					×	×	×	×
<i>Mediterranea depressa</i> (Sterki, 1880)	×	×	×	×	×	×	×	×
<i>Merdigera obscura</i> (O. F. Müller, 1774)				×				
<i>Monachoides incarnatus</i> (O. F. Müller, 1774)	×	×		×				
<i>Nesovitrea hammonis</i> (Strøm, 1765)	×							×
<i>Orcula dolium</i> (Draparnaud, 1801)								×
<i>Oxychilus alliarius</i> (J. S. Miller, 1822)		×						
<i>Oxychilus cellarius</i> (O. F. Müller, 1774)	×	×	×			×		×
<i>Oxychilus draparnaudi</i> (H. Beck, 1837)								×
<i>Oxychilus navarricus helveticus</i> (Blum, 1881)		×			×	×		
<i>Phenacolimax major</i> (A. Férussac, 1807)	×	×						
<i>Trochulus villosus</i> (Draparnaud, 1805)				×	×	×	×	×
<i>Vitrea crystallina</i> (O. F. Müller, 1774)				×		×	×	×
<i>Vitrea subrimata</i> (Reinhardt, 1871)	×			×		×	×	×
<i>Vitrina pellucida</i> (O. F. Müller, 1774)		×		×	×		×	



APPENDIX 2

Gastropod species (hydrobioids and slugs excluded) at the western limit of their range in the north-eastern quarter of France after KERNEY & CAMERON (1999), WELTER-SCHULTES (2012) and BICHAIN et al. (2021) (species marked with an asterisk are only found in France in this region, species marked with a double asterisk have disjoint populations in the Pyrenees or in Spain).

<i>Aegopinella minor</i> (Stabile, 1864)**	<i>Laciniaria plicata</i> (Draparnaud, 1801)*
<i>Aegopinella nitens</i> (Michaud, 1831)	<i>Macrogastrea attenuata</i> (Rossmässler, 1835)**
<i>Cochlodina fimbriata</i> (Rossmässler, 1835)	<i>Macularia sylvatica</i> (Draparnaud, 1801)
<i>Cochlodina orthostoma</i> (Menke, 1828)*	<i>Mediterranea depressa</i> (Sterki, 1880)
<i>Columella columella</i> (G. von Martens, 1830)	<i>Nesovitrea petronella</i> (L. Pfeiffer, 1853)
<i>Clausilia corynodes saxatilis</i> (W. Hartmann, 1843)*	<i>Orcula dolium</i> (Draparnaud, 1801)
<i>Clausilia cruciata</i> (S. Studer, 1820)*	<i>Platyla polita</i> (W. Hartmann, 1840)
<i>Daudebardia brevipes</i> (Draparnaud, 1805)*	<i>Pupilla alpicola</i> (Charpentier, 1837)
<i>Daudebardia rufa</i> (Draparnaud, 1805)*	<i>Pupilla sterrii</i> (Voith, 1840)
<i>Edentiella edentula</i> (Draparnaud, 1805)	<i>Semilimax semilimax</i> (J. Férussac, 1802)*
<i>Eucobresia diaphana</i> (Draparnaud, 1805)	<i>Trochulus clandestinus</i> (W. Hartmann, 1821)*
<i>Gyraulus rosmaessleri</i> (Auerswald, 1852)*	<i>Trochulus montanus</i> (S. Studer, 1820)
<i>Helicopsis striata</i> (O. F. Müller, 1774)*	<i>Trochulus villosus</i> (Draparnaud, 1805)
<i>Hessemilimax kotulae</i> (Westerlund, 1883)*	<i>Vallonia declivis</i> Sterki, 1893*
<i>Isognomostoma isognomostomos</i> (Schröter, 1784)	<i>Vitrinobrachium breve</i> (A. Férussac, 1821)*