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Predatory boreholes in Tournaisian (Lower Carboniferous) spiriferid brachiopods

BERNARD MOTTEQUIN AND GEORGE SEVASTOPULO

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A brachiopod fauna from the uppermost part of the Tournaisian Tournai Formation (Belgium) contains an undetermined species of *Crurithyris* (Spiriferida, Ambocoeliidae), which displays numerous bored shells. About 8% of the 432 specimens with conjoined valves display single, small (≤ 1 mm) boreholes, which are smooth-sided, cylindrical or weakly conical, circular to slightly elliptical in plan view, perpendicular to the shell surface and generally complete. Of the 35 bored articulated specimens, 27 were drilled on the ventral valve. Most of the boreholes are located in the posterior half of the shell, and no case of edge-drilling has been observed. The boreholes were drilled by a predator, or possibly a parasite, which selected individuals greater than 2.5 mm long. *Crurithyris* sp. may have represented an attractive (in terms of energy cost) and easy target for a small-sized predator because of its thin shell and ornament of minute spines. ☐ *Belgium*, *borehole*, *brachiopods*, *Carboniferous*, *predation*, *Tournaisian*.

Bernard Mottequin [mottequb@tcd.ie] and George Sevastopulo [gsvstpul@tcd.ie], Department of Geology, Trinity College, Dublin 2, Ireland; manuscript received 11/04/2008; accepted 18/08/2008

Holes drilled in fossil shells are among the more commonly reported examples of biotic interactions in the geological past. The majority of records are from late Mesozoic and Cainozoic assemblages of molluscs, where the drilling frequencies can attain more than 20% (e.g. Kelley & Hansen 1993, 1996; Hoffmeister & Kowalewski 2001). Most reported borings in brachiopod shells are from the Palaeozoic (e.g. Fenton & Fenton 1931; Brunton 1966; Brunton & Champion 1974; Rohr 1976; Chatterton & Whitehead 1987; Legrand-Blain & Poncet 1991; Baumiller *et al.* 1999; Hoffmeister *et al.* 2002), where drilling frequencies rarely exceed 10% (Hoffmeister *et al.* 2003). Reports of post-Palaeozoic and Recent brachiopods with drill holes are less numerous (e.g. Harper & Wharton 2000; Baumiller & Bitner 2004; Harper 2005; Baumiller *et al.* 2006; Simões *et al.* 2007). The identity of the boring organisms as well as the type of relationship (parasitism or predation) have been discussed extensively (Leighton 2001). In Recent communities, muricid and naticid gastropods are important predators of molluscs, but representatives of other gastropod families are also able to drill shells (Harper *et al.* 1998); the boreholes are made by a combination of physical abrasion through the action of the radula and chemical attack (Carricker 1981). Other boring predators in Recent seas include platyhelminths, polychaetes and octopods.

This paper examines the evidence for predation (or parasitism) of a small Mississippian (Lower Carboniferous) spiriferid brachiopod, *Crurithyris* sp., from the Tournai Formation (Tournai area, Belgium). Although Bassett & Bryant (1993) have reported the presence of borings in the late Tournaisian micromorphic rhynchonellid *Lambdarina glaphyra* from Belgium, this is the first quantitative study of borings in Mississippian brachiopods from Western Europe.

Material and methods

The material originates from Lemay quarry at Vaulx-lez-Tournai, south-east of Tournai (Figs 1, 2) and is reposited in the collections of the Geological Museum, Trinity College, Dublin (catalogue numbers prefixed TCD). The brachiopods are from the uppermost part of the Tournai Formation (Vaulx Member) of Tournaisian age (Ivorian regional Substage). The Tournai Formation comprises dark, thin-bedded, siliceous and argillaceous limestones with shaly intercalations and with abundant chert at some levels. Six members have been identified within this lithostratigraphic unit, which is up to 145 m thick in its type area. They are from the base to the top: the Crampon, Allain, Providence, Pont-à-Rieu, Vaulx and Vignobles members. Where the Vignobles Member is not developed (as is the case at the Lemay Quarry), the Vaulx Member (up to 35 m thick), consisting of dark grey, argillaceous, crinoidal limestones with abundant cherts and macrofossils, extends up to the 'Gras Délit' (Poty *et al.* 2002), a thin clay marker probably of volcanic origin (Gaillard *et al.* 1999),

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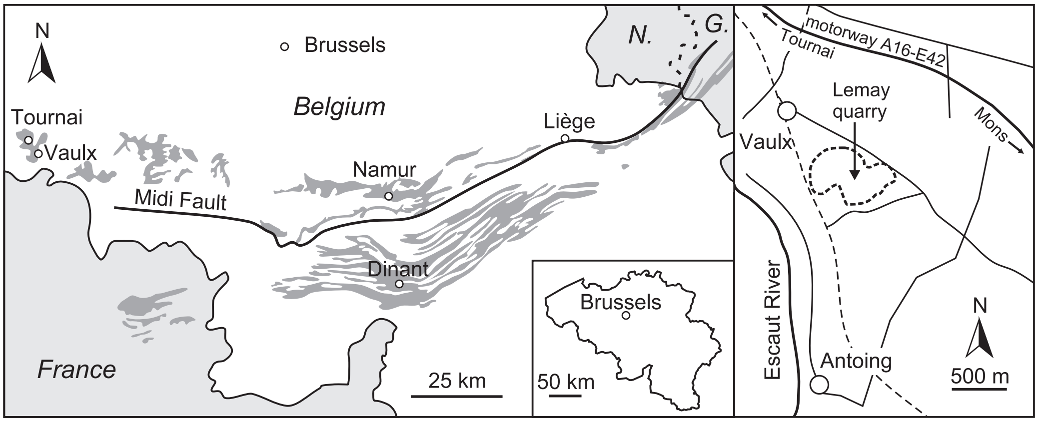

Fig. 1. Distribution of the Lower Carboniferous ('Dinantian') rocks in southern Belgium (modified from Hance *et al.* 2006); location of Lemay quarry (modified from Gaillard *et al.* 1999). N., the Netherlands; G., Germany.

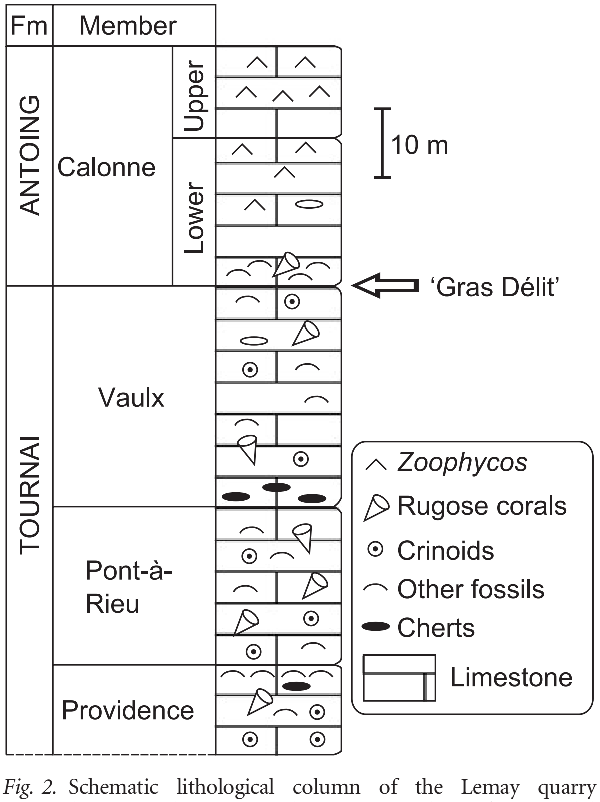

Fig. 2. Schematic lithological column of the Lemay quarry (Vaulx-lez-Tournai) showing the position of the 'Gras Délit' (modified from Devuyst *et al.* 2005). Fm, Formation.

which marks the top of the formation. The Tournai Formation represents the nearly *in situ* accumulation of remains from a relatively deep water, crinoid-brachiopod-bryozoan community with associated tabulate and solitary rugose corals, gastropods, bivalves, nautiloids and trilobites (Gaillard *et al.* 1999). The biostratigraphical range of this formation, in terms of the Mississippian Foraminifer Zones (MFZ) of Devuyst & Hance (2006), spans the interval MFZ4 to MFZ5 according to Hance *et al.* (2006). Groessens (1975) listed and illustrated conodonts from boreholes in the Tournai region and discussed their stratigraphical significance. He reported that the 'Gras Délit' at the top of the Vaulx Member coincides with a change from older faunas containing *Pseudopolygnathus multistriatus* to younger containing *Polygnathus* ex gr. *longiposticus*. His main conclusions have been supported by the results of the study of the conodont faunas from a borehole at Barry, 6.4 km east of the Lemay Quarry (Larangé *et al.* 1998). In the present study, a specimen of *Pseudopolygnathus multistriatus* (TCD 54346) was recovered from weathered shales on loose blocks, which are judged to have come from just below the 'Gras Délit'. These data suggest that the brachiopod-bearing horizon may be correlated with the younger part of the *Pseudopolygnathus multistriatus* Biozone recognized at Hook Head, County Wexford, Ireland, by Johnston & Higgins (1981) and other sections in the south of Ireland (Varker & Sevastopulo 1985). In terms of the international conodont zonation proposed by Lane *et al.* (1980), this horizon can be correlated with the Lower *Gnathodus typicus* Biozone. For more details concerning the Tournai Formation, as well as the Lower Carboniferous succession in the Tournaisis, see Hennebert & Doremus (1997a, b) and Poty *et al.* (2002).

Bulk samples were collected by Professor Gary Webster from weathered, thin shale partings between 1 and 2 m below the 'Gras Délit'. The shale was simmered in Quarternary O (Zingula 1968) to disaggregate it and the residue was screened through a stack of sieves. Brachiopods and other fossils were picked from the dried residues under a binocular microscope. The sample from 2 m below the 'Gras Délit' proved to be the most productive.

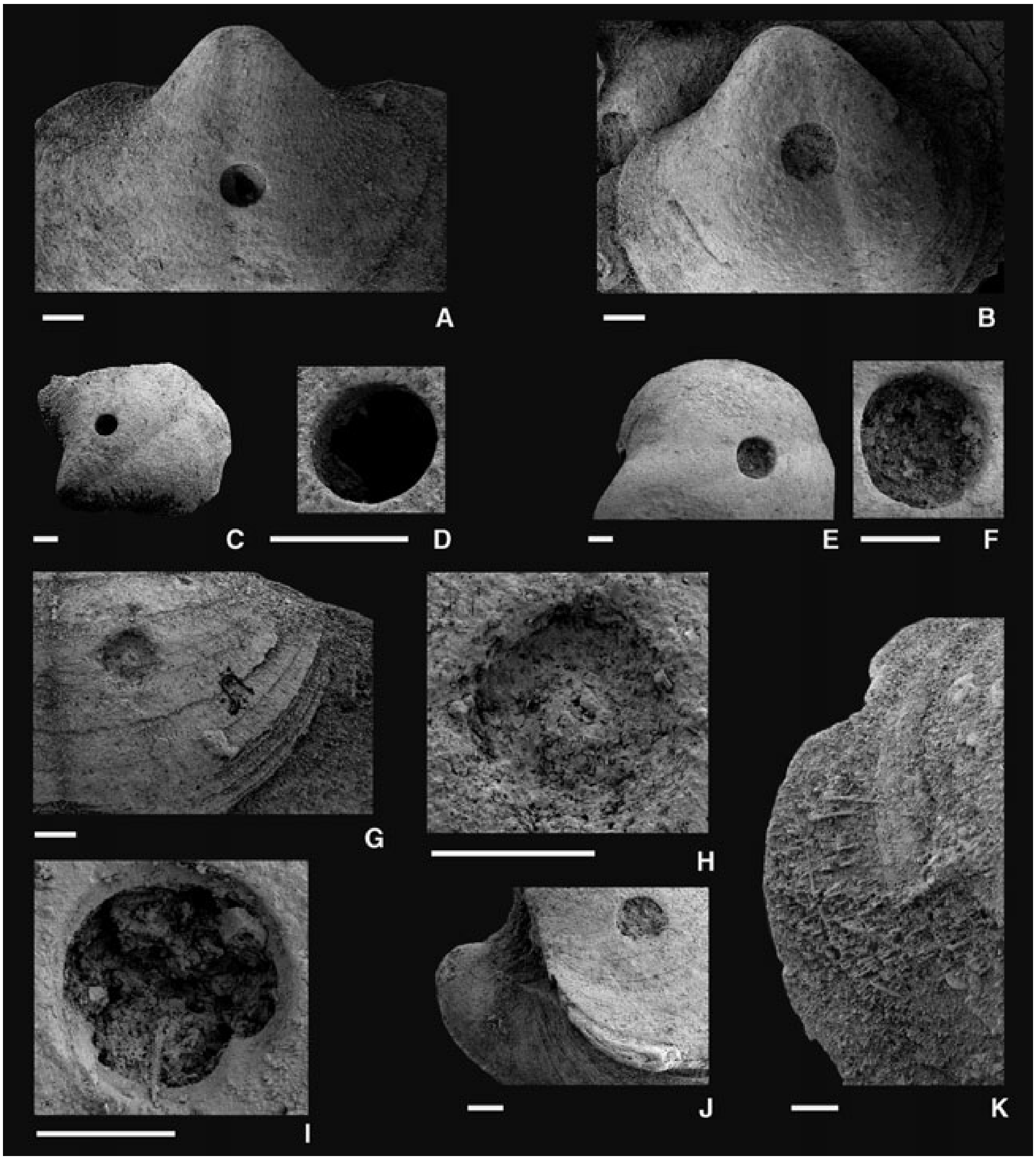

Fig. 3. Drilled specimens of *Crurithyris* sp. from the Tournai Formation (top of Vaulx Member), southern Belgium. □A. TCD 54347, ventral valve. □B. TCD 54348, ventral valve. □C, D. TCD 54349, ventral valve and close-up of the drill hole. □E, F. TCD 54350, ventral valve and close-up of the drill hole. □G, H. TCD 54351, ventral valve with a failed drill hole and close-up of the failed drill hole. □I, K. TCD 54352, close-up of a drill hole located in ventral valve and with an irregularity on one side and close-up of the left side of the valve showing the microspinous ornamentation. □J. TCD 54353, articulated specimen with drill hole on dorsal valve. Scale bars are 0.5 mm for all.

All but one of the drilled specimens investigated belong to an unidentified species of the spiriferid genus *Crurithyris* (Ambocoeliidae) (Fig. 3). They are characterized by a strongly ventribiconvex shell displaying a rounded outline and the presence in most specimens of a sulcus in both valves. These specimens are probably conspecific with those from Tournai illustrated (but not described) by de Koninck (1887, pl. 36, figs 17–25), who died before completing his monograph on the Carboniferous brachiopods from Belgium. They are probably also conspecific with a new species proposed by Demanet (1958), which was stated to occur in abundance within the 'Calcaire de Vaulx et de Chercq' (now the Vaulx Member of the Tournai Formation). Demanet named it *C. sulcata* (not *C. sulcata* Stehli, 1954), but he failed to provide a description or a definition of the species. *C. sulcata* Demanet, 1958 is considered here to be a *nomen nudum*. De Koninck's taxa have not been revised since their first description and a modern systematic study of the brachiopods from Tournai is urgently needed. The bulk samples from 2 m below the 'Gras

Table 1. Abundance of brachiopods from samples used in this study.

Genus (or order/suborder)	Number of specimens
1 m below the 'Gras Délit'	
Unidentified Productidina	2
Rhipidomella	3
Schizophoria	2
Cleiothyridina	2
Nucleospira	1
Unidentified Athyridida	6
*Crurithyris**	3
Parallelora?*	58
2 m below the 'Gras Délit'	
Petrocrania	1
Unidentified Productidina	1
Schizophoria	1
*Crurithyris**	918
Spiriferellina	2

*drilled taxa.

Délit' also yielded other brachiopod taxa (Table 1), as well as microcrinoids, small blastoids, echinoids (isolated plates), bryozoans, solitary rugose corals, gastropods (very rare euomphalids) and trilobites. This rich fauna was first reported by Hibo & Tourneur (1989) from weathered shales on top of large limestone blocks lining the quarry roadway. They considered that it was derived from immediately above the 'Gras Délit' but comparison with in situ material clearly indicates that it is from below. An additional bulk sample from 1 m below the 'Gras Délit' yielded a few specimens of *Crurithyris* sp., as well as representatives of other brachiopod genera (Table 1), bryozoans and solitary rugose corals.

Each drilled specimen of *Crurithyris* sp. was examined under a stereomicroscope and measured with callipers (length of the shell and diameter of the drill hole). Specimens were coated with gold and examined using a scanning electron microscope.

Results

A total of 918 specimens of *Crurithyris* sp. were collected from the shale layer 2 m below the 'Gras Délit' (Table 2). Of these, 432 have conjoined valves; 35 of them had been bored, a drilling intensity (Baumiller *et al.* 2006) of 8.1%. Of the 486 separated valves, 25 had been bored. The drilling intensity of ventral valves is 6.25% in both conjoined and disarticulated specimens. For the dorsal valves, drilling intensity is 1.85% in conjoined and 1.69% in separated valves. The difference in intensity in dorsal valves is not statistically significant ($P > 0.66$; one-tailed Fisher's exact test). The drilling intensity recorded for *Crurithyris* sp. is within the range reported by Kowalewski *et al.* (2005, table S4) for Mississippian taxa.

Uncrushed, drilled and undrilled shells were measured (Fig. 4A, B). The length of the ventral valve, which is used here as a measure of size, ranges from 1.12 mm to 8.30 mm (mean = 2.95 mm; S.D. = 1.66 mm). Young specimens are overrepresented in the set of measured specimens because they are better preserved than larger specimens, which are generally crushed as a result of compaction and could not be measured accurately. Because there is no statistically significant difference in the drilling intensity of the ventral valves of specimens with conjoined valves and that of dissociated ventral valves, the data for drilling intensity of different size categories of conjoined and dissociated ventral valves were pooled. Drilling intensity was compared for different size classes of ventral valves (using the size classes 1–2.5 mm, 2.5–4 mm, 4–5.5 mm, 5.5–9 mm: Table 3). The hypothesis that the probability of drilling across all size classes was the same can be rejected (χ^2 test; $P < 0.01$). However, if the size class 1–2.5 mm is removed from the dataset, the hypothesis cannot be rejected ($P > 0.8$).

Table 2. Statistics of boring intensity and stereotypy in specimens of *Crurithyris* sp.

Total number of specimens from 2 m below the 'Gras Délit'	Conjoined valves			Separated valves			
				Ventral		Dorsal	
	Not bored	Ventral valve bored	Dorsal valve bored	Not bored	Bored	Not bored	Bored
918	397	27	8	345	23	116	2

Table 3. Statistics of boring intensity vs shell size of *Crurithyris* sp. from the Vaulx Member, Tournai Formation, 2 m below the 'Gras Délit', Lemay Quarry, Vaulx-lez-Tournai, Belgium.

Size class	1–2.5 mm	2.5–4 mm	4–5.5 mm	5.5–9 mm	Total
Number of measured specimens	135	54	33	23	245
Number of bored specimens	7	15	10	4	36

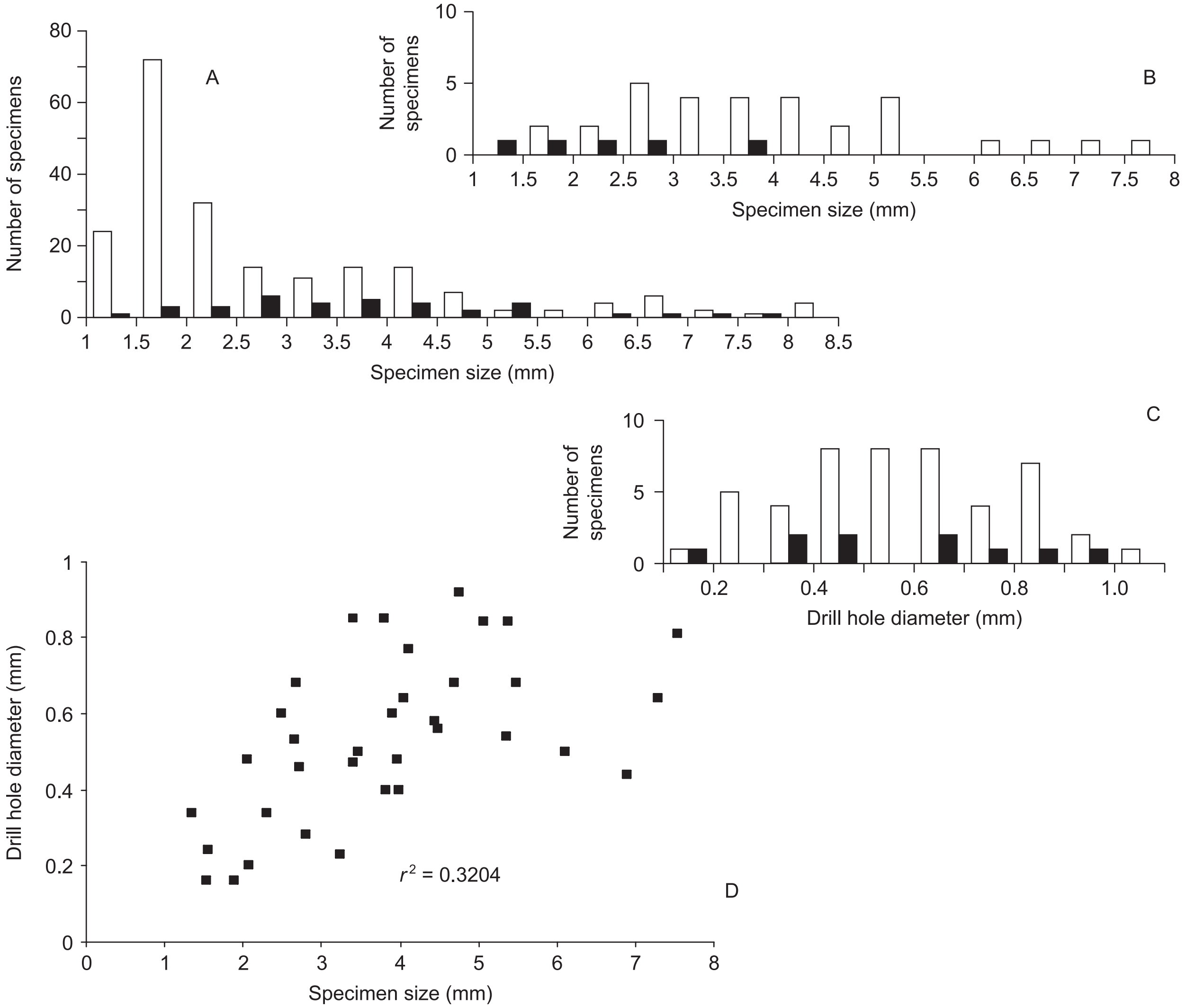

Fig. 4. □A. Size (length of the ventral valve) frequency diagrams for both unbored (white; $n = 209$) and bored specimens (black; $n = 36$). □B. Size frequency diagrams for both ventrally bored specimens (white) and dorsally bored ones (black); $n = 36$. □C. Drill hole diameter frequency diagrams for both ventrally bored specimens (white) and dorsally bored ones (black); $n = 58$. □D. Relationship between specimen size of *Crurithyris* sp. and drill hole diameter. The correlation coefficient, $r = 0.57$. $N = 35$.

This suggests that the driller organism selected specimens with the ventral valve longer than 2.5 mm, but showed no preference for different sized categories above this limit.

Of the 60 drill holes identified overall, 58 are well preserved and range in diameter from 0.16 mm to 1.08 mm (mean = 0.57 mm; standard deviation (SD) = 0.22 mm) (Fig. 4C). The diameter of the drill hole and the length of the brachiopod are positively correlated ($r = 0.57, P < 0.01$) (Fig. 4D). The borings are smooth sided, cylindrical or weakly conical, circular to slightly elliptical in plan view, and perpendicular to the surface of the shell (Fig. 3A–D, J). They penetrate the shell completely and correspond to type A borings of Ausich & Gurrola (1979). A single case of a drill hole with an irregularity on one side has been recognized (Fig. 3I); it is similar to that illustrated by Carricker & Yochelson (1968, pl. 1, fig. 18), which was made by a gastropod.

Of the 35 bored specimens with conjoined valves, 27 were drilled on the ventral valve, while eight were drilled on the dorsal valve; this preference is statistically significant ($P < 0.001$, using the binomial equation and assuming that P, the probability of a borehole on the ventral valve, equals 0.5). No specimen has more than one borehole. On both the ventral and the dorsal valves, most of the drill holes are located in the posterior half of the valve (Fig. 5). No case of edge-drilling (Vermeij 1980), as described in the small orthid *Perditocardinia* cf. *dubia* by Deline *et al.* (2003), has been observed.

Of the more than 1000 specimens of brachiopods recovered from Lemay quarry, only *Crurithyris* sp.

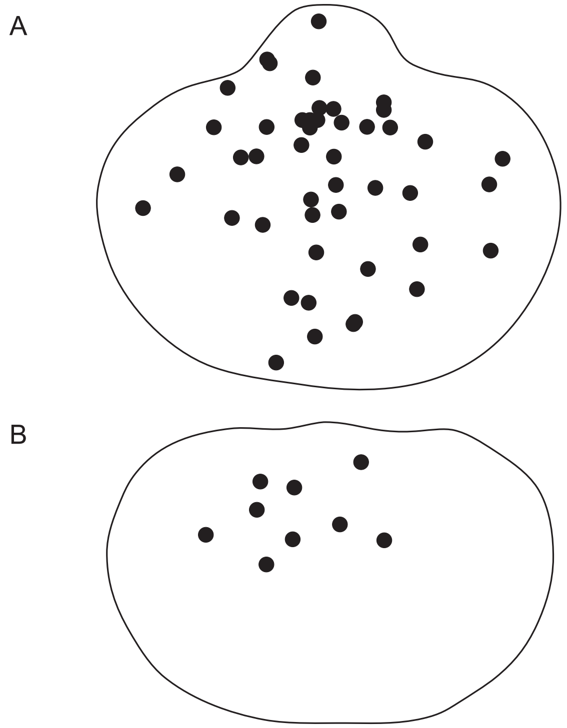

Fig. 5. Distribution of drill hole centres on normalized specimens of *Crurithyris* sp. from the Tournai Formation (Vaulx Member) in ventral (A) and dorsal (B) valve.

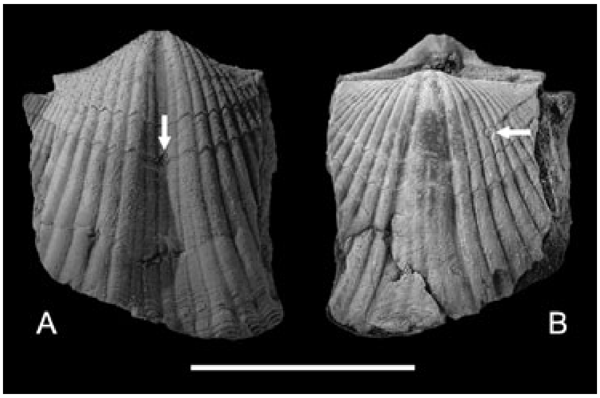

Fig. 6. Drilled specimen of *Parallelora*? sp. (TCD 54415) from the Tournai Formation (top of Vaulx Member) in ventral (A) and dorsal (B) views. Arrows indicate the drill hole positions. Scale bar is 10 mm.

and a single articulated specimen of *Parallelora*? sp. of the 58 collected from 1 m below the 'Gras Délit' were bored. It displays two boreholes, one in the central part of each valve (Fig. 6).

Discussion

The drill holes in *Crurithyris* sp. described above are clearly not the result of an organism boring randomly into hard substrates. They are also completely unlike the borings produced by brachiopod pedicles (Bromley & Surlyk 1973; Alexander 1994). There is no evidence of healed and multiple borings or attachment scars, which Baumiller (1990) listed as criteria for distinguishing parasitic from predatory drilling. The drill holes display the criteria listed by Leighton (2001, table 1) for identifying predatory drill holes, such as a single, complete perforation at right angles to the surface of the shell. We conclude, therefore, that the borings in *Crurithyris* sp. from the Lemay quarry were probably made by a predator. Most of the holes record successful attacks because they penetrate the shell completely; only one specimen shows an incomplete borehole bearing a central boss in the bottom (Fig. 4G, H). Such a boss has been also reported by Ausich & Gurrola (1979, p. 336) in their type B borehole and Carricker & Yochelson (1968, pl. 2, fig. 6) have illustrated a comparable structure in a drill hole, which resulted from an abortive attack by a gastropod on a bivalve.

Representatives of the genus *Crurithyris* are markedly ventribiconvex and display an open delthyrium bordered by narrow deltidial plates for the passage of the pedicle, which provided permanent anchorage and permitted rotational movements (a tether: Alexander 1977). Ferguson (1962) found numerous shells of the Viséan species *Crurithyris urei* with their dorsal valves normal to or highly inclined to the bedding planes and with the posterior part of the ventral valve pointing downwards and interpreted this to be the life position of this pedunculate brachiopod. This mode of life has been also suggested for *Crurithyris* by Rollins & Donahue (1975, fig. 14) and for the Devonian amboecoeliid genera *Ambocoelia* by Thayer (1974, fig. 18D) and *Crurispina* by Racki (1992, fig. 29). Bowen *et al.* (1974) proposed that *Ambocoelia* lived attached to plants or animals. This epibiont mode of life has been clearly demonstrated by Schneider (2003), who illustrated numerous individuals of *C. planoconvexa* preserved either touching, or in very close association with individual spines of the echinoid *Archaeocidaris* from the Pennsylvanian of Texas. Such an association has not been found in our material though isolated echinoid plates occur commonly in the samples. If *Crurithyris* sp. from Lemay Quarry had a mode of life similar to that suggested by Ferguson (1962) for *C. urei*, it would have represented an attractive (in terms of energy cost) and easy prey for a predator. Its shell is thin (less than 0.5 mm thick), practically smooth and was probably not buried in the sediment. Only growth lines are observable on most of the shells but the best preserved specimens display minute spinose projections (Fig. 3K) comparable to those illustrated by

Brunton (1976, 1984). However, these very small spines seem to have been ineffective in deterring the drilling predator.

The stereotyped behaviour of the driller organism is marked in the case of *Crurithyris* sp. because more than 77% of the drill holes occurring in articulated specimens are located in the ventral valve. In most cases of stereotypy reported in the literature (e.g. Brunton 1966; Ausich & Gurrola 1979), the posterior-medial area of the brachiopod shell, which corresponds internally to the body cavity, was the favoured site of attack (Leighton 2001). Ausich & Gurrola (1979) noted that boring was concentrated in the ventral valve of brachiopods that lived with the commissure parallel to the substrate. Examples of the ventral valve having been preferentially bored are found in the order Productida, representatives of which lived with their ventral valve resting on the substratum (Brunton 1966; Watkins 1974; Leighton 2001). Ausich & Gurrola (1979) suggested that borers showed no preference for either valve in brachiopods with the commissure perpendicular to the sediment. It is clear, however, that the borers of *Crurithyris* sp. showed a marked preference for drilling the ventral valve, despite the fact that the brachiopod lived with the commissure probably perpendicular, or highly inclined to the surface of the sediment. An explanation for this might be that it was easier for the drilling organism to topple the brachiopod shell over to rest on its ventral rather than its dorsal valve, which would be consistent with Ferguson's (1962) interpretation of the life position of *C. urei*. The numerous boreholes recorded in this study do not support the hypothesis of Leighton (1998, 2001) that brachiopods with an open delthyrium are unlikely to have been bored because predators would have had direct access to the interior of the shell via the pedicle opening.

The identity of the organisms responsible for the boreholes in Palaeozoic shells (gastropods versus soft-bodied animals) has been widely discussed, notably by Leighton (2001). On one hand, the soft-bodied animal hypothesis (Carricker & Yochelson 1968; Rohr 1976; Ausich & Gurrola 1979) is difficult, perhaps impossible to verify, but cannot be discounted. On the other hand, platyceratid gastropods, which represent a common element of Palaeozoic marine communities (Baumiller 1996), are frequently associated with drilled brachiopods (e.g. Lespérance & Sheehan 1975; Rohr 1976; Ausich & Gurrola 1979; Baumiller *et al.* 1999; Deline *et al.* 2003). Baumiller (1990, 1993, 1996) and Baumiller & Gahn (2002, 2003) gave numerous examples of platyceratids attached to crinoids and to blastoids, a relationship that has been interpreted as parasitic, and demonstrated that some archaeogastropods were capable of drilling well before the mid-Mesozoic or the Late Triassic, the times of origination of the modern shell-boring gastropods according to Carricker & Yochelson (1968) and Fürsich & Jablonski (1984), respectively. Representatives of the genus *Platyceras* occur within the Tournai Formation but Demanet (1958) did not report any in the 'Calcaire de Vaulx et de Chercq' (now the Vaulx Member), which is the source of the material under investigation. It is not possible to identify unequivocally the organisms responsible for the drill holes because we have only a truncated view of the palaeontological record, but we regard gastropods as one of the more plausible candidates. However, only two minute specimens of Euomphalidae are associated with our material from 2 m below the 'Gras Délit'.

Even though the identity of the drilling animal is not known, borings, whether made by predators or parasites, are evidence of biotic interactions that may have affected the evolution of the prey species (Harper & Wharton 2000). According to Johnson *et al.* (in Carter *et al.* 2006), no major change occurred in the shell morphology or body size of *Crurithyris* in the course of its long geological history (Upper Devonian to Permian). Presumably, the intensity of drilling was generally too low to produce any major change in its morphology to deter potential predators, as suggested by Hoffmeister *et al.* (2002) for the long ranging athyridid genus *Composita*.

Conclusions

Numerous drill holes have been recognized in a Tournaisian population of *Crurithyris* (Ambocoeliidae) where the drilling frequency attains about 8%. Other brachiopods in the assemblage, with a single exception, are not drilled. The features of the drill holes, especially the strong stereotypy in the selection of the ventral valve, lead us to interpret them as probably predatory boreholes possibly made by gastropods. The boring organisms preferentially selected individuals with a ventral valve longer than 2.5 mm.

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