

First evidence of cannibalism in
Crassimurex (s. s.) calcitraba (Lamarck, 1803)
(Gastropoda, Muricidae) from the Lutetian
of the Paris Basin (France)

Didier MERLE, Donald H. GOLDSTEIN & Michael L. MCKINNEY



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First evidence of cannibalism in *Crassimurex (s. s.) calcitraba* (Lamarck, 1803) (Gastropoda, Muricidae) from the Lutetian of the Paris Basin (France)

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ABSTRACT

Reports of cannibalistic behavior in fossil muricids are scarce and are only known from the Quaternary. This study presents evidence of cannibalism among *Crassimurex (s. s.) calcitraba* (Lamarck, 1803), from the Lutetian of the Paris Basin (France). The studied material comes from the quarry of La Ferme de l'Orme (Yvelines, France) and was collected in a unit (unit 6) in which this species is the lone drilling predator. The paleoenvironment of this bed corresponds to intertidal or shallow subtidal brackish facies and *C. (s. s.) calcitraba* is associated with an assemblage containing other euryhaline species. The samples collected include 132 specimens, among which 14 display predatory holes attributed to conspecifics, thus suggesting cannibalism. Small specimens between 2-7 mm are the most commonly drilled and the size of drill holes indicates that juveniles as well as adults are responsible of these attacks. We also observed a global selection of drilling sites that are well oriented to the weak points of the shell (between the varices and avoiding the spines). Finally, this study shows that behaviors such as predation on juveniles, selection of weak parts of the shell and multiple drill holes on the same prey are similar to Quaternary and extant cases. The precise conditions leading to cannibalism are difficult to highlight, but subtidal brackish facies are accompanied by many environmental stressors that can promote opportunistic behaviors such as occasional cannibalism. Also, the sudden appearance of cohorts of hatchlings adds to these stressors.

KEY WORDS

Eocene,
muricid,
cannibalism,
drill holes,
Paris Basin.

RÉSUMÉ

Première observation d'un comportement cannibale chez Crassimurex (s. s.) calcitraba (Lamarck, 1804) (Gastropoda, Muricidae) du Lutétien du bassin de Paris (France).

Les signalisations de comportement cannibale chez les fossiles de Muricidae sont rares et ne sont connus que du Quaternaire. Dans cette étude, nous présentons le cas très ancien de *Crassimurex (s. s.) calcitraba* (Lamarck, 1803) du Lutétien du bassin de Paris (France). Le matériel étudié provient de la carrière de La Ferme de l'Orme (Yvelines, France) et a été recueilli dans le niveau 6, dans lequel cette espèce est le seul prédateur. Le paléoenvironnement correspond à un faciès intertidal lagunaire et *C. (s. s.) calcitraba* est associé à un assemblage contenant quelques autres espèces d'euryhaline. L'échantillonnage a permis de collecter 132 spécimens dont 14 présentent des perforations attribuées à des congénères, suggérant ainsi un cannibalisme. Les petits spécimens entre 2 et 7 mm sont principalement perforés et la taille des trous indique que les juvéniles, aussi que les adultes, sont responsables de ces attaques. De plus, le choix global des emplacements de perforation est nettement orienté vers les points faibles de la coquille (entre les varices et en évitant les épines). Enfin, cette étude montre que des comportements tels que la prédation sur les juvéniles, la sélection des parties faibles de la coquille ou les perforations multiples sur une même proie sont similaires aux cas déjà observés dans le Quaternaire et l'actuel. Les conditions précises conduisant à un comportement cannibale sont difficiles à élucider. Cependant, les faciès intertidaux lagunaires s'accompagnent de nombreux facteurs de stress environnementaux, auxquels s'ajoute l'apparition soudaine de cohortes de nouveau-nés, ce qui peut favoriser des comportements opportunistes tels qu'un cannibalisme occasionnel.

MOTS CLÉS

Eocène,
Muricidae,
cannibalisme,
perforations,
bassin de Paris.

INTRODUCTION

Drill holes, *Oichmus* (Bromley, 1981), made by gastropods constitute a highly visible part of the bioerosion process, and a clear record of fossil predation in the geological record. They have been widely used by biologists and paleontologists to study predator-prey interactions over a wide range of spatial, temporal and phylogenetic scales. Cenozoic and modern drill holes have been reported in muricid and naticid families by many authors (for reviews and references see Carriker 1981; Kitchell *et al.* 1981; Vermeij 1983, 1987; Kabat 1990; Leighton 2002; Kowalewski & Kelley 2002; Kelley *et al.* 2003; Kowalewski 2004; Kelley & Hansen 2007; Goldstein *et al.* 2014), particularly in the ranellid (*Argobuccinum* Herrmannsen, 1846 [Day 1969]) and nassarid (*Nassarius* Duméril, 1805 [Morton & Chan 1997]) groups.

For paleontologists, the recognition of these drill hole morphologies gives one of the few cases of direct evidence of feeding for both families (Taylor 1970; Hofman *et al.* 1974; Kojumdjieva 1974 in Kabat 1990; Chattopadhyay *et al.* 2014; Bošnjak *et al.* 2021). Moreover, this opportunity to discriminate muricid from naticid drill holes allows documentation of cannibalism, i.e., an intraspecific interaction having the potential to alter the functional relationship of predator-prey interactions (Rudolf 2008). The objective of this paper is to describe cases of cannibalism in the Eocene *Crassimurex (s. s.) calcitraba* (Lamarck, 1803) from the Paris Basin, the earliest occurrence of this behavior in the muricid fossil record. These were discovered by random sampling at the outcrop of La Ferme de l'Orme (middle Lutetian). We will successively detail the geological context of these findings and the different lines of evidence supporting a hypothesis of cannibalism in this species.

MATERIAL AND METHODS

COLLECTION OF THE SPECIMENS OF *CRASSIMUREX (S. S.) CALCITRABA*

Random bulk samples were collected in 2011 from unit 6, at 10 meter intervals across the face of the old quarry of La Ferme de l'Orme. In 2014 another location 150 m west, also within the actual protected site, was also collected. The samples of about 5 kg in 2011, and 2 kg in 2014, were dry sieved through sieves of 5 mm, 2 mm, 1 mm, and 53 microns in order to collect complete and subcomplete specimens of *Crassimurex (s. s.) calcitraba* of all sizes.

DRILL HOLE IDENTIFICATION

After sieving, specimens of *C. (s. s.) calcitraba* were extracted from the rest of the fauna for study. All identifiable shells were counted, whether complete or partial. Each specimen was carefully examined with a binocular microscope to look for the presence of drill holes. The location of the drilling trace was photographed for each specimen bearing drill holes.

MEASUREMENTS

Measurements of the height of the specimens were taken with a micrometer, and drill hole diameters were measured using image J (Schneider *et al.* 2012).

ABBREVIATIONS

Institutional abbreviations

AMNH American Museum of Natural History, New York;
MNHN.F Muséum national d'Histoire naturelle, Paris, paleontological collections.

Other abbreviation

EDS Elementary Depositional Sequence.

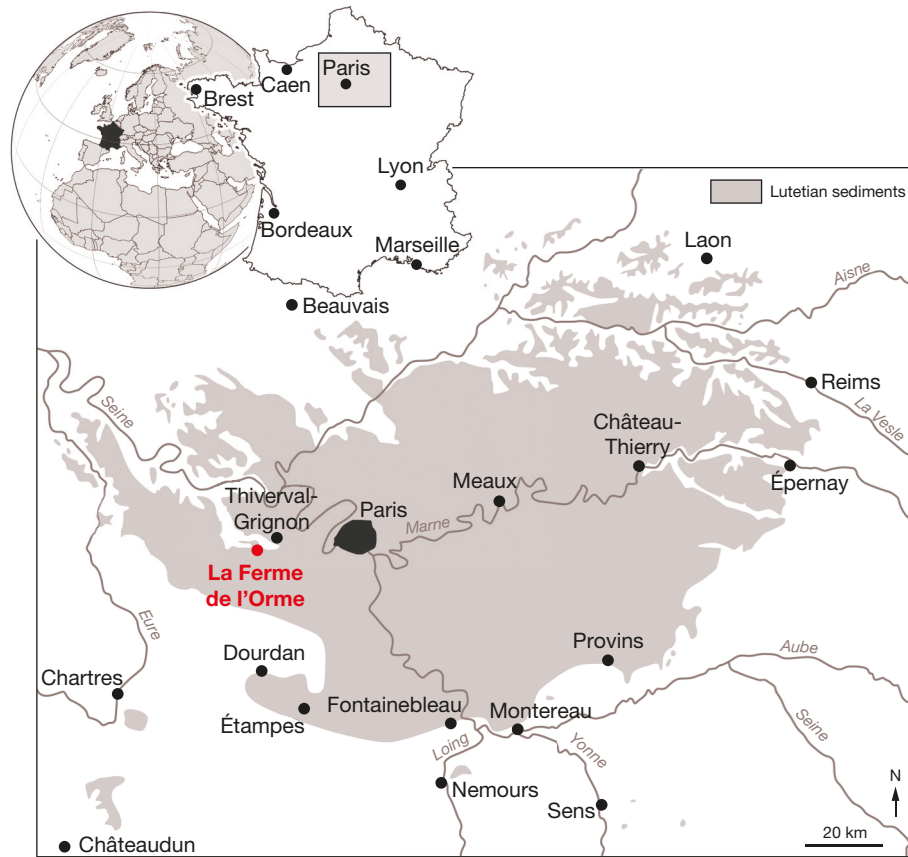


FIG. 1. — Geographical location of La Ferme de l'Orme (Beynes, Yvelines, France). The locality (in red font) is indicated on the map of the extension of the Lutetian sediments (modified from de Wever & Cornée 2008).

GEOLOGICAL SETTING

GEOGRAPHICAL LOCATION OF THE SITE

The quarry of La Ferme de l'Orme is located in the commune of Beynes, 36 km West of Paris (Fig. 1), on the left of the D11 in the direction of Saulx-Marchais in Neauphle-le-Château. The location of the quarry is indicated in the guide of Pomerol & Feugueur (1974).

DESCRIPTION OF THE SECTION

The exposure includes the uppermost middle Lutetian, but few strata are visible (Fig. 2). Several sections have been logged and published, notably those of Goubert (1863), Abrard (1925), Merle & Courville (2008) and Chattopadhyay *et al.* (2016). The present state of the quarry unfortunately does not allow examination of the lower part of the section, which includes a white limestone rich in *Orbitolites complanatus* Lamarck, 1801. The upper part is the only one that is visible and displays five beds (units 1-5). Among them one can identify the *Seraphs* Montfort, 1810 and *Avicularium* Gray, 1853 limestone bed (unit 4) that can be seen at the top of La Falunière at Grignon. These beds correspond to the top of the EDS 4 (Elementary Depositional Sequence) of Chattopadhyay *et al.* (2016: fig. 1). Approximately 1 m above this bed can be distinguished a *Potamides lapidorum* (Lamarck, 1804), batillariids and *Crassimurex* (*s. s.*) *calcitrata* bed (unit 6 = EDS 5 of Chat-

topadhyay *et al.* 2016), indicative of an intertidal brackish facies (Figs 2; 3). The material of *C. (s. s.) calcitrata* collected for this study comes exclusively from this unit. Closer to the top, a stratum of green marls (unit 7) contains a freshwater fauna with numerous *Staliola* Brusina, 1870, lymnaeids and vertebrate remains (Goubert 1863). The section is overlain by a limestone bed with powdery molluscs, indicating a return of the marine environment (unit 8 = EDS 6 of Chattopadhyay *et al.* 2016). During the 1880s, Cossmann (1886-1913, 1904-1913) mentioned La Ferme de l'Orme several times in his publications on molluscs and Fritel (1910) wrote that the site was famed as one of the most species-rich of the Paris basin. By relying on the programs of Strategy of Creation of Protected metropolitan Areas (SCAP) and the National Inventory of the Geological Heritage (INPG), this paleontological site of international value threatened by anthropic activities was selected in 2018 for the APPG (Prefectural Decree of the Protection of the Geotope) along with the site of Grignon (Auberger *et al.* 2018).

PALEOECOLOGY OF *CRASSIMUREX* (*S. S.*) *CALCITRATA*

Crassimurex (*s. s.*) *calcitrata* is a euryhaline Lutetian species and clearly prefers intertidal or shallow subtidal brackish facies. In the middle Lutetian of the Paris Basin, it is common in several localities (La Ferme de l'Orme (at Beynes), Grignon, Villiers-Saint-Frédéric, Montchauvet, etc.).

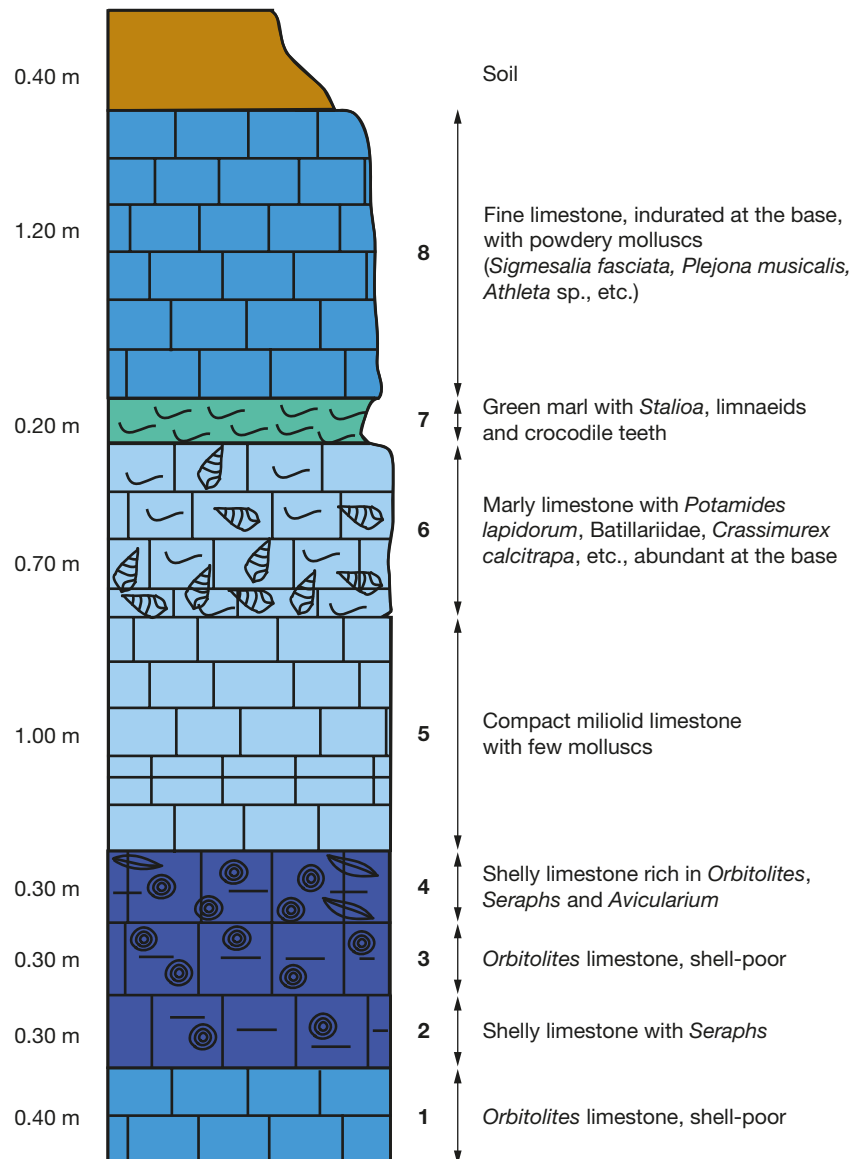


FIG. 2. — The section of La Ferme de l'Orme (Beynes, Yvelines, France) from Merle & Courville (2008). The material of *Crassimurex* (*s. s.*) *calcitraba* (Lamarck, 1803) collected for this study comes exclusively from the unit 6.

At La Ferme de l'Orme (unit 6), the identification work allowed to recognize 46 species of mollusks (31 gastropods and 15 bivalves) including only one driller, *Crassimurex* (*s. s.*) *calcitraba*. It is the sole driller as no naticid and no other muricid is recorded in this paucispecific assemblage. This observation is very important, because in the absence of other predators, we can hypothesize that all the drill holes can only come from *C. (s. s.) calcitraba*. In the same locality, it is associated with other euryhaline species. These include: *Potamides lapidorum* (Lamarck, 1804), *Vicinocerithium calcitraboides* (Lamarck, 1804), *Serratocerithium denticulatum* (Lamarck, 1804) and *Saxolucina saxorum* (Lamarck, 1806). It is responsible for drill holes on *V. calcitraboides* and *S. serratum* (Fig. 4A-C). *Crassimurex* (*s. s.*) *calcitraba* can be also a prey and traces of peeling by crabs are observed in seven specimens (Fig. 4D).

RESULTS

Different aspects of the growth of the shell of *C. (s. s.) calcitraba* and the characteristics of the drill holes are developed below as follows: 1) growth and appearance of the sculpture is given to evaluate when the sculptural elements can protect the individuals; 2) prey size and predation pressure; 3) relationship of the size of the prey to the size of the predator based on the diameter of drill holes; 4) drill hole site selection; and 5) occurrence of multiple drill holes.

GROWTH AND APPEARANCE OF THE SCULPTURE

Adults of *Crassimurex* (*s. s.*) *calcitraba* have small armoured shells and sculptural elements (spiral rows of cords, alignments of cord spines, reinforced varices) that can be considered as a deterrence to shell drillers. However, they are missing



FIG. 3. — View of the unit 6 of La Ferme de l'Orme section (Beynes, Yvelines, France) in which *Crassimurex* (*s. s.*) *calcitrapa* (Lamarck, 1803) was collected. Credits: Isabelle Rouget (MNHN). Length of the meter: 20 cm.

TABLE 1. — Characteristics of the specimens of *C. (s. s.) calcitrapa* (Lamarck, 1803) bearing drill holes. The star (*) indicates the specimens bearing two drill holes.

Specimens number	Specimen length mm	Number of teleoconch whorls	Drilled whorl	Diameter of hole (in mm)	Complete or not	Location of the hole	Comment on the location of the holes
MNHN.F.A91214	19.38	5 incomplete	Fifth	1.20	No	Abapertural side	On the shoulder, near the suture
MNHN.F.A91213	18.47	5 incomplete	Fifth	1.05	No	Apertural side	On the varix
MNHN.F.A91212	12.87*	4 incomplete	Third	0.8	Yes	Abapertural side	In an intervarice
MNHN.F.A91212	12.87*	4 incomplete	Fourth	0.6	No	Abapertural side	On the shoulder, in an intervarice
MNHN.F.A91211	10.69*	4 incomplete	Fourth	0.95	Yes	Abapertural side	On the shoulder, in an intervarice
MNHN.F.A91211	10.69*	4 incomplete	Third	1.00	No	Adapertural side	On the top of the whorl, in an intervarice
MNHN.F.A91210	7.06	3 incomplete	1-2 th (suture)	1.20	Yes	Adapertural side	On the suture, in an intervarice, single hole with two opening
MNHN.F.A91209	4.45*	5	Fourth	0.4	Yes	Abapertural side	On the top of the whorl, in an intervarice
MNHN.F.A91209	4.45*	5	Third	0.25	Yes	Abapertural side	On the suture, in an intervarice
MNHN.F.A91208	4.37	3.5	1.5 th	0.10	Yes	Abapertural side	On the shoulder, in an intervarice
MNHN.F.A91207	3.15	3.5	Third	0.35	Yes	Abapertural side	On the top of the whorl, in an intervarice
MNHN.F.A91206	3.43	3	2-3 th (suture)	0.10	Yes	Abapertural side	Near the shoulder, in an intervarice, single hole with two openings
MNHN.F.A91205	3.30	3.25	Third	0.50	Yes	Abapertural side	On the centre of the whorl, in an intervarice
MNHN.F.A91204	3.95	1.5	Second	0.85	Yes	Abapertural side	On the top of the whorl, in an intervarice, large hole
MNHN.F.A91203	3.25	2.5	Beginning of the first	0.60	Yes	Adapertural side	On the centre of the whorl, in an intervarice
MNHN.F.A91202	3.10	2.5	Protoconch/ first (suture)	0.70	Yes	Abapertural side	In an intervarice, single hole with two openings
MNHN.F.A91201	2.50	1.5	First	0.40	Yes	Apertural side	In an intervarice

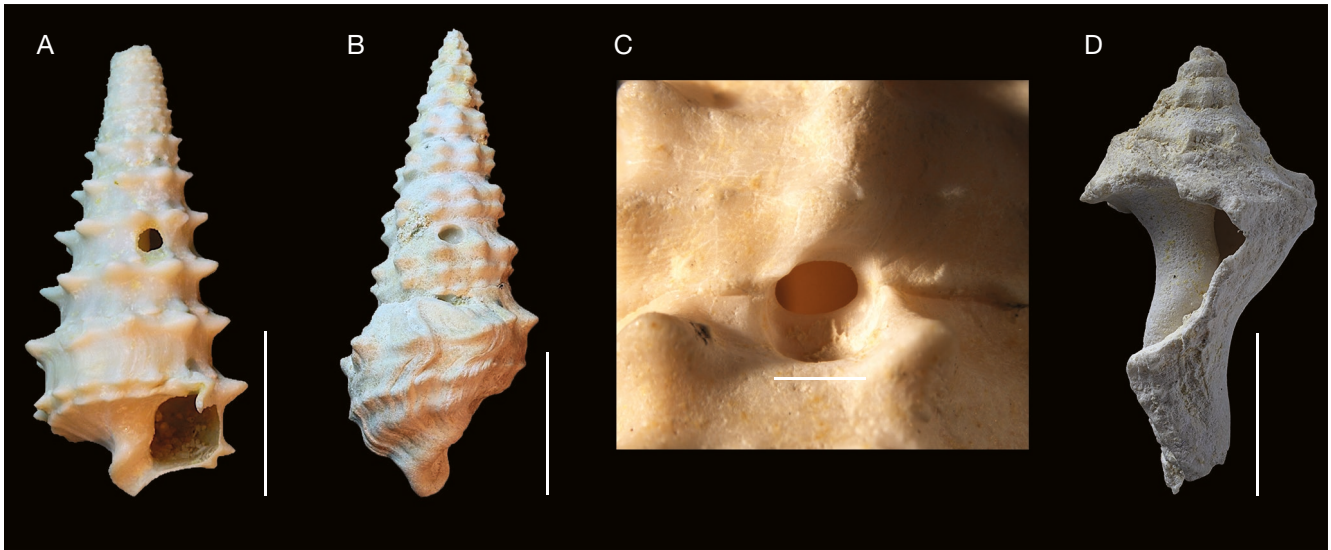


FIG. 4. — Different paleobiological aspects of *C. (s. s.) calcitraba* (Lamarck, 1803) at La Ferme de l'Orme (unit 6): **A-C**, feeding (drill holes) on cerithioids: **A**, *Serrato-cerithium denticulatum* (Lamarck, 1804), D. Goldstein coll.; **B**, *Vicinocerithium calcitrapoides* (Lamarck, 1804), D. Goldstein coll.; **C**, same species, detailed view of a drill hole, D. Goldstein coll.; **D**, MNHN.F.A91215 (Goldstein leg), specimen peeled by a crab. Scale bars: A, D, 5 mm; B, 10 mm; C, 1 mm. Credits: D. Goldstein.

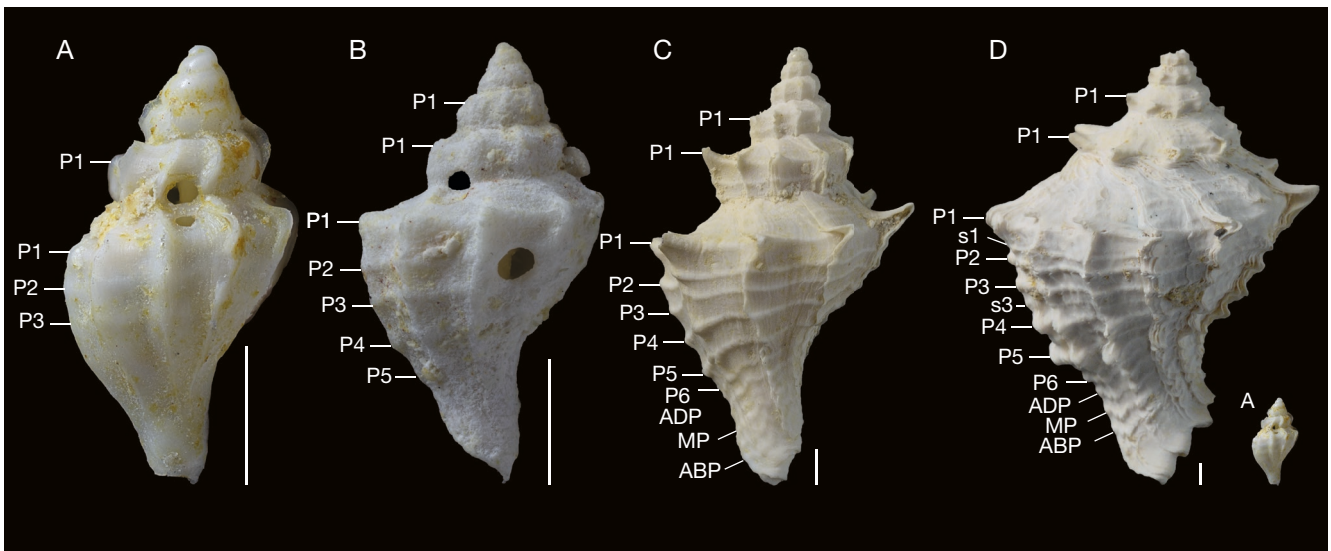


FIG. 5. — Growth of the sculpture of *Crassimurex (s. s.) calcitraba* (Lamarck, 1803) with the appearance of spiral cords and cord spines: **A**, MNHN.F.A91206 (Goldstein leg), spm of three teleoconch whorls; **B**, MNHN.F.A91209 (Goldstein leg), spm of four teleoconch whorls; **C**, MNHN.F.A91216 (Goldstein leg), spm of five teleoconch whorls; **D**, MNHN.F.A31217 (Goldstein leg), spm of ?seven teleoconch whorls with spm A of the same relative size for comparison. Scale bars: 1 mm. Credits: L. Cazes. The identification of the spiral cords adopts the terminology suggested by Merle (2001, 2005).

or thin in juveniles and appear during ontogeny. Therefore, an understanding of shell growth can help explain which areas of the shell were more easily drilled by predators during the life of individuals. We thus note that the ontogeny of these elements. *Crassimurex (s. s.) calcitraba* bears a multispiral protoconch indicating planktotrophic larvae (Merle *et al.* 2011: text-fig. 61F) such that the protoconch is devoid of sculpture. The development of the spiral sculpture on the teleoconch was partly described by Merle & Pacaud (2002) who showed that all primary cords and cord spines on the convex part of the whorl (P1 to P5, see Merle 2001 for the terminology) are present on the 5th teleoconch whorl.

Observations of younger specimens demonstrate that P1 to P3 are already present on the third teleoconch whorl (Fig. 5A). More abapical cords on the siphonal canal (ADP, MP and ABP) appear during the fifth teleoconch whorl (Fig. 5C) and secondary cords appear later (Fig. 5D). Cord spines are present in the typical morphotype of the species present at La Ferme de l'Orme (unit 6). The ontogeny of the sculpture demonstrates a progressive appearance of its elements (spiral rows of cords and axial alignments of cord spines) and suggests that individuals become less vulnerable to predation as they grow, particularly when they reach the 5th whorl (see Fig. 5C). Also, the appearance of sculptural

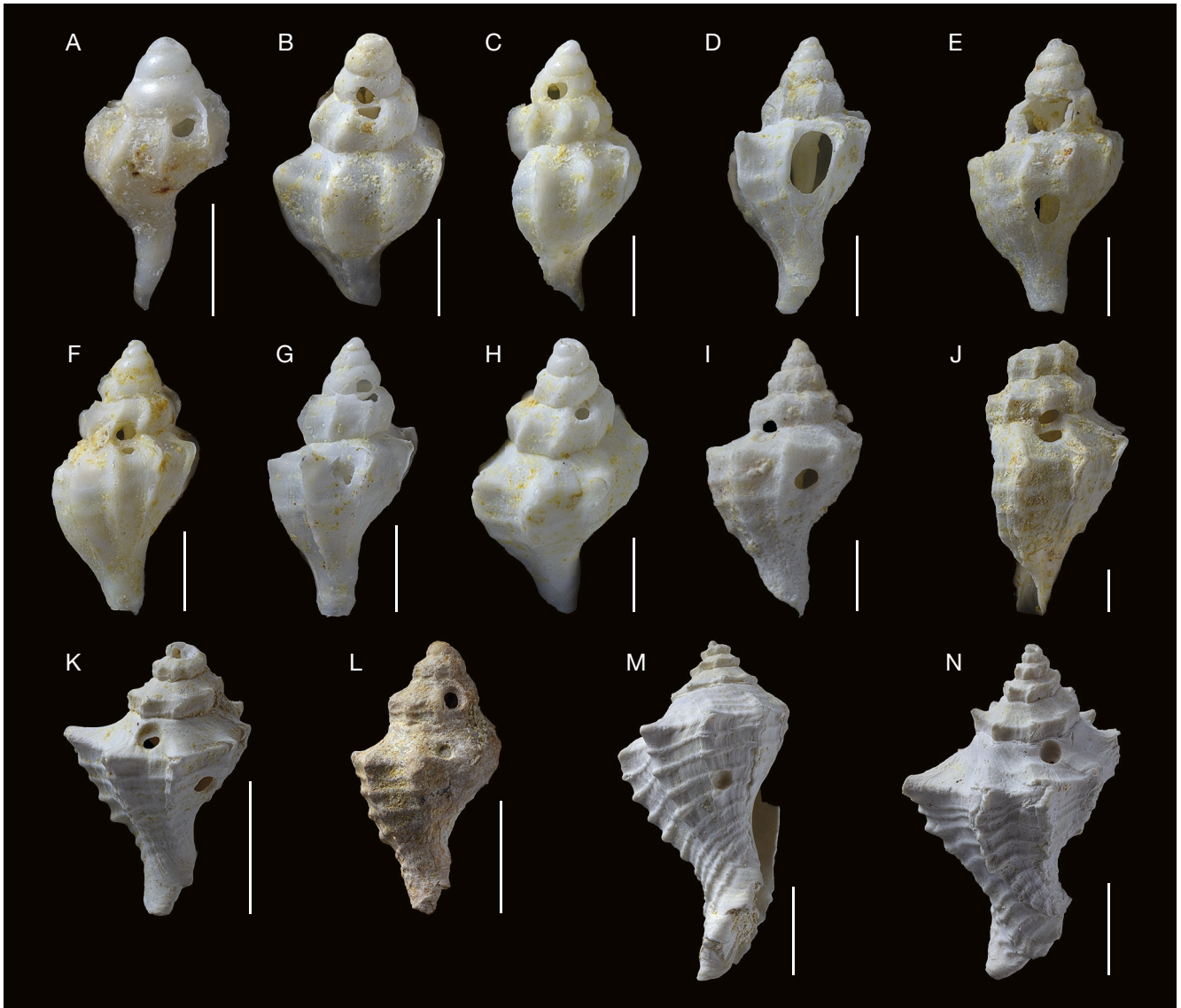


FIG. 6. — Specimens of *C. (s. s.) calcitrata* (Lamarck, 1803) from La Ferme de l'Orme (Beynes, Yvelines) bearing muricid drill holes: **A, C, D, E, H**, complete single holes with one opening: **A**, MNHN.F.A91201; **C**, MNHN.F.A91203; **D**, MNHN.F.A91204; **E**, MNHN.F.A91205; **G**, MNHN.F.A91207; **H**, MNHN.F.A91208; **B, F, J**, complete single holes with two openings: **B**, MNHN.F.A91202; **F**, MNHN.A91206; **J**, MNHN.F.A91210; **I, K, L**, two complete holes: **I**, MNHN.F.A91209; **K**, MNHN.F.A91211; **L**, MNHN.F.A91212; **M, N**, incomplete holes: **M**, MNHN.F.A91213; **N**, MNHN.F.A91214. Scale bars: A–J, 1 mm; K–N, 5 mm. Credits: L. Cazes (MNHN/CNRS).

elements occurs with the thickening of the shell, which reinforces its resistance to drilling. In addition, cord spines and particularly P1 spine, which is more developed than the other cord spines, constitute an important mean of defense against predators.

PREY SIZE AND PREDATION PRESSURE

Sieving of samples from the unit 6 allowed us to collect 132 specimens of *C. (s. s.) calcitrata* of which 14 specimens (Fig. 6; Table 1) display drill holes representing 10.61% of the total. The smallest specimen with signs of attack is 2.5 mm in length. The largest drilled specimen, an adult of 18.47 mm in height, has an incomplete hole, indicating an interrupted drilling process under unknown circumstances (e.g., another predator or perhaps abandonment from lack of success). Thus, 10.61% of all specimens are drilled during various ontoge-

netic phases ranging from very young specimens to young adults not exceeding 19 mm in height. Figure 7 illustrates the proportion of specimens not drilled versus drilled. These are divided into three size class intervals, one ranging from 0 to 9 mm in height (class I) and corresponding to juveniles very exposed to drilling, another ranging from 10 to 19 mm (class II) in which the drill holes are scarcer, and a class above 20 mm to 32 mm (class III) in which the specimens no longer have drill holes. The class I records 71% of the drill holes and clearly demonstrates that it is the most vulnerable class to this type of predation. In the class II, only four specimens, having a size varying from 10 to 19 mm, bear drill holes. This result is in accordance with observations demonstrating that the sculptural elements (cords and cord spines) appear in young adults and contribute to drill resistance via reinforcement of the shells by increasing its thickness.

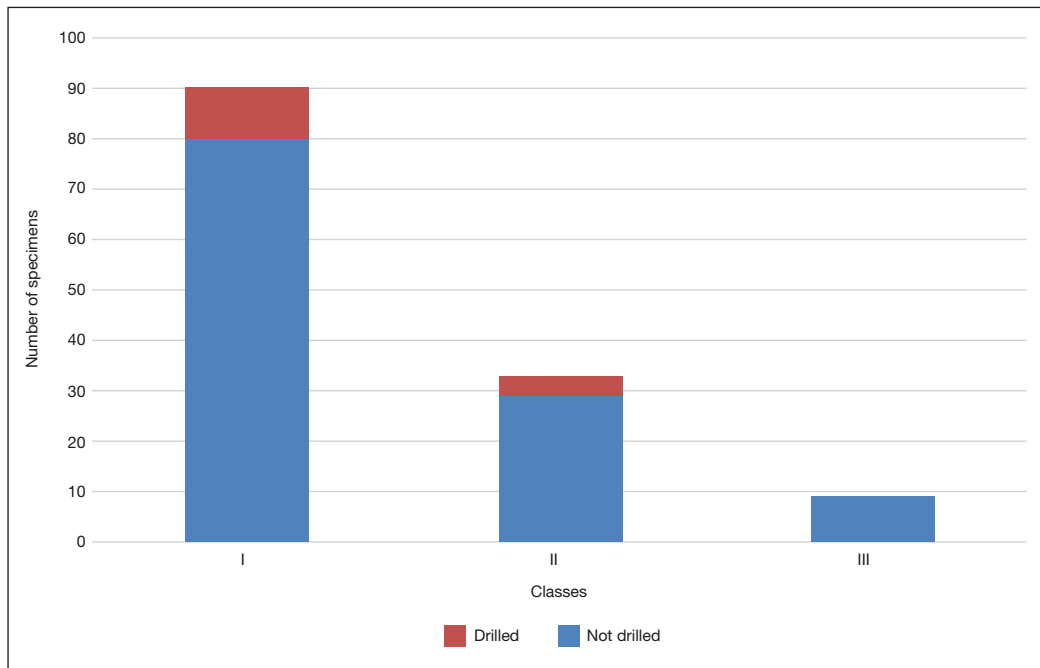


FIG. 7. — Drilled versus non-drilled *Crassimurex* (*s. s.*) *calcitraba* (Lamarck, 1803) shells in three size classes. Size classes (shell length): I, 0-9 mm; II, 10-19 mm; III, 19-32 mm.

RELATIONSHIP OF THE SIZE OF THE PREY TO THE SIZE OF THE PREDATOR

Based on the drill hole diameters, which can be correlated to the size of the attacker (Kowalewski 2004), individuals of all sizes drill conspecifics. On the bivariate plot Figure 8, we can observe that the class 0-7 mm displays the widest range of size hole ranging from 0.10 mm (for a specimen of 3.43 mm) to 1.2 mm (for a specimen of 7.06 mm). The hole of 0.10 mm is the smallest that we found and it was made likely by a very young individual. Conversely, 1.2 mm corresponds to the largest hole encountered. Therefore, we can deduce that juveniles as well as adults were potential predators of juvenile and sub-adult individuals. In the class 7-32 mm, the size range of the holes is narrower, ranging from 0.95 mm to 1.2 mm, and seems to be the result of the action of larger individuals. This observation indicates that only adults only attack other adults. Furthermore, the two larger specimens of this class (H: 19.38 mm and 18.47 mm) bear unsuccessful attacks with unfinished holes, suggesting greater predation difficulty on larger individuals.

DRILL HOLE SITE SELECTION

All of the drilling attacks are based on an operating principle which consists of attacks systematically located between two varices (in the intervarices) and avoiding P1 spines that represent reinforcement of the shell. The only attack that does not follow this principle was made on the varix of an individual of 18.14 mm and ended in failure. On the spire of young specimens, the holes can be at different places (top of the whorl near the adapical suture, centre of the whorl or base of whorl, near the abapical suture). On the last whorl, holes are more commonly located on the centre of the whorl in the thinner part of the shell.

MULTIPLE DRILL HOLES

Three specimens have two drill holes. One is a small specimen of 4.45 mm in height and two, larger, are of 10.69 mm and 12.87 in height. We have also observed on *C. (s. s.) calcitraba* prey species that multiple drill holes are a frequent occurrence (21.43% of the total) and that most swarming attacks involve predators of different sizes, determined by their drilling diameter; typically, one adult and several juveniles.

DISCUSSION

As Octopid species are also predatory and produce drill holes, it is necessary for our cannibalism hypothesis to confirm that the drill holes described herein are not produced by Octopid predation. The morphological characters allowing us to distinguish *Octopus* and naticid drill holes from the muricid drill holes observed on *C. (s. s.) calcitraba* will be discussed first in this section. Then, the predation on *C. (s. s.) calcitraba* will be placed in the stratigraphic context of muricid drill holes, followed by discussion of the cannibalistic behavior of this Lutetian species.

OCTOPUS, NATICIDS OR MURICID DRILL HOLES MADE ON *CRASSIMUREX* (*S. S.*) *CALCITRABA*?

Differences from *Octopus* drill holes

Fuchs *et al.* (2009) reported the occurrence of the oldest Octopodidae d’Orbigny, 1840 from the the Upper Cenomanian Lagerstätte of Hâqel (Lebanon) with *Stylectopus annae* Fuchs, Bracchi & Weis, 2009. In the Cenozoic, there is no documented report of octopid specimens, but octopod

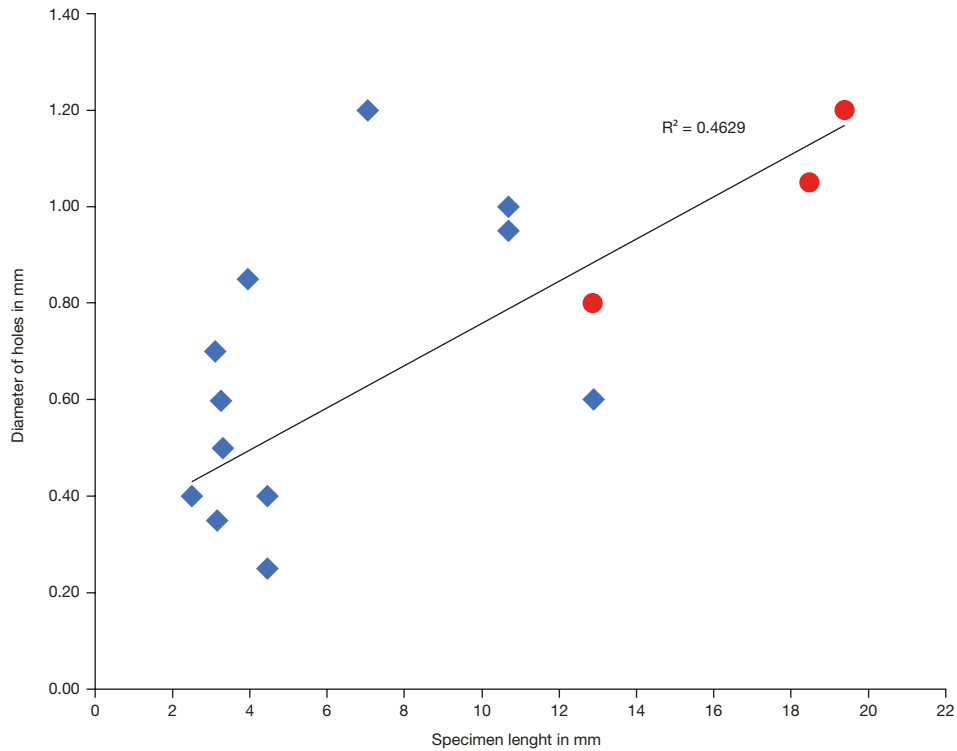


FIG. 8. — Bivariate plot of specimen length against drill hole diameter in *Crassimurex* (s. s.) *calcitrata* (Lamarck, 1803). **Red circles**, unsuccessful drills.

TABLE 2. — Morphological and functional patterns of holes associated with gastropod and *Octopus* predation (modified from Gordillo *et al.* 2022).

Characteristic	Pattern A	Pattern B	Pattern C
Shape	A hole, round to oval	Paired breaks	A hole, rounded to irregular
Outline character	Regular outline	Irregular breakage	Regular to irregular
Profile cross section	Straight or sloping sides or parabolic outline	Random breakage	Width and direction of hole vary with depth
Drill hole location	Primarily Abapertural, dorsal to ventral	Unspecified	Apertural, ventral to dorsal, parietal (left)
Produced by	Secretions of the ABO and rasping by the radula	Possible chemical softening and biting marks of upper and lower beaks	Secretion of salivary glands and rasping by radula and teeth of the papillary shield and terminal process
Potential predator	Drilling gastropods	<i>Octopus</i>	<i>Octopus</i>
Present in this sampling	Yes	No	No

feeding traces were found in the large bivalve of *Venericor clarendonensis* (S. W. Wood, 1871) from the early Eocene of Southern England (Todd & Harper 2011).

Octopus breach the shells of their prey in two ways, breaking the shell with their beaks, leaving characteristic paired irregular breaks, (Table 2 pattern B), and drilling through the shells to inject a paralyzing venom (Arnold & Arnold 1969). This method of drilling is described as grasping and positioning the prey. Gastropod prey is held with the shell aperture downward (Arnold & Arnold 1969), then rasping the shell with the papillary teeth (Nixon *et al.* 1980), repositioning the shell and rasping again. This sequence is repeated until the shell is penetrated (Arnold & Arnold 1969). Rasping is done in straight lines but because of the rotation, variable shapes are produced (Hiemstra 2015). The resulting drill holes range from irregular ovals corresponding to *Oichnos*

ovalis (Bromley, 1993), to rounded holes corresponding to *Oichnos simplex* (Bromley, 1981) (Fig. 9A1, B-E). The edges of the drill holes are not as crisp or clearly defined as those made by muricids (Fig. 9F-I; Table 2), and the holes are not as perfectly circular even when corresponding to *Oichnos simplex* (Todd & Harper 2011).

In depth, the drill holes of *Octopus* frequently show changes of width and direction (see Table 2 pattern C, Arnold & Arnold 1969 and Fig. 9A2). There is a marked preference for octopodoids to drill in the ventral-left-posterior (parietal) part of gastropods (Table 2 pattern C) because that is closest to the columellar muscle (Arnold & Arnold 1969; Nixon *et al.* 1980; Klompemaker & Kittle 2021).

In contrast to the above, muricid drill holes are typically *Oichnos simplex*. In thicker shells the round cross section and straight to slightly sloping sides are evident (Table 2

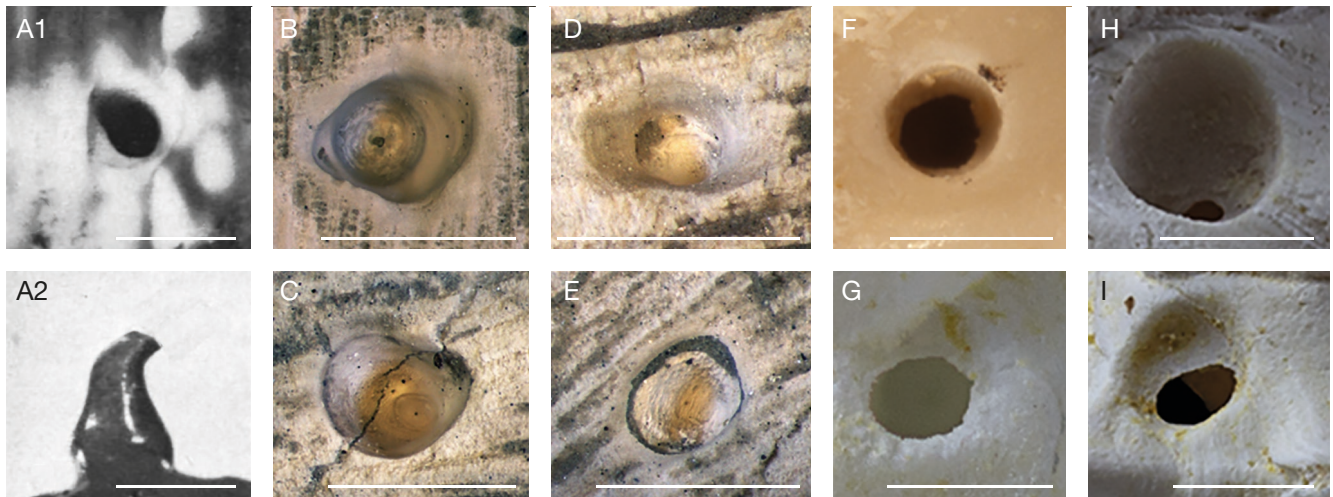


FIG. 9. — Comparison between drill holes made by octopids (A-E) and drill holes made by *Crassimurex* (s. s.) *calcitraba* (Lamarck, 1803) (F-I): A1, B-E, plan view of holes drilled by octopids; A2, mold of an octopid drill hole showing the variable path through the shell; A1, A2, drill hole made by the extant *Octopus vulgaris* Cuvier, 1797; B-E, drill holes made by octopids from the upper Campanian of Meade (South Dakota) on a specimen (AMNH 99175) of *Nymphalucina occidentalis* (Morton, 1842); F, *Serratocerithium denticulatum* (Lamarck, 1804) (Goldstein coll.); G-I, *C. (s. s.) calcitraba*: G, MNHN.F.A9120; H, MNHN.F.A91214; I, MNHN.F.A91211. Credits: A1, A2, Arnold & Arnold (1969) slightly modified; B-E, Klompmaker & Landman (2021: fig. 1) slightly modified; F, D. Goldstein; G-L, L. Cazes (MNHN/CNRS). Scale bars: A-E, H-I, 1 mm; F, G, 0.5 mm.

pattern A), but this is not so clearly defined in thinner shells and especially where there has been some diagenetic dissolution (Fig. 9G). The Figure 6D illustrates one of these holes in a thin, small specimen. In this case the hole is constrained to the intervarical area and appears to be *Oichnos ovalis*. The edges of this hole are well defined, lacking irregularity and the location of the drill hole is abapertural.

Naticid versus muricid drill holes

Although it appears independently during their evolution, muricids and naticids share a similar drilling method. In muricids, the accessory boring organ (ABO), is withdrawn snugly within a sac in the mid-anterior part of the sole of the foot, and is everted only in operation. In naticids, it lies under the distal tip of the proboscis that, as in muricids, remains inverted within the cephalic hemocoel of the snail except when exploring, drilling, and feeding (Carriker & Yochelson 1968). However, the resulting holes are rather different between both families, and this allows them to be distinguished separately.

The muricid hole is straight-sided or tapers slightly inwards, the outer parts may be ragged and irregular; a beveled rim is sometimes produced, but it is never as wide or pronounced as that of the naticids (Fretter & Graham 1962; Taylor 1970). In addition, incomplete holes of naticids bear usually a characteristic central boss (Fretter & Graham 1962; Taylor 1970), whereas the bases of incomplete muricid holes are shallowly concave (Carriker 1969). The drill holes observed on the specimens of *C. (s. s.) calcitraba* at La Ferme de l'Orme (unit 6) are round in contour (with one exception discussed above). Except for an eroded specimen they have crisp, unbeveled edges, are straight sided, and some show irregular breakage of the final shell and thus indicate a muricid origin. Incomplete holes are shallowly concave as described by Carriker (1969), see Figure 6M, N.

STRATIGRAPHIC APPEARANCE OF MURICID DRILL HOLES AND MODERN CASES OF CANNIBALISM

Muricid gastropods are a very rich family of predatory snails, comprising more than 1 700 living species (Houart 2018) and 1 200 fossil Cenozoic species (Merle *et al.* 2011, 2022). The oldest indisputable Cretaceous muricid is *Flexopteron cretaceum* (Garvie, 1991) from the Maastrichtian formation of Kemp Clay (Texas, United States, Garvie 1991). The Paleogene period represents a rapid growth phase for the familial diversification with the appearance of around 330 species (Merle 1999), the earliest members of the twelve accepted subfamilies (Merle *et al.* 2022), and the colonization of various environments from shallow to deep waters. Evidence of muricid drill holes are known since the Ypresian from the Paris and Aquitaine Basins (personal observations DM). Concerning the Paris Basin, Taylor (1970) suspected that *Timbellus crenulatus tricarinatus* (Lamarck, 1803) and *Eofavartia frondosa* (Lamarck, 1803) were potential drillers of straight-sided holes observed in the middle Lutetian assemblages of Damery (Marne, France). *Crassimurex* (s. s.) *calcitraba* is now added to the list of Lutetian drillers. This evidence shows that the ability to drill shells for food is ancient for this family and suggests the hypothesis that individuals were able to drill shells of intraspecific congeners from the early Paleogene.

According to Gordillo (2013), research on cannibalism in fossil muricid gastropods is extremely scarce. From the Late Oligocene of Hungary (Chattian), Dávid (1997) noted that muricid borings can be observed on the shells of muricid gastropods, but it is not possible to prove that these borings are intraspecific predation, because several species are implicated. Paine (1966) reported cases with *Chicoreus* (s. s.) *ramosus* (Linnaeus, 1758) from the Holocene of the Red Sea and Spanier (1986) and Rilov *et al.* (2004) reported cases with *Hexaplex (Trunculariopsis) trunculus* (Linnaeus, 1758) from the

Holocene of the Mediterranean Sea (Israel). Gordillo (2013) reported cases with *Trophon geversianus* (Pallas, 1774) from the Holocene of South America (Beagle Channel).

Carriker (1955) and noted that cannibalism occurred among living *Urosalpinx cinerea* (Say, 1822) of all ages in the presence of other prey both in the field and in confinement. Pope (1911) reported that in one observation, 100 newly hatched drills hatched in captivity were reduced to 36. However, Nelson (1922) doubted that such extreme cannibalism occurs in nature, since drills do not all hatch simultaneously and tend to scatter. Stauber (1943) also detected cannibalism among recently hatched drills in aquaria, but with an amount fewer than the extremes reported by Pope. Pope (1911), Haskin (1935), Galtsoff *et al.* (1937), Stauber (1943), and Flower (1954) reported cannibalism among adult drills in both the laboratory and in the field. Flower (1954) during a series of dredgings in the lower Delaware Bay (United States) collected bottom material retained on a $1/4 \times 3$ (= 0.64×7 cm) inch mesh screen. In this material he counted 937 dead drills and 76 of these had been drilled by other *Urosalpinx* Stimpson, 1865 and *Eupleura* Adams, 1853.

CHARACTERISTICS OF THE CANNIBALISM BEHAVIOR OF *CRASSIMUREX* (s. s.) *CALCITRAPA*

Our results reveal three characteristics of the cannibalistic behavior of *C. (s. s.) calcitrata*: 1) it is not uncommon and affects about 10.61% of individuals; 2) predation is directed primarily towards juveniles (preferentially class 0-7 mm); the decrease in the number of holes above 7 mm in height corresponds to a thickening of the shell (coarser cords and cord spines) during the growth forming armor and making predation more difficult; and 3) hole location selection is clearly oriented towards the weak points of the shell. This is consistent to a global selection of drilling sites that is well oriented to the weak points of the shell and maximizes chances of successful predation.

The strategy of preferentially selecting juvenile prey and precise hole locations suggests that the predators have sought to maximize their chances of success and lower their risk of a dangerous interaction. In addition, the presence of multiple drill holes in three specimens and the 10.61% predation rate on vulnerable specimens suggest that this conspecific predation is probably more than simply a matter of using an available resource. Carriker (1981) noted that in cases where a muricid was interrupted during the drilling process, it often went back to the same hole to continue drilling. Muricids moreover, have been known to attack their prey in groups (Belding 1910; Carriker 1981; Kelley 1991).

Finally, we propose that the attacks on juveniles by adult *C. (s. s.) calcitrata* may meet criteria of an intense competition or an opportunist behavior for limited food resources. This falls under the concept of density dependent cannibalism (Paine 1965) which has been demonstrated in laboratory conditions with the modern muricid, *Rapana venosa* (Valenciennes, 1846) (Yu *et al.* 2018). This hypothesis is consistent with the presence of the species in the assemblage of *Potamides lapidorum*, batillariids and bivalves indicative of

intertidal facies. This type of facies is accompanied by many environmental stressors related to tides and emersion, such as desiccation, high temperatures, salinity fluctuations, ultraviolet (UV) radiation and wave disturbance. Because of these stressors, the mortality rate can be high and the search for food more difficult. It is highly notable that Chattopadhyay *et al.* (2016), working with material from a bed deposited in an open embayment to offshore environment at la Ferme de l'Orme, by comparison, found a 0% predation rate. The sudden addition of cohorts of hatchlings and juveniles simultaneously adds a food resource for conspecifics, but also puts pressure on what was likely a minimally adequate food supply. Such conditions represent factors that can promote opportunistic behaviors such as occasional cannibalism.

CONCLUSION

Cases of cannibalism in fossil muricid gastropods are extremely scarce and are only reported in the Holocene from the Red Sea (Paine 1966), Mediterranean Sea (Spanier 1986; Rilov *et al.* 2004) and South America, Tierra de Fuego (Gordillo 2013). This case of muricid cannibalism in *Crassimurex* (s. s.) *calcitrata* dates back to about 45 million years (Lutetian, Eocene), a period corresponding to the beginning of the diversification of the family (Merle *et al.* 2011). It shows that behaviors such as predation on juveniles, selection of weak parts of the shell or multiple perforations on the same prey are similar to cases in the Quaternary (Paine 1966; Rilov *et al.* 2004; Gordillo 2013) and today (Pope 1911; Haskin 1935; Galtsoff *et al.* 1937; Stauber 1943; Flower 1954; Carriker 1955). Cannibalistic behaviors are thus likely already in place as early as middle Eocene. However, the conditions leading to cannibalistic behavior are difficult to precisely determine. Cannibalism in gastropods has been attributed to many factors including energy maximization or the selective utilization of available resources (Kitchell *et al.* 1981; Kelley 1991; Chattopadhyay *et al.* 2014), the lack of alternate prey (Stanton & Nelson 1980; Spanier 1986) or the influence of ontogenetic stage (Zlotnik 2001; Chattopadhyay *et al.* 2014).

One limitation of cannibalism is the risk of injury or death from attacking a larger conspecific (Dietl & Alexander 2000; Kelley & Hansen 2007). In the present case, we propose that the natural challenges of the subtidal brackish environment and additional hatchlings increasing the competition for resources are contributing factors. This hypothesis requires further study. To demonstrate that the cannibalism is more than a simple case of utilizing an available food source, we will need to quantify the predation pressures on the prey species of *C. (s. s.) calcitrata*, and characterize the pattern of predation on the prey species. In doing so we would need to show whether there is direct competition for prey within and between the juveniles and adults, and that the predation pressure on the conspecifics is at a higher level than can be explained by mere food source utilization. A preliminary study, in progress, of multiple attacks on two of the most common prey species, *Vicinocerithium calcitrapoides* and *Serratocerithium*

denticulatum, indicates that juveniles and adults attack these larger prey species simultaneously. The study of other brackish facies characterized by assemblages containing few species and only one predator among the muricid family can be a good way to highlight other cases and further document the repeated occurrence of this behavior during the Cenozoic.

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