Predatory scars in the shells of a Recent lingulid brachiopod: Paleontological and ecological implications

MICHAŁ KOWALEWSKI, KARL W. FLESSA, and JONATHAN D. MARCOT

Kowalewski, M., Flessa, K.W., & Marcot, J.D. 1997. Predatory scars in the shells of a Recent lingulid brachiopod: Paleontological and ecological implications. — *Acta Palaeontologica Polonica* **42**, 4, 497–532.

The paper presents the detailed quantitative study of predatory scars in the shells of an inarticulate brachiopod: the lingulid *Glottidia palmeri* Dall, 1870. The scars include four morphological types: u-shaped, pocket, crack, and miscellaneous scars. They concentrate and open up toward the anterior shell edge. They commonly consist of a pair of scars on the opposite valves. The analysis of 820 specimens live-collected from two intertidal localities in the northern Gulf of California indicates that (1) 23.4% specimens bear repair scars; (2) the scars vary in size from 1.5 to 24 mm^2 (mean = 2.5 mm^2) and all scar types have similar size-frequency distributions; (3) the spatial distribution of scars on the shell is non-random; (4) the anterior-posterior distribution of scars is strongly multimodal and suggests seasonal predation in the late fall and winter months; and (5) the frequency of scarred specimens increases with brachiopod size and differs between the two sampled localities, but does not vary among brachiopod patches from the same locality. The repair scars record unsuccessful attacks by epifaunal intertidal predators with a scissors-type weapon (birds or crabs). The high frequency of attacks, seasonal winter predation, and previous ecological research suggest that scars were made by wintering shorebirds (willets or/and curlews). However, crabs cannot be entirely excluded as a possible predator. Because repair scars represent unsuccessful predation, many of the quantitative interpretations are ambiguous. Nevertheless, the study suggests the existence of strong seasonal interactions between inarticulate brachiopods and their predators. Because shorebirds, crabs, and lingulids may have co-existed in intertidal ecosystems since the late Mesozoic, predatory scars in lingulid shells may have potentially a 100 million year long fossil record.

Key words: predation, lingulids, brachiopods, *Glottidia palmeri*, shorebirds, Recent, Baja California.

Michał Kowalewski [michael.kowalewski@uni-tuebingen.de], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.
Karl W. Flessa [kflessa@geo.arizona.edu], Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA.
Jonathan D. Marcot [dinosaur@geo.arizona.edu], Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA.

Introduction

Predatory attacks by durophagous organisms (i.e., those that damage the prey's exoskeleton) create marks on the hard skeletons of their prey. In present-day benthic marine ecosystems traces of predation are very diverse (see Vermeij 1987 for details and references) and include drillholes made by snails, octopods, and flatworms (e.g., Bromley 1981; Kabat 1990; Kowalewski 1993); irregular punch holes made by stomatopod crabs (e.g., Geary *et al.* 1991); multiple holes caused by fish (e.g., Norton 1988); and fracture and breakage inflicted by crabs, birds, and other predators (e.g., Schoener 1979; Vermeij 1987, 1992; Cadée 1968, 1989; Vale & Rex 1988, 1989; Kropp 1992; Walker & Yamada 1993; Cadée *et al.* in press).

Predatory traces provide quantifiable data on prey-predator interactions, and thus, they have been intensely studied by biologists interested in the behavior of prey and predators, foraging strategies, population biology and ecosystem dynamics (e.g., Berg 1976; Wiltse 1980; Garrity & Levings 1981; Fairweather 1985; Vale & Rex 1988, 1989). Moreover, predatory traces are commonly preserved in the geological record. Indeed, they have a diverse and impressive fossil record and have been documented, in a great variety, from all the periods of the Phanerozoic (e.g., Vermeij 1987); and even from the Late Precambrian (Bengtson & Zhao 1992). Such fossilized traces of predation (Praedichnia; see Ekdale 1985; Bromley 1996) offer paleontologists invaluable insights into ancient ecosystems (e.g., Hoffman *et al.* 1974; Thomas 1976; Robba & Ostinelli 1975; Sheehan & Lesperance 1976; Kitchell *et al.* 1981; Schindel *et al.* 1982; Hoffman & Martinell 1984; Kowalewski 1990; Andersen *et al.* 1991), into the behavior of extinct species (e.g., Berg & Nishenko 1975; Kitchell 1986; Kelley 1989), and into macroevolutionary and coevolutionary processes (e.g., Vermeij 1977, 1987; Vermeij *et al.* 1980, 1981, 1982; Taylor *et al.* 1980; Fürsich & Jablonski 1984; Allmon *et al.* 1990; Kelley 1989, 1991; Kelley & Hansen 1996).

Here we present a detailed quantitative analysis of the repair scars found on the shells of the Recent lingulid (family Lingulidae) brachiopod *Glottidia palmeri* Dall, 1870, a living fossil that inhabits the present-day macrotidal flats of the northeastern Baja California, Mexico. In sharp contrast to repair scars in extant mollusks and articulate brachiopods, which have been intensely researched (e.g., Vale & Rex 1988, 1989; Thayer & Allmon 1991; Alexander 1992; Kropp 1992; Walker & Yamada 1993; Walker & Voigt 1994; Cadée *et al.* in press), repair scars in extant lingulid brachiopods have not been investigated. In fact, ecological interactions between Recent inarticulate brachiopods and their predators have rarely been investigated in a rigorous fashion (see James *et al.* 1992; Emig in press; and below for references).

This study has both biological and paleontological goals. We document the morphological types of repair scars and attempt to identify the most likely predators. By doing so, not only do we hope to improve the ecological knowledge of present-day inarticulate brachiopods and their predators, but also to provide an actualistic description that may be helpful in identifying predatory traces encountered in the fossil record of lingulid brachiopods and other shelly organisms. Also, this study illustrates difficulties inherent to the interpretation of repair scars. Repair scars represent unsuccessful predation events, and thus, provide ambiguous data on the ecology and behavior of prey-predator interactions, both Recent and fossil (see also Shoener 1979; Schindel *et al.* 1982; Vermeij 1983; Walker & Voigt 1994).

We use repair scars to evaluate issues such as the size and site selectivity of predatory attacks, variation in frequency of predatory attacks through time and among different brachiopod populations, and seasonality of predation. Our quantitative analysis serves also to illustrate some statistical methods useful in analyzing repair scars, both modern and fossil. In particular, we discuss quantitative techniques that allow for the assessment of randomness in the spatial distribution of scars and for the recognition of seasonality of predation in modern and ancient ecosystems.

Previous research on durophagous predation on lingulid brachiopods

In striking contrast to the Recent mollusks (e.g., Vermeij 1987, 1992; Kabat 1990), the Recent lingulids has been poorly researched for traces of predation. Marginal remarks and a few rigorous observations scattered in the literature suggest that shells of the two Recent lingulid genera, *Glottidia* and *Lingula*, occassionally bear predatory marks. Drillholes has been relatively best documented. Paine (1963), in his monograph on *G. pyramidata*, reported that drilled specimens were commonly found (14% of shells contained drillholes) on a sandbar near the mouth of Stum Pass (west coast of Florida). A predatory drillhole, most likely caused by a muricid gastropod, was found in *G. palmeri* (Kowalewski & Flessa 1994). Drillholes were also documented in fossil lingulids from the Tertiary of Seymour Island (Wiedman *et al.* 1988; Bitner 1996) and the eastern USA (Cooper 1988). Among other inarticulate brachiopods, predatory drillholes were reported in Recent craniids (Emig in press) and in fossil acrotretids (Miller & Sundberg 1984; Chatterton & Whitehead 1987).

Breakage and repair scars are poorly studied in lingulids. The only more detailed observation was reported by Paine (1963) who investigated holes made by willets (*Catoptrophorus semipalmatus)* and found many partially consumed specimens of *G. pyramidata*: 'In most instances, the pedicle and one valve were left, although in others the anterior ends of both valves had been broken off. If shell and other damage is not too extensive, the brachiopod can regenerate its lost portions' (Paine 1963: pp. 192–193). Repair scars, most likely caused by crabs, were also found in shells of extant *Lingula* (C.C. Emig written communication 1997). Breakage and repair scars, caused by durophagous predators, are much better documented among articulate brachiopods, both Recent and fossil (e.g., Brunton 1966; Thayer 1985; Alexander 1986a, 1986b, 1990, 1992; Thayer & Allmon 1991; Ruggiero 1991; James *et al.* 1992; Baliński 1993).

To our knowledge, not only traces of predation but also predators that prey on lingulids have rarely been investigated rigorously. Nevertheless, previous researchers of lingulid brachiopods (e.g., Paine 1963; Worecester 1968; Emig *et al.* 1978; Emig 1982, 1983) have listed prosobranch gastropods, crabs, fish, and shorebirds as potential predators. In the most comprehensive review so far, Emig (in press) provided a detailed list of predators including: (1) crustaceans (hermit crabs, stone crabs, portunid crabs, crangonids, stomatopods, shrimps, amphipods); (2) echinoderms (asteroids, ophiuroids, echinoids); (3) gastropods (muricids and naticids); (4) fishes (demersal fishes and sturgeons); (5) shorebirds; and (6) humans.

Gut content studies provide unquestionable evidence for successful predation. The gut content of *Catoptrophorus semipalmatus* from the Gulf of Mexico (Paine 1963) as well as the gut contents of *Limnodoromus grieus*, and *C. semipalmatus* from the Pacific coast of Costa Rica (Pereira 1990; Emig & Vargas 1990) indicate that those birds commonly prey on *Glottidia*. Also, the asteroid *Amphipolis germinata* frequently (43%) contains shells of *Glottidia pyramidata* (Emig in press). Fish may also be important predators of lingulids. In the Gulf of Mexico, *G. pyramidata* is preyed upon by estuarine sturgeons (Mason & Clugston 1993) and tonguefish (Cooper 1973). As reported by Campbell & Campbell (manuscript), one specimen of sturgeon in the Florida Museum collections contained 500 specimens of *G. pyramidata*. *Lingula anatina* was commonly found in the stomachs of demersal fishes (Emig in press).

In sum, this brief review indicates that, in present-day ecosystems, a variety of predators prey upon lingulid brachiopods and can potentially leave predatory traces on shells of their victims.

Material and methods

Study Area. — The study area is the intertidal mudflat of the southernmost delta plain of the Colorado River, north of San Felipe, Baja California, Mexico (Fig. 1). The tidal flat experiences extremely high semi-diurnal tides with tidal ranges reaching up to 10 meters (Sykes 1937; Roden 1964; Thompson 1968; Bray & Robles 1991). The intertidal flat reaches up to several kilometers in width. This exceptional macrointertidal environment is inhabited by an abundant macroinvertebrate fauna (see Thompson 1968; Batten *et al.* 1994) that includes the infaunal lingulid brachiopod *Glottidia palmeri* Dall, 1870 (Dall 1920; Thompson 1968; Kowalewski 1996a). The climate of the area is hot and arid with a maximum summer temperature of 50°C and less than 60 mm precipitation per year (Ezcurra & Rodrigues 1986; Thomson 1993). The water of the northern Gulf of California has a salinity of 36–39‰ (Brusca 1980). Mean monthly water temperature reaches about 30°C in the summer and drops to 15°C in the winter (Thomson 1993).

The tidal flat is a progradational feature composed of fine-grained clastic sediments consisting predominately of silts and fine-grained sands. Several series of longitudinally oriented, shell-rich beach ridges occur in the area (Thompson 1968; Kowalewski *et al.* 1994). The facies development of the tidal flat, discussed in detail by Thompson (1968), has largely been controlled by the activity of the Colorado River (see also Kowalewski *et al.* 1994; Kowalewski & Flessa 1995).

On *Glottidia palmeri* Dall, 1870. — This species is endemic to the Gulf of California and the Pacific coast of California (Dall 1870, 1871, 1920; Lowe 1933; Hertlein & Grant 1944; Thompson 1968; Emig 1983; Kowalewski 1996a). It was described first by Dall (1870) from the intertidal mudflats of northeastern Baja California, where it is patchily distributed, but locally very abundant (Thompson 1968; Kowalewski 1996a). Like all other Recent lingulids (e.g., Paine 1963; Emig *et al.* 1978; Emig 1982;

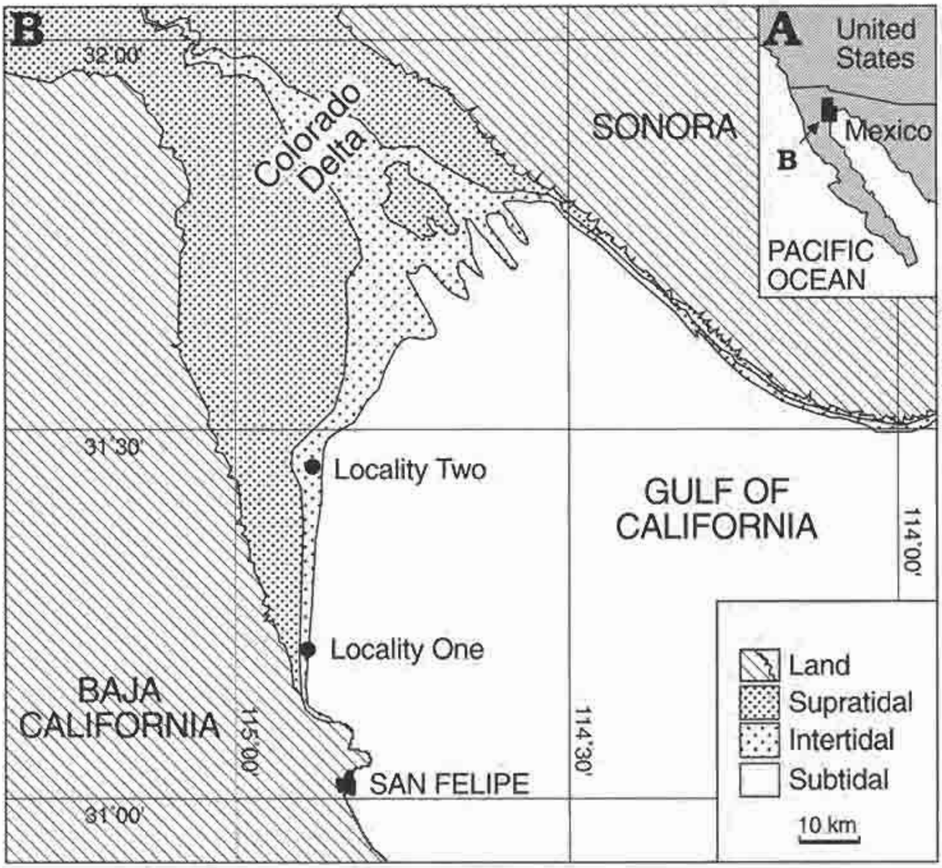

Fig. 1. Map of the study area showing the location of the two sampling localities. **A**. Regional map (Baja California and the Gulf of California). **B**. The northern Gulf of California and the Colorado River Delta (Fig. 1B modified from Thompson 1968; Kowalewski *et al.* 1994).

Treuman & Wong 1987), it is an infaunal suspension-feeder that lives in deep vertical burrows and is anchored by a long pedicle (see also Kowalewski & Demko 1996). Its shell is thin (0.2–0.3 mm), spatulate, and linguliform in outline, and reaches up to 45 mm in length. The shell has low internal septa – a diagnostic feature of the genus *Glottidia* (Rowell 1965; Emig 1983). The ventral, or pedicle, valve has two septa diverging from the beak. The dorsal, or brachial, valve has one median septum and is slightly shorter than its ventral counterpart. The shell consists of calcium phosphate and contains as much as 50% organic matter (G. Goodfriend personal communication). Shells display yellow or occasionally green or dark brown color banding. Concentric growth lines are often visible.

Previous work on *G. palmeri* concentrated primarily on its taxonomy and morphology (e.g., Dall 1920; Hatai 1938; Hertlein & Grant 1944; Emig 1983). A recent study by Kowalewski (1996a) indicated that *G. palmeri* occurs in densely inhabited patches dominated by single age-cohorts (see below for more details). Little is known about causes of mortality in *G. palmeri*. Predation and seasonal mortality during winter months – when storms erode and redeposit intertidal sediments or when water temperatures drop beyond the brachiopod's tolerance – are most likely factors (Kowalewski & Flessa 1994; Kowalewski 1996a).

Field, laboratory and analytical methods. — This analysis is based on the samples collected by our research group to investigate the taphonomy, population biology, biometry, and natural history of *G. palmeri* (see Kowalewski & Flessa 1994; Batten & Kowalewski 1995; Smith *et al.* 1995; Kowalewski 1996a; Kowalewski *et al.* 1997; Anand *et al.* submitted). The samples were collected from two localities on the macrotidal flat of the lower Colorado Delta (Fig. 1).

Six patches from the two localities (Fig. 1) were sampled in March 1993, November 1993, and February 1994. This analysis includes the live-collected specimens, which were previously measured (Kowalewski 1996a), but not analyzed for scars ($n = 599$), as well as additional live-collected specimens not included in the previous study ($n = 221$). All additional specimens were measured to the nearest 0.1 mm using electronic or dial calipers. Size of the shell was measured as the length of the longer, ventral valve. This procedure is consistent with the one employed previously (Kowalewski 1996a).

The population data, based on 820 specimens, are summarized in Table 1. Previous quantitative analysis (Kowalewski 1996a) indicated that patches from Locality One represented single age-cohorts from single spatfalls and consisted of mature, slowly growing specimens that were 3–4 years old at the time of collection. The new population data, with an increased sample size (number of specimens), are consistent with the previous work. Note that the mean specimen size in Locality One increased by 2.4 mm from March 1993 to November 1993, but did not increase in size form November 1993 to February 1994 (Table 1). This is consistent with growth ring analyses (Batten & Kowalewski 1995; Anand *et al.* submitted) which indicates that *G. palmeri* ceases or slows its growth during winter months. Locality Two, in the north, included younger patches of various age, representing 1–2 year old cohorts (Table 1).

Table 1. Size data for the *Glottidia palmeri* patches sampled in March 1993, November 1993, and February 1994. This analysis, based on 820 specimens, updates the previous analysis, based on 599 specimens (see Kowalewski 1996a: table 1).

Variable	March 1993	November 1993	February 1994
Locality One			
Sample size	154	325	172
Mean (mm)	36.8	39.2	39.1
Standard deviation (mm)	1.42	1.86	1.53
Maximum size (mm)	39.5	44.8	45.8
Minimum size (mm)	32.2	33.5	35.4
Locality Two			
Sample size	–	45	124
Mean (mm)	–	28.2	24.7
Standard deviation (mm)	–	4.58	2.00
Maximum size (mm)	–	36.3	28.4
Minimum size (mm)	–	21.6	19.1

Each specimen was carefully examined under magnification for any marks (scars, cracks, growth disruptions, etc.). Marks were classified according to their presumed origin as: (1) reliable marks that were, in our opinion, predatory in origin; and (2) questionable marks which were fresh-looking, unnaturally straight, much larger than other scars, and cut randomly across the shells at various angles (most likely these were caused by our shovels when we were digging for specimens or during subsequent transport – see also Flessa *et al.* 1992). We confined our analysis primarily to the reliable scars.

The size and location of each scar was measured using a transparent grid. A sector in the grid covered approximately 3 mm^2. The scar size was estimated visually by comparing the area covered by the scar to the grid. For example, the size of the scar that covered area corresponding to 1.5 sector was recorded as 4.5 mm^2. The precision of the estimate was ±1.5 mm^2 (i.e., ±0.5 sector). To estimate the position of the scar, the grid was placed over each specimen with the lateral sector '1' placed at the anterior shell edge (Fig. 2A). Note that scar location can be described consistently using a single grid system only for specimens that are similar in size and were collected at the same time (the apparent position of scars in relation to the grid 'shifts' with shell growth).

To estimate the relative age of the scar, we measured, to the nearest 0.1 mm, the distance (d) from the youngest shell growth ring disrupted by the scar to the anterior (growing) edge of the shell. Assuming that scars were made at the growing edge of the shell, d can be used to estimate the relative age of the scar, as well as to calculate the size of the brachiopod at the time of attack (S_a) (see Fig. 2B). The assumption that scars were made at the anterior shell margin seems reasonable in view of Paine's (1963) observations on predatory damage in *G. pyramidata* (see above for details). Nevertheless, we will note some alternative interpretations for our data, when this assumption is relaxed. Note that both, d and S_a, estimate the relative age of the scar (Fig. 2B). However, d is a more appropriate measure because it minimizes the noise introduced by variation in brachiopod growth rate: modern lingulids show an asymptotic growth rate (e.g., Chuang 1961; Paine 1963; Worcester 1969; Kenchington & Hammond 1978), and thus, the variation introduced by differences in the growth rate among specimens should substantially decrease toward the anterior shell edge. In the case of complementary (paired) scars, the distance was measured for the scar closer to the anterior shell margin.

Note that the distance analysis is appropriate only for Locality One, because all specimens in that locality belong to the same age/size cohort (i.e., d is directly comparable among the specimens). Because the brachiopod population grew 2.4 mm between March 1993 and November 1993 (see above and Table 1), we corrected d values for shell growth for the March 1993 sample (i.e., $d = d + 2.4$). Because the specimens did not grow significantly between November 1993 and February 1994, the November samples were not corrected. After the correction is applied, all distance measurements can be treated as if they were taken at the same time in February 1994.

The morphology of each scar was described and a schematic drawing of the scars outline was made. Most of the scars could be classified into three morphological categories hereafter referred to as: 'u-shaped scars', 'pocket scars', and 'crack scars' (see Fig. 3), scars with other morphologies were classified as 'miscellaneous'. The scars were also classified as either healed (complete repair of all shell layers) or unhealed (incomplete repair with external shell layers still disrupted). A substantial

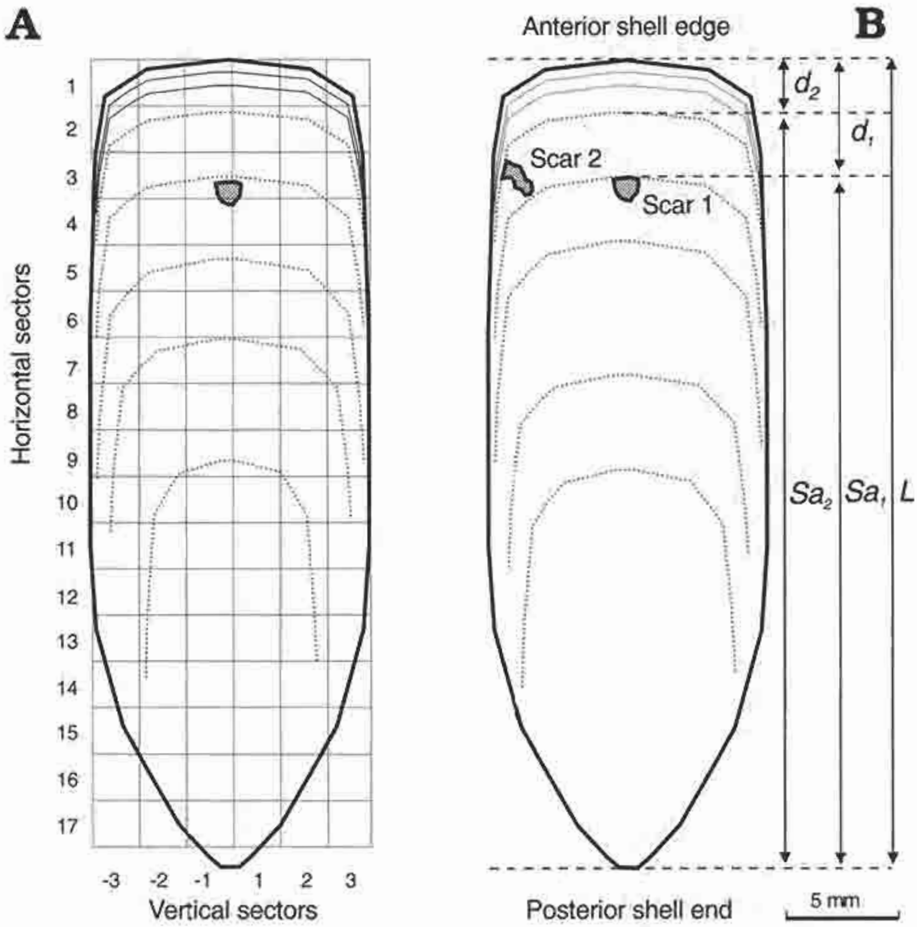

Fig. 2. **A**. Grid system employed in this study to estimate the position of a scar on the brachiopod shell in plan view. A hypothetical scar is located in sector -1,3. One sector of a grid represents a square =3 mm^2 in area. **B**. Schematic illustrating the measurement method used to estimated the relative age of the scar and the brachiopod size at the time of the attack. Two hypothetical scars are used as examples. Scar 2 is younger than Scar 1 (i.e., $d_1 > d_2$) and was inflicted on a larger specimen ($Sa_1 < Sa_2$). Symbols: d_1 – distance of Scar 1 from the anterior shell edge, d_2 – distance of Scar 2 from the anterior shell edge, Sa_1 – the size of the brachiopod at the time of attack recorded by Scar 1, Sa_2 – the size of the brachiopod at the time of attack recorded by Scar 2, L – the anterior-posterior length of the shell.

proportion of the scars consisted of two complementary disruptions on opposite valves. Such paired scars were treated in our analysis as single observations and measurements were taken only for one of the two disruptions: whichever was more appropriate for a given measurement (see the example of distance measurement above).

All statistical analysis were performed using Statistical Analysis System (SAS) on the University of Arizona interactive VAX system. The statistical analyses were performed using the SAS/STAT procedures (SAS Institute 1989, 1990a). Statistical randomizations and simulations were written in the SAS and SAS-IML languages (SAS Institute 1990a, 1990b, 1991).

Results

Out of 820 live-collected specimens of *Glottidia palmeri*, 267 (32.6%) contained at least one disruption (Table 2). Among them, 75 specimens (9.1% of all specimens) bear 'questionable disruptions'. Thus, we classified only 23.4% of collected specimens (n = 192) as having 'scars' of unquestionably biogenic origin. The quantitative analysis, presented below deals primarily with the unquestionable scars.

Because some specimens bear multiple scars, the total number of scars exceeds the total number of specimens (Table 2). For example, there are 213 unquestionable scars, but only 192 specimens that bear them. Similarly, 75 specimens bear only questionable disruptions, but there is a total of 85 questionable disruptions. Thus, the sample sizes and results vary depending on the objective of analysis. Note that it is important to distinguish between the analysis that targets scars and the analysis that targets specimens. In general, the analysis of scars provides information about the predator and analyses of specimens provides information about the prey. For example, 65 (33.9%) specimens bear healed scars but there are total of 70 (32.9%) healed scars. Obviously, 33.9% of the attacked brachiopods were able to heal their shells completely by the time of collection, and not 32.9%. Similarly, we identified total of 84 u-shaped scars but there are only 78 specimens bearing them. When studying the site-selectivity of predation, one should analyze all 84 scars, even though there are only 78 specimens that contain them. We explicitly distinguish between the two types of analysis by presenting them in the two separate sections. Although this distinction may appear to be trivial, not distinguishing between 'traces' and 'specimens with traces' would seriously undermine the clarity of any quantitative analysis.

Types of scars. — Although scars vary in shape, most of them can be categorized into one of the three main morphological types (Fig. 3) referred to here as 'u-shaped scars', 'pocket scars', and 'crack scars'. The remaining scars (17.8%) could not be assigned to any of these morphological types and were classified into the 'miscellaneous' category.

Ninety disruptions were identified as u-shaped disruptions. Only six of them were questionable disruptions and 84 were identified as true scars (39.4% of all scars). The scars have a regular u-shaped outline (Fig. 3A) with their two arms typically open directly toward the anterior edge of the shell (i.e., the scar axis is parallel to the shell axis). The ratio between the length of the arms and the width of the 'U' ranges from 2:1 to 3:1. In many cases, u-shaped scars consist of two complementary disruptions of similar size located on the opposite valves and situated at a similar distance from the anterior edge of the shell.

Fifty seven disruptions were identified as pocket disruptions. Only seven of them were questionable disruptions and 50 were identified as true scars (23.5% of all scars). Pocket scars (Fig. 3B) have a much more complicated outline than u-shaped scars and can be described as deep pockets that form irregular disruptions in the shell. They also open toward the anterior but they are much more elongated than u-shaped scars with the ratio between the length of the arms and the width of the scar ranging typically from 5:1 to 10:1. Unlike the u-shaped scars, the majority of the pocket scars have their axis at an acute angle (10–20°) to the shell axis. In many cases, the pocket scars consist of

Table 2. Summary of quantitative data on predatory scars in shells of *Glottidia palmeri.*

Variable	Total		Locality One		Locality Two	
	number	percent	number	percent	number	percent
Specimens	820	100.0	651	100.0	169	100.0
without any disruptions	553	67.4	397	61.0	156	92.3
with disruptions	267	32.6	254	39.0	13	7.7
with scars	192	23.4	183	28.1	9	5.3
with questionable disruptions	75	9.1	71	10.9	4	2.4
with 2 disruptions	27	3.3	26	4.0	1	0.6
with 2 scars	17	2.1	16	2.4	1	0.6
with 3 disruptions	2	0.2	2	0.3	0	0.0
with 3 scars	2	0.2	2	0.3	0	0.0
Specimens with scars	192	100.0	183	100.0	9	100.0
with 2 scars	17	8.8	16	8.7	1	11.1
with 3 scars	2	1.0	2	1.1	0	0.0
with u-shaped scars	78	40.6	76	41.5	2	22.2
with pocket scars	45	23.4	42	23.0	3	33.3
with crack scars	35	18.2	33	18.0	2	22.2
with miscallaneous scars	34	17.7	32	17.5	2	22.2
with healed scars	65	33.9	119	65.0	8	88.9
with unhealed scars	127	66.1	64	35.0	1	11.1
with a scar on a ventral valve	68	35.4	66	36.1	2	22.2
with a scar on a dorsal valve	88	45.8	83	45.4	5	55.6
with a paired scar on both valve	36	18.8	34	18.6	2	22.2
Disruptions	298	100.0	284	100.0	14	100.0
questionable disruptions	85	28.5	81	28.5	4	28.6
scars	213	71.5	203	71.5	10	71.4
Scars	213	100.0	203	100.0	10	100.0
unhealed scars	143	67.1	134	66.0	9	90.0
healed scars	70	32.9	69	34.0	1	10.0
u-shaped scars	84	39.4	82	40.4	2	20.0
pocket scars	50	23.5	46	22.7	4	40.0
crack scars	41	19.2	39	19.2	2	20.0
miscellaneous scars	38	17.8	36	17.8	2	20.0
scars on ventral valve	81	38.0	78	38.4	3	30.0
scars on dorsal valves	94	44.1	89	43.8	5	50.0
paired scars on both valves	38	17.8	36	17.8	2	50.0
U-shaped disruptions	90	100.0	88	100.0	2	100.0
questionable disruptions	6	7.1	6	6.8	0	0.0
scars	84	92.9	82	93.2	2	100.0
Pocket disruptions	57	100.0	53	100.0	4	100.0
questionable disruptions	7	12.3	7	13.2	0	0.0
scars	50	87.7	46	86.8	4	100.0
Crack disruptions	82	100.0	78	100.0	4	100.0
questionable disruptions	41	50.0	39	50.0	2	50.0
scars	41	50.0	39	50.0	2	50.0
Miscellaneous disruptions	69	100.0	65	100.0	4	100.0
questionable disruptions	31	44.9	29	44.6	2	50.0
scars	38	55.1	36	55.4	2	50.0

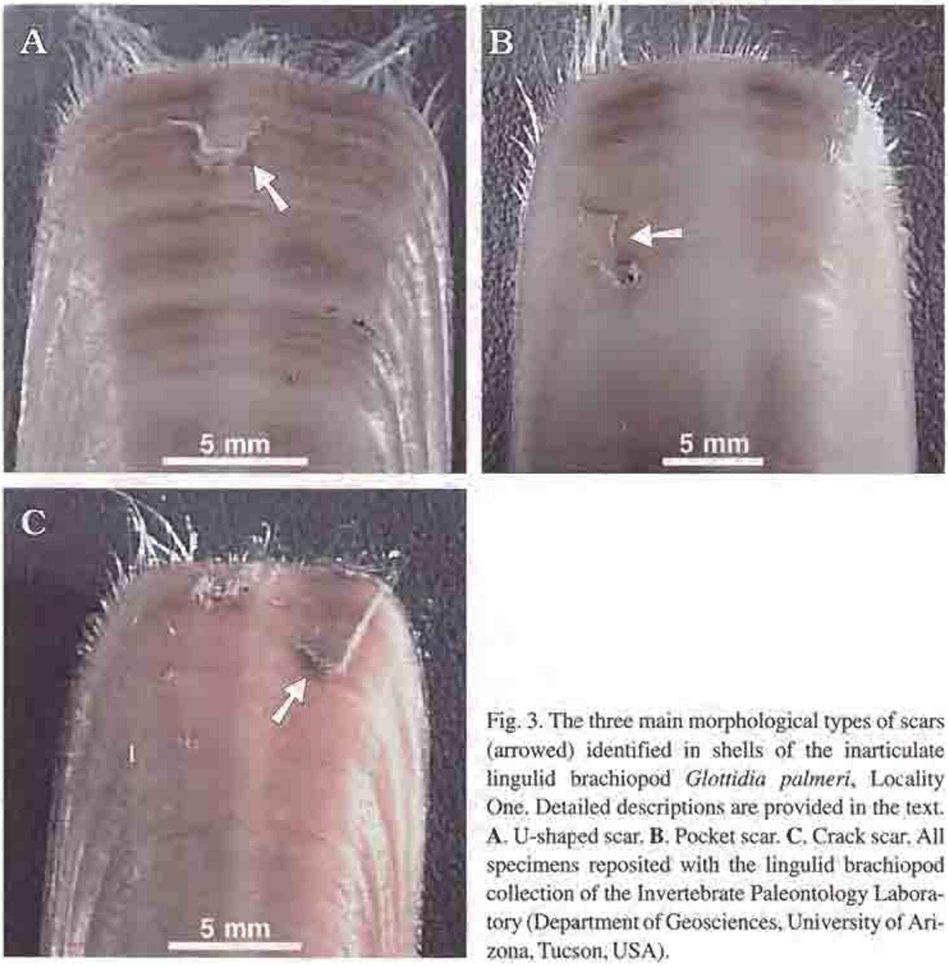

Fig. 3. The three main morphological types of scars (arrowed) identified in shells of the inarticulate lingulid brachiopod *Glottidia palmeri*, Locality One. Detailed descriptions are provided in the text. **A**. U-shaped scar. **B**. Pocket scar. **C**. Crack scar. All specimens reposited with the lingulid brachiopod collection of the Invertebrate Paleontology Laboratory (Department of Geosciences, University of Arizona, Tucson, USA).

two complementary scars of similar size located on opposite valves and situated at a similar distance from the anterior edge of the shell. Thanks to all those differences, and the fact that very few scars displayed intermediate morphological characteristics, the pocket scars were easy to distinguish from the u-shaped scars in our samples.

Eighty two disruptions were identified as crack disruptions. Half of them were questionable disruptions and only 41 were identified as true scars (19.2% of all scars). Crack scars are linear disruptions (Fig. 3C). In many cases, the scars consist of a pair of cracks that form a v-shaped disruption which invariably opens toward the anterior edge of the shell (Fig. 3C). In many cases, the cracks consist of two complementary scars of similar size located on the opposite valves and situated at a similar distance from the anterior edge of the shell.

Sixty nine disruptions could not be classified in any of the three morphological categories and were, therefore, classified as 'miscellaneous'. Almost half of them were questionable disruptions, and only 38 were classified as true scars (17.8% of all scars). Some of the miscellaneous scars also open toward the anterior edge of the shell. In

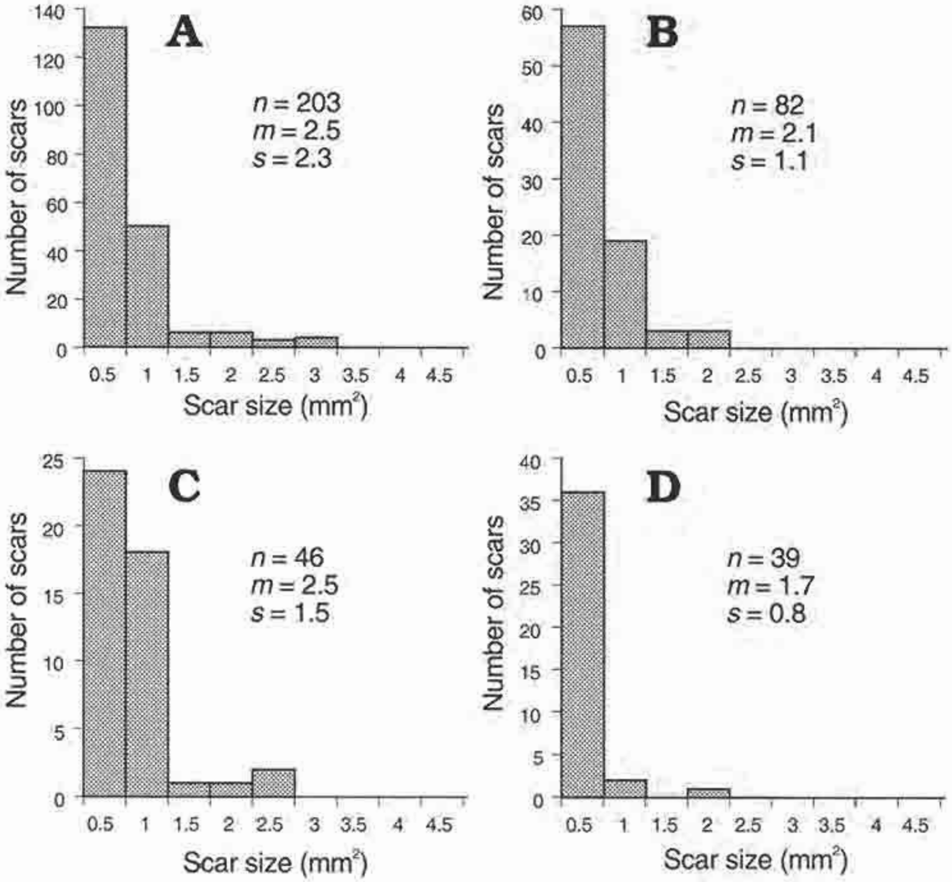

Fig. 4. **A–D**. Size-frequency distribution of scars from Locality One. **A**. Pooled data for all scar types. **B**. U-shaped scars. **C**. Pocket scars. **D**. Crack scars. Symbols: *n* – sample size, *m* – mean, *s* – standard deviation.

many cases, the scars consist of two complementary scars of similar size located on the opposite valves and situated at a similar distance from the anterior edge of the shell.

Quantitative analysis of scars. — The overwhelming majority of disruptions (95.3%) were found in specimens collected from Locality One. The quantitative analysis can, therefore, be confined to Locality One without substantially reducing sample sizes (see Table 2). This allows us to eliminate any potential uncontrollable variation in the data caused by biotic and/or environmental differences between the two localities. The analysis was performed both for all scar types pooled together, as well as, separately for each of the three morphological types of scars (miscellaneous scars were not analyzed separately).

The size of scars varies from 1.5 mm^2 to 24 mm^2 and averages 2.5 mm^2 (Fig. 4A). The variation in scar size is relatively small, with standard deviation of 2.3 mm^2 and coefficient of variation, cv = 91%. The size-frequency distribution is highly right-skewed (skewness = 5.4) and very peaked (kurtosis = 41.8) with the majority of scars

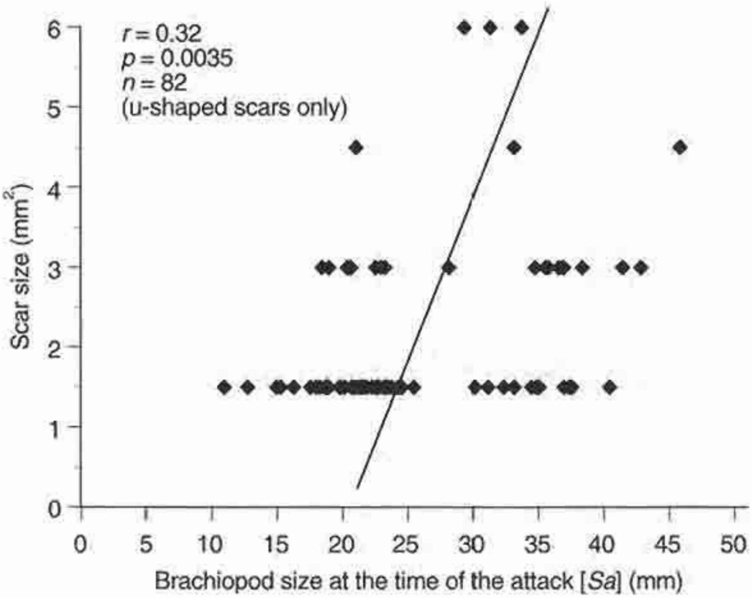

Fig. 5. Scatter plot of *Sa* (size of the brachiopod at the time of the attack) *vs.* scar size. Data for u-shaped scars from Locality One (the other two scar types do not show any significant correlation). Symbols: r – Spearman rank correlation coefficient, p – significance of the correlation coefficient, n – sample size.

being small. The analysis by scar type reveals a very similar pattern in all three cases. All distributions are strongly right-skewed, vary in a similar size range (Fig. 4B–D), and are statistically indistinguishable from one another in their overall shape (pairwise Kolmogorov-Smirnov test, $p > 0.05$ in all three cases). Moreover, the u-shaped scars and the pocket scars do not differ significantly from one another in their median size (Wilcoxon test, $p = 0.06$). The only exception is the significantly smaller size of crack scars in comparison with the two other scar types (Wilcoxon test, $p \ll 0.05$ in both cases). However, given that the scar size, as defined here, is an area measure, the relatively smaller size of the crack scars should not be surprising.

As explained above, the distance of the scar to the anterior shell edge can be used to calculate the brachiopod size at the time of the attack (S_a) (see Fig. 2B). Spearman rank correlation analysis indicates that only in the case of the u-shaped scars, does the scar size (S) and the brachiopod size at the time of the attack (S_a) show a significant positive correlation ($p = 0.0035$, Fig. 5). However, although significant, the correlation is not very strong (Spearman rank coefficient, $r = 0.32$, Fig. 5).

Out of 203 scars from Locality One, 17.8% of the scars occurred on both valves of the brachiopod (i.e., scars were represented by a pair of disruptions). Out of 167 single scars, 46.7% were located on ventral valves and 53.3% on dorsal valves. This proportion does not differ significantly from 50:50, $p = 0.28$ (binomial test with normal approximation, see Zar 1984). The dorso-ventral distribution of scars is very uniform among the three scar types: in all cases, the paired scars represent less than 20% (Fig. 6). The proportion of single scars on dorsal vs. ventral valves does not differ significantly from 50:50 (in all three cases $p \gg 0.05$, binomial test). Also, the homo-

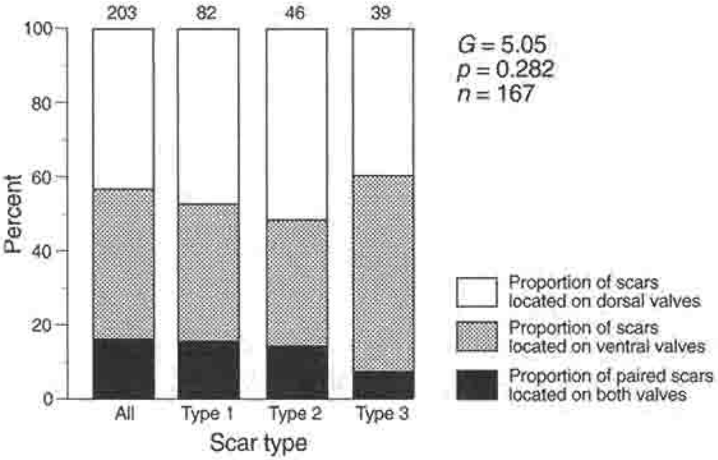

Fig. 6. Dorso-ventral distribution of scars shown for the pooled data and separately for each of the three main scar types. Data for Locality One only. The numbers above each bar represent the sample size of that bar. Symbols: G – log-likelihood ratio (G-statistic), p – significance of G, df – number of degrees of freedom, n – sample size.

geneity G-test (Fig. 6) fails to indicate any statistically significant variation in dorso-ventral distribution of scars among different scar types.

Analysis of the spatial distribution of scars in the plan view was limited to November 93 and February 94 samples from Locality One. We excluded the March 1993 sample because, due to the shells' growth, the apparent position of scars 'shifted', on average by 2.4 mm (see above). Thus, we analyzed total of 182 scars. For all three scar types, the spatial distribution of scars appears highly non-random with the majority of scars located in the anterior part of the shell and concentrated along the shell's median axis (Fig. 7A–C). Note that even though there are potentially 17 horizontal sectors (see Fig. 2A), only sectors 1 through 12 contain scars. The only obvious difference among the three scar types is in their distribution parallel to the anterior shell edge (i.e., along lateral sectors). U-shaped scars concentrate along the median shell axis, whereas pocket scars and crack scars are more evenly distributed and include many scars located along the lateral margins.

The apparent non-randomness in scar distribution (Fig. 7) can be analyzed rigorously using a Poisson model. In this paper, we propose an approach which uses a Monte Carlo simulation based on the Poisson probability function (for details see Appendix 1; see also Reyment 1971). The simulations indicate that the spatial distribution of scars is significantly different from random for each of the three scar types, $p < 0.0001$ (the same result is obtained for the pooled data).

Out of 203 scars from Locality One, only 33% are completely healed (Fig. 8). There is a statistically significant variation in the proportion of healed scars among the different scar types (see Fig. 8). U-shaped scars show the highest rate (over 52%), whereas only ≈25% of crack and ≈13% of pocket scars are healed. Healed scars and unhealed scars differ dramatically in their distribution away from the anterior shell edge. The mean distance d is 5.9 mm (median = 3.3 mm) for unhealed scars, and

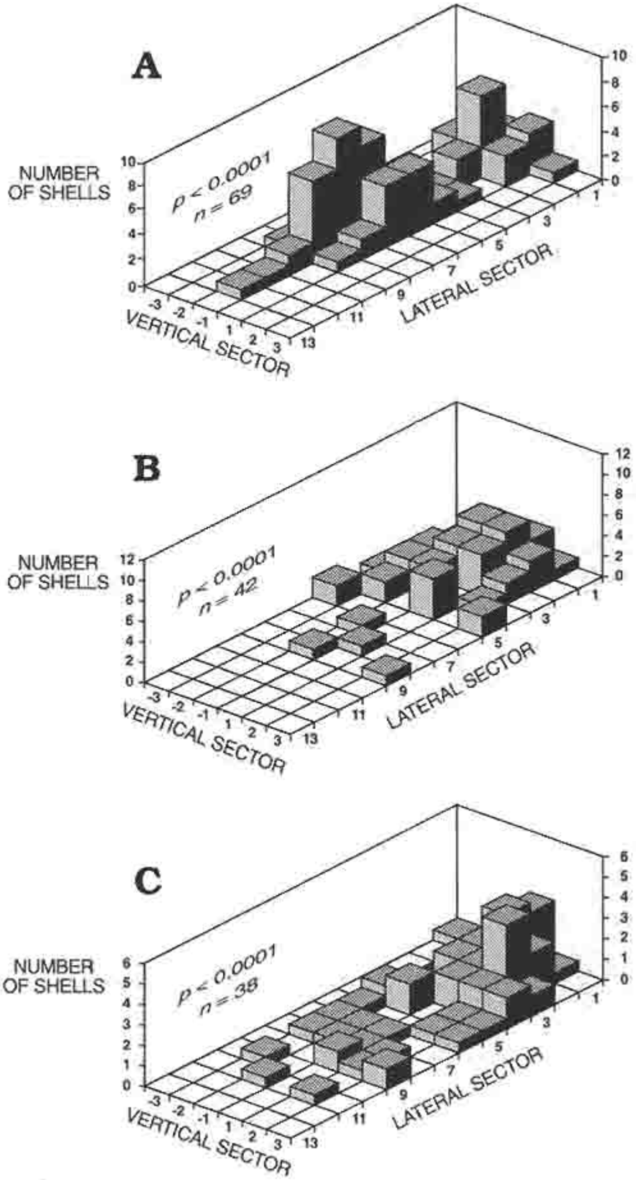

Fig. 7. Spatial distribution of scars on brachiopod shells in plan view. Data for the November 1993 and February 1994 samples from Locality One only. Note that lateral sector '1' corresponds to the anterior shell edge (to relate the charts to the brachiopod shell see also Fig. 2A). Symbols: p – probability that spatial distribution of scars is random (based on Monte Carlo simulations, see text and Appendix 1), n – sample size. **A**. U-shaped scars. **B**. Pocket scars. **C**. Crack scars.

13.8 mm (median = 16.1 mm) for healed scars. This difference is highly significant statistically ($p \ll 0.05$, Wilcoxon test). The increase in the proportion of healed scars away from the anterior shell edge is not surprising considering the fact that the more posterior scars are older, and thus, more time was available for their healing.

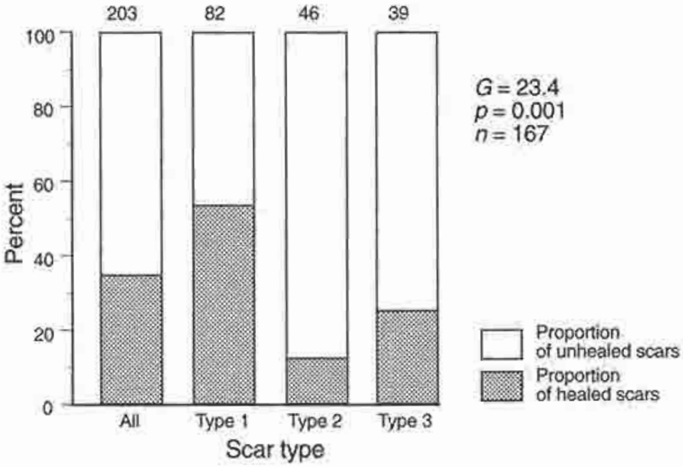

Fig. 8. The proportion of healed to unhealed scars shown for the pooled data and separately for each of the three main scar types. Data for Locality One only. The numbers above each bar represent the sample size of that bar. Symbols: *G* – log-likelihood ratio (*G*-statistic), *p* – significance of *G*, *df* – number of degrees of freedom, *n* – sample size.

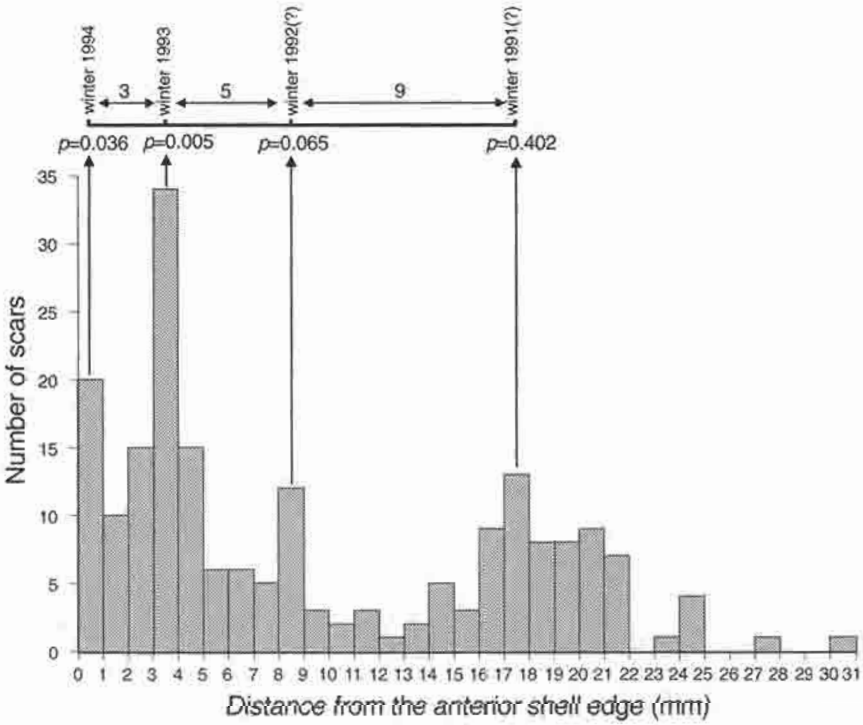

Fig. 9. The anterior-posterior distribution of scars on the brachiopod shell (i.e., distance-frequency distribution). Data for Locality One only. Four major modes may represent seasonal (winter) predation. Note the increase in spacing between the modes away from the anterior shell edge. The two anterior modes are statistically significant according to 10,000-iteration bootstrap (see Appendix 2). Symbol: *p* – bootstrap estimate of local significance of a mode.

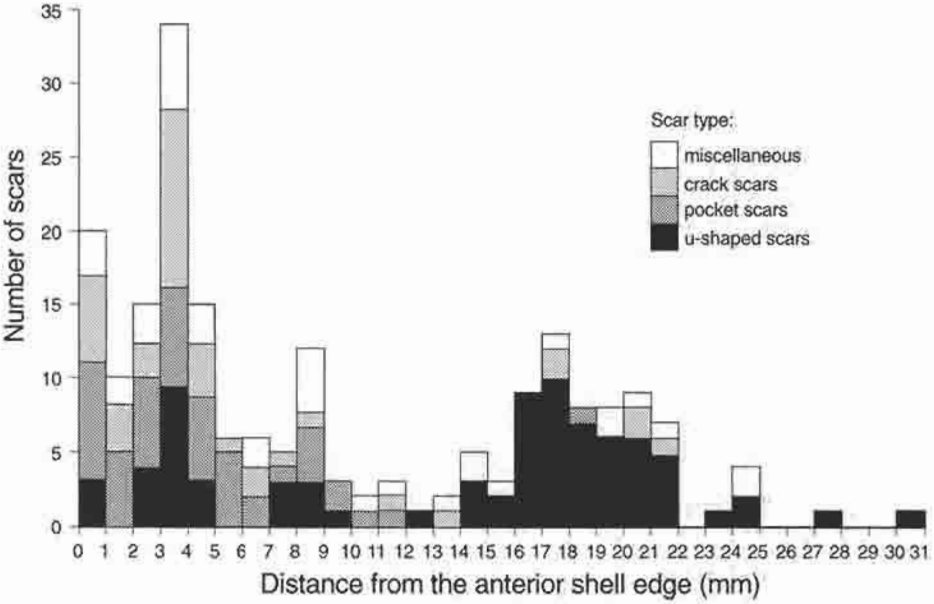

Fig. 10. The anterior-posterior distribution of scars on the brachiopod shell (i.e., distance-frequency distribution). Data the same as for Fig. 9, re-plotted here to show the variation among the scar types in their anterior-posterior distribution.

Scars vary in their distance to the anterior shell edge from 0 to 31 mm. This means, given the average size of specimens (see Table 1), that scars are absent in the most posterior part of the shell (6–9 mm; see also Fig. 7). The distribution of scars away from the anterior shell edge is strikingly multimodal (Fig. 9), with four well defined modes. The first mode is located at the anterior shell edge (0–1 mm distance class), the second and largest mode is located 3 mm toward the posterior from the first mode (3–4 mm distance class). In addition, there are two smaller modes toward the posterior of the shell: 8–9 mm and 17–18 mm distance classes respectively. Note that the spacing of the modes increases away from the anterior edge (Fig. 9). We used a bootstrap procedure to test whether the modes are statistically significant (for details see Appendix 2). The analysis suggests that two anterior modes are statistically significant, whereas the two smaller posterior modes are not (see Fig. 9). The two posterior modes became significant, however, when chart resolution is decreased to 2-mm bins (not shown here).

The three main scar types differ notably in their anterior-posterior distribution (Fig. 10). Crack scars and pocket scars concentrate mostly in the anterior part of the shell (0–11 mm distance classes), whereas u-shaped scars dominate farther away from the anterior edge (12–31 mm distance classes). Given that the frequency of healed scars increases away from the anterior edge, the more posterior distribution of u-shaped scars is consistent with their significantly higher frequency of healing (Fig. 8). The u-shaped scars differ statistically in their anterior-posterior distribution from the two other scar types (in both comparisons $p \ll 0.05$, pairwise Kolmogorov-Smirnov test).

Quantitative analysis of brachiopod shells. — Out of 820 brachiopod specimens, 23.4% bear repair scars (see Table 2 for quantitative summary). Out of 192 specimens

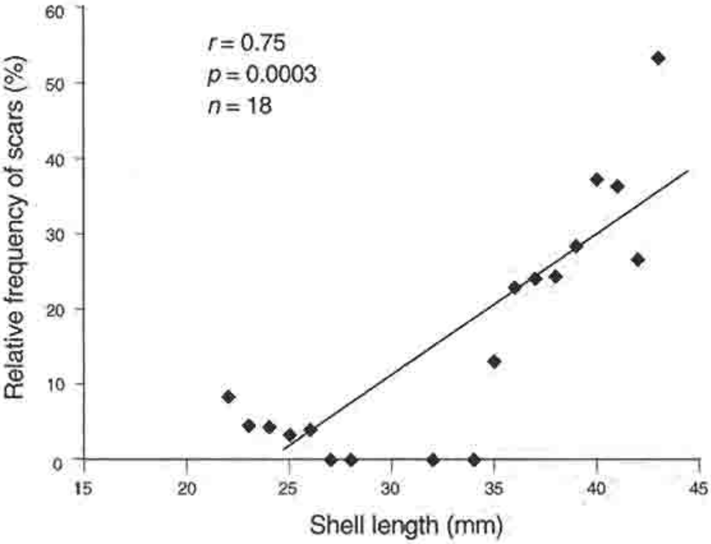

Fig. 11. Scatter diagram showing frequency of scars in a given size-class of brachiopods plotted against brachiopod size-classes. Only the size-classes with $n > 5$ are considered. Data pooled for Localities One and Two. Symbols: r – Spearman rank correlation coefficient, p – significance of the correlation coefficient, n – sample size.

with unquestionable scars, 90.2% specimens bear single scars, 8.8% bear two scars, and only 2 (1%) bear three scars. Specimens bearing more than three scars were not identified among our samples.

The frequency of attacked specimens increases with brachiopod size: whereas shells with scars are rare in the smaller size classes, they became increasingly frequent among larger specimens. Indeed, there is a very strong positive correlation between the frequency of attacked specimens and their size (Fig. 11). Also, the frequency of specimens with multiple scars increases with the brachiopod size. The mean shell size of specimens bearing multiple scars is significantly greater than the mean size of specimens with single scars ($Z = 2.51$, $p = 0.012$, Wilcoxon test). The specimens with multiple scars are confined to larger brachiopod size-classes. Smallest specimen with multiple scars has length of 35.6 mm, whereas specimens as small as 20 mm contain single scars.

The frequency of attacked individuals of *G. palmeri* varies at the three comparative levels that are available given our sampling design: (1) between localities; (2) within Locality One among brachiopod patches; and (3) within Locality One through time.

1. Variation between the two localities. The most dramatic variation can be observed between the two sampled localities (Fig. 12; Table 2). Specimens with scars are over three times more frequent in Locality One than in Locality Two. In both localities, the frequency of attacked specimens increases in the larger size-classes. However, only in the case of Locality One is this pattern statistically significant (see Fig. 12). The lack of significance for data from Locality Two may be a consequence of the smaller sample size (only 9 specimens with scars).

2. Variation within Locality One. Because three patches from Locality One were sampled simultaneously in November 1993, it is possible to analyze local (within-lo-

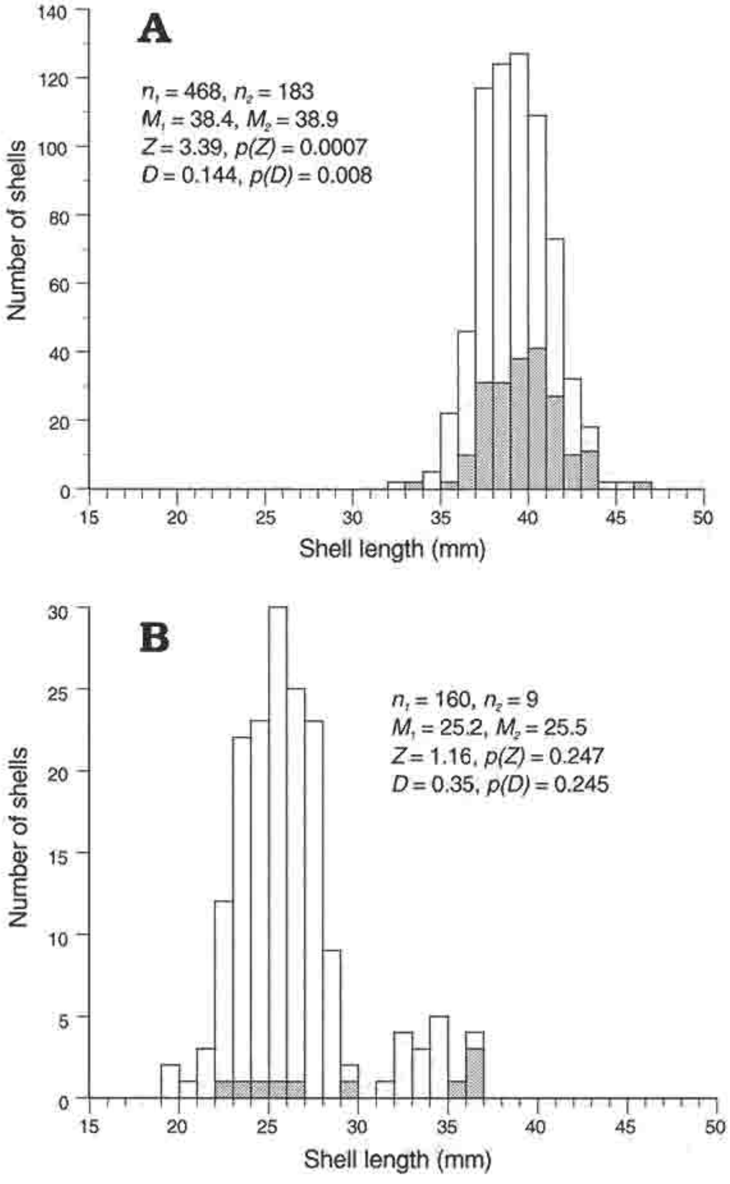

Fig. 12. Size-frequency distributions of *G. palmeri*; the white parts of bars represent specimens without scars and the gray parts specimens with scars. Symbols: n_1 – number of specimens without scars, n_2 – number of specimens with scars, M_1 – median size of specimens without scars, M_2 – median size of specimens with scars, Z – statistic for the Wilcoxon Median test with normal approximation and continuity correction, *p(Z)* – significance of *Z*, *D* – Kolmogorov-Smirnov statistic, *p(D)* – significance of *D*. **A**. Locality One. **B**. Locality Two.

cality) variation in frequency of attacked individuals among brachiopod patches. The apparent variation among the three sampled patches is not statistically significant (Fig. 13).

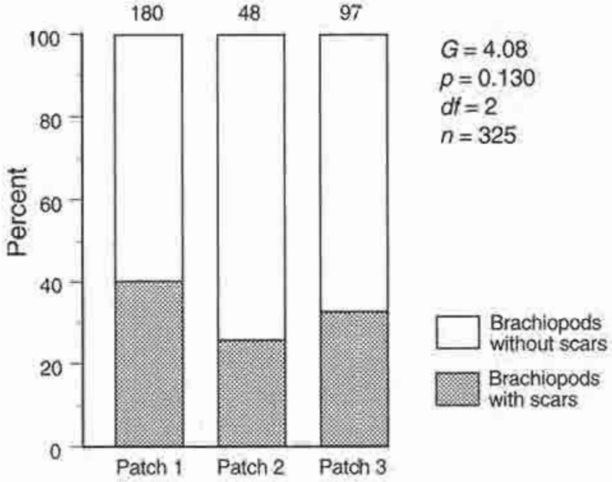

Fig. 13. The variation in relative frequency of specimens with scars among three brachiopod patches sampled in November 1993 in Locality One. The numbers above each bar represent the sample size of that bar. Symbols: G – log-likelihood ratio (G-statistic), p – significance of G, df – number of degrees of freedom, n – sample size.

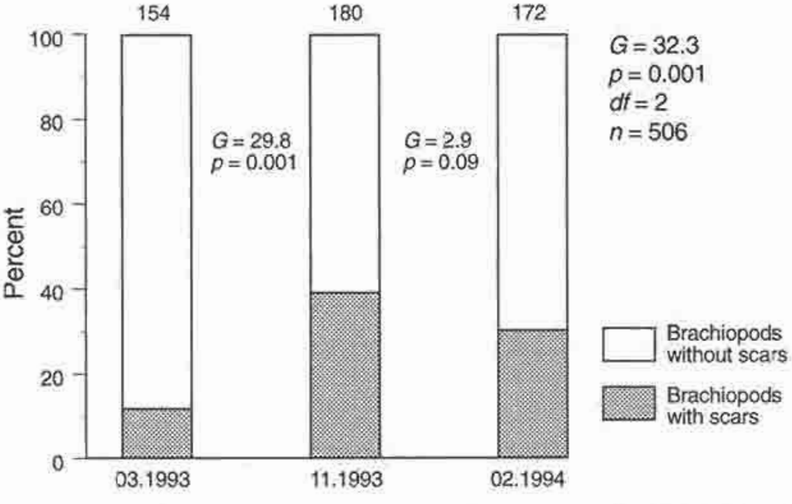

Fig. 14. The variation in relative frequency of specimens with scars through time (Patch 1, Locality One). The numbers above each bar represent the sample size of that bar. Symbols: G – log-likelihood ratio (G-statistic), p – significance of G, df – number of degrees of freedom, n – sample size.

3. Variation in time. Patch 1 from Locality One was sampled three times: in March 1993, in November 1993, and in February 1994. There is a significant variation in the frequency of specimens with scars across the seasons (Fig. 14). The frequency of specimens with scars is substantially lower in the March 1993 sample than in the samples from the two subsequent seasons. There is no significant difference in the frequency of attacked specimens between November 1993 and February 1994 (for statistical details see Fig. 14).

Interpretation

The origin of scars. — Despite several weeks of observation, we have never been able to directly observe the agent responsible for scars, and thus, our interpretation of the origin of scars is somewhat speculative. In addition, many abiotic and non-predatory biotic factors exist that can cause damage, and consequently, repair scars in shelly organisms. These include self-inflicted damage of burrowers and predators, abiotic damage due to impacts of wave-borne stones, and human activity (for more details and references see Cadée *et al.* in press). Nevertheless, it seems quite certain that scars (1) are biotic in origin; (2) record attempts at predation; and (3) were made by an epifaunal organism with a scissors-type weapon (e.g., claws, beak).

The small localized scars, that cut across the shell growth rings, clearly indicate an external agent of destruction. The evidence pointing to the biotic origin of scars includes the very limited size variation among the scars (Fig. 4); their non-random distribution concentrated near the anterior shell edge (Fig. 7); the fact that it is possible to group scars into morphological types (Fig. 3; Table 2); and the presence of complementary scars on opposite valves (Fig. 6). The non-random distribution of scars (Fig. 7), the overwhelming dominance of single scars (Table 2), and the correlation between shell size and scar size (in the case of u-shaped scars; Fig. 5) all suggest the predatory origin of scars. The fact that scars concentrate near the anterior shell edge (Fig. 7) and, regardless of the scar type, open toward the anterior edge suggest predatory attacks from the anterior side of the brachiopod. Lingulid brachiopods are infaunal organisms that live in vertical burrows and when active position themselves with their anterior-side up and with their anterior shell edge aligned near the sediment-water interface (e.g., Emig 1982). Thus, the scars must have been produced by an epifaunal organism. The fact that many scars (again, regardless of the morphological type of scar) consist of a pair of disruptions (Fig. 5) – that are of similar size and situated on opposite valves at a similar distance from the anterior shell edge – suggest predatory attacks with a scissors-type weapon such as the claws of a crab or the beak of a bird.

The identity of predator(s?). — The most likely epifaunal intertidal predators with a scissors-type weapon include crabs and shorebirds (for review of shell-crushing predators see Vermeij 1987, 1992). Both crabs and shorebirds are common in the study area. For several reasons, we believe that shorebirds are more likely predators. In particular, two species of sandpipers should be considered: the willet, *Catoptrophorus semipalmatus*, and the long-billed curlew, *Numenius americanus*.

Shorebirds, especially willets and long-billed curlews, are common in the study area (Wilbur 1987). They can, in fact, be extremely abundant seasonally; coastal areas, from California to Peru are their wintering grounds (Johnsgard 1981; Hayman *et al.* 1986; Wilbur 1987; Richards 1988). Moreover, shorebirds tend to form dense aggregations when foraging (e.g., Recher 1966), and thus, can account for the very high frequency of scars (Table 2). Finally, both long-billed curlews and willets are armed with long bills which make them particularly well adapted for preying on lingulids. Bill length ranges from 113 to 219 mm in long-billed curlews and from 50 to 67 mm in willets (Hayman *et al.* 1986). Because willets were observed preying on *Glottidia* and damaging the anterior shell edge (Paine 1963) and because *Glottidia* has previously been found in the gut content of willets (Paine 1963; Pereira 1990), it seems more likely to us that the willet rather than the long-billed curlew is responsible for the scars. There is, however, no direct emprical evidence which would allow us to decide the predator's identity with certainty. For the same reason, crabs cannot be entirely excluded as possible predators. In contrast, shell-crushing fish such as rays – although present in the area, as indicated by frequent ray pits – should be excluded as possible predators. It seems unlikely that their toothed jaws would generate a localized and complementary pair of scars with regular outlines, even if we assume that they are able to capture fully infaunal organisms such as *Glottidia*.

Two important caveats. — Two concerns need to be stressed before proceeding with the interpretation of our data. First, as stressed above, we are uncertain whether the scars were all created by one predatory species. Thus, the presence of the three morphological types of scars may either suggest that there is more than one predator, or that there is a single predator which produces more than one type of scar. In the latter case, the variation may be attributable to behavioral variation in predatory attacks or in the response of the prey (see below). The data do not provide an unequivocal solution. The statistical similarities among the different scar types (i.e., similar size, distribution around the anterior edge, similar dorso-ventral distribution), may indicate that scars were made by one predator, but may also indicate a similar behavior (and weapon size) of two or more predators. Similarly, the anterior-posterior differences in distribution of scar types (Fig. 9), can be used to argue either for the presence of two different predators that preyed on brachiopods at different times, or changes in predatory behavior with prey size.

Second, repair scars record unsuccessful predation events, and thus, are inherently difficult to interpret (see Schoener 1979; Schindel *et al.* 1982; Vermeij 1983; Walker & Voight 1994; Cadée *et al.* in press). Most importantly, they cannot be used to estimate predation intensity: a prey population with 20% of repair scars may in fact be preyed upon at much higher rates by an efficient predator or at much lower rates by a clumsy predator. In fact, some predators are known to repeatedly attack unsuitable prey (e.g., Vermeij 1982), and thus, it is feasible that a 'prey' with frequent repair scars is never subjected to predation. Also, if a predator is (at least occasionally) successful, the repair scars represent only a subsample of all attacks. Unless the unsuccessful and successful attacks are the same in their ecological and behavioral aspects (e.g., prey size, site of attack), a quantitative analyses of repair scars may provide misleading insights into predation. We will assume in the subsequent interpretation that the repair scars provide representative sample for all attacks, but some alternative interpretations will also be noted.

Behavior of the predator. — If all, or most of the scars, were made by one species of predator (e.g., the willet), the variation in scar morphology reflects the variable foraging behavior of that predator. Stenzel *et al.* (1976), for example, observed willets to display as much as five foraging behaviors when searching for prey: peck, multiple peck, probe, multiple probe, and theft. Changes in searching method may introduce variation in the strength of the attack and the angle at which an attack is attempted. This, in turn, may affect the morphology of a scar produced in an unsuccessful attack.

Alternatively, variation in the scar morphology may be a function of the prey escape response. *G. palmeri* is capable of rapid withdrawal into the deeper parts of its burrow with a surprising strength (personal observations). According to our field observations (see also Kowalewski & Demko 1996), the *G. palmeri* burrows can easily exceed 50 cm. Thus, the depth of burrows exceeds notably the length of the crab's claws and even the length of the bills of both willets (up to 7 cm; after Hayman *et al.* 1986) and curlews (up to 22 cm; after Hayman *et al.* 1986). It seems likely that both the capturing method of the predator as well as the escape response of *G. palmeri* is likely to change with brachiopod size. Indeed, the differences in the anterior-posterior distribution of different scar types (Fig. 10) suggest that the variation in scar morphology may be related to brachiopod size.

It is also possible that variation in scar morphology reflects variation in the crystallography and mineralogy of the lingulid shell. The orientation of apatite crystals, the orientation of organic matrix, and proportion of organic to non-organic phases tend to vary strongly across the shell. In *Lingula*, for example, the length of the c-axis in apatite, the degree of orientation of crystals, and proportion of apatite relative to the organic matter all increase toward the shell center (Iijima *et al.* 1988; Iijima & Moriwaki 1990). Finally, as stressed earlier, variation in scar morphology may simply reflect the fact that there is more than one species of predators that attempt to prey on lingulids.

Site-selective durophagous predation can be evaluated by assessing randomness in the spatial distribution of predatory traces on a shell. This line of evidence has been repeatedly used for predatory drillholes, both Recent and fossil (e.g., Reyment 1971; Negus 1975; Kowalewski 1990; Anderson 1992). In case of our data, however, the non-random distribution of scars (Fig. 7) most likely reflects the fact that the direction of attack is strongly constrained spatially: a shorebird (or crab) that attempts to pull a brachiopod out of its burrow is most likely to seize the anterior shell edge. In addition, the dorso-ventral distribution of scars (Fig. 6) does not suggest a valve-selective predation, and the distribution of scars along the anterior shell edge (Fig. 7) also shows a lack of any site-selective tendencies. Note, that the lack of site-selectivity is consistent with behavior of willets, which frequently prey upon infaunal organisms by randomly probing burrows or by detecting prey movement under water (e.g., Stenzel *et al.* 1976).

The correlation between prey size and scar size (Fig. 5) may be used as an argument for size-selective predation. Note that although the correlation was found only for u-shaped scars, this most likely reflects that fact that other scar types were all made in large specimens (Fig. 10); i.e., the independent variable S_a varies so little that any potential correlation cannot be detected. It is, however, debatable whether the scar size is well correlated with the predator size, and we have no rigorous data on the size-variation in shorebird and crab populations in the area. A seemingly more convincing argument for size-selectivity is provided by the strong correlation between prey size and the frequency of attacks (Fig. 9). Alternative explanations exist here, however (e.g., Vermeij & Dudley 1982). First, larger/older individuals have potentially had more chance to encounter a predator than the smaller/younger ones. Second, a larger individual may be more likely to survive the attack than a smaller one because the damage done by the predator is smaller relative to the brachiopod size and, possibly,

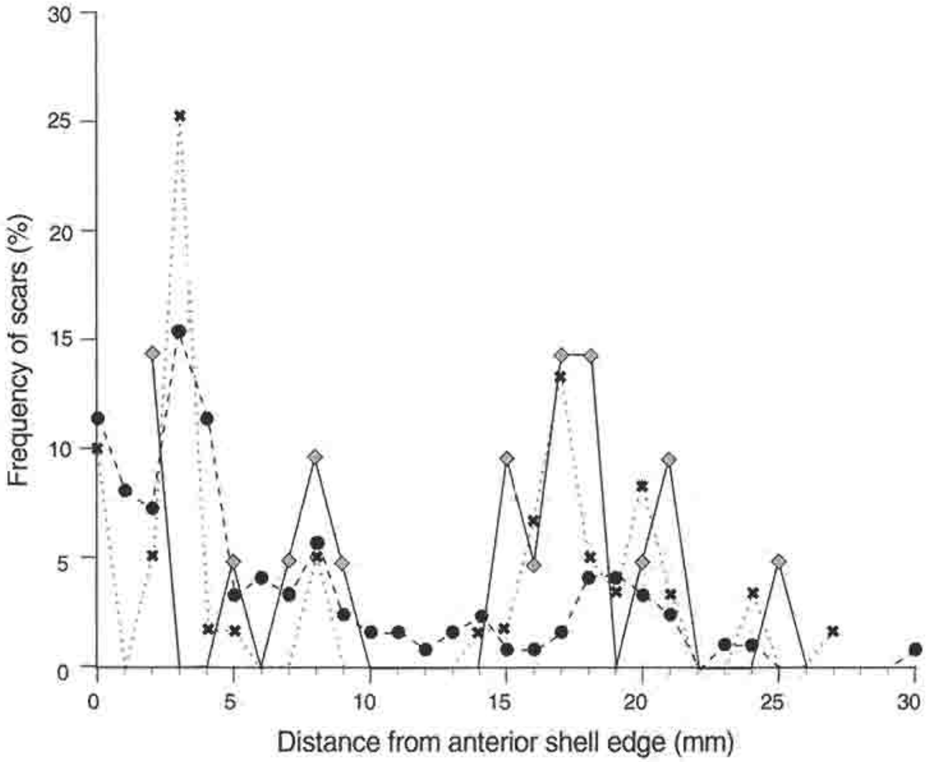

Fig. 15. The anterior-posterior distribution of scars on the brachiopod shell. Data the same as in Fig. 9, but presented separately for each of the three sampling seasons (rhombs – March 1993, black circles – November 1993, x – February 1994).

because the larger brachiopods may be able to withdraw their shell into their burrows with more strength.

Seasonality of predation. — The most interesting and least ambiguous line of evidence regarding predator behavior is provided by the anterior-posterior distribution of scars (Fig. 9). The significantly multimodal distribution suggests substantial variation in predatory attacks through time. We believe that the modes reflect seasonal, late fall/winter predation attempts.

The youngest mode is located at the anterior edge (Fig. 9). The distance data, plotted separately for each of the three sampling seasons (Fig. 15), indicate that this mode is present both in the November 1993 as well as the February 1994 samples. All scars in the November 1993 anterior mode must have been made, therefore, in late Fall 1993, a short time before the collection of the samples. The scars in the anterior mode of the February 1994 sample, may have also been made in the late Fall 1993 (*G. palmeri* ceases or slows its growth during the winter months; Batten & Kowalewski 1995; Anand *et al.* submitted), or during the 1993/1994 Winter. The second anterior mode, both in the November and February samples, is located 3 mm from the anterior shell edge. The distance between the modes corresponds very well to the annual growth of the *G. palmeri* population of 2.4 mm (Table 2). Thus, the second mode corresponds to the late Fall 1992 and/or Winter 1993. This is confirmed by the March 1993 sample which contains a significant mode at the anterior edge. When the March 1993 sample is corrected for growth, the mode coincides with the second anterior mode in the November 1993 and February 1994 samples (Fig. 15).

Unfortunately, we do not have data on the brachiopod populations prior to March 1993, and thus, we do not know how much the brachiopod populations grew in previous seasons. However, the growth ring analysis suggests that the two posterior modes coincide with seasonal growth rings (Batten & Kowalewski 1995; Anand *et al.* submitted). Also, in all extant lingulids, the rate of growth slows down with increasing size/age (see Chuang 1961; Paine 1963; Worcester 1969; Kenchington & Hammond 1978), and consequently, the annual growth increments decrease toward the anterior shell edge. Thus, the increase in the distance between the modes away from the anterior shell edge (Fig. 9) strongly suggests that the two posterior modes also represent seasonal, fall/winter predation. The third mode, most likely, represents the late Fall 1991 and/or Winter 1992 and the fourth mode the late Fall 1990 and/or Winter 1991.

The seasonal pattern of predation recorded in the anterior-posterior distribution of scars is consistent with the hypothesis that the wintering shorebirds are responsible for scars. Willets and curlews are migratory birds that winter on the oceanic coasts of North and Central America (Johnsgard 1981; Hyman *et al.* 1986; Richards 1988). The coasts of Baja California and California are their major wintering grounds (Johnsgard 1981; Hayman *et al.* 1986; Wilbur 1987; Richards 1988). Those seasonal populations can be extremely abundant and often become the dominant predator in the intertidal communities (Wilbur 1987). Moreover, migratory shorebirds such as willets are known to occasionally remain in their wintering grounds for the entire year (Haymen *et al.* 1986), which would account for the presence of some scars in-between the modes (Figs 9, 15).

Impact on *Glottidia* populations. — Scars in live-collected specimens (or repair scars in fossil specimens) represent unsuccessful predation attempts, and thus, as pointed out above, the frequency of specimens with scars does not necessarily correlate with predation intensity. Nevertheless, it is worth noting that the frequency of specimens with scars is high: comparable to the frequencies observed in modern mollusks (e.g., Vermeij *et al.* 1981) and higher than those observed in articulate brachiopods (e.g., Thayer & Allmon 1991). The high frequency of brachiopods with scars may mean that shorebirds (or crabs) are very unsuccessful predators of lingulids and either cannot learn from, or can afford, their frequent failures. This 'clumsy-but-stubborn-predator model' is, however, inconsistent with gut content studies (Paine 1963; Pereira 1990), that show that shorebirds *are* successful predators of lingulids. Thus, the high frequency of brachiopods with scars indicates, we think, a high intensity of predation (unless birds are successful predators and scars record an unsuccessful predation by crabs). The high predation intensity is corroborated by the fact that specimens with multiple scars are not frequent which suggests, in turn, a high rate of successful attacks. Note also, that even if all predation events were unsuccessful, the wound caused by the attack is likely to affect the brachiopod's chances of survival: unhealed scars are often found several mm away from the anterior shell margin suggesting that brachiopods require months or even years to fully repair injuries caused by predators (alternatively, these unhealed scars may have been fresh scars made away from the anterior margin).

At least four explanations can be offered for the fact that specimens with scars are significantly more frequent in Locality One than in Locality Two. First, the older populations from Locality One (at least 3–4 years old; see Kowalewski 1996a; Anand *et al.* submitted) have had more opportunity to encounter a predator than the younger populations from Locality Two (1–2 years old). Thus, even if there were no differences in frequency of attacks between the two localities, populations from Locality One would be expected to include a higher proportion of specimens with scars. Second, it is possible that predators are more successful when preying on smaller brachiopods. Third, when hunting predators may select for larger preys (but see above). Finally, some subtle microhabitat differences between the two localities – in particular, the substantially finer granulometry of the intertidal sediment in Locality Two (see Kowalewski 1996a) – may influence the intensity and effectiveness of foraging by predator's (especially shorebirds, see Quammen 1982).

The increase in the frequency of specimens with scars through time, between March 1993 and November 1993, most likely reflects the cumulative increase in specimens attacked by predators. In addition, the variation in predation intensity among the subsequent winters and the increased rate of failed attacks with increased age of the brachiopod may also have contributed to the observed pattern. The available data are insufficient to evaluate the relative importance of those factors. The lack of variation in frequency of specimens with scars among the three patches that range in microhabitat from the uppermost intertidal to the lower middle intertidal (Kowalewski 1996a), suggests that predators prey equally intensely in the upper and middle intertidal.

Implications

Biological implications. — Despite the many ambiguities that hamper the interpretation of repair scars, we believe that our study indicates the existence of strong seasonal interactions between shorebirds (and/or crabs?) and inarticulate brachiopods. Moreover, given the very high population densities of *G. palmeri* in the area (Kowalewski 1996a), not only may the shorebirds (and/or crabs?) be an important predator of the brachiopod, but the brachiopod may be an important part of the predators diet, especially during the winter months.

The predation on Recent articulate brachiopods is in general much less intense that that on mollusks (e.g., Thayer & Allmon 1991; Thayer 1985; James *et al.* 1992). This relatively lower predation intensity has been attributed to poor palatability and low energetic value of the articulate brachiopods (Thayer 1985; Baliński 1993). This study suggests that in contrast to articulate brachiopods, lingulids are not repellent to predators. Indeed, a simple field experiment suggests that they may be a very palatable invertebrate prey: we fed live-collected specimens of *G. palmeri* to seagulls and observed the same individual seagull happily returning for more. Our study is consistent with gut content data suggesting that many groups of predators eat lingulids (Paine 1963; Cooper 1973; Pereira 1990; Mason & Clugston 1993; Emig in press; Campbell & Campbell manuscript). Lingulids are also eaten by humans (e.g., Stimpson 1860; Yatsu 1902; Emig in press), and in some areas they form their '...favorite article of food...' (Stimpson 1860: p. 445).

The data presented here suggest that further biological research on brachiopod-shorebird/crab interactions in the Colorado Delta may bring forth important contributions toward better understanding of the intertidal ecosystems of the innermost Gulf of California. This may also prove important for understanding the marine ecology and conservation biology of nearshore marine ecosystems in general because lingulids can be very abundant in intertidal habitats (Emig 1983; Kenchington & Hammon 1978; Savazzi 1991; Kowalewski 1996a).

Finally, this study shows that repair scars may offer insights into the seasonality of predation, and thus, into the ecology of migratory animals and their impact on their transient ecosystems.

Paleontological implications. — Repair scars in lingulid shells may be preserved in the fossil record. This study shows that predators (most likely shorebirds) are capable of scarring the shells of a large proportion of the intertidal populations of *G. palmeri*. Moreover, repair scars in *Glottidia* are also known from at least two other localities: (1) the intertidal flats of the Gulf of Nicoya, Costa Rica (specimens of *G. audebarti* collected and provided to us by J.A. Vargas 1996), and (2) the Florida coast of the Gulf of Texas, USA (Paine 1963). Clearly, predatory repair scars are common in intertidal populations of lingulids.

Unquestionable lingulids (family Lingulidae) are known since the Late Devonian (Williams 1977) whereas sandpipers (order Chadriiformes, family Scolopacidae) – a monophyletic (Jehl 1968), exclusively predatory family, which includes willets and long-billed curlews – are known from the fossil record since the Late Cretaceous (Brodkorb 1963, 1967). The genus *Numenius* appears in the fossil record by the Middle Miocene and the genus *Tringa* (a close relative of *Catoptrophorus*) by the Oligocene (Brodkorb 1967). Clearly, predatory shorebirds and lingulid brachiopods have co-existed in intertidal ecosystems since at least the middle Tertiary, but may have co-existed as early as the Late Cretaceous (molluscivorous birds are known from the fossil record since at least the Late Eocene; Cracraft 1973; Vermeij 1977). The shell-crushing ability of modern predatory arthropods (e.g. stomatopods, spiny lobsters, crabs) may have evolved in the Late Mesozoic or Paleogene (see Vermeij 1977, 1987). Thus durophagous arthropods and lingulid brachiopods have co-existed in benthic ecosystems since at least the early Tertiary.

To our knowledge, however, repair scars have never been reported in fossil lingulids. This may be partly due to the fact that lingulids have very low fossilization potential (Worcester 1969; Emig 1990; Kowalewski 1996a). Indeed, post-Jurassic lingulids have very poor fossil record (Kowalewski & Flessa 1996), and thus, are rarely preserved well enough, or in a sufficient number, to allow for the recognition of repair scars. Also, and perhaps more likely, fossil lingulids may have been rarely examined for repair scars by paleontologists. We hope that the criteria and quantitative data offered here will stimulate future paleoecological research on lingulids and will lead to the identification of repair scars in fossil lingulids.

If repair scars in brachiopods are predominately made by shorebirds, then specimens with scars may offer a useful paleoenvironmental indicator as such brachiopods must have lived in the intertidal zone. The confinment of scarred specimens to intertidal populations indeed seems to be the case for extant *Glottidia*. In the course of a morphometric project (Kowalewski *et al.* 1997), we obtained specimens from six localities. Specimens from three intertidal localities (Localities One and Two from Baja California, and one locality from Costa Rica) bear repair scars, whereas those from three subtidal localities (musuem collections form the subtidal of southern California, North Carolina, and the Gulf of Mexico) lack scars. This suggests that repair scars that might be found in Tertiary fossil lingulids could be used as an evidence that those brachiopods lived in the intertidal environment; especially if other lines of evidence exist to suggest that shorebirds were responsible for the scars. It should be noted, however, that scars were found in subtidal populations of *Lingula* (C.C. Emig written communication 1997).

Because scars in the brachiopod shell can record seasonal predation by migratory birds, the identification of fossil populations of brachiopods with frequent repair scars may be particularly exciting. Such populations may help in identifying seasonal predation in ancient migratory birds. Because post-Jurassic lingulids have had a very low fossilization potential (Kowalewski 1996a; Kowalewski & Flessa 1996), they are less prone to time-averaging than mollusks (Kowalewski 1996b, 1997), and thus, Tertiary lingulid assemblages may offer temporal resolution sufficiently fine for the analysis of seasonal predation.

In summary, we hope that this paper will stimulate paleontological research on predatory traces on lingulids – in particular, their implications for ecological and co-evolutionary interactions between lingulids and their predators.

Acknowledgments

This study was supported by the NSF grant EAR-9417054 to Karl Flessa. Michał Kowalewski gratefully acknowledges support of the Alexander von Humboldt Foundation during the final stages of this project and thanks Wolfgang Oschmann and Jimmy Nebelsick from Tübingen Universität for their hospitality. We thank Diana Hallman and Julie Anand for help at various stages of this project, Christian Emig for many useful comments and valuable information, and Andrzej Baliński and Gerhard Cadée for careful and helpful reviews of the final manuscript. This is publication number 26 of C.E.A.M. (Centro de Estudios de Almejas Muertas).

References

Alexander, R.R. 1986a. Frequency of sublethal shell-breakage in articulate brachiopod assemblages through geologic time. *In:* P.R. Racheboeuf & C.C. Emig (eds), Les Brachiopodes Fossiles et Actuels. — *Biostratigraphie du Paleozoique* **4**, 159–167.

Alexander, R.R. 1986b. Resistance to and repair of shell breakage induced by durophags in Late Ordovician brachiopods. — *Journal of Paleontology* **60**, 273–285

Alexander, R.R. 1990. Mechanical strength of shells of selected extant articulate brachiopods: implications for Paleozoic morphologic trends. — *Historical Biology* **3**, 169–188.

Alexander, R.R. 1992. Survival and repair of the natural and surgical damage in the articulate brachiopod *Terebratulina retusa* (Linnaeus). — *Historical Biology* **6**, 221–231.

Allmon, W.D., Nieh, J.C., & Norris, R.D. 1990. Drilling and peeling of turritelline gastropods since the Late Cretaceous. — *Palaeontology* **33**, 595–611.

Anand, J., Flessa, K.W., & Kowalewski, M. (submitted). Seasonal growth banding in the shell of the Recent lingulid brachiopod *Glottidia palmeri* Dall.

Anderson, L.C. 1992. Naticid gastropod predation on corbulid bivalves: effect of physical factors, morphological features, and statistical artifacts. — *Palaios* **7**, 602–620.

Anderson, L.C., Geary, D.H., Nehm, R.H., & Allmon, W.D. 1991. A comparative study of naticid gastropod predation on *Varicorbula caloosa* and *Chione cancellata*, Plio-Pleistocene of Florida, U.S.A. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **85**, 283–290.

Baliński, A. 1993. A recovery from sublethal damage to the shell of a Devonian spiriferoid brachiopod. — *Acta Palaeontologica Polonica* **38**, 111–118.

Batten, J. & Kowalewski, M. 1995. Seasonal growth banding and predation scars in the shells of a Recent lingulide brachiopod. — *Geological Society of America Abstracts with Programs* **27 (6)**, A–445.

Batten, J., Chesley, K.B., Graybill, J.K., Marcot, J.D., Ramsey, M., Riley, B.C.D., Shinker, J.J., Smith, O.A., & Speer, J.H. 1994. Geomorphology, sedimentary structures, and biota of the Lower Colorado delta, Baja California, Mexico. — *University of Arizona Gesocience Symposium, Program and Abstracts* **1994**, 6.

Bengtson, S. & Zhao, Y. 1992. Predatorial borings in Late Precambrian mineralized exoskeletons. — *Science* **257**, 367–369.

Berg, J.C. 1976. Ontogeny of predatory behavior in snails (Prosobranchia: Naticidae). — *Nautilus* **90**, 1–4.

Berg, J.C. & Nishenko, S. 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. — *Paleobiology* **1**, 258–260.

Biernat, G. & Emig, C.C. 1993. Anatomical distinction of the Mesozoic lingulide brachiopods. — *Acta Palaeontologica Polonica* **38**, 1–20.

Bitner, M.A. 1996. Brachiopods from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. *In:* A. Gaździcki (ed.), Palaeontological Results of the Polish Antarctic Expeditions. — *Palaeontologia Polonica* **55**, 65–100.

Bray, N.A. & Robles, J.M. 1991. Physical oceanography of the Gulf of California. *In:* J.P. Dauphin & B.R.T. Simoneit (eds), The Gulf and Peninsular Provinces of the Californias. — *American Association of Petroleum Geologists Bulletin* **47**, 511–553.

Brodkorb, P. 1963. Birds from the Upper Cretaceous of Wyoming. — *Proceedings of the XIII International Ornithological Congress* **1**, 55–70.

Brodkorb, P. 1967. Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). — *Bulletin of the Florida State Museum* **11**, 99–220.

Bromley, R.G. 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. — *Acta Geologica Hispanica* **16**, 55–64.

Bromley, R.G. 1996. *Trace Fossils: Biology and Taphonomy*. 2nd ed. 361 pp. Unwin Hyman, London.

Brunton, H. 1966. Predation and shell damage in a Visean brachiopod fauna. —*Palaeontology* **9**, 355–359.

Brusca, R.C. 1980. *Common Intertidal Invertebrates of the Gulf of California*. 513 pp. University of Arizona, Tucson, USA.

Cadée, G.C. 1968. Molluscan biocoenoses and thanatocoenoses in the Ria de Arosa, Galicia, Spain. — *Zoologische Verhandelingen Leiden* **95**, 1–121.

Cadée, G.C. 1989. Size-selective transport of shells by birds and its palaeoecological implications. — *Palaeontology* **32**, 429–437.

Cadée, G.C., Walker, S.E., & Flessa, K.W. (in press). Gastropod shell repair in the intertidal of Bahia la Choya. — *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Campbell, L.D. & Campbell, C.C. (manuscript). Distribution and paleoecology of *Glottidia inexpectans* Olsson (Brachiopoda: Lingulidae).

Chatterton, B.D.E. & Whitehead, H.L. 1987. Predatory borings in inarticulate brachiopod *Artiotreta* from the Silurian of Oklahoma. — *Lethaia* **20**, 67–74.

Chuang, S.H. 1961. Growth of the postlarval shell in *Lingula unguis* (L.) (Brachiopoda). — *Proceedings of the Zoological Society of London* **137**, 299–310.

Cooper, G.A. 1973. Brachiopods (Recent). — *Memoirs of the Hourglass Cruises* **3**, part 3, 1–14. Marine Research Laboratory, Florida Department of Natural Resources.

Cooper, G.A. 1988. Some Tertiary brachiopods of the East Coast of the United States. — *Smithsonian Contributions to Paleobiology* **64**, 1–54.

Cracraft, J. 1973. Continental drift, palaeoclimatology, and the evolution and biogeography of birds. — *Journal of Zoology, London* **169**, 455–545.

Dall, W.H. 1870. A revision of the Terebratulidae and Lingulidae, with remarks and descriptions of some recent forms. — *American Journal of Conchology* **6**, 88–168.

Dall, W.H. 1871. Supplement to the 'revison of the Terebratulidae', with additions, corrections and a revision of the Craniidae and Discinidae. — *American Journal of Conchology* **7**, 39–79.

Dall, W.H. 1920. Annotated list of the Recent brachiopods in the collection of the United States National Museum, with description of thirty-three new forms. — *Proceedings of the United States National Museum* **57**, 261–377.

Diaconis, P. & Efron, B. 1983. Computer-intensive methods in statistics. — *Scientific American* **248**, 116–130.

Efron, B. 1979. Bootstrap methods: another look at the jackknife. — *The Annals of Statistics* **7**, 1–26.

Ekdale, A.A. 1985. Paleoecology of the marine endobenthos. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **50**, 63–81.

Emig, C.C. 1982. Terrier et position des Lingules (Brachiopodes, Inarticulés). — *Bulletin de la Société Zoologique de France* **107**, 185–194.

Emig, C.C. 1983. Taxonomie du genre *Glottidia* (Brachiopodes, Inarticulés). — *Bulletin de Museum nationale d'Histoire naturalle, Paris* **4 (5)**, section A(2), 469–489

Emig C.C. (in press). Ecology and biogeography of the inarticulated brachiopods. *In:* R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, 1.* Geological Society of America and University of Kansas Press, Boulder Colorado, and Lawrence Kansas, USA.

Emig, C.C. & Vargas, J.A. 1990. *Glottidia audebarti* (Broderip), (Brachiopoda, Lingulidae) from the Gulf of Nicoya, Costa Rica. — *Revista de Biologia Tropical* **38**, 251–258.

Emig, C.C., Gall, J.C., Pajaud, D., & Plaziat, J.C. 1978. Réflexions critiques sur l'écologie et la systématique des lingules actuelles et fossiles. — *Géobios* **11**, 573–609.

Ezcurra, E. & Rodrigues, V. 1986. Rainfall patterns in the Grand Desierto, Sonora, Mexico. — *Journal of Arid Environments* **10**, 13–28.

Fairweather, P.G. 1985. Differential predation on alternative preys, and the survival of rocky intertidal organisms in New South Wales. — *Journal of Experimental Marine Biology and Ecology* **89**, 135–156.

Flessa, K.W., Kowalewski, M., & Walker, S.E. 1992. Post-collection taphonomy: shell destruction and the Chevrolet. — *Palaios* **7**, 553–554.

Fürsich, F.T. & Jablonski, D. 1984. Late Triassic naticid drillholes: carnivorous gastropods gain a major adaptation but fail to radiate. — *Science* **224**, 78–80.

Garrity, S.D. & Levings, S.C. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effect. — *Ecological Monographs* **51**, 267–286.

Geary, D.H., Allmon, W.D., & Reaka-Kudla, M.J. 1991. Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. — *Journal of Paleontology* **65**, 355–360.

Hatai, K. 1938. On some Cenozoic Brachiopoda from the North American region. — *American Midland Naturalist* **19**, 706–722.

Hayman, P., Merchant, J., & Prater, T. 1986. *Shorebirds: An Identification Guide to Waders of the World.* 412 pp. Crrom Helm, London.

Hertlein, L.G. & Grant IV, U.S. 1944. The Cenozoic Brachiopoda of western North America. — *University of California Los Angeles Publications in Mathematical and Physical Sciences* **3**, 1–236.

Hoffman, A., Pisera, A., & Ryszkiewicz, M. 1974. Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica Clays. — *Acta Geologica Polonica* **24**, 249–260.

Hoffman, A. & Martinell, J. 1984. Prey selection by naticid gastropods in the Pliocene of Emporda (Northeast Spain). — *Neues Jahrbuch für Geologie und Paläontologie, Monatshaft* **1984**, 393–399.

Iijima, M. & Moriwaki, Y. 1990. Orientation of apatite and organic matrix in *Lingula unguis* shell. — *Calcified Tissue International* **47**, 237–242.

Iijima, M., Moriwaki, Y., Doi, Y., & Kuboki, Y. 1988. The orientation of apatite crystals in *Lingula unguis* shell. — *Japanese Journal of Oral Biology* **30**, 20–30.

James, M.A., Ansell, A.D., Collins, M.J., Curry, G.B., Peck, L.S., & Rhodes, M.C. 1992. Biology of living brachiopods. — *Advances in Marine Biology* **28**, 175–387.

Jehl, J.R., Jr. 1968. Relationships in the Charadrii (Shorebirds): a taxonomic study based on color patterns of the downy young. — *San Diego Society of Natural History Memoir* **3**, 1–54.

Johnsgard, P.A. 1981. *The Plovers, Sandpipers, and Snipes of the World.* 492 pp. The University of Nebraska Press, Lincoln, Nebraska.

Kabat, A.R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. — *Malacologia* **32**, 155–193.

Kelley, P.H. 1989. Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods. — *Historical Biology* **2**, 139–156.

Kelley, P.H. 1991. The effects of predation intensity on rate of evolution of five Miocene bivalves. — *Historical Biology* **5**, 65–78.

Kelley, P.H. & Hansen, T.A. 1996. Naticid gastropod prey selectivity through time and the hypothesis of escalation. — *Palaios* **11**, 540–556.

Kenchington, R.A. & Hammond, L.S. 1978. Population structure, growth and distribution of *Lingula anatina* (Brachiopoda) in Queensland, Australia. — *Journal of Zoology, London* **184**, 63–81.

Kitchell, J.A. 1986. The evolution of predator-prey behavior: naticid gastropods and their molluscan preys. *In*: M.H. Nitecki & J.A. Kitchell (eds), *Evolution of Animal Behavior: Paleontological and Field Approaches*, 88–110. Oxford, New York.

Kitchell, J.A., Boggs, C.H., Kitchell, J.F., & Rice, J.A. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. — *Paleobiology* **7**, 533–552.

Kowalewski, M. 1990. A hermeneutic analysis of the shell-drilling gastropod predation on mollusks in the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). — *Acta Geologica Polonica* **40**, 183–213.

Kowalewski, M. 1993. Morphometric analysis of predatory drillholes. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **102**, 69–88.

Kowalewski, M. 1996a. Taphonomy of a living fossil: the lingulide brachiopod *Glottidia palmeri* Dall from Baja California, Mexico. — *Palaios* **11**, 244–265.

Kowalewski, M. 1996b. Time-averaging, overcompleteness, and the geological record. — *Journal of Geology* **104**, 317–326.

Kowalewski, M. 1997. The reciprocal taphonomic model. — *Lethaia* **30**, 86–88.

Kowalewski, M. & Demko, T.M. 1996. Trace-fossils and population paleoecology: comparative analysis of size-frequency distributions derived from burrows. — *Lethaia* **29**, 113–124.

Kowalewski, M. & Flessa, K.W. 1994. A predatory drillhole in *Glottidia palmeri* Dall (Brachiopoda; Lingulidae) from Recent tidal flats of northeastern Baja California, Mexico. — *Journal of Paleontology* **86**, 1403–1405.

Kowalewski, M. & Flessa, K.W. 1995. Comparative taphonomy and faunal composition of the shelly cheniers from the northeastern Baja California, Mexico. — *Ciencias Marinas* **21**, 155–177.

Kowalewski, M. & Flessa, K.W. 1996. Improving with age: the fossil record of lingulide brachiopods and the nature of the taphonomic megabiases. — *Geology* **24**, 977–980.

Kowalewski, M., Flessa, K.W., & Aggen, J.A. 1994. Taphofacies analysis of Recent shelly cheniers (beach ridges), northeastern Baja California, Mexico. — *Facies* **31**, 209–242.

Kowalewski, M., Dyreson, E., Marcot, D., Vargas, J.A., Flessa, K.W., & Hallman, D.P. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. — *Paleobiology* **23**, 444–469.

Kropp, R.K. 1992. Repaired shell damage among soft-bottom mollusks on the continental shelf and upper slope north of Point Conception, California. — *Veliger* **35**, 36–51.

Lowe, H.N. 1933. At the head of the Gulf of California. — *Nautilus* **47**, 45–47.

Mason, W.T., Jr. & Clugston, J.P. 1993. Food of the Gulf Sturegoen in the Suwannee River, Florida. — *Transactions of the American Fisheries Society* **122**, 378–385.

Miller, R.H. & Sundberg, F.A. 1984. Boring Late Cambrian organisms. — *Lethaia* **17**, 185–190.

Neugus, M. 1975. An analysis of boreholes drilled by *Natica catena* (da Costa) in the valves of *Donax vittatus* (da Costa). — *Proceedings of the Malacological Society of London* **41**, 353–356.

Norton, S.F. 1988. Role of the gastropod shell operculum in inhibiting predation by fishes. — *Science* **241**, 92–94.

Paine, R.T. 1963. Ecology of the brachiopod *Glottidia pyramidata*. — *Ecological Monographs* **33**, 187–213.

Pereira, A.I. 1990. Ecología de la alimentación de *Limnodromus griseus*, *Catoptrophorus semipalmatus* y *Numenius phaeopus* (Aves, Scolopacidae) en Chomes, Costa Rica. M.Sc. Thesis, Universidad de Costa Rica.

Quammen, M.L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. — *Marine Biology* **71**, 339–343.

Recher, H.F. 1966. Some aspects of the ecology of migrant shorebird. — *Ecology* **47**, 393–407.

Reyment, R.A. 1971. *Introduction to Quantitative Paleoecology*. 227 pp. Elsevier, Amsterdam.

Richards, A. 1988. *Birds of the Tideline: Shorebirds of the Northern Hemisphere.* 224 pp. Dragons World, Surrey, England.

Robba, E. & Ostinelli, F. 1975. Studi paleoecologici sul Pliocene Ligure. I. Testimoniaze di predazione sui molluschi Pliocenici de Albenga. — *Rivista Italiana di Paleontologia e Stratigrafia* **81**, 309–372.

Roden, G.I. 1964. Oceanographic aspects of the Gulf of California. *In:* T.H. van Andel & G.G. Shor (eds), Marine Geology of the Gulf of California. — *American Association of Petroleum Geologists Memoir* **3**, 30–58.

Rowell, A.J. 1965. Inarticulate. *In:* R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda 1*, H260–H296. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, USA.

Ruggiero, E.T. 1991. A study of damage evidence in brachiopod shells. *In:* D.I. MacKinnon, D.E. Lee, & J.D. Campbell (eds), *Brachiopods Through Time*, 203–210. Balkema, Rotterdam.

SAS Institute. 1989. *SAS/STAT User's Guide (version 6)*, 4th ed. 943 pp. (vol. 1), 846 pp. (vol. 2), SAS Institute, Cary, USA.

SAS Institute. 1990a. *SAS Procedures Guide (version 6)*, 3d ed. 705 pp. Sas Institute, Cary, USA.

SAS Institute. 1990b. *SAS/IML*. 235 pp. Sas Institute, Cary, USA.

SAS Institute 1991. *SAS Language Guide*. 755 pp. Sas Institute, Cary, USA.

Savazzi, E. 1991. Burrowing in the inarticulate brachiopod *Lingula anatina*. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **85**, 101–106.

Schindel, D.E., Vermeij, G.E., & Zipser, E. 1982. Frequencies of repaired shell fractures among the Pennsylvanian gastropods of North-Central Texas. — *Journal of Paleontology* **56**, 729–740.

Schoener, T.W. 1979. Inferring properties of predation and other injury-producing agents from injury frequencies. — *Ecology* **60**, 1110–1115.

Sheehan, P.M. & Lesperance, P. 1978. Effects of predation on the population dynamics of a Devonian brachiopod. — *Journal of Paleontology* **52**, 812–817.

Smith, O.A., Hallman, D.P., & Batten, J. 1995. Comparative taphonomy of Recent lingulide brachiopod and bivalve shells: an experimental study. — *Geological Society of America Abstracts with Programs* **27 (6)**, A–135.

Stenzel, L.E., Huber, H.R., & Page, G.W. 1976. Feeding behavior and diet of the long-billed curlew and willet. — *The Willson Bulletin* **88**, 315–332.

Stimpson, W. 1860. A trip to Beaufort, N. Carolina. — *American Journal of Science* **29**, 2nd series, 442–445.

Sykes, G.G. 1937. The Colorado Delta. — *Carnegie Institution Washington Publication* **460**, 1–193.

Taylor, J.D., Morris, N.J., & Taylor, C.N. 1980. Food specialization and the evolution of predatory prosobranch gastropods. — *Palaeontology* **23**, 375–409.

Thayer, C.W. 1985. Brachiopods versus mussels: competition, predation, and palatability. — *Science* **228**, 1527–1528.

Thayer, C.W. & Allmon, R.A. 1991. Unpalatable thecideid brachiopods from Palau: Ecological and evolutionary implications. *In:* D.I. MacKinnon, D.E. Lee, & J.D. Campbell (eds), *Brachiopods Through Time*, 261–264. Balkema, Rotterdam.

Thayer, C.W. & Steele-Petrovic, H.M. 1975. Burrowing of the lingulid brachiopod *Glottidia pyramidata*: its ecologic and paleoecologic significance. — *Lethaia* **8**, 209–221.

Thomas, R.D.K. 1976. Gastropod predation on sympatric Neogene species of *Glycymeris* (Bivalvia) from the eastern United States. — *Journal of Paleontology* **50**, 488–499.

Thompson, R.W. 1968. Tidal flat sedimentation on the Colorado River delta, northwestern Gulf of California. — *Geological Society of America Memoir* **107**, 1–133.

Thomson, D.A. (ed.) 1993. *1993 Tide calendar for the northern Gulf of California*. [No page numbers]. Printing and Publishing Support Services, University of Arizona, Tucson, USA.

Treuman, E.R. & Wong, T.M. 1987. The role of the coelem as a hydrostatic skeleton in lingulid brachiopods. — *Journal of Zoology, London* **213**, 221–232.

Vale, F.K. & Rex, M.A. 1988. Repaired shell damage in deepsea prosobranch gastropods from the western North Atlantic. — *Malacologia* **28**, 65–79.

Vale, F.K. & Rex, M.A. 1989. Repaired shell damage in a complex of rissoid gastropods from the upper continental shelf south of New England. — *Nautilus* **103**, 105–108.

Vermeij, G.J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. — *Paleobiology* **3**, 245–258.

Vermeij, G.J. 1982. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. — *Malacologia* **23**, 1–12.

Vermeij, G.J. 1983. Traces and trends in predation, with special reference to bivalved animals. — *Palaeontology* **26**, 455–465.

Vermeij, G.J. 1987. *Evolution and Escalation*. 527 pp. Princeton University, Princeton.

Vermeij, G.J. 1992. *A Natural History of Shell*. 207 pp. Princeton University, Princeton.

Vermeij, G.J. & Dudley, E.C. 1982. Shell repair and drilling in some gastropods from Ripley Formation (Upper Cretaceous) of the South-eastern U.S.A. — *Cretaceous Research* **3**, 397–403.

Vermeij, G.J., Zipser, E., & Dudley, E.C. 1980. Predation in time and space: peeling and drilling in terebrid gastropods. — *Paleobiology* **6**, 352–364.

Vermeij, G.J., Schindel, D.E., & Zipser, E. 1981. Predation through geological time: evidence from gastropod shell repair. — *Science* **214**, 1024–1026.

Vermeij, G.J., Zipser, E., & Zardini, R. 1982. Breakage-induced shell repair in some gastropods from the upper Triassic of Italy. — *Journal of Paleontology* **56**, 233–235.

Walker, S.E. & Yamada, S.B. 1993. Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. — *Palaeontology* **36**, 735–741.

Walker, S.E. & Voigt, J.R. 1994. Paleoecologic and taphonomic potential of deepsea gastropods. — *Palaios* **9**, 48–59.

Wiedman, L.A., Feldmann, R.L., Lee, D.E., & Zinsmeister, W.J. 1988. Brachiopoda from the La Meseta Formation (Eocene), Seymour Island, Antarctica. *In*: R.M. Feldmann & M.O. Woodburn (eds), Geology and Paleontology of the Seymour Island, Antarctic Penninsula. — *Geological Society of America Memoir* **169**, 531–539.

Wilbur, S.R. 1987. *Birds of Baja California*. 253 pp. University of California, Berkeley, USA.

Wiltse, W.I. 1980. Predation by juvenile *Polinices duplicatus* (Say) on *Gemma gemma* (Totton). — *Journal of Experimental Marine Biology and Ecology* **42**, 187–199.

Worcester, W. 1969. On *Lingula reevei*. Unpublished Master Science Thesis. 49 pp. University of Hawaii, Hawaii.

Yatsu, N. 1902. On the habits of the Japanese *Lingula*. — *Annotationes zoologicae Japonensis* **4**, 61–67.

Zar, J.H. 1984. *Biostatistical Analysis*. 718 pp. Prentice, Englwood Cliffs.

Appendix 1

The Monte-Carlo model based on the Poisson distribution. The SAS program (for SAS release 6.11) that performs the procedure described here is available upon request from M. Kowalewski.

The approach proposed here is based on the method described by Reyment (1971) to analyze the spatial distribution of predatory marks. In contrast to the Reyment's approach, we employ here a non-parametric, computer-intensive technique that would not have been feasible 25 years ago, when the Reyment's approach was published. The test evaluates whether the spatial distribution of scars is different from random. In this approach, the scar-frequency distribution calculated for the actual data was compared to the distribution expected for random data predicted by the Poisson distribution with mean λ.

$$\lambda = N/s \tag{1}$$

where λ – poisson distribution mean; N – number of scars; and s – number of sectors.

A given scar-frequency distribution includes s observations where N equals:

$$N = \sum_{i=1}^{s} y_i \tag{2}$$

where y is a number of scars in an *i-th* sector. Consider a 3×3 grid of 9 sectors that contains 7 scars. Suppose, for example, that there is 1 sector with 3 scars, 4 sectors with 1 scar, and 4 sectors with 0 scars. The scar-frequency distribution is thus based on 9 observations (3,1,1,1,1,0,0,0,0) that sum up to 7.

The null hypothesis that the data have a random spatial distribution can be evaluated by comparing the sector-frequency distribution to the theoretical distribution predicted by Poisson function with $\lambda = N/s$. In the above example of 9 sectors and 7 scars, the expected distribution should be calculated for $\lambda = 0.7778$. The significant difference between the actual distribution and the expected distribution rejects the null hypothesis that data came from the population with a random spatial distribution. In Reyment's approach the two distributions are compared directly using the X^2 statistic. However, such an approach requires an arbitrary *a priori* lumping of the categories that contain small percentage of observations (Reyment 1971) and also requires assumptions of X^2 test which can be avoided when using a computer-intensive method (e.g., Diaconis & Efron 1983).

Our approach consists of the following steps:

Step 1. 10 000 random datasets with sample size s, are drawn from the Poisson distribution with mean λ, where λ is calculated from the actual data. In the simulation, we used the Poisson function provided by SAS (see SAS 1991).

Step 2. Each of the random datasets is compared to the expected Poisson distribution with mean λ. The difference between the two distributions is estimated by G (a log likelihood ratio), the parameter which is often considered superior to the X^2 statistic1).

$$G = 2 \sum_{i=1}^{n} f(i)_o \ln\left(\frac{f(i)_e}{f(i)_o}\right) \tag{3}$$

where G – likelihood ratio, $f(i)_o$ –number of observation in category i, $f(i)_e$ – number of expected observation in category i as expected from Poisson distribution.

Note, that 10 000 G–values derived in the simulation provide an estimate of the probability distribution for random datasets with sample size s drawn from Poisson function with a mean λ.

Step 3. A single G-value for the actual data is calculated using the same expected Poisson distribution as used in Step 2. The probability associated with the obtained G-value (p) is then estimated using empirical distribution of G-values obtained in Step 2. We used the percentile method (also called nave bootstrap approach, see Efron 1979):

$$p = x/i \tag{4}$$

where p – is probability that data came from a Poisson-distributed population, x – a number of randomly derived G-values greater than or equal to the G-value calculated for the actual data, and i – number of iterations (10 000 in our case). Note that i defines the number of decimal places that can be reported for p; when $p = 0$, then $p < 1/i$ (i.e., 0.0001 in our case).

---

1) Note, that the choice of the goodness-of-fit statistic is not critical in our approach because the probability function is built empirically through a Monte-Carlo simulation. Thus, X^2 or Kolmogorov-Smirnov D could be used equally successfully in our approach.

Appendix 2

Bootstrap procedure for local significance of modes (employed here to analyze data presented on Fig. 10). The program written in SAS/IML is available upon request from M. Kowalewski.

In order to assess the statistical significance of multiple modes in a single distribution, we propose here a simple bootstrap procedure. The procedure estimates the probability of whether a given mode is locally significant – i.e., significant in respect to the directly adjacent bins (frequency classes) – or locally insignificant (i.e., could be produced by sampling of a population which lacks that mode). The procedure is based on the resampling of the actual data according to the following protocol.

Step 1. The modes to be evaluated are identified[1] in the original data (in our case, 4 modes indicated on Fig. 10).

Step 2. A sample (in our case 203 distance measurements presented on Fig. 10) is resampled with replacement. The resulting bootstrap sample is used to calculate a new frequency distribution.

Each mode is then evaluated according to the simple criterion. If the number of observation in the mode is greater than in any of the two adjacent frequency-classes, the bootstrap sample is assigned value of '1'. If any of the two adjacent classes has equal or greater number of observation than the mode, the sample is assigned value of '0'.

Step 3. Step 2 is repeated n number of times. In our analysis $n = 10{,}000$. The null hypothesis for a given mode is rejected[2)] if $p < 0.05$. Where p (probability that sample came from a population where the 'mode' has fewer or equal number of observations than at least one of the two directly adjacent bins) is given by the following formula:

$$p = 1 - \frac{x}{n} \tag{1}$$

where x – number of bootstrap samples which were assigned '1' in the procedural Step 2, and n – number of iterations.

---

1) Note that position and height of modes depend on how we define the bins. In case of our data, bins are 1-mm intervals (Fig. 10).

2) Although the analysis evaluates four hypothesis, the tests are dependent (i.e., based on the same bootstrap samples) and Bonferroni correction should not be applied.

Blizny drapieżnicze w muszlach współczesnego ramienionoga lingulidowego *Glottidia palmeri* i ich znaczenie paleontologiczne i ekologiczne

MICHAŁ KOWALEWSKI, KARL W. FLESSA i JONATHAN D. MARCOT

Streszczenie

Szczegółowa analiza ilościowa blizn drapieżniczych w muszli ramienionoga bezzawiasowego z grupy lingulidów oparta jest na 820 okazach *Glottidia palmeri* Dall, 1870. Okazy zebrano z dwóch stanowisk z równi międzypływowych północno-wschodniej Zatoki Kalifornijskiej w Meksyku. Blizny drapieżnicze występują w 23.4% osobników. Można je podzielić na cztery kategorie: blizny u-kształtne, kieszeniowe, spękaniowe oraz pozostałe. Niezależnie od ich morfologii, blizny koncentrują się przy przedniej krawędzi muszli. Większość blizn zorientowana jest rozwartą stroną w kierunku przedniej krawędzi muszli i wiele z nich składa się z dwóch blizn zlokalizowanych naprzeciwlegle na brzusznej i grzbietowej skorupce ramienionoga. Analiza ilościowa wskazuje, że (1) blizny wahają się w wielkości od 1,5 do 24 mm^2 (średnia = 2,5 mm^2) i wszystkie cztery kategorie blizn mają podobne rozkłady wielkości; (2) rozmieszczenie blizn na powierzchni muszli nie jest losowe, podczas gdy ich rozkład grzbieto-brzuszny wydaje się być losowy; (3) proporcja zagojonych blizn wzrasta w kierunku tylnej części muszli; (4) rozkład blizn jest uderzająco multimodalny i sugeruje sezonalne drapieżnictwo skoncentrowane późną jesienią i zimą; (5) częstość blizn wzrasta wraz z wielkością ramienionoga; i (6) częstość okazów z bliznami waha się znacząco pomiędzy dwoma badanymi stanowiskami, jak również w obrębie stanowiska 1 w czasie, ale nie waha się znacząco pomiędzy różnymi miejscami opróbowania w obrębie stanowiska 1.

Blizny reprezentują nieudane ataki jakiegoś epifaunalnego drapieżnika, wyposażonego w nożycowy narząd chwytny (np. szczypce kraba, dziób ptaka). Wysoka częstość ataków, ich sezonalność i poprzednie badania ekologiczne zgodnie sugerują, że blizny są wynikiem ataków drapieżnych ptaków (*Catoptrophorus semipalmatus* lub *Numenius americanus*). Wybrzeża Półwyspu Kalifornijskiego są miejscem zimowania drapieżnych ptaków i goszczą ich liczne populacje. Nie można jednak całkowicie wykluczyć, że drapieżnikami były kraby. Ponieważ blizny reprezentują nieudane ataki, ilościowe analizy dotyczące selektywności miejsca ataku, selektywności wielkości ofiary i wpływu drapieżnictwa na dynamikę populacji ramienionoga są trudne do jednoznacznego zinterpretowania. Niemniej jednak, wyniki sugerują istnienie silnej sezonalnej zależności ekologicznej pomiędzy ptakami (krabami?) i ramienionogami. Analiza ilustruje metody ilościowe użyteczne w badanich współczesnych i kopalnych blizn drapieżniczych i ma istotne implikacje paleontologiczne. Drapieżne ptaki, kraby i ramienionogi mogły współzamieszkiwać strefy międzypływowe począwszy od późnego mezozoiku. Tak więc, blizny drapieżnicze w muszlach ramienionogów mogą mieć długi zapis kopalny, interesujący dla paleontologii, szczególnie z punktu widzenia paleoekologii ewolucyjnej. Ponieważ blizny w muszlach lingulidów pozwalają rozpoznać sezonalne drapieżnictwo, kopalne blizny mogą potencjalnie dostarczyć danych ekologicznych i etologicznych, które są zazwyczaj rzadko dostępne w paleontologii.