

FIRST REPORT OF SUBLETHAL BREAKAGE-INDUCED PREDATION ON DEVONIAN BIVALVES

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ABSTRACT

Here we report on the frequency, shape, and position of sublethal, predatory-induced breakage on shells of the common pterineid bivalve genus *Ptychopteria* from the Middle Devonian of New York. Twenty-six of the 115 well-preserved shells of *Ptychopteria* examined displayed evidence of at least one repair scar. The capacity to retract the vulnerable mantle deep within the shell and squeeze the valve margins together tightly to seal the shell enabled *Ptychopteria* to sustain marginal shell damage that was often severe. Repair scars resemble traces made by modern shell-breaking predators, especially decapod arthropods. Stereotyped positioning of the repair scars on the posterior portion of the valve also suggests active selection of an attack site by unknown shell-breaking predators. The relatively high repair frequency for *Ptychopteria* supports a growing body of evidence that suggests predation pressure intensified in the middle Paleozoic.

Key words: durophagous predation, *Ptychopteria*, Pterineidae, shell repair, mid-Paleozoic marine revolution

INTRODUCTION

Predators have profound effects on the phenotypes and distributions of their prey, as well as the structure of ecosystems (Signor and Brett, 1984; Smith et al., 1985; Vermeij, 2002; Brett and Walker, 2002; Brett, 2003). A critical time interval in which predation has been hypothesized to have influenced the evolution of benthic communities is the middle Paleozoic, the so-called mid-Paleozoic Marine Revolution (Signor and Brett, 1984; Aronson, 1991; Leighton, 2001; Brett, 2003). Many predatory groups, especially those that possessed powerful jaws and claws for crushing hard-shelled prey (Fig. 1), such as phyllocarid arthropods and placoderm fishes, diversified during this time interval (Brett and Walker, 2002). At the same time, the incidence of defensive prey armor increased in many groups; possible examples include spines on crinoids, and shell-strengthening ribs on brachiopods and nautiloids (Signor and Brett, 1984; Brett, 2003).

Direct evidence of middle Paleozoic predation comes from the record of species interactions—the traces left behind by predators, following their successful and failed attacks, on the shells of their prey, such as circular drillholes or repaired scars (healed sublethal breakage). Drillholes have been found in brachiopods (e.g., Smith et al., 1985; Baumiller et al., 1999; Deline et al., 2003; Leighton, 2003), blastoids (Baumiller, 1993, 1996), crinoids (Baumiller, 1990; Gahn et al., 2003), colonial metazoans (Wilson and Taylor, 2006), and possibly bivalves (Liljedahl, 1985; Cosma and Baumiller, 2005). Repaired breakage-induced injuries have been found in ammonoids (Bond and Saunders, 1989), gastropods (e.g., Vermeij et al., 1981; Schindel et al., 1982), brachiopods (Alexander, 1990), rugose corals (Galle and Mikuláš, 2003), and even tentaculites (Berkyová et al., 2007). The frequency of these predation traces peaks in the middle Paleozoic (Kowalewski et al.,

1998; Huntley and Kowalewski, 2007). Taken together, these lines of evidence suggest that predation intensified in the mid-Paleozoic, with a far-reaching influence on evolution and the history of life.

Here we report the first documented examples of sublethal, breakage-induced shell damage on the common pterineid bivalve genus, *Ptychopteria*, from the Middle Devonian of New York. Our study addresses: (1) traits that enabled *Ptychopteria* to survive after marginal shell damage, (2) evidence supporting a biological origin of shell breakage, and (3) the utility of bivalve fossils as a resource for future tests of the evolutionary role of durophagous predators in the middle Paleozoic.

MATERIAL AND METHODS

We examined Middle Devonian pterineid bivalves of the genus *Ptychopteria* for evidence of breakage-induced shell repair (see Supplementary Data¹). Members of this genus are characterized by strong valve asymmetry, with a convex left valve and a lid-shaped, flat to slightly convex right valve. Two morphological groups of *Ptychopteria* are evident from the ornamentation of the shell. The left valve of *Ptychopteria* (*Actinopteria*) is ornamented with weak radial ribs (Figs. 2B–C), while *Ptychopteria* (*Ptychopteria*), which is also commonly named *Cornellites* in the literature, is armored with additional strong radial ribs (Fig. 2A). The right valve of both taxa lacks radial ornamentation. We have not attempted to revise the systematics of this group given the ecological focus of our analysis (for further discussion, see McAlester, 1962; Bailey, 1983).

Ptychopteria is an excellent candidate for an analysis of predation scars because members of this taxon were exclusively epibenthic suspension feeders that dwelled on the surface of the substrate, either byssally attached or in pleurothetic (reclining) life position. This mode of life would have made them vulnerable to an array of potential Devonian jawed and clawed, shell-crushing epibenthic predators (Fig. 1). Also, in some exceptional cases, the original shell microstructure was preserved as fine-grained calcite (Carter and Tevesz, 1978a, 1978b), which lessens any potential taphonomic bias associated with the identification of shell repairs.

All of the *Ptychopteria* samples we studied are from the Middle Devonian Hamilton Group of western and central New York, which represents a typical, mid-Paleozoic benthic fauna with sessile, epibenthic suspension feeders, endobenthic deposit feeders, and moderate bioturbation (Brower and Nye, 1991). *Ptychopteria* developed locally dense populations, some approximating biostromal accumulation (Carter and Tevesz, 1978a). These marine deposits represent anaerobic to fully oxygenated environments, which developed at the northern end of the Appalachian Basin following the early phases of the Acadian Orogeny (Brett et al., 1986, 2007). The Hamilton fauna is inferred to record relatively shallow, euphotic to dysphotic epeiric environments, with water depths ranging from ~20 to 80 meters (Vogel et al., 1987). The stratigraphic and facies framework for the region has

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TABLE 1—Summary of 26 *Ptychopteria* specimens with evidence of breakage-induced shell repair. PRI = Paleontological Research Institution; YPM = Yale Peabody Museum; USNM = U.S. National Museum.

Catalog number	Shell height (mm)	Sculpture	Number of scars	Scar shape	Depth of scar (mm)	Scar position	Length at incidence of injury (mm)
PRI 9809	31	fine	1	scalloped	1.3	posterior	18.0
PRI 9810	43	fine	2	embayed	1.3	median	13.9
				scalloped	8.8	median	39.0
PRI 9811	53	coarse	1	scalloped	4.8	posterior	31.8
PRI 9812	38	coarse	1	scalloped	3.0	posterior	31.5
PRI 9813	29	coarse	1	scalloped	1.5	posterior	23.8
PRI 9814	55	coarse	1	embayed	4.7	posterior	31.0
PRI 9815	48	coarse	2	scalloped	2.0	posterior	17.0
				scalloped	4.3	median	44.0
PRI 9816	38	coarse	1	scalloped	1.3	median	17.5
PRI 9817	15	fine	1	scalloped	1.1	median	7.0
PRI 9818	61	coarse	1	scalloped	7.0	med./post.	45.9
PRI 9819	40	coarse	2	scalloped	1.1	posterior	14.1
				scalloped	1.0	anterior	31.1
PRI 9820	29	fine	1	scalloped	1.5	median	14.0
PRI 9821	28	coarse	1	scalloped	1.6	posterior	9.4
USNM 100586	45	coarse	1	scalloped	1.3	posterior	36.0
USNM 100593	41	coarse	2	scalloped	3.3	posterior	28.2
				scalloped	2.8	posterior	40.6
USNM 100902-B	22	fine	1	scalloped	0.8	posterior	10.3
USNM 537876	27	coarse	1	embayed	1.7	median	13.5
USNM 537882	50	coarse	1	scalloped	1.3	anterior	33.0
YPM 2388	42	coarse	1	scalloped	2.2	posterior	34.6
YPM 222269	31	coarse	1	scalloped	1.1	posterior	25.5
YPM 222271	28	fine	1	scalloped	1.7	posterior	20.4
YPM 222272	40	coarse	1	scalloped	0.9	posterior	30.1
YPM 222275	23	coarse	1	scalloped	1.9	posterior	14.8
YPM 222276	38	coarse	1	scalloped	0.6	median	28.5
YPM 223545	25	coarse	1	scalloped	1.1	posterior	15.1
YPM 223546	17	coarse	1	scalloped	1.1	median	10.1

because marginal shell damage in bivalves lacking such traits is often lethal. The exposure of the mantle following sublethal marginal breakage is an open invitation for bacteria, or it may signal the position of an injured individual to parasites and other predators (Vermeij, 1983; Dietl and Alexander, 2005). This inability of most bivalve taxa to sustain marginal damage typically results in low repair-frequency values in comparison to other prey taxa, such as gastropods, that can withdraw deep within their shell. Only bivalve taxa with traits that enable them to sustain shell damage exhibit high frequencies of repair. Studies on shell repair in modern bivalves indicate that thin, flexible shell margins and a highly retractable mantle permit a high degree of tolerance to marginal shell damage (Vermeij, 1983, 1993; Dietl and Alexander, 2005).

The pallial line and adductor muscle scars of the mid-Paleozoic *Ptychopteria* are situated close to the umbo. This soft-body organiza-

tion would have enabled them to retract their vulnerable mantle deep within the shell; it also allowed a wider portion of the shell margin to be damaged without being life threatening to an individual. We found one individual of *Ptychopteria* that had ~22% of its shell margin broken back by a predator, but still survived to repair the shell. *Ptychopteria* also exhibits a shell microstructure consisting of a simple, exterior prismatic calcite and interior nacreous shell layer; the nacreous layer is restricted to the dorsal region of the shell (Carter and Tevesz, 1978a). This microstructure made the ventral margins of the shell flexible, enabling the bivalve to squeeze its valves together to form a tight seal (Carter and Tevesz, 1978a). While *Ptychopteria* developed the typical pterineid shell microstructure in the right valve, its left valve was characterized by the loss of the simple prismatic calcite layer, making it rigid; this evolutionary change thus resulted only in the right valve being flexible (Carter and Tevesz, 1978a). Such an arrangement would have made *Ptychopteria* more resistant to shell-breaking predators because of the increased strength of the rigid left valve together with the capacity for tight valve closure. The type of flexible, rigid margin that is evident in *Ptychopteria* can be observed in modern pteriomorph groups, such as anomids, ostreids, and propeamussiids (Carter and Tevesz, 1978a; Esteban-Delegado et al., 2008).

Thus, both shell microstructure and soft-body organization indicate that the Middle Devonian bivalve *Ptychopteria* was well defended against shell-breaking predators. The persistence of these traits in modern taxa also underscores their evolutionary success in the face of a dangerous environment. Despite the long evolutionary history of these traits, however, which originated in the early Middle Ordovician (Pojeta and Runnegar, 1985), they are not as widespread taxonomically today as one might expect, perhaps due to the evolution and increasing influence of a battery of powerful shell-crushing predators since the Devonian (Vermeij, 1987). For instance, modern pteriomorph bivalve taxa that possess flexible prismatic layers in both valves and highly retractable mantles, such as the families Pinnidae, Pteriidae, Malleidae,

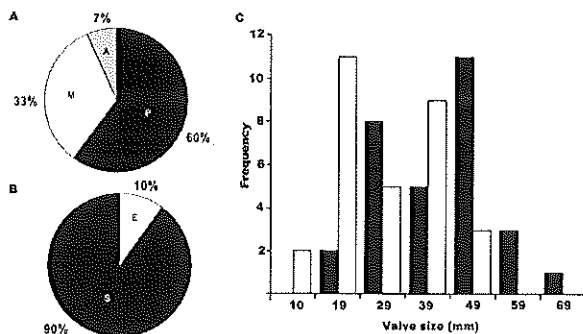


FIGURE 3—Distribution of scar morphology, position, and valve size in studied samples of *Ptychopteria*. A) Scar position; A = anterior, M = medial, P = posterior. B) Scar type; E = embayed, S = scalloped. C) Size-frequency distribution; black bars = valve size at death; white bars = valve size at time of injury.

and Isognomonidae, are relatively genus poor and restricted to epi- and endobyssate life habits, mostly in subtropical to tropical regions (Esteban-Delgado et al., 2008). In striking contrast, pteriomorph groups, such as the ostreoids and pectinoids, which have evolved more rigid shells made of foliated calcite, are geographically widespread, genus rich, and have repeatedly evolved more derived lifestyles, such as cementing and swimming (Esteban-Delgado et al., 2008). The decline in diversity and ecological importance of groups that have retained flexibility in both valves within the pteriomorph bivalve group, thus, may represent a tradeoff between the possession of traits that provide valve flexibility—such as an outer prismatic shell layer—and traits, such as foliated microstructure, that enable the development of pronounced shell armor but also tend to make the margins more rigid (Esteban-Delgado et al., 2008). These features may have opened up different, more predator-resistant, pathways for the evolution of shell form in the Pteriomorphia, such as markedly convex and strongly ribbed or spiny shells; the defensive advantages of these shell morphologies against shell-breaking predators are well known (Vermeij, 1987, 1993).

A biological origin of the repaired injuries on the shells of *Ptychopteria* is supported by three lines of evidence. First, the embayed- and scalloped-repair scars resemble traces made by modern shell-breaking predators (Alexander and Dieltz, 2003). Potential shell-breaking predators capable of making such scars in the Devonian include phyllocarid arthropods. These predators diversified in the Devonian (Signor and Brett, 1984) and possessed molariform, calcified mandibles that may have functioned to break the skeletons of hard-shelled benthic prey. Nautiloid and ammonoid cephalopods with chitinous beaks were also capable of breaking at least thin-shelled prey (Alexander, 1986; Brett and Walker, 2002). Jawed placoderm fishes (e.g., ray-like rhenanids and ptyctodonts), armed with crushing plates, diversified during the Early to Middle Devonian and may have been important predators of shelled prey (Fig. 1). Other Middle Devonian fish that were potential predators of *Ptychopteria* include marine dipnoan and dipterid lobed-finned fishes (Vermeij, 1987; Campbell and Barwick, 1990) and early ray-finned fishes, such as the gonatodontids (Janvier, 2003). Little is known, however, about the activities of these predators (Brett and Walker, 2002). Other shell-crushing predators that are often considered as participants in the mid-Paleozoic Marine Revolution, such as paleostomatopods, eurypterids, and helodontid chimaeras and other sharks, evolved later in the Late Devonian or Carboniferous, or were restricted to marginal marine or freshwater environments (Vermeij, 1987; Brett and Walker, 2002). The shell-breaking predators of *Ptychopteria*, thus, remain unknown, but it is clear that an array of potential predators equipped with an arsenal of varied weapons could have made scars found in this study.

The second line of evidence is the disproportionate (93%) stereotyped positioning of the scars on the posterior and medial region of *Ptychopteria* shells, which is suggestive of active selection of an attack site by shell-breaking predators. These areas occur in the inhalant and exhalant current regions of the shell, which may have attracted the predators. The life position of *Ptychopteria* (either byssally attached or reclining) also would have made the posterior portion of the shell vulnerable to foraging, epibenthic predators (for further discussion of life position, see Stanley, 1972; Bailey, 1983; Johnston, 1993; Bradshaw, 1999).

The third line of evidence supporting a biological origin of the scars relates to the possibility of a size refuge from sublethal damage (*sensu* Alexander and Dieltz, 2003) suggested by the data (Fig. 3C), which may imply a limit to the functional capabilities of the predators. It is important to recognize, however, that the absence of sublethal repairs in the largest size classes of shells does not necessarily imply that the largest specimens were safe from shell-crushing predation. Such a gap between the largest size at which sublethal breakage occurred (46 mm for *Ptychopteria* in this study) and the largest sizes of individuals at death (61 mm) may indicate that predation attempts on larger

individuals were either absent, always successful, or unsuccessful but without any trace evidence of the event (Alexander and Dieltz, 2003).

Lastly, the high repair frequency for Devonian *Ptychopteria* supports the hypothesis that predation was an important selective agency in the mid-Paleozoic (see Signor and Brett, 1984; Brett, 2003). Our findings further suggest that the Paleozoic bivalve record represents a largely untapped resource for tests of the mid-Paleozoic Marine Revolution hypothesis (Signor and Brett, 1984).

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REFERENCES

- ALEXANDER, R.R., 1986, Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods: *Journal of Paleontology*, v. 60, p. 273–285.
- ALEXANDER, R.R., 1990, Mechanical strength of shells of selected extant articulate brachiopods: Implication for Paleozoic morphology trends: *Historical Biology*, v. 3, p. 169–188.
- ALEXANDER, R.R., and DIETZ, G.P., 2003, The fossil record of shell-breaking predation on marine bivalves and gastropods, in Kelley, P.H., Kowalewski, M., and Hansen, T.A., eds., *Predator-Prey Interactions in the Fossil Record: Topics in Geobiology*, v. 20, Kluwer/Plenum Publishers, New York, p. 141–176.
- ARONSON, R.B., 1991, Escalating predation on crinoids in the Devonian: Negative community-level evidence: *Lethaia*, v. 24, p. 123–128.
- BAILEY, J., 1983, Middle Devonian Bivalvia from the Solville Member (Marcellus Formation), central New York State: *Bulletin of the American Museum of Natural History*, v. 174, p. 193–326.
- BAIRD, G.C., 1979, Sedimentary relationships of Portland Point and associated Middle Devonian rocks in central and western New York: *New York State Museum Bulletin*, v. 433, p. 1–23.
- BATT, R.J., 1996, Faunal and lithologic evidence for small-scale cyclicity in the Wanakah Shale (Middle Devonian) of western New York: *PALAIOS*, v. 11, p. 230–243.
- BAUMILLER, T.K., 1990, Non-predatory drilling of Mississippian crinoids by platyceratid gastropods: *Palaeontology*, v. 33, p. 743–748.
- BAUMILLER, T.K., 1993, Boreholes in Devonian blastoids and their implications for boring by platyceratids: *Lethaia*, v. 26, p. 41–47.
- BAUMILLER, T.K., 1996, Boreholes in the Middle Devonian blastoids *Heteroschisma* and their implications for gastropod drilling: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 123, p. 343–351.
- BAUMILLER, T.K., LEIGHTON, L.R., and THOMPSON, D.L., 1999, Boreholes in Mississippian spiriferid brachiopods and their implications for Paleozoic gastropod drilling: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 147, p. 283–289.
- BERKYOVA, S., FRYDA, J., and LUKE, P., 2007, Unsuccessful predation on Middle Paleozoic plankton: Shell injury and anomalies in Devonian dacryoconarid tentaculites: *Acta Palaeontologica Polonica*, v. 52, p. 407–412.
- BOND, P.N., and SAUNDERS, W.B., 1989, Sublethal injury and shell repair in Upper Mississippian ammonoids: *Paleobiology*, v. 15, p. 414–428.
- BRADSHAW, M.A., 1999, Lower Devonian bivalves from the Reefton Group, New Zealand: *Memoir of the Association of Australasian Palaeontologists*, v. 20, p. 1–171.
- BRETT, C.E., 2003, Durophagous predation in Paleozoic marine benthic assemblages, in Kelley, P.H., Kowalewski, M., and Hansen, A., eds., *Predator-Prey Interactions in the Fossil Record: Topics in Geobiology*, v. 20, Kluwer/Plenum Publishers, New York, p. 55–92.
- BRETT, C.E., and BAIRD, G.C., 1985, Carbonate shale cycles in the Middle Devonian of New York: An evaluation of models for the origin of limestones in terrigenous shelf sequences: *Geology*, v. 13, p. 324–327.
- BRETT, C.E., and BAIRD, G.C., 1986, Symmetrical and upward shallowing cycles in the Middle Devonian of New York: Implications for the punctuated aggradational cycle hypothesis: *Paleoceanography*, v. 1, p. 1–16.
- BRETT, C. E., and BAIRD, G. C., 1996, Middle Devonian sedimentary cycles and sequences in the Northern Appalachian Basin, in Witzke, B.J., Ludvigson, G.A., and Day, J., eds., *Paleozoic Sequence Stratigraphy: Views from the North American Craton: Geological Society of America Special Paper 306*, p. 213–241.
- BRETT, C.E., and WALKER, S.E., 2002, Predators and predation in Paleozoic marine environments, in Kowalewski, M., and Kelley, P.H., eds., *The Fossil Record of Predation: The Paleontological Society Papers*, v. 8, p. 93–118.

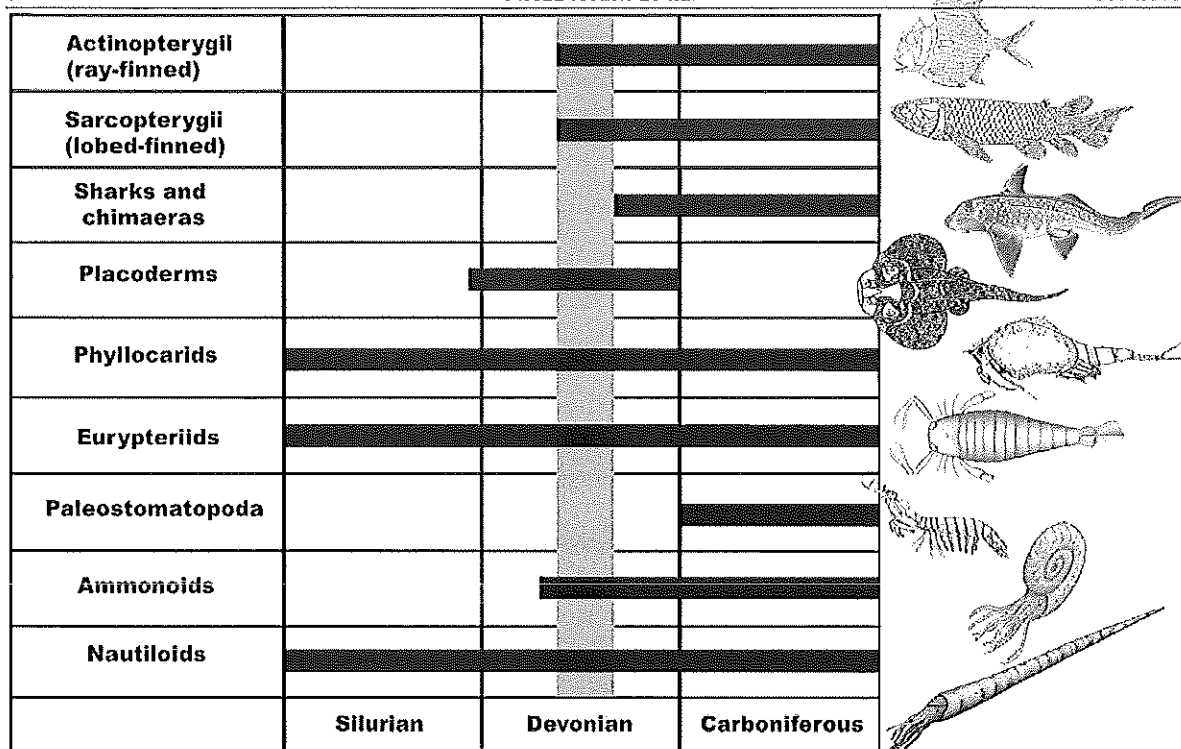


FIGURE 1.—Stratigraphic ranges of mid-Paleozoic shell-crushing predators (based on Brett, 2003).

been thoroughly established over the last several decades (for reviews, see Cooper, 1929; Cooper and Williams, 1935; McCave, 1973; Baird, 1979; Brett and Baird, 1985, 1986, 1996; Landing and Brett, 1991; Batt, 1996).

Breakage-induced shell damage that resulted from unsuccessful attacks by predators is differentiated from other non-biological taphonomic processes, such as sediment compaction, by the presence of characteristic features of damage and repair, including scar geometry (jagged, scalloped, or embayed *sensu* Alexander and Dietl, 2003), changes in growth line banding, and loss or offsetting of radial surface ornamentation (Fig. 2A). The frequency of shell repair (f) was calculated as the total number of repair scars divided by the total number of individuals in the sample—the scars per shell method (Alexander and Dietl, 2003). This method was chosen over others that are available (see Alexander and Dietl, 2003) because of our focus on the effectiveness of *Ptychopteria* shell traits in sustaining marginal shell injuries. The scars per shell method is sensitive to the presence of multiple scars that accumulate on the shell of a single individual. For purposes of standardization of data presentation, however, our data were also tabulated in such a way that other repair-frequency metrics can be calculated by future researchers. Only the left valve was used in this repair-frequency analysis, so that we are confident of the number of unique individuals in our sample.

Because of poor preservation, 228 shells were excluded from the repair-frequency analysis and are not discussed further (see Supplementary Data¹). Data were also pooled for weakly and strongly ribbed *Ptychopteria* shells in the analysis because no differences were evident between them in the accumulation of shell injuries.

RESULTS

The frequency of shell repair in samples was 0.26. Of the 115 well-preserved shells of *Ptychopteria* examined, 26 displayed evidence of at least one repair scar. Four specimens had two scars preserved on the

shell (Fig. 2B). Ninety percent ($n = 27$) of the repair scars displayed the characteristic scalloped shape (Figs. 2A–C; Table 1) that Alexander and Dietl (2003) described for attacks on Cenozoic bivalves by various clawed and jawed predators. The geometry or outline of this type of scar involves shell breakage that is subparallel to concentric growth lamellae, often cutting across radial ornamentation, if present (Alexander and Dietl, 2003). Only 3% ($n = 3$) of the scars were severe embayments of the shell (Figs. 2C, 3B; Table 1), in which a large piece of the shell was removed (Alexander and Dietl, 2003). Similar breakage-induced repair scars on specimens of *Ptychopteria* from other regions of the world during the Devonian also are evident in a cursory examination of material figured in systematic monographs, such as Bailey (1983; fig. 7.A), Johnston (1993; fig. 23N), and Bradshaw (1999; fig. 68H).

The mean ratio of the depth of the repaired scar to the height of the valve at the incidence of repair was 0.09, with a range of 0.02–0.22; the latter value suggests the removal of about 1/5 of the left valve margin. Nearly a third (30%) of the shells displayed evidence of a loss or offsetting of the primary ribbing pattern on the valve surface following the repair of the injury (Fig. 2A; Table 1). This offsetting is restricted to the immediate area of the repair scar. The majority (60%) of the scars were located on the posterior portion of the left valve (Fig. 3A; Table 1). Only 7% occurred on the anterior portion of the valve, with the remaining third positioned medially along the shell commissure (Fig. 3A; Table 1). The mean shell height of scarred *Ptychopteria* at the time of injury was 22 mm; the largest individual at the incidence of marginal injury measured ~46 mm, while the smallest was 7 mm (Fig. 3C; Table 1), although several specimens in our samples obtained sizes >50 mm.

DISCUSSION

The frequency of repair found in the samples of *Ptychopteria* is surprisingly comparable to values calculated for many modern bivalves.

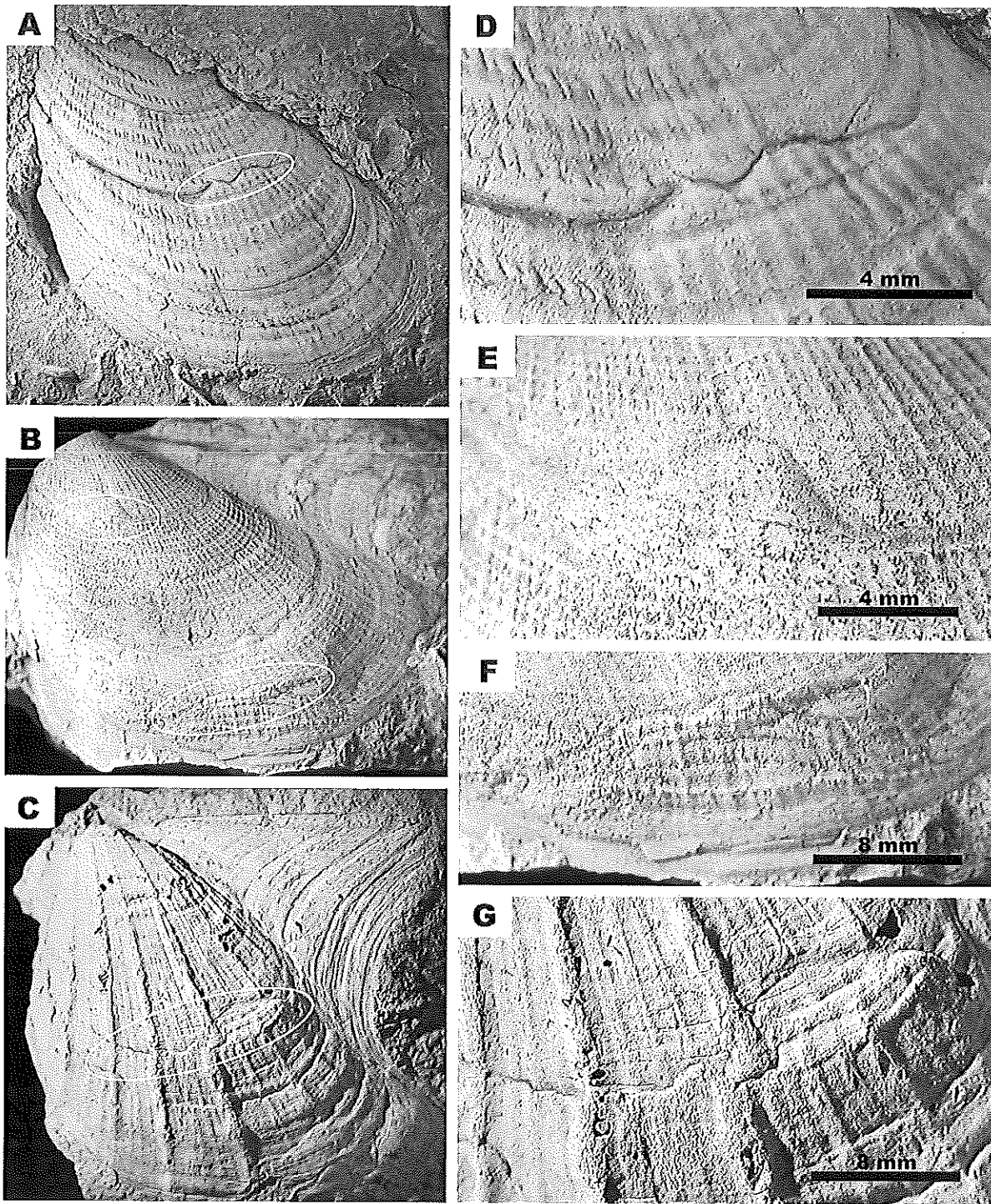


FIGURE 2—Repair scars on *Ptychopteria*. A, D) *P. (Actinopteria) decussata*, PRI 9809, with single scar; entire specimen (A), $\times 2.25$, and close up (D) showing scalloped scar. B, E–F) *P. (Actinopteria) decussata*, PRI 9810, with two scars; entire specimen (B), $\times 1.4$, and close ups of embayed (E) and scalloped scars (F). C, G) *P. (Ptychopteria) flabella*, PRI 9811, with single scar; entire specimen (C), $\times 1.25$, and close up (G) showing scalloped scar and offset of primary rib.

Modern taxa, such as the pinnids *Pinna* and *Atrina*, show higher repair-frequency values ($f = 0.31$ – 1.14 , Dietl and Alexander, 2005) than the Devonian *Ptychopteria* ($f = 0.26$), but the majority of modern taxa have lower repair frequencies ($f \leq 0.1$; Dietl and Alexander, 2005). High

frequencies of repair for *Ptychopteria* imply that its shell was an effective defense against local shell-breaking agents (Vermeij et al., 1981; Alexander and Dietl, 2003); high values also suggest that *Ptychopteria* possessed traits that functioned to withstand shell injury

USE THESE MARKS IN CORRECTING PROOFS

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| <i>tu</i> | Transpose; indicate by <i>N</i> in text | ⊙ | Period |
| <i>cap</i> | Capital; circle letter or word in text | ↵ | Comma |
| <i>sc</i> | Small capital; circle letter or word in text | ⊖ | Colon |
| <i>lc</i> | Lowercase; circle letter or word in text | ↗ | Semicolon |
| <i>ital</i> | Italic; circle letter or word in text | ↘ | Apostrophe |
| <i>rom</i> | Roman; circle letter or word in text | ↙ | Quotation marks |
| <i>spell out</i> | Give complete spelling; circle abbreviation in text | ⊖ | Hyphen |
| bold | Boldface; circle letter or word in text | $\frac{1}{n}$ | One-en dash |
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The *s* ~~s~~ *cap* presents a complex interfingering of deltaic and marine subenvironments with the delta dominating. Southern progradation of the present Ganges-Brahmaputra delta is a continuation of the deltaic system that was initiated at the end of the pleistocene. *cap*

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Surma Group (Early Miocene-Quaternary)

The *Surma Group* is a diachronous unit consisting of a succession of alternating shales, sandstones, siltstones, and sandy shales with occasional thin conglomerates, indicative of repetitive deposition from pro-delta, delta front, and facies paralic with intermittent, wholly marine facies (Holthrop and Kazajev 1970).
 The group is divided into the Bhuban and the Bokabil Formations, based on differences in their gross lithologies (Mather and Evans 1964).

rom ~~Tipam Group (Middle Miocene-Quaternary)~~ ital
Tipam Group is a diachronous unit representing a sequence of predominantly arenaceous sediments of fluvial origin overlying the Surma Group. Compared with the Surma Group, the Tipam Group contains a much smaller proportion of shales.
 The group is divided into three formations, The Tipam Sandstone Formation, The Girujan Clay Formation, and the uppermost Dupitila Sandstone Formation. The Tipam Sandstone Formation is composed of massive to cross-bedded, medium-grained sandstones with subordinate (10-20 %) shale interbeds. The Girujan Clay is only locally developed and in its absence it is often difficult to distinguish the cross-bedded ferruginous sandstone of the Dupitila Sandstone Formation from the basal Tipam Sandstone Formation.
 The eigenvector *V*, refers to the "direction" of maximum clustering and *V*, that of minimum clustering. The eigenvalues represent the "degree" of clustering or fabric strength, and it is these that

When answering queries:

Please answer questions "yes" or "no," or make the correction needed. Please do not use "OK." ("OK" could mean "yes, change it" or "no, it is correct as set.")

Revision Charges

Revision charges will be based on principles illustrated below.

- A *Facies* --? *Crossopodia* is found in the offshore hummocky crossbedded sandstone at measured section 1A only tu # (Figure 1) ⊖
- B understand how the drill movement is yet another example *was controlled* under such difficult conditions; the technique

Figure 1. In A and B one charge is incurred by one revision. In both cases the revision involves the addition of contiguous words. One charge is assessed in each case.

La lluvia en EspaZa ~~de~~ tu principalmente en el plano ~~de~~

Figure 2. There are three noncontiguous corrections in this line and therefore three charges are assessed.

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Figure 3. New material is added to the end of an existing paragraph. One charge is assessed.

- BRETT, C.E., BAIRD, G.C., and MILLER, K.B., 1986, Sedimentary cycles and lateral gradients across a Middle Devonian shelf to ramp, Ludlowville Formation, Cayuga Basin, in Cisne, J., ed., New York State Geological Association Guidebook: 58th Annual Meeting, p. 81-127.
- BRETT, C.E., BARTHOLOMEW, A.J., and BAIRD, G.C., 2007, Biofacies recurrence in the Middle Devonian of New York State: PALAIOS, v. 22, p. 306-324.
- BROWER, J.C., and NYE JR, O.B., 1991, Quantitative analysis of paleocommunities in the lower part of the Hamilton Group near Cazenovia, New York, in Landing, E., and Brett, C.E., eds., Dynamic Stratigraphy and Depositional Environments of the Hamilton Group (Middle Devonian) in New York State, Part II: New York State Museum and New York Geological Survey Bulletin, v. 469, p. 37-74.
- CAMPBELL, K.S.W., and BARWICK, R.E., 1990, Paleozoic dipnoan phylogeny: Functional complexes and evolution without parsimony: Paleobiology, v. 16, p. 143-169.
- CARTER, J.G., and TEVESZ, M.J.S., 1978a, Shell microstructure of a Middle Devonian (Hamilton Group) bivalve fauna from central New York: Journal of Paleontology, v. 52, p. 859-880.
- CARTER, J.G., and TEVESZ, M.J.S., 1978b, The shell structure of *Ptychodesma* (Cyrtodontidae: Bivalvia) and its bearing on the evolution of the Pteriomorpha: Philosophical Transactions of the Royal Society of London, Series B, Biological Science, v. 284, p. 367-374.
- COOPER, G.A., 1929, Stratigraphy of the Hamilton Group: Unpublished Ph.D. dissertation, Yale University, New Haven, 485 p.
- COOPER, G.A., and WILLIAMS, H.S., 1935, Tully Formation of New York: Bulletin of the Geological Society of America, v. 46, p. 781-868.
- COSMA, T.N., and BAUMILLER, T.K., 2005, A trace fossil on a Silurian bivalve: Evidence of predatory boring? Ichnos, v. 12, p. 135-139.
- DELINE, B., BAUMILLER, T., KAPLAN, P., KOWALEWSKI, M., and HOFFMEISTER, A.P., 2003, Edge-drilling on the brachiopod *Perditocardia* cf. *P. dubia* from the Mississippian of Missouri (USA): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 201, p. 211-219.
- DIETL, G.P., and ALEXANDER, R.R., 2005, High frequency and severity of breakage-induced shell repair in western Atlantic Pinnidae (Bivalvia): Journal of Molluscan Studies, v. 71, p. 307-311.
- ESTEBAN-DELGADO, F.J., HARPER, E.M., CHECA, A.G., and RODRIGUEZ-NAVARRO, A., 2008, Origin and expansion of foliated microstructure in pteriomorph bivalves: The Biological Bulletin, v. 214, p. 153-165.
- GAIN, F.J., FABIAN, A., and BAUMILLER, T.K., 2003, Additional evidence for the drilling behaviour of Paleozoic gastropods: Acta Palaeontologica Polonica, v. 48, p. 156-156.
- GALLE, A., and MIKULAS, R., 2003, Evidence of predation on the Rugose coral *Sandalina calcicola* (Devonian, Czech Republic): Ichnos, v. 10, p. 41-45.
- HUNTLEY, J.W., and KOWALEWSKI, M., 2007, Strong coupling of predation intensity and diversity in the Phanerozoic fossil record: Proceedings of the National Academy of Sciences, USA, v. 104, p. 15,006-15,010.
- JANVIER, P., 2003, Early Vertebrates: Oxford Monographs on Geology and Geophysics 33: Oxford University Press, 408 p.
- JOHNSTON, P.A., 1993, Lower Devonian Pelecypoda from southeastern Australia: Memoir of the Association of Australasian Palaeontologists, v. 14, p. 1-134.
- KOWALEWSKI, M., DULAI, A., and FÖRSICHT, F.T., 1998, A fossil record full of holes: The Phanerozoic history of drilling predation: Geology, v. 27, no. 10, p. 959-960.
- LANDING, E., and BRETT, C.E., eds., 1991, Dynamic Stratigraphy and Depositional Environments of the Hamilton Group (Middle Devonian) in New York State, Part II: New York State Museum Bulletin, v. 469, p. 1-177.
- LEIGHTON, L.R., 2001, New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 165, p. 53-69.
- LEIGHTON, L.R., 2003, Morphological response of prey to drilling predation in the Middle Devonian: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 201, p. 221-234.
- LILJEDAHN, L., 1985, Ecological aspects of a silicified bivalve fauna from the Silurian of Gotland: Lethaia, v. 18, p. 53-66.
- MCALISTER, L.A., 1962, Upper Devonian pelecypods of the New York Chemung stage: Peabody Museum Bulletin, v. 16, p. 1-88.
- MCCAVE, I.N., 1973, The sedimentology of a transgression: Portland Point and Cooksburg Members (Middle Devonian), New York State: Journal of Sedimentary Research, v. 43, p. 484-504.
- POJETA, J., and RUNNEGAR, B., 1985, The evolution of diasome molluscs, in Trueman, E.R., and Clarke, M.R., eds., The Mollusca, Volume 10: Evolution: Academic Press, Orlando, p. 296-336.
- SCHINDEL, D.E., VERMEJ, G.J., and ZIPSER, B., 1982, Frequencies of repaired shell fractures among the Pennsylvanian gastropods of north-central Texas: Journal of Paleontology, v. 56, p. 729-740.
- SIGNOR, P.W., and BRETT, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic Marine Revolution: Paleobiology, v. 10, p. 229-245.
- SMITH, S.A., THAYER, C.W., and BRETT, C.E., 1985, Predation in the Paleozoic: Gastropod-like drillholes in Devonian brachiopods: Science, v. 230, p. 1033-1035.
- STANLEY, S.M., 1972, Functional morphology and evolution of byssally attached bivalve mollusks: Journal of Paleontology, v. 46, p. 165-212.
- VERMEJ, G.J., 1983, Traces and trends of predation, with special reference to bivalved animals: Palaeontology, v. 26, p. 455-465.
- VERMEJ, G.J., 1987, Evolution and Escalation: An Ecological History of Life: Princeton University Press, Princeton, 527 p.
- VERMEJ, G.J., 1993, A Natural History of Shells: Princeton University Press, Princeton, 207 p.
- VERMEJ, G.J., 2002, Evolution in the consumer age: Predators and the history of life, in Kowalewski, M., and Kelley, P.H., eds., The Fossil Record of Predation: The Paleontological Society Papers, v. 8, p. 375-393.
- VERMEJ, G.J., SCHINDEL, D.E., and ZIPSER, B., 1981, Predation through geological time: Evidence from gastropod shell repair: Science, v. 214, p. 1024-1026.
- VOGEL, K., GOLUBIC, S., BRETT, C.E., 1987, Endolith associations and their relation to facies distribution in the Middle Devonian of New York State, U.S.A.: Lethaia, v. 20, p. 263-290.
- WILSON, M.A., and TAYLOR, P.D., 2006, Predatory drillholes and partial mortality in Devonian colonial metazoans: Geology, v. 34, p. 565-568.

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Sandalina calcicola