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AN EXPERIMENTAL INVESTIGATION OF POST-DEPOSITIONAL TAPHONOMIC BIAS IN CONODONTS

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Abstract: The different types of elements that occurred together in conodont apparatuses are not recovered from the fossil record in the expected numbers. The causes of this are complex and difficult to study. Numerous complete articulated skeletons of *Ozarkodina excavata* (Branson and Mehl) have been recovered from the Eramosa Member at Hepworth, Ontario, and as a consequence, several of the potential biases affecting recovery of isolated conodont elements can be ruled out *a priori*. Based on processing ten replicate samples ('runs') of nodular carbonate and bituminous shale, we tested the role of post-mortem compaction, laboratory processing and difficulties in element identification in biasing the expected, or predicted, recovery of apparatus elements.

Although the numbers of different elements of *O. excavata* reported in the literature do not exhibit as marked a bias as do Late Palaeozoic conodont faunas, they are biased nonetheless. This is also true of elements recovered from the Eramosa Member. In both carbonate and shale samples, P_1 and $S_{1/2}$ elements are significantly under-represented, whereas P_2 and S_0 elements are significantly over-represented. In the carbonate runs, this bias is a consequence of the difficulties in differentiating between broken remains of morphologically similar elements. When this factor is taken into account in the shale runs, however, the fauna still exhibits significant bias, and we are able to rule out all potential biases except one. Surprisingly, apparent over-representation of P elements and under-representation of S elements can arise as a result of element fragmentation during sediment compaction and diagenesis alone.

Key words: conodont, elements, bias, fossil record, post-mortem, breakage, diagenesis.

WE now know that the fossil record of conodonts is fundamentally biased. Decades of research provides clear evidence that the elements of the conodont skeletal apparatus are not found in the relative abundances that they should be. But this simple statement masks an important issue: recognition that this bias exists, and assessment of the degree to which it obscures our view of conodont evolutionary history, is predicated on our understanding of the conodont skeleton as it was in life, and as other papers in this volume (Purnell and Donoghue 2005*a*) attest this is still a matter of some discussion.

The debate over the nature of the conodont skeleton was among the most important in the history of conodont research. Did each conodont, whatever organism that might be, possess a single element, multiple elements of the same type, or several different types of element? Without resolution of this fundamental question there could be no stable taxonomy, no meaningful scientific investigation of conodont evolution, and limited understanding and interpretation of stratigraphical distributions. Of central importance in this debate were fossils that have come to be known as 'bedding plane assemblages', fossils that, in contrast to the isolated elements that comprise a standard conodont sample, preserve a number of conodont elements clustered together. It was the discovery of one such fossil that led Hinde (1879) to suggest that the conodont skeleton had numerous elements of different types. Unfortunately, the assemblage described by him as *Polygnathus dubius* is a faecal or regurgitated pellet resulting from several conodonts being consumed by an unknown predator, and this is how all bedding plane assemblages were interpreted by some early conodont authorities. But as more and more were discovered through the first part of the twentieth century the recognition of patterns of element association within the clusters made this interpretation increasingly untenable. Scott (1942, p. 296) for example observed recurrent patterns in Carboniferous bedding plane assemblages from the Heath Formation of Montana and in answer to those that advocated a faecal origin noted dryly that 'it would be strange indeed to find a group of animals that had such a perfectly balanced diet the excretal material would consist time after time of one pair of prioniods [M elements], one pair of spathognaths [P_1 elements], one pair of prioniodells [P_2 elements], and approximately four pairs of hindeodells [S elements]'. It took another 30 years before the implications of this for conodont taxonomy became fully accepted (see Sweet and Donoghue 2001 for a recent review), but today nobody would suggest that conodonts bore only one element.

Ironically, it is the acceptance and implementation of multi-element taxonomy that has highlighted the bias in the conodont fossil record. Bedding plane assemblages clearly indicate that S elements should be the most commonly occurring components of the skeleton, but this is far from what we find. The Carboniferous *Idiognathodus* (*sensu* Baesemann 1973; Grayson *et al.* 1991) provides the most compelling example of this. Bedding plane assemblages have been known for decades (Du Bois 1943; Rhodes 1952) and are the most abundantly preserved of any conodont. They provided templates for the first applications of multi-element methods to Upper Palaeozoic conodonts (von Bitter 1972; Baesemann 1973), and the structure of the apparatus is also among the best known (Purnell and Donoghue 1997, 1998). Like many other ozarkodinid taxa, an unbiased collection should contain elements in the ratio of 2 M elements, 4 $S_{3/4}$ elements, 4 $S_{1/2}$ elements, 1 S_0 element, 2 P_2 elements, and 2 P_1 elements (see Purnell *et al.* 2000 for discussion of element notation), but von Bitter (1972) and subsequent authors found massive over-representation of P_1 elements (or under-representation of all other parts of the apparatus). Of the 20,244 elements of *Idiognathodus* spp. recovered by von Bitter (1972), only 379 were M elements (14% of the expected number), 330 were S_{1-4} elements (3% of expected), 56 were S_0 elements (0·04% of expected) and 1326 were P_2 elements (49% of expected). In stark contrast, 18,153 were P_1 elements (675% of expected) (Table 1).

Bias and Ozarkodina excavata

The unique nature of our data (discussed below) means that the focus of this paper is *Ozarkodina excavata* (Text-figs 1–3, Pls 1–3). In many ways this is fortuitous. As apparatus H (Walliser 1964), this species was among the first to have its complement of elements reconstructed, and it was also among the first conodonts for which the taxonomic consequences of the multi-element skeleton were properly explored (Jeppsson 1969).

Klapper and Murphy (1974, p. 36) considered *Ozarkodina excavata* to be 'among the most convincing of all reconstructions of Silurian multielement species', but in the absence of natural assemblages, opinion concerning the number of elements in the apparatus has varied. Jeppsson (1969) included *O. excavata* among members of his genus *Hindeodella*, and suggested that the apparatus probably included 16 paired elements, four P_1 elements (as two pairs), two P_2, two S_0, two $S_{1/2}$, four $S_{3/4}$ (as two pairs) and two M elements (using current element notation). Rexroad and Nicoll (1972) used the statistical methods of Kohut (1969) to look for associations of elements in their collections that might correspond to multi-element *Ozarkodina excavata*. Despite employing a statistical approach, they were among the first to articulate the view that the use of ratios of occurrence of element types to recognize apparatuses was suspect. Nevertheless, they did discuss ratios for *O. excavata*, suggesting that they cast serious doubt on Walliser's (1964) and Jeppsson's (1969) reconstructions. They tabulated ratios of elements for *O. excavata* in the Bainbridge Formation as eight P_1 elements, five P_2, six S_0, two $S_{1/2}$, zero $S_{3/4}$ and 7·5 M elements. In retrospect, it is clear that rather than undermining the reconstructions of *O. excavata* their data support their opinion that element ratios

TABLE 1. *Idiognathodus* spp., discrete elements recovered and identified from the four cyclothems of the Shawnee Group (Virgilian, Pennsylvanian) of eastern Kansas by von Bitter (1972). Percentage of each element is of the total recovered shown in parentheses under each element category. Expected percentage of each element, based on 15 element ozarkodinid model, shown in bottom row.

	P_1	P_2	S_0	$S_{1/2,\ 3/4}$	M	Total
Topeka Limestone	8088	399	23	131	166	8807
	(91·836%)	(4·531%)	(0·261%)	(1·487%)	(1·885%)	(100%)
Deer Creek Limestone	2395	250	9	67	50	2771
	(86·431%)	(9·022%)	(0·325%)	(2·418%)	(1·804%)	(100%)
Lecompton Limestone	4155	324	9	50	77	4615
	(90·033%)	(7·021%)	(0·195%)	(1·083%)	(1·668%)	(100%)
Oread Limestone	3515	353	15	82	86	4051
	(86·769%)	(8·714%)	(0·370%)	(2·024%)	(2·123%)	(100%)
mean percentage	88·77%	7·32%	0·29%	1·75%	1·87%	100%
Total Conodont Elements	18,153	1326	56	330	379	20244
% of Total	(89·671%)	(6·550%)	(0·277%)	(1·630%)	(1·872%)	(100%)
% Expected	(13·333%)	(13·333%)	(6·667%)	(53·334%)	(13·333%)	(100%)

are fundamentally biased. Table 2 summarizes literature reports of recovery for the elements of the apparatus of *O. excavata*. It is clear that although element recovery is less biased than that of *Idiognathodus*, P_1 elements are consistently over-represented, whereas S_{1-4} elements are generally under-represented.

CAUSES OF BIAS IN CONODONT ELEMENT RECOVERY

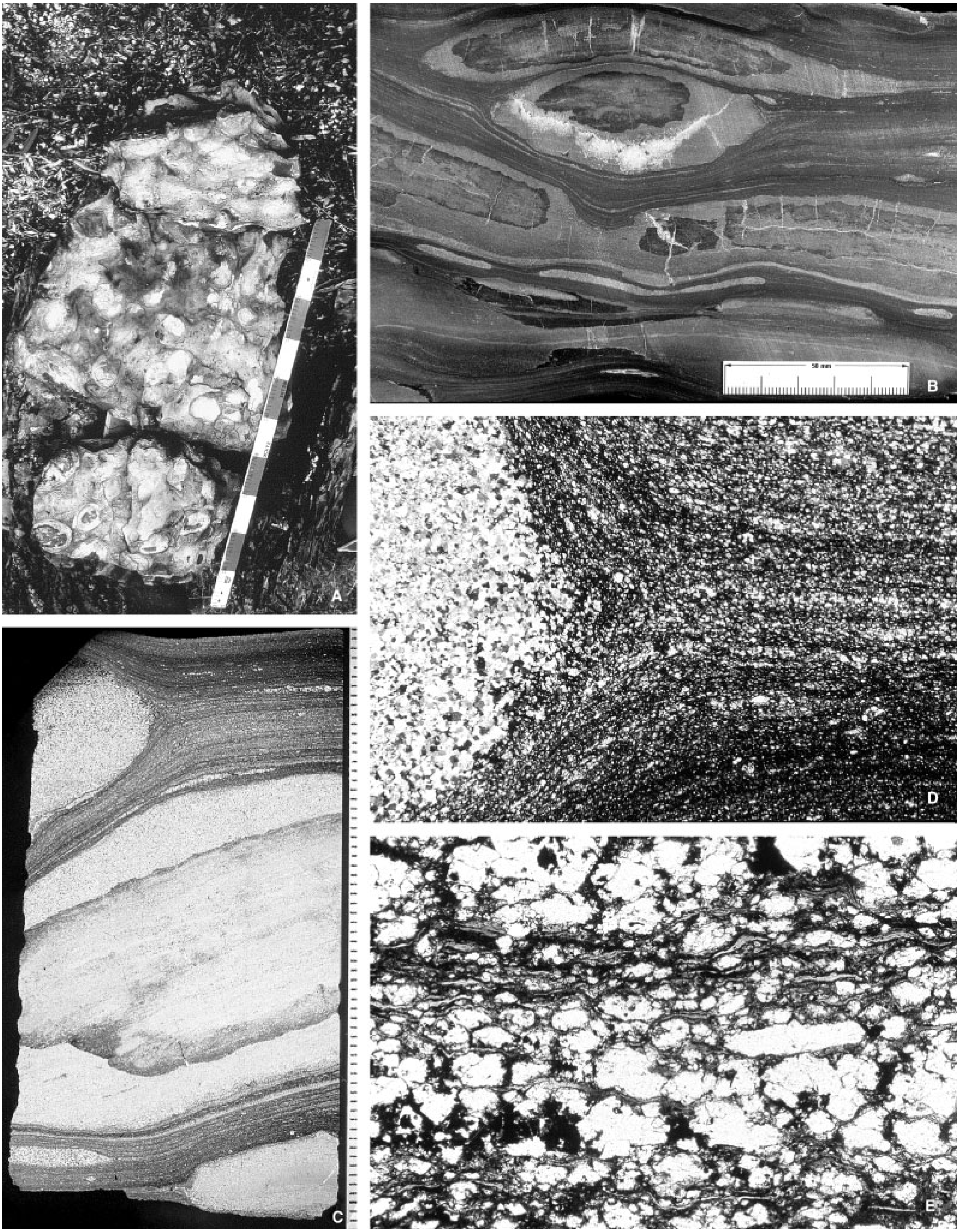
To a greater or lesser degree, the bias in element numbers discussed above affects all collections of conodonts recovered through standard sampling practice from all parts of the stratigraphical column (i.e. elements derived from laboratory dissolution or disaggregation of rock, followed by sieving, and picking). The potential causes of this bias are numerous and complex (see e.g. Carls 1977 for a review); here we consider seven potential factors.

1. Variability in the element composition of the skeletal apparatus

Do apparently biased numbers of elements reflect repeated shedding and replacement of over-represented elements or resorption and loss of under-represented elements? Hypotheses that the number of elements in conodont apparatuses was variable and under some sort of biological or

TABLE 2. Summary of element recovery of *Ozarkodina excavata* as reported in selected literature. Only elements of *O. excavata* are included in calculation of totals and percentages. Data include those of Jeppsson (1974, table 2), Klapper and Murphy (1974, tables 2–8), Simpson and Talent (1995, tables 2–5), Helfrich (1980, tables 1, 3–5), Aldridge [1972, tables 1–5, except that we have excluded samples which lack *O. excavata* P elements because, as noted by Jeppsson 1974, some '*N. excavatus*' may include M elements of *Oulodus* (his *Ligonodina*), and the same may be true of other counts] and Rexroad *et al.* (1978, table 1). Data are listed in approximate stratigraphical order, younging upwards. N, number of samples containing *O. excavata*.

Element	P_1	P_2	S_0	$S_{1/2}$	$S_{3/4}$	M	$P_1 + P_2$	$M + S_0 + S_{1/2}$	Total
Expected proportion of fauna	13·33%	13·33%	6·67%	26·67%	26·67%	13·33%	26·67%	46·67%	
Klapper and Murphy 1974									
$n = 126$									
total	1902	634	210	398	487	339	2536	947	3970
mean percentage of total	53·54%	13·71%	4·73%	9·07%	9·80%	9·14%	67·26%	22·94%	
ratio observed:expected	4·016	1·029	0·710	0·340	0·367	0·640	2·522	0·492	
Jeppsson 1974									
$n = 44$									
total	454	267	193	263	509	337	721	793	2023
mean percentage of sample	23·47%	13·18%	7·66%	9·22%	27·64%	18·84%	36·64%	35·72%	
ratio observed:expected	1·760	0·988	1·149	0·346	1·036	1·413	1·374	0·765	
Simpson and Talent 1995									
$n = 72$									
total	213	113	35	76	127	55	326	166	619
mean percentage of sample	41·88%	19·19%	2·93%	9·72%	20·13%	6·15%	61·07%	18·80%	
ratio observed:expected	3·141	1·439	0·440	0·365	0·755	0·461	2·290	0·403	
Rexroad *et al.* 1978									
$n = 5$									
total	22	19	9	8	16	24	41	41	98
mean percentage of sample	21·52%	10·25%	8·75%	6·25%	19·27%	33·95%	31·77%	48·95%	
ratio observed:expected	1·614	0·769	1·313	0·234	0·723	2·547	1·191	1·049	
Helfrich 1980									
$n = 17$									
total	78	55	105	117	27	36	133	258	418
mean percentage of sample	19·66%	24·46%	19·94%	23·18%	3·90%	8·85%	44·13%	51·97%	
ratio observed:expected	1·475	1·835	2·991	0·869	0·146	0·664	1·655	1·008	
Aldridge 1972									
$n = 15$									
total	111	98	43	41	66	39	209	123	398
mean percentage of sample	37·61%	22·61%	9·57%	6·04%	14·91%	9·27%	60·22%	24·88%	
ratio observed:expected	2·82	1·696	1·435	0·226	0·559	0·695	2·258	0·533	


A
50 mm
B
C
D
E

developmental control have involved several interrelated ideas. The first of these, that conodonts repeatedly shed and replaced individual elements during their lifetime, began with Gross (1954), and was followed by Carls (1977) and Krejsa *et al.* (1990). Interestingly Carls' conclusions derived from a detailed analysis of element ratios and were proposed as an explanation for under-representation of S and M elements. Jeppsson (1976), however, drew on evidence of repair to damaged elements to conclude that rather than being shed, conodont elements were permanent structures. Similarly, Purnell's (1994) investigation of natural assemblages of *Idiognathodus* and *Gnathodus* found no evidence in the element composition of assemblages, or in the ontogeny of the apparatus, for element shedding or replacement. The accumulating evidence of natural assemblages of a broad range of taxa (Purnell and Donoghue 1998) provides strong support for the hypothesis that the number of elements in an apparatus was stable throughout the life of the animal that bore it, and in the face of this direct evidence it is now difficult to sustain Merrill and Powell's (1980) inference that elements were lost from the apparatus during ontogeny.

The second line of reasoning to do with variability in apparatus composition began with Müller and Nogami (1971). They interpreted discontinuities within conodont elements to be surfaces along which resorption of phosphatic crown tissue had occurred during growth. Von Bitter and Merrill (1980) built on this idea by postulating that conodonts resorbed and removed calcium phosphate from their elements as a body weight control mechanism. More recently, Zhuravlev (1999) has continued to develop these concepts. It is difficult to exclude confidently post-mortem or laboratory processes as the cause of the etched features he illustrates, but what is relevant for the present discussion is that even if the features he observed are accepted as evidence of resorption, they are too rare for resorption and shedding to account for P_1 element over-representation (Zhuravlev 1999). The hypothesis that resorption of elements has a role in explaining bias is further undermined by the recent suggestion (Purnell 1995; Donoghue and Purnell 1999) that internal discontinuities are not the result of resorption, but are wear surfaces that formed during periods of function and were subsumed during subsequent element growth. Donoghue and Purnell (1999) documented the correlation between surface wear and internal discontinuities, and noted that this provides strong evidence that elements are retained and not shed.

2. Differential breakage and dissolution during ingestion, digestion and excretion by predators

Although several authors, including von Bitter and Merrill (1998) and Tolmacheva and Purnell (2002), have studied conodont apparatuses that have gone through the gut of a predator, the effects of these ingestive, digestive and excretory processes on the completeness of individual apparatuses, or on individual elements, have apparently not been studied in a systematic way. One of the more interesting possibilities is that during these processes calcium phosphate is removed from conodont elements by bacteria (von Bitter *et al.* 1996). It is also pertinent to note, however, that complete articulated apparatuses are known from coprolites (e.g. Purnell and Donoghue 1998, text-figs 15–16) and from within the digestive tract of predators (Nicoll 1977; Purnell 1993; Purnell and Donoghue 1998).

3. Post-mortem sorting due to differential current entrainment and settling

Ellison (1968) was among the first to interpret variation in the number and kind of elements from sample to sample as evidence of sorting during deposition. Other authors (e.g. von Bitter 1972) considered this and related factors to account for under- and over-representation; however, it was not until the early 1990s that post-mortem sorting began to be studied more formally. Broadhead *et al.* (1990) studied gravitational settling of conodont elements and its implications for palaeoecological interpretations of conodont samples; similarly, McGoff (1991) determined the hydrodynamic properties of a number of different types of element. These studies confirmed previous suspicions that the susceptibility of

TEXT-FIG. 1. Conodont-bearing lithologies in the Eramosa Member, Hepworth, Bruce County, Ontario. A, bedding-plane surfaces of carbonate nodules in bituminous shale; scale represents 1 m. B, cross-section of nodular carbonate alternating with bituminous shale; carbonate has core of grey chert, and both chert and carbonate were fractured, and subsequently cemented by white, fluorescent calcite; scale represents 50 mm. C, thin-section of nodular carbonate alternating with dark, bituminous shale; darker core of chert in the largest (central) carbonate nodule, also 'pinching and swelling' of bituminous shale, ROM thin-section 99PB15A, crossed nicols; scale represents 64 mm. D, uppermost part of thin-section ROM 99PB15A, carbonate nodule on left, showing compaction of bituminous shale laminae around nodule. Carbonate nodules alternate with darker organic material that has a 'knitted', cellular texture, crossed nicols; ×30. E, enlargement of bituminous shale portion of D showing lighter carbonate in a matrix of darker layered organic material. Elongated organic material is golden yellow in colour, both under plane and polarized light. Thin-section ROM 99PB15A, crossed nicols; ×259.

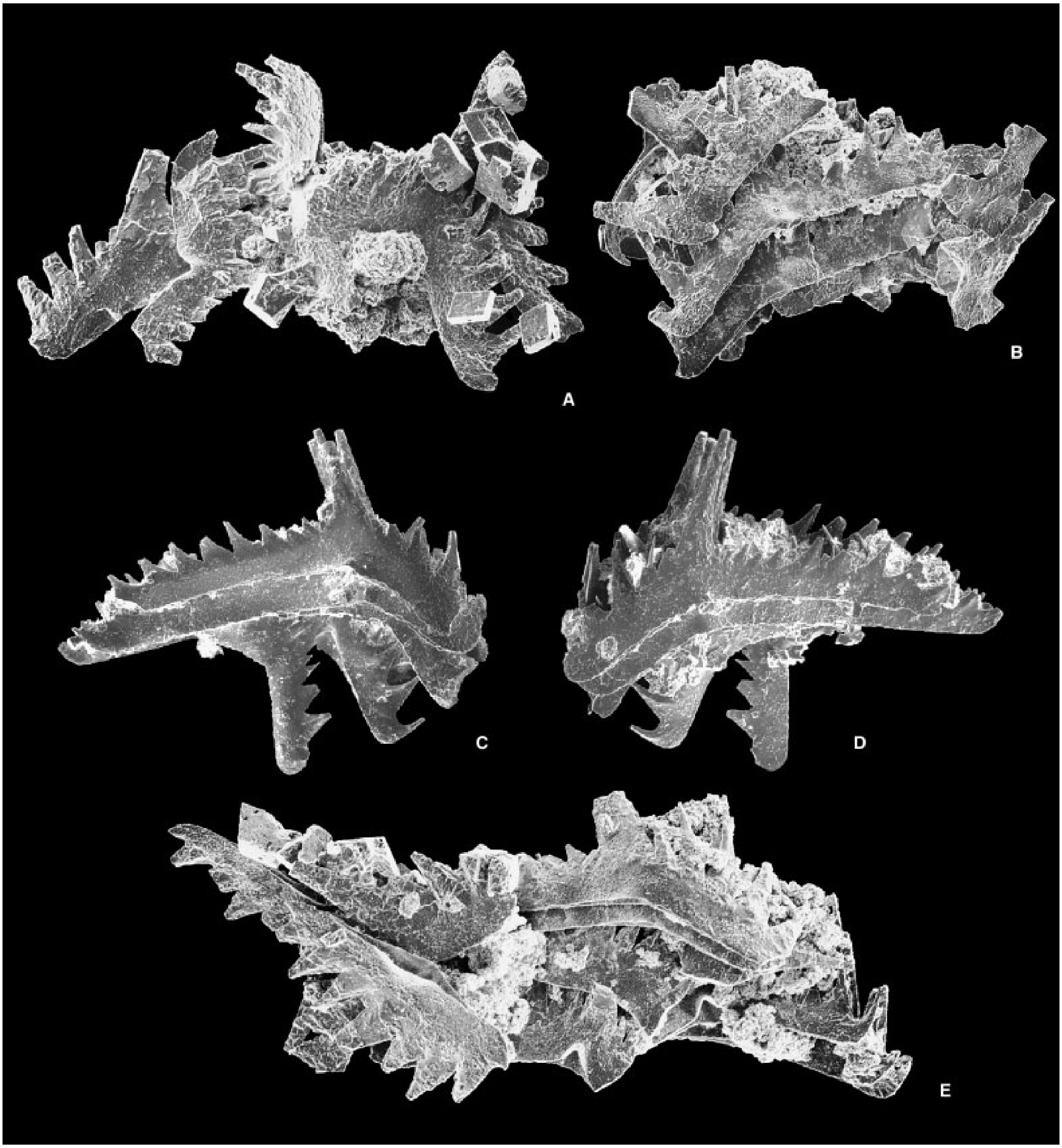
TABLE 3. Discrete elements and 'clusters' of *Ozarkodina excavata* (Branson and Mehl) recovered and identified from the Eramosa Member (Silurian), Hepworth, Bruce County, Ontario, in ten carbonate (CO_3) and shale (Sh) laboratory processing runs. Some processing data and calculated conodont element yield per kilogram also shown. Asterisks refer to inclusion of counts from fused element pairs (clusters).

Run	P_1	P_2	$P_{indet.}$	S_0	$S_{1/2}$	$S_{3/4}$	M	Total	Clusters	Litho.	Amount proc.	Breakdown	Yield	Preservation
CO_3/1	5*	13	5	11	10	16	13	73	3	Mixed CO_3/Sh	2943 g	2018 g (69%)	36/kg	mod.good
CO_3/2	11*	24*	–	11	15*	20	15	96	19	CO_3	4558 g	2746 g (54%)	35/kg	mod.good
CO_3/3	3	7	–	2	3	11	3	29	3	CO_3	2082 g	1220 g (59%)	24/kg	mod.good
CO_3/4	9*	13	6	10	22	34*	17	111	~22	CO_3	4183 g	2741 g (66%)	40/kg	good to excellent
CO_3/5	15	28	4	17	41	40	34	179	9	CO_3	4275 g	3100 g (73%)	58/kg	mod.good to good
Sh/6	–	1	1	–	–	1	2	5	–	Shale	4005 g	1068 g (27%)	5/kg	poor
Sh/7	5*	42*	22	26	32	33	21	181	24	Shale	1303 g	576 g (44%)	314/kg	poor
Sh/8	2	102	48	53	62	116	56	439	36	Shale	1300 g	668 g (51%)	657/kg	poor
Sh/9	1	9	4	5	7	20	3*	49	1	Shale	2526 g	1543 g (61%)	32/kg	poor
Sh/10	–	8	3	3	2	10	6	32	–	Shale	1063 g	120 g (11%)	266/kg	poor
Summary														
5 CO_3 runs	43	85	15	51	91	121	82	488	~56	Mostly CO_3	18041 g	11,555 g (64%)	42/kg	good
% of total	8·811	17·418	3·074	10·45	18·648	24·795	16·803	100%						
5 shale runs	8	162	78	87	103	180	88	706	61	Shale	10197 g	3975 g (39%)	178/kg	poor
% of total	1·133	22·946	11·05	12·32	14·589	25·496	12·465	100%						
5 CO_3 and 5 shale runs combined	51	247	93	138	194	301	170	1194	~117	Nodular CO_3 and bituminous shale	28238 g	15,530 g (55%)	77/kg	
% of total	4·271	20·687	7·789	11·56	16·248	25·209	14·238	100%						

elements to current entrainment, transport and sorting is correlated with their size and shape. Broadhead and Driese (1994) addressed the related question of the effects of abrasion on conodont elements during current transport. They concluded that when suspended in water abrasion of elements is limited and that their destruction through abrasion is highly unlikely.

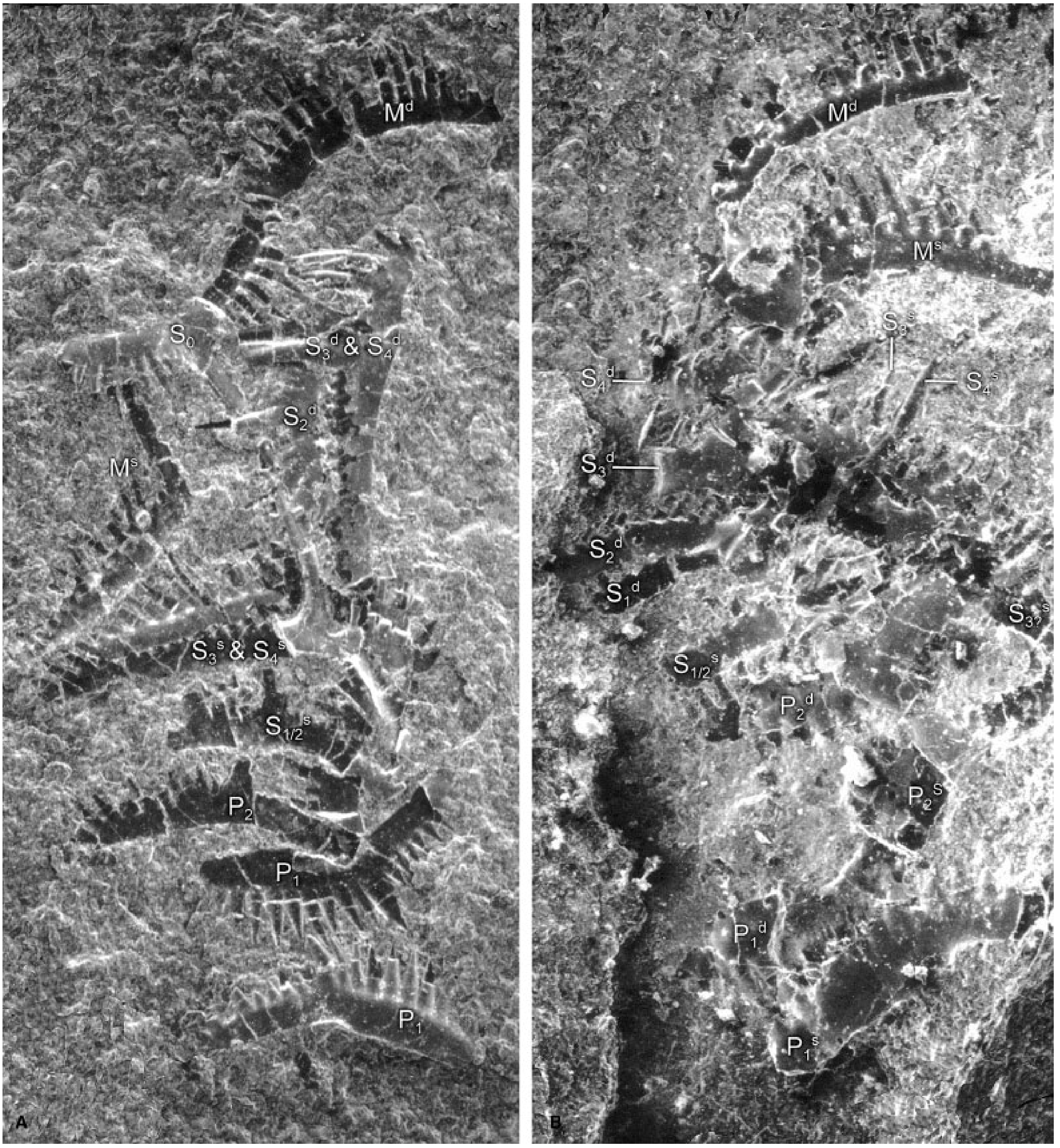
4. Lithological sampling bias

Almost all conodonts are collected blind, and although most conodont workers intuitively develop their own strategies regarding which lithologies are worth collecting, to our knowledge none of these has ever been put to the test. Aside from avoiding non-marine lithologies and



TEXT-FIG. 2. *Ozarkodina excavata* (Branson and Mehl) fused natural assemblages ('clusters') from Eramosa Member carbonate (Silurian), Hepworth, Bruce County, Ontario. A, B, E, three almost complete apparatuses, specimens ROM 56390, 56391, 56393; C–D, both sides of an almost complete S element array, specimen ROM 56392. All ×139.

those that will not yield to laboratory processing it is by no means clear that there is a general strategy that can be applied to rocks from all depositional settings through all parts of the conodont stratigraphical record. The consequence of these intuitive approaches to collecting is that lithologies that are difficult to break down, or which experience suggests are not worth the effort (too few informative conodont elements to justify the difficulty of processing), will tend not to be collected unless there is a pressing biostratigraphical (or other) need to obtain material. Among those that have recently touched on the subject of lithological sampling bias are Orchard (2002, 2005) and Broadhead and Repetski (2002); see also Purnell and Donoghue (2005*b*) for more detailed discussion.



TEXT-FIG. 3. *Ozarkodina excavata* (Branson and Mehl) bedding plane assemblages from Eramosa Member shale (Silurian), Hepworth, Bruce County, Ontario. Elements show extensive fracturing. A, specimen ROM 56394; ×42; B, specimen ROM 56395; ×52.

5. Differential breakage and solution of elements during sediment compaction and diagenesis

Jeppsson (1976) and Carls (1977) were among the first to consider this factor. Questions of differential breakage and solution are an important part of our own study, and we consider these topics elsewhere in this paper.

6. Differential loss of elements during laboratory processing

Since Ziegler *et al.* (1971) and von Bitter (1972) observed that differential destruction of elements during laboratory processing may be a significant factor in the 'loss' of conodont elements, a number of papers have suggested ways of reducing, or measuring, that loss. Among the techniques for decreasing or minimizing the loss of elements, those to do with buffering the acids used during dissolution of carbonates (Jeppsson *et al.* 1985, 1999; Jeppsson and Anehus 1995) have been particularly effective and important. Introducing known 'spikes' into a sample provides a means of checking on possible processing bias as it enables phosphate dissolution during processing, element loss during separation, and effectiveness of picking to be assessed (von Bitter and Millar-Campbell 1984).

7. Bias resulting from differences in element identifiability

It is clear from natural assemblages that although the number and locations of elements in ozarkodinid and prioniodinid apparatus are stable (Purnell and Donoghue 1998), the degree to which the elements within the apparatus differ from one another varies. In many taxa S_3 and S_4 elements, for example, are extremely similar to one another. The S_1 and S_2 elements are usually more similar to one another than either is to the $S_{3/4}$ elements, but this varies considerably. Further confusion can arise in taxa which have digyrate elements in $S_{1/2}$ positions: these elements are easily distinguished from $S_{3/4}$ elements, even when broken, but may be more easily confused with digyrate elements from P positions. Clearly, if different elements vary in the ease with which they can be identified when broken, or in their similarity and potential confu-

TABLE 4. Laboratory processing data for runs 1–5 (carbonate, CO_3), and 6–10 (shale, Sh), from the Eramosa Member, Hepworth, Bruce County, Ontario.

Run	Sample	Rock type	Preparation	Acid/ chemical used	Amount processed (g)	Amount coarse fraction (g)	Weight fine fraction (g)	Amount breakdown (g)	Percentage breakdown	Comments
CO_3/1	99PB15	Interbedded carbonate and shale	Crushed	Acetic acid	2943	925	139	2018	69	
CO_3/2	01PB1	Mostly carbonate	Not crushed	Acetic acid	4558	2082	127	2476	54	
CO_3/3	01PB1	Mostly carbonate	Coarse fraction from run 2	Formic acid	2082	862	15	1220	59	coarse fraction is mostly shale
CO_3/4	01PB1	Mostly carbonate	Not crushed	Acetic acid	4183	1442	158	2741	66	coarse fraction is mostly shale
CO_3/5	02PB1	Mostly carbonate	Not crushed	Acetic acid	4275	949	214	3100	73	
Sh/6	01PB2	Shale	Not crushed	Acetic acid	4005	2603	20	1068	27	
Sh/7	01PB2	Shale	Large pieces of coarse fraction from run 6	Acetic acid	1303	727	16	576	44	poor breakdown
Sh/8	01PB2	Shale	Small pieces of coarse fraction from run 6	Sodium hypochlorite	1300	632	112	668	51	
Sh/9	02PB2	Shale	Not crushed	Acetic acid	2526	983	76	1543	61	
Sh/10	02PB2	Shale	Small pieces not crushed	Sodium hypochlorite	1063	943	28	120	11	poor breakdown

TABLE 5. *t*-test results determining whether the number of each element type recovered from the five carbonate and five shale runs processed from the Eramosa Member, Hepworth, Bruce County, Ontario, differ significantly from the number that would be expected from complete apparatuses of *Ozarkodina excavata* (Branson and Mehl). For raw data see Table 3. *t* is calculated as $(\bar{x} - \mu)/s_e$, where, in this case, $\bar{x}$ is the mean per cent recovery for an element, μ is the per cent expected recovery of that element; s_e is the standard error [calculated as $s\sqrt{(1/n)}$ where *s* is the standard deviation of the runs, and *n* is the number of runs]. The critical values of *t* for rejection of the null hypothesis at a significance level, *P*, of 0·05 are ± 2·132 [for 4 degrees of freedom (= $n - 1$); 5 carbonate runs, 5 shale runs) and ± 2·353 [for 3 degrees of freedom; 4 shale runs in analysis, excluding aberrant (shale) run 6]. This is a one-tailed test, because we are testing for significant over- or under-representation (positive and negative values of *t*, respectively), not simply difference from the expected value.

	P_1	P_2	S_0	$S_{1/2}$	$S_{3/4}$	M	Total P	$S_0 + S_{1/2}$	$S_0 + S_{1/2}$ + M
Carbonate runs									
% Expected	13·333	13·333	6·667	26·667	26·667	13·333	26·667	33·333	46·667
mean (%)	9·028	18·860	10·386	16·479	26·732	15·618	30·786	26·865	42·482
s_e	0·826	2·531	1·377	2·220	3·300	1·485	2·211	2·557	4·006
t	–5·211	2·184	2·700	−4·590	0·020	1·539	1·866	−2·528	−1·045
H0 rejected? ($P < 0·05\%$)	yes	yes	yes	yes	no	no	no	yes	no
Shale runs									
mean (%)	1·052	21·961	9·203	10·468	27·344	17·846	35·138	19·671	37·517
s_e	0·569	1·208	2·456	3·220	4·090	5·890	1·956	6·334	2·273
t	–21·589	7·145	1·033	−5·031	0·166	0·766	4·332	−2·157	−4·025
H0 rejected? ($P < 0·05\%$)	yes	yes	no	yes	no	no	yes	yes	yes
Shale runs (excluding run Sh/6)									
mean (%)	1·315	22·452	11·504	13·085	29·181	12·308	33·923	24·589	36·896
s_e	0·651	1·425	1·108	2·421	4·718	2·589	1·978	3·398	2·823
t	–18·454	6·400	4·366	−5·610	0·533	−0·396	3·671	−2·573	−3·461
H_0 rejected? ($P < 0·05\%$)	yes	yes	yes	yes	no	no	yes	yes	yes

sion with other elements from the apparatus, this has the potential to introduce bias in the numbers of the different elements reported.

AN EXPERIMENTAL APPROACH TO EVALUATING UNDER- AND OVER-REPRESENTATION OF CONODONT ELEMENTS

The principal difficulty in trying to assess the cause of bias in recovered collections of conodont elements is that any given sample is likely to have been affected by many or all of biases 2–7 outlined above. Because it is often impossible to disentangle the effects of one bias from another, determining the relative importance of each is problematic to say the least. We have been able to take advantage of the unique nature of the preserved conodont fauna of the Eramosa Member at Hepworth, Ontario, to provide new insights into the contribution of individual biases to the fauna recovered from this unit.

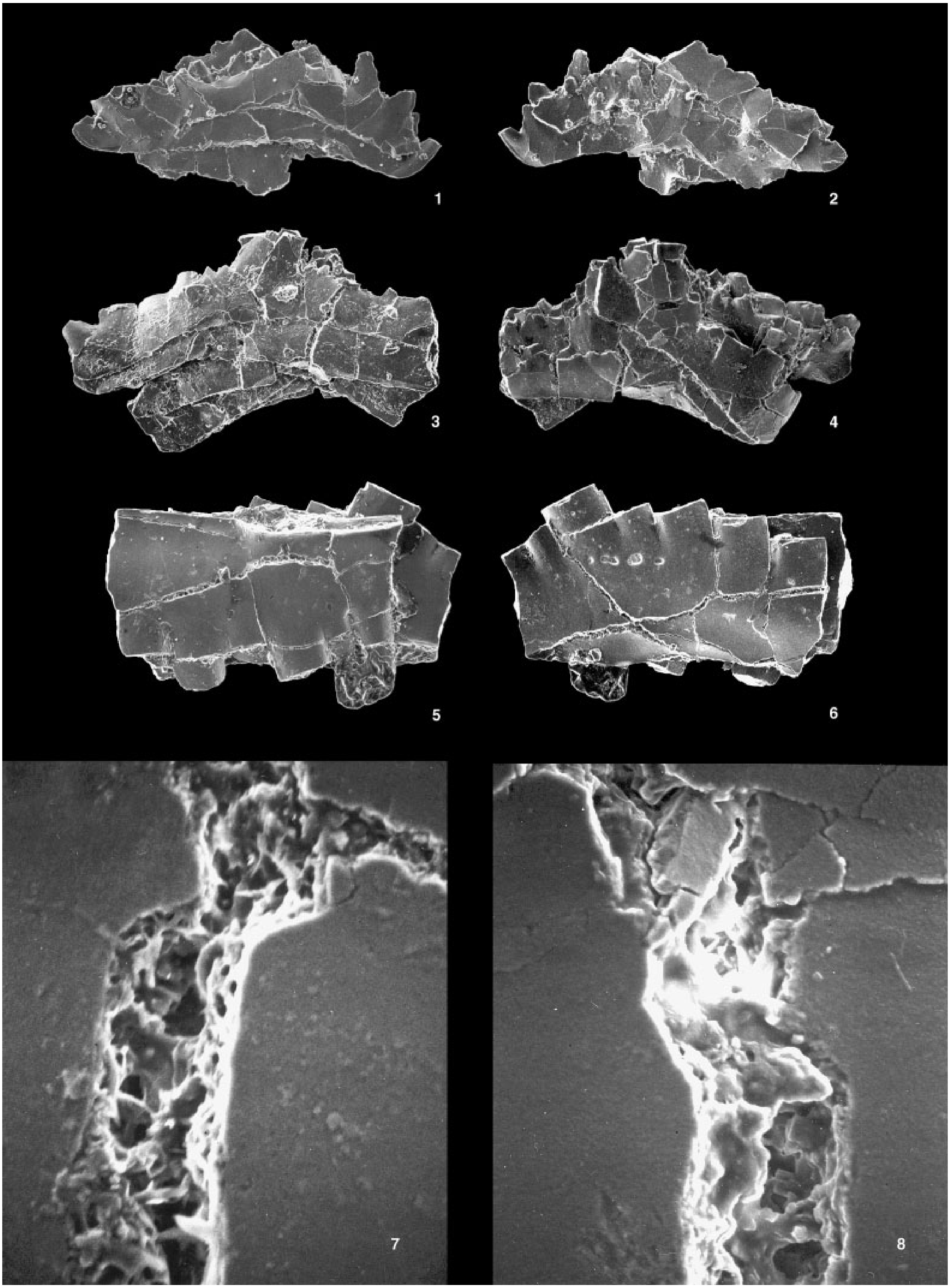
Materials, methods and experimental design

Material. The Eramosa Member of the Guelph Formation (Silurian, Wenlock) on the Bruce Peninsula of southern Ontario is commonly regarded as a dolostone (Armstrong and Meadows 1988; Armstrong 1989; Armstrong and Goodman 1990), but at Hepworth it occurs as nodular, lightly dolomitized limestone that alternates with bituminous shale. It crops out in a small roadside section, approximately 30 cm thick, with no exposed top or bottom. No excavations were possible, and all material was collected as loose material thrown up by ditch-clearing and maintenance operations. The shaly, bituminous nature of these beds, and the presence of abundant carbonate nodules, suggests that these two alternating lithologies represent the 'Interbedded Unit' of the upper part of the Eramosa Member (Armstrong and Meadows 1988).

The beds sampled are characterized by the presence of abundant carbonate nodules (Text-fig. 1A) around which bituminous shale thickens and thins (Text-fig. 1B). The carbonate nodules are generally between 5 and 12 cm

EXPLANATION OF PLATE 1

Figs 1–8. *Ozarkodina excavata* (Branson and Mehl) fused natural assemblages ('clusters') showing severe fracturing. All specimens from Eramosa Member shale (Silurian), Hepworth, Bruce County, Ontario. 1–2, fused S elements, ROM 56396; ×150. 3–4, fused S elements, ROM 56397; ×150. 5–8, a pair of P elements in apposition (i.e. fused in near functional position), ROM 56398; 5–6, ×100; 7–8, repair of fractures, possibly by mobilized phosphate; ×2035.



VON BITTER and PURNELL, *Ozarkodina*

in diameter, but are often considerably elongated along bedding (Text-fig. 1B); they generally possess a core of silica (Text-fig. 1B–C), sometimes replacing fossils, and they generally show evidence of early diagenetic shrinkage in the form of syneresis cracks (Text-fig. 1B). The chert is succeeded in an outward direction by lightly dolomitized limestone (Text-fig. 1D). Common accessory minerals in the nodules are sphalerite and brown fluorite, the latter often possessing an unusual acicular crystal habit. The shale enclosing the nodules is bituminous, and contains abundant elongated organic fragments parallel to bedding (Text-fig. 1E), fragments that are honey-yellow in colour under both plane polarized light and crossed nicols.

When processed for conodonts, this mixed lithology yielded a well-preserved discrete-element fauna dominated by *Ozarkodina excavata* (run 1, Table 3). From this and subsequent runs (Table 3), we also recovered clusters of elements (Text-fig. 2) representing partial to nearly complete natural assemblages in which the elements are fused together in original life position.

Subsequent to processing run 1, carbonate and shale were processed separately and this revealed that both lithologies contained conodont clusters (Table 3); however, those recovered from carbonate are noticeably better preserved than are those from shale. Unexpectedly, manual splitting of the shale and carbonate from Hepworth also produced abundant bedding plane assemblages (Text-fig. 3), natural assemblages in which the conodont elements are preserved in original, or near original, life position. These occur flattened on the convex and concave surfaces of the shale separated from around carbonate nodules. To date more than 200 bedding plane assemblages of *Ozarkodina excavata* have been recovered from Hepworth.

The fauna is dominated by *Ozarkodina excavata*, but rare associates, both as discrete elements and as natural assemblages, include *Ctenognathodus* sp., *Panderodus* sp., *Pseudooneotodus* sp. and an undescribed taxon with an apparatus of diminutive, finely denticulated elements. This small species is known from Sweden (L. Jeppsson, pers. comm. 2002) and has been illustrated from Britain (Aldridge 1985, pl. 3.4, fig. 2) as *Ozarkodina*? sp. nov. None of these elements was included in the counts that form the basis for the present study.

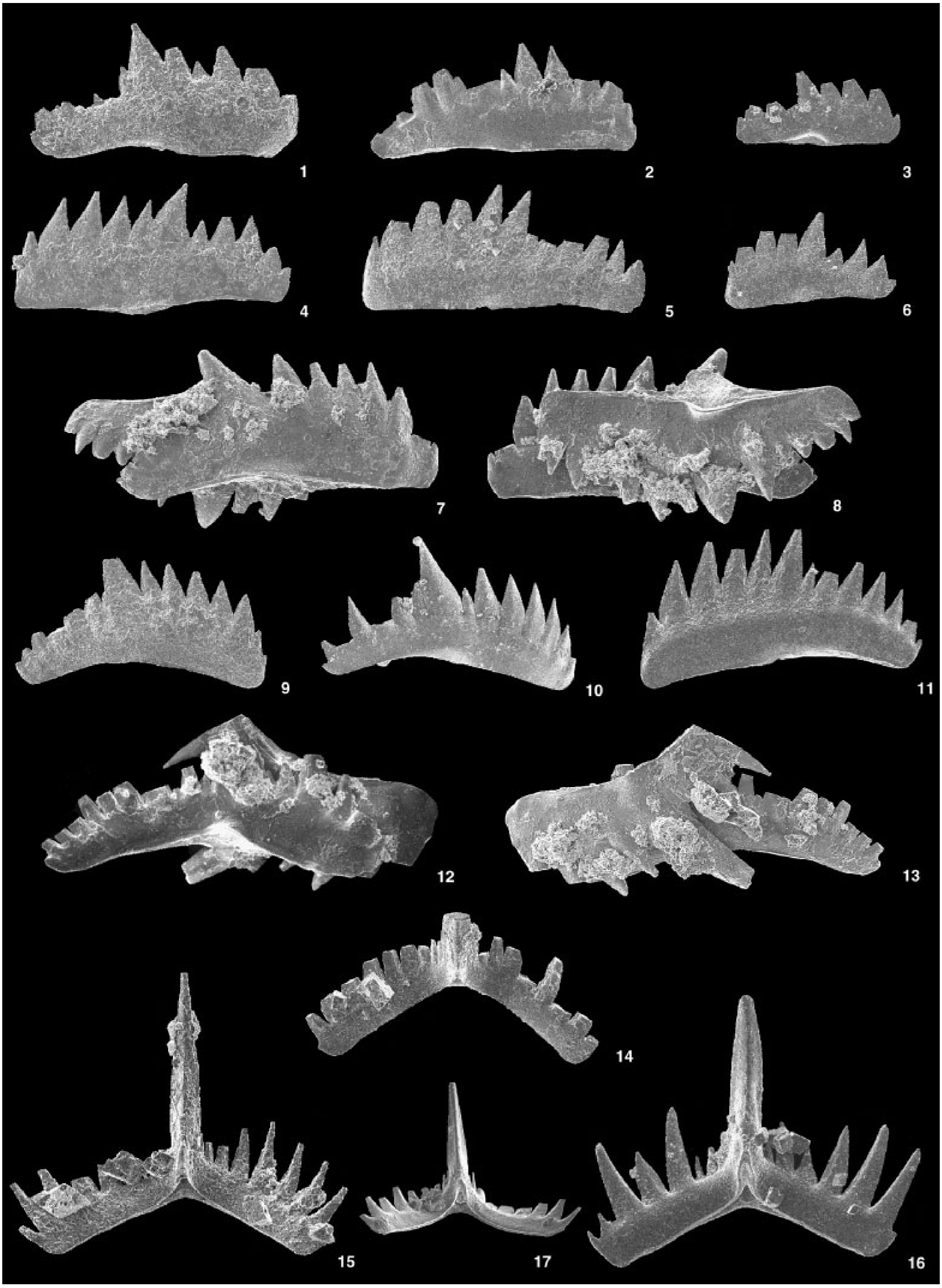
Experimental design and method. This conodont fauna is unique in that the dominance of *Ozarkodina excavata* and the completeness of the natural assemblages make it possible to rule out biases discussed above under headings 1–4. The natural assemblages of *Ozarkodina excavata* from nodular carbonate and from bituminous shale demonstrate unequivocally that the apparatus contained 15 elements in the usual ozarkodinid configuration. We doubt that the number of elements in the apparatus of ozarkodinid conodonts varied from 15 (see discussion of bias 1 above), but the evidence from the Hepworth fauna allows us to rule out this potential bias from the outset. The natural assemblages are generally complete and, although we recovered a few faecal element concentrations, there is remarkably little evidence of predator ingestion, digestion and excretion (allowing us to discount bias 2, the effects of predation). The natural assemblages show little or no evidence of sedimentological dismemberment and sorting (allowing us to eliminate bias 3, post-mortem sorting). Because we recovered relatively complete natural assemblages from both carbonate and shale, and because we processed both lithologies, we concluded that bias 4, lithological sampling bias, could also be safely discounted.

The elimination of these four factors leaves only differential breakage and solution during sediment compaction and diagenesis (bias 5), differential loss of elements during laboratory processing (bias 6) and identification bias (bias 7) as the possible causes of any deviation in recovery of elements from the numbers in which they occurred in the apparatus during life.

Light and scanning electron microsocopy of both natural assemblage types, and of conodont elements recovered by laboratory processing of both nodular carbonate and bituminous shale, allowed us to evaluate bias 5, differential breakage and solution during sediment compaction and diagenesis. Bias 6, loss of elements during laboratory processing, was evaluated by processing the two lithologies in a number of different ways, and processing each lithology in a number of ‘runs’ (see Table 4). The expected number of elements was then compared with the actual number and kinds of elements recovered. Ten runs (Table 3) were processed by Ms Kathy David of the Palaeobiology Department, Royal Ontario Museum (ROM), utilizing acetic and formic acids individually, or successively, to break down the nodular carbonates, and acetic acid and sodium hypochlorite to disaggregate the bituminous shale (Table 4). The processing of the runs was monitored using introduced ‘spikes’ (von Bitter and

EXPLANATION OF PLATE 2

Figs 1–17. *Ozarkodina excavata* (Branson and Mehl) from Eramosa Member carbonate (Silurian), Hepworth, Bruce County, Ontario. 1–6, P_1 elements, ‘lateral’ views, ROM 56355–56361. 7–8, P_1 element pair, ‘lateral’ views, fused in near life position; ROM 56362. 9–11, P_2 elements, ‘lateral’ views; ROM 56363–56365. 12–13, P_2 element pair, ‘lateral’ views, fused in near life-position; ROM 56366. 14–17, S_0 elements; ROM 56366–56369; 14–16, ‘posterior’ views, 17, oblique aboral view. All × 58.



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Millar-Campbell 1984), controlled by the use of buffered acids, and by the daily removal of conodont elements from unspent acid. The residues from the first run were picked by Mr Christopher Stott, presently of the University of Western Ontario, whereas the remaining runs were picked by Ms David and/or PvB. Picking of samples is here regarded as part of standard laboratory processing procedure. Bias 7, identification bias, was evaluated by comparing individual counts and combined element counts to the expected frequency of occurrence of the elements (based on natural assemblage data).

Our data are summarized in Table 3. Rather than simply evaluating these data subjectively, we performed *t*-tests (Table 5) to determine whether the numbers of each element type recovered from the carbonate and shale fractions of the Eramosa Member differ significantly from the numbers that would be obtained from complete apparatuses [summaries of *t*-test methodology as applied to such problems appear in general statistical textbooks for geologists and biologists, such as Bailey (1981) or Davis (1986)]. For example, P_1 elements should make up 13·33 per cent (2/15) of an unbiased sample; does the mean value for P_1 element recovery from the Eramosa Member carbonate samples (9·028%) differ significantly from this value or not? This equates to a null hypothesis that the mean relative contribution of an element to the samples does not differ significantly from the proportion of a complete apparatus that the element makes up.

RESULTS: EVALUATION OF BIAS IN CONODONT FAUNAS FROM THE ERAMOSA MEMBER

The degree of conodont element over- and under-representation

Table 5 summarizes the results of *t*-tests applied to our data for recovery of elements of *O. excavata* from the Eramosa Member. The critical values of *t* for rejection of the null hypothesis was taken at a significance level of $P = 0{\cdot}05$ (although for several elements, *t*-values indicate that the null hypothesis could be rejected at a much higher level of significance).

One unusual potential bias in the data that must be dealt with arises because several runs yielded fused clusters of elements, in some cases in moderately large numbers (Table 3). The difficulty with these is that the S elements are very closely juxtaposed and it is extremely difficult to identify and count them. Consequently, the elements in clusters have not been included in the totals, except where the cluster comprises only a pair of elements. If this was a significant bias, then those runs with the fewest clusters should have S levels closest to those expected. However, this is not the case: in runs with few or no clusters (e.g. 1, 3, 9, 10) $S_{1/2}$ elements, for example, are strongly under-represented.

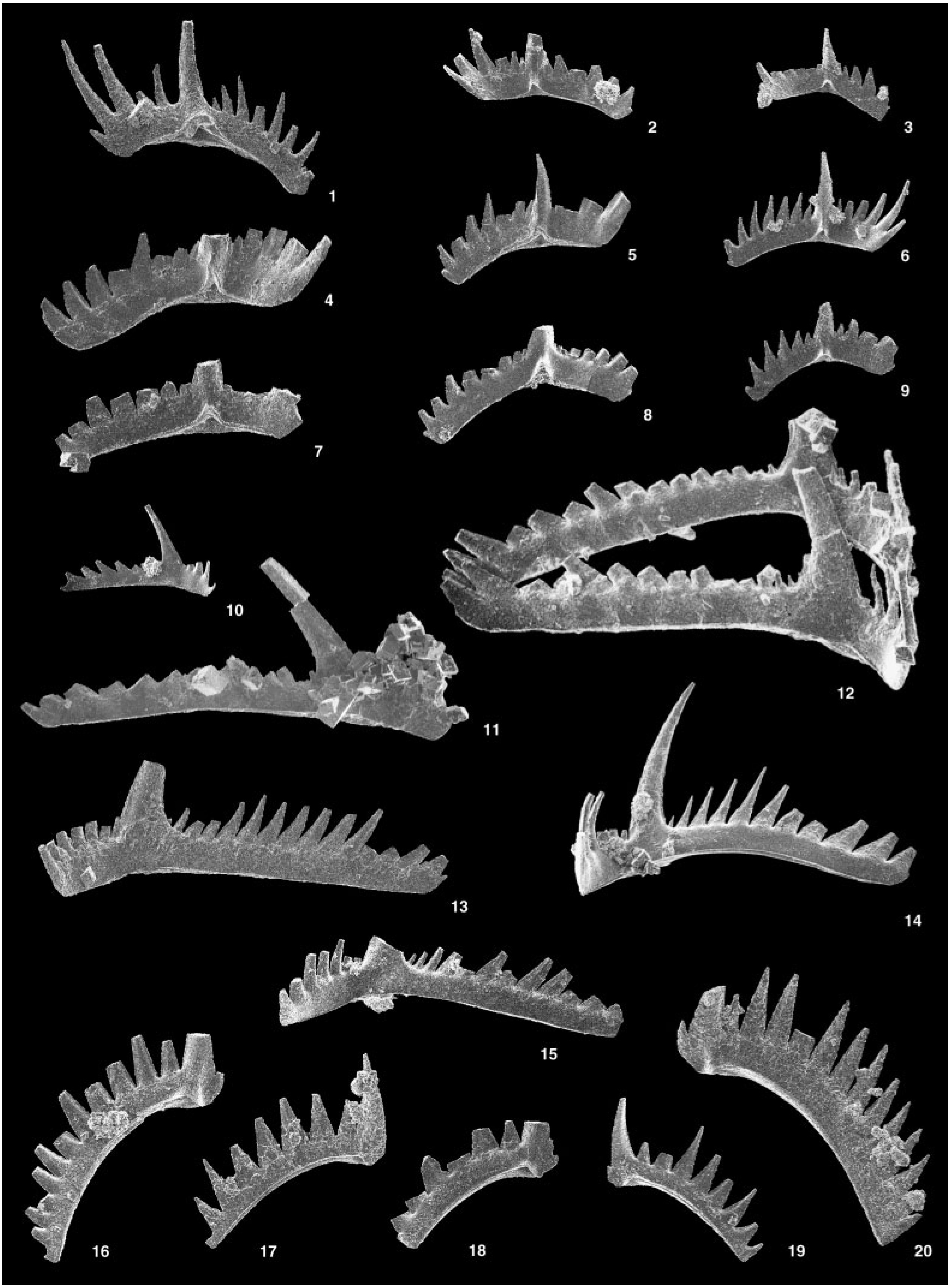
For the five carbonate runs, the null hypothesis is rejected for P_1, P_2, S_0 and $S_{1/2}$ elements, P_1 and $S_{1/2}$ elements being significantly under-represented, and P_2 and S_0 elements being significantly over-represented. The contribution of $S_{3/4}$ and M elements to the fauna does not differ significantly from the numbers expected in an unbiased sampling of the complete apparatuses. When S_0, $S_{1/2}$ and M element numbers are combined, however, the null hypothesis cannot be rejected, so the bias in S_0 and $S_{1/2}$ element numbers is probably due, at least in part, to broken $S_{1/2}$ elements being included in the counts for S_0 and M elements. Similarly, when P element numbers are combined, including indeterminate P elements (i.e. those that because of breakage cannot be assigned to P_1 or P_2 positions), the number of P elements does not differ significantly from the number expected. Laboratory processing of the carbonate fraction therefore yields an unbiased fauna, and other than the errors in assigning elements to positions noted above, post-depositional and laboratory processes have almost no effect on the numbers of elements recovered.

These results differ markedly from the pattern of element recovery of these elements in Late Palaeozoic faunas (Table 1), where strong positive bias in P_1 element recovery is the norm. It also differs from the published data for *O. excavata* recovery (Table 2), but it is worth noting that although P_1 element over-representation is usual, both Jeppsson (1974) and Rexroad *et al.* (1978) documented positive bias in M element recovery, and the data of Jeppsson (1974), Rexroad *et al.* (1978) and Aldridge (1972) all showed over-representation of S_0 elements (Table 2).

The results for the shale runs 6–10 from the Eramosa Member are quite different. The null hypothesis is rejected for P_1 elements (extreme under-representation), P_2 elements (over-representation) and $S_{1/2}$ elements (under-representation). The numbers of S_0, $S_{3/4}$ and M elements do not differ significantly from the numbers expected in an

EXPLANATION OF PLATE 3

Figs 1–20. *Ozarkodina excavata* (Branson and Mehl) from Eramosa Member carbonate (Silurian), Hepworth, Bruce County, Ontario. 1–9, $S_{1/2}$ elements, 'inner lateral' view; ROM 56370–56378. 10–11, 13–15, $S_{3/4}$ elements, 'inner lateral' view; ROM 56379, 56380, 56382–56384. 12, S_3 and S_4 element pair fused together in near life-position, 'inner lateral' view; ROM 56381. 16–20, M elements, 'posterior' view; ROM 56385–56389. 1–15, ×58; 16–20, ×50.



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unbiased sample, although when the aberrant run 6 (Table 3) is excluded from analysis, S_0 elements are significantly over-represented. The extreme under-representation of P_1 elements is due primarily to the difficulty in recognizing broken P_1 elements and differentiating them from broken P_2 elements; when P element numbers are combined they differ significantly from the expected numbers in being over-represented. The over-representation of S_0 elements and the under-representation of $S_{1/2}$ elements may in part result from broken $S_{1/2}$ elements being mistakenly included in S_0 element counts, but this is not the whole story, as when S_0, and $S_{1/2}$ counts, and S_0, $S_{1/2}$ and M counts are combined, these elements are still significantly under-represented. In the case of shale runs 6–10 (Table 3), then, post-depositional and/or laboratory processes have biased recovery of elements, leading to significant over-representation of P elements and significant under-representation of $S_{1/2}$ elements. The fact that laboratory processes have no significant effect on recovery of elements from the carbonate runs strongly supports the hypothesis that the bias in the shale runs is a result of post-depositional processes, probably connected to sedimentary compaction, leading to elements being broken to the point at which their identity cannot be determined.

Differential breakage and solution during diagenesis and sediment compaction (bias 5)

The nature of the nodular carbonate and bituminous shale at the Hepworth exposure of the Eramosa Member (see discussion above) is important in explaining one of the more startling differences between the shale and carbonate runs: the much greater abundance of conodont elements in the bituminous shale (Table 3). In the most productive shale run (Table 3), 558 conodont elements per kg were recovered, with an average yield of 159 elements per kg for the five runs. In contrast, the best yielding carbonate run produced only 49 elements per kg, with an average of 46 per kg for the five runs (Table 3). This is consistent with early diagenetic growth of the nodules preventing compaction of the carbonate. In the bituminous shales, on the other hand, loss of carbonate and later compaction will have significantly increased the number of elements per unit volume. This is also consistent with differences in preservation between the two lithologies. Compaction and possible pressure solution are both potentially important to conodont element abundance and preservation. Evidence from bedding plane assemblages on shale surfaces (Text-fig. 3), and from clusters obtained from residues of laboratory processed shale (Pl. 1), demonstrates that sediment compaction, and resultant differential breakage of conodont elements, is the norm in the bituminous shales at Hepworth, whereas elements and clusters derived from residues of laboratory-processed carbonate (Text-fig. 2, Pls 2–3) are whole, unfractured and well preserved.

Evidence for diagenetic removal of individual conodont elements or of clusters in the shale by solution is lacking. Bedding plane assemblages in the bituminous shale, although often highly fractured as a result of compaction (Text-fig. 3), are remarkably complete, and there is no evidence that individual elements, or groups of elements, were differentially removed by solution. The best evidence for solution lies in the fracture fillings in clusters (Pl. 1) and in isolated elements from the bituminous shale. The mineral(s) filling the fractures, most likely mobilized calcium phosphate, were probably introduced shortly after the differential breakage of the conodont elements, i.e. during or shortly after sediment compaction. It is probably these same fracture filling minerals that have fused together both the broken elements and the clusters.

Dolomite crystals adhering to conodont clusters (Text-fig. 2), as well as white powdery coatings on some conodont clusters from the carbonate runs, suggest that dolomitization may have been both early and a factor in the preservation of the often exquisite conodont clusters in the carbonate. Potential phosphatic fracture fillings, of the kind observed and documented in the shale-derived conodont clusters (Pl. 1), have not been detected in the unfractured conodont elements and clusters from the carbonates.

CONCLUSIONS

Because nodular carbonate and bituminous shale from Hepworth, Ontario, Canada, contain abundant natural assemblages of *Ozarkodina excavata*, we can eliminate *a priori* four of seven factors, or biases, thought to lead to conodont element under- and over-representation. In processing five runs of each lithology by standard laboratory methods, we found that there was remarkably little under- or over-representation of elements, that the overall yields of the elements of the apparatus of *Ozarkodina excavata*, the dominant taxon, were relatively balanced, and that there was little or no evidence for differential loss of elements due to laboratory processing (elimination of bias 6).

Nevertheless, statistically significant under- and over-representation was detected. In both carbonate and shale runs, P_1 and $S_{1/2}$ elements are significantly under-represented, whereas P_2 and S_0 elements are over-represented. We interpret this as being largely due to bias 5, element breakage during sediment diagenesis and compaction, compounded by bias 7, the difficulty of correctly differentiating between fragments of morphologically similar elements. In the carbonate runs, when numbers of P_1 and P_2 elements are combined and numbers of S_0, $S_{1/2}$ and M elements are combined, element numbers do not differ significantly from those in articulated assemblages. In shale samples, however, that exhibit much higher levels of element fragmentation, P elements remain significantly over-represented and S elements significantly under-represented even when individual element counts are combined.

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