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Orientation of agnostid shields in Alum Shale (Upper Cambrian): Implications for the depositional environment

JOHAN EKLÖF, JENS RYDELL, JEMIMA FRÖJMARK, MARIA JOHANSSON, and ADOLF SEILACHER

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Abstract: Polar angles (azimuth orientations) and vertical positions (convex side up or down) of cephala and pygidia of *Agnostus pisiformis* were recorded from 18 shale surfaces within a 0.85 m sequence of Upper Cambrian Alum Shale in Västergötland, Sweden. The absence of articulated specimens, and of thoracic segments, on the surfaces suggest that the agnostids did not live in the depositional area, but that exuviae had been transported into this area, possibly following storms. Two of the surfaces, where most of the shields were deposited with the convex side down, indicated absence of bottom currents. On the other 16 surfaces shields were deposited with the convex side up, indicating that their position had been affected by currents. On 12 of these 16 surfaces the orientations were significantly bipolar, suggesting a wave regime. Hence the results indicate that the sediments forming the Alum Shale (of the *A. pisiformis* Zone) were deposited above storm wave base (<50 m deep).

Keywords: *Agnostus pisiformis*, sedimentation, trilobites, Västergötland, wave currents.

J. Eklöf, J. Rydell, J. Fröjmark & M. Johansson, Zoology Department, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden, e-mail johan.eklof@zool.gu.se and jens.rydell@zool.gu.se. A. Seilacher, Geologisches Institut, Universität Tübingen, Sigwartstraße 10, DE-72076 Tübingen, Germany, and Kline Geology Lab., Yale University, New Haven CT 06520-208109, USA. *Manuscript received 3 November 1998. Revised manuscript accepted 8 September 1999.*

The Middle and Upper Cambrian of Scandinavia are generally dominated by finely laminated black shales, with lenses and beds of limestone, so called anthraconite or "orsten" (Nielsen 1996; Buchard et al. 1997). The shales are called Alum Shales and have a high organic carbon content (5–20%; Andersson et al. 1985). The orsten often contains an abundance of extremely well preserved fossils, and usually shows a low-diversity fauna of "opportunistic" trilobite species (e.g. Westergård 1922; Henningsmoen 1957; Müller & Walossek 1987; Ahlberg & Ahlgren 1996; Clarkson 1973; Clarkson & Taylor 1995; Clarkson et al. 1998) and other arthropods (e.g. Müller & Walossek 1985, 1988).

The deposition of the Alum Shale was very slow (1–10 mm per 1000 years; Thickpenny 1984) as was the subsequent formation of the orsten. It is traditionally believed to have taken place in a stratified epicontinental sea, with anoxic or dysoxic conditions prevailing in deep, stagnant waters (Bergström & Gee 1985; Thickpenny 1987; Thickpenny & Leggett 1987) at high latitudes (45–60°S; Scotese & McKerrow 1990). The often perfect preservation of delicate exoskeletons in the "orsten" has been taken to imply an environment undisturbed by water currents (Anderson et al. 1985).

On the other hand, there is geological evidence that Alum Shales could also have been formed in shallow water near the shore (Westergård 1922, p. 108; Martinsson 1968, 1974, p. 251; Nielsen 1996; Buchardt et al. 1997). For example, sediments over- and underlying the Alum Shales are of shallow water affinities, and the lithology of these strata suggests that the prevailing water depth was less than 200 m (Thickpenny 1987). The aim of our work was to test the prevailing hypothesis that the agnostids of the Alum Shale and the associated orsten were deposited in deep water, or, more specifically, below storm wave base.

Agnostids generally occur in abundance in the lower part of the Upper Cambrian, and *Agnostus pisiformis* (Wahlenberg) is one of the most abundant of all species. In the *A. pisiformis* Zone this species forms virtually monospecific assemblages (Müller & Walossek 1987; Ahlberg & Ahlgren 1996). The morphology and mode of life of *A. pisiformis* have been thoroughly investigated by Müller & Walossek (1987), who concluded that the species most likely was benthic or necto-benthic. It probably swam or floated with the shields only partly open, and fed on detritus in a rich flocculent layer near the bottom. However, since many agnostids have wide-ranging distributions, earlier authors have suggested that they were either pelagic (Robison 1972; Jago 1973), or that they lived attached to floating vegetation or even as ectoparasites (Bergström 1973).

Preservation and orientation of *A. pisiformis*

In the Alum Shale and the associated orsten in Västergötland, where this study was made, the trilobites are usually disarticulated. Complete, articulated specimens are generally rare. In the case of agnostids, articulated specimens are extremely rare or absent altogether. Although this may be a common pattern for agnostids (Öpik 1979), it seems to be accentuated in the material from the Alum Shale of Västergötland (Ahlberg & Ahlgren 1996). The disarticulation of the bodies suggests transportation and deposition of isolated cephalic and pygidial shields, i.e. of exuvia, rather than of entire, live or dead, specimens (Öpik 1979).

In Västergötland, fossils are typically recognizable only in the orsten and not at all in the associated shale. The quarry at Kakeled on Kinnekulle is an exception (J. Ahlgren, pers. comm.). In this quarry fossils are preserved in the shale throughout the *A. pisiformis* Zone, although this is not the case higher up in the exposure. This unusual circumstance allowed us to investigate a continuously fossiliferous sequence within the *A. pisi-formis* Zone (the lowermost part of the Upper Cambrian), consisting of reasonably homogeneous and easily split black shale.

Agnostus pisiformis shells occur in abundance throughout the sequence. They are in places densely packed and occasionally cover most of the surface (Fig. 1A). In most cases, however, packing of the shields is less dense, so that they are usually not in contact with each other (Fig. 1B). In all cases the cephalic and

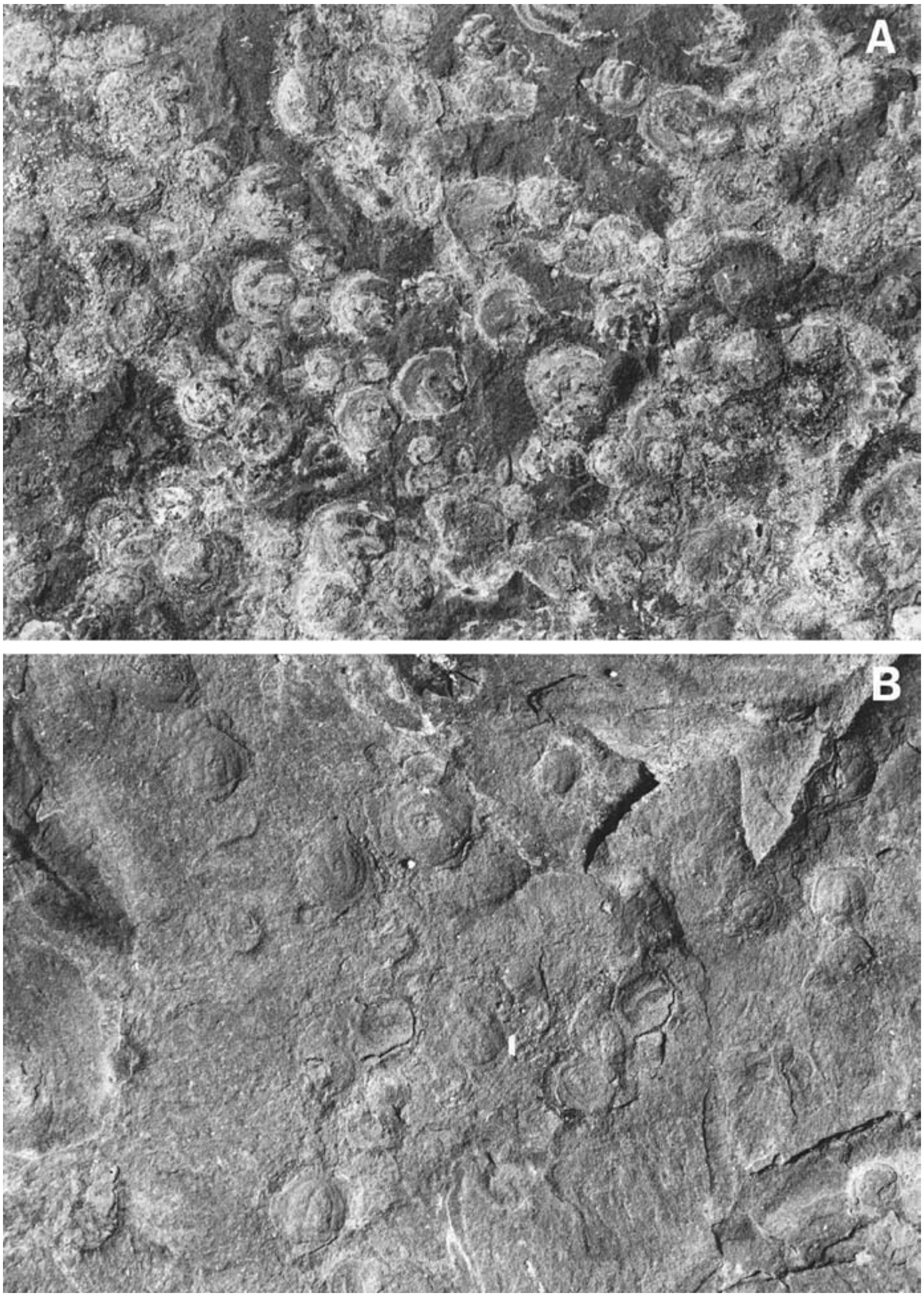

Fig. 1. Examples of shale surfaces with *Agnostus pisiformis* shields occurring densely packed (A) and scattered (B). Slabs from Kakeled quarry at Kinnekulle, Västergötland, Sweden.

pygidial shields are disarticulated, and thoracic segments are virtually absent on most surfaces. In the following, we do not distinguish cephalic shields from pygidial ones, because their similar morphology suggests that the two would respond to physical forces in a similar way (see below). The relatively poor preservation of the fossils in the shale (see Fig. 1) would have made such a distinction difficult anyway.

Hypotheses and assumptions

The orientation of the shields on the shale surfaces would be expected to be influenced by packing, because there may be spatial restrictions imposed by neighbouring shields. However, assuming that the shields originated from the water column (and not from the sea floor; Robison 1972), their position must also have been affected by gravity and by the prevailing direction of water movements during deposition (Menard & Boucot 1951; Nagle 1967; Bergman 1983), perhaps including the turbulence caused by already deposited shields (Futterer 1982).

In the absence of water movements, where gravity was the only major force acting on a shield in the water, we would, for hydrodynamic reasons, expect it to sink to the bottom with the convex side down (Fig. 2A). However, this position would be unstable if any horizontal water movements occurred, in which case the shield would be likely to tip over and come to rest with the convex side up (Menard & Boucot 1951; Bergman 1980). Hence, preservation of *A. pisiformis* shields with the convex sides down suggests deposition in an environment with little or no water movement. Under such conditions the shields would not be turned around or flipped over, and therefore their polar angle would be expected to be almost random.

By the same token, preservation of shields with their convex sides up would indicate that the deposition was influenced not only by gravity but also by horizontal water movements of some kind (Trusheim 1931). Shields with the convex sides up would have remained in this stable position until a current acting against the articulating margin (i.e. the posterior margin of a cephalic shield or the anterior margin of a pygidial shield) either tipped it over or rotated it (Nagle 1967). If there was one prevailing current direction, as would be the case for a tidal or a turbidity current, the shields would be expected to be unimodally oriented with the longitudinal axis parallel to the prevailing current direction and the articulating margin facing downcurrent (Fig. 2B). However, because a shield would also be in a stable position if the current acts laterally, deviations of up to 90° in each direction would be expected.

Deposition of the shields may also have occurred under the influence of waves, i.e. in shallow water. Since waves are bidirectional by definition, a shield would be in a stable position only when the currents act laterally, i.e. perpendicular to the longitudinal axis. Hence, in this case, we would expect the shields to be deposited with the convex side up and with the longitudinal axes perpendicular to the two prevailing current directions (and opposite to each other; Fig. 2C), i.e. their orientation would be bipolar (Nagle 1967; Futterer 1982).

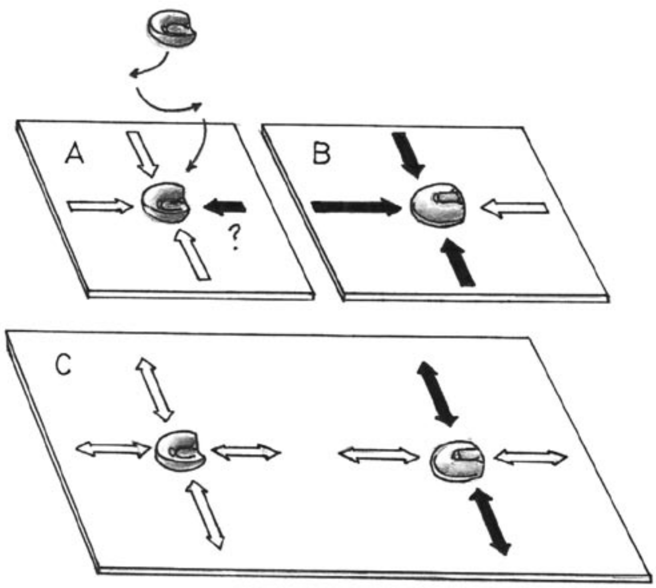

Fig. 2. Hypothetical influence of unimodal water currents on agnostid shields deposited with the convex side down (A) and up (B), respectively, and of bimodal water currents (waves) on shields deposited convex side down (C). Black arrows represent directions from which a current along the bottom would not be expected to alter the position of the shield (stable positions), while the white arrows are directions from which a current would be expected to tip it over (unstable positions).

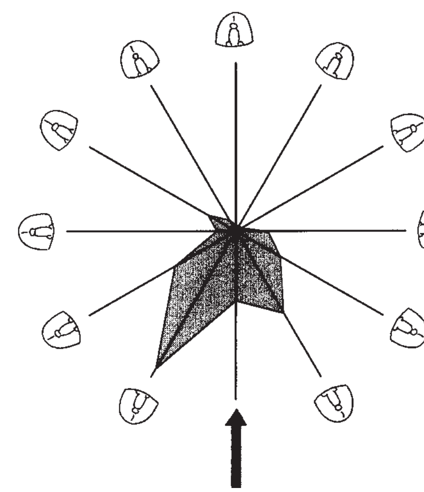

Fig. 3. Result of the model experiment. Polar angle distribution (azimuth orientation) of shield models (10:1 scale; 3 cephalic and 3 pygidial, all pooled) coming to rest on the sand-covered bottom of a flow tank under the influence of a unidirectional current (0.11 m s^{-1}). The vectors represent the frequency of each azimuth orientation (N=88). Arrow indicates current direction.

Model experiment

To test the assumptions that (a) cephalic and pygidial shields reacted in the same way to currents and that (b) unidirectional currents result in unipolar distribution of the deposited shields, and not in a bipolar one, we made scale models of *A. pisiformis* exuvia (after Müller & Walossek 1987, p. 7); three cephalic and three pygidial shields. The models were of vacuum-formed 0.5 mm thick PVC plastic (mass = 1.0 g) and were 35 mm long, 40 mm wide and 18 mm high, i.e. the scale was ca. 10:1.

The behaviour of the models under the influence of a unidirectional current was then tested in a flow tank at Tjärnö Marine Biology Field Station (Göteborg University). The bottom of the tank, which was filled with sea water, was covered by sand. Water depth in the tank was 15 cm and the flow rate was 0.11 m s^{-1}. This current was strong enough to tip the models over when they were in an unstable position but weak enough to allow the model to be completely stable in some positions.

The models were tested one by one. Their orientations relative to the current direction was recorded (to the nearest 30°) after they had come to rest on the sediment. We made 72 tests without any current and 96 with a current. In each case half of the tests were made with models of cephalic shields and half with pygidial ones. We alternated between convex side down and convex side up when introducing the models into the tank and we also varied their initial polar angle systematically.

Without a current, the models always (N=72), came to rest with the convex side down, regardless of how they were put into the water (convex side up, N=36; convex down, N=36). With current, however, only eight (8.3%) of the 96 tests resulted in the model coming to rest with the convex side down. In these cases the resting place was in a shallow depression, undeliberately formed when we introduced the sand into the tank.

In the other 88 cases (91.7%) the model came to rest with the convex side up, and in 83 of these (94.8%) with the articulating margin pointing downcurrent (i.e., with the anterior end of the cephalic shield or the posterior end of the pygidial shield facing the current; Fig. 3). The orientations of the shields show a highly significant unipolar distribution ($P<0.001$; Rayleigh test of randomness; Batschelet 1981). Cephalic and pygidial shields oriented in the same way. It made no difference whether the convex side was up or down or how the model was oriented relative to the current when introduced into the tank.

The results of these experiments agree with what we expected (see above) and therefore justify our assumptions. First, there was no difference between cephalic and pygidial shields, and second, a unidirectional current resulted in a significantly unimodal distribution of the polar angles of the shields, which came to rest with the convex side up.

Materials and methods

The Alum Shale samples were collected in the quarry Kakeled on Kinnekulle, 13 km northeast of Lidköping, Västergötland, Sweden (UTM VE030922). This quarry exposes an Upper Cambrian sequence of Alum Shale and orsten from the Zone of *A. pisiformis* to that of *Peltura scarabaeoides* (Fig. 4). Eighteen lamination surfaces within a 0.85 m sequence of the *A. pisiformis* Zone were sampled *in situ* from the exposure with intervals of ca. 0.05 m. The uppermost sample was taken 0.3 m below the major bank of orsten (or "Great Stinkstone Bed"; Westergård 1922). The orsten bank comprises the uppermost part of the *A. pisi-formis* Zone and also most of the overlying *Olenus*/*Agnostus obesus* Zone.

Within an area of 225 cm^2 (15×15 cm) on each surface, the number of shields was counted under a binocular microscope. We also counted the number of shields that were in contact with another shield, thus quantifying the shield density and the extent to which the shields were tightly packed on each surface. We recorded the polar angle of each shield, i.e., the compass direction of the anterior end of the cephalon or the posterior end of the pygidium (within ±15°), and also its vertical position, i.e., whether

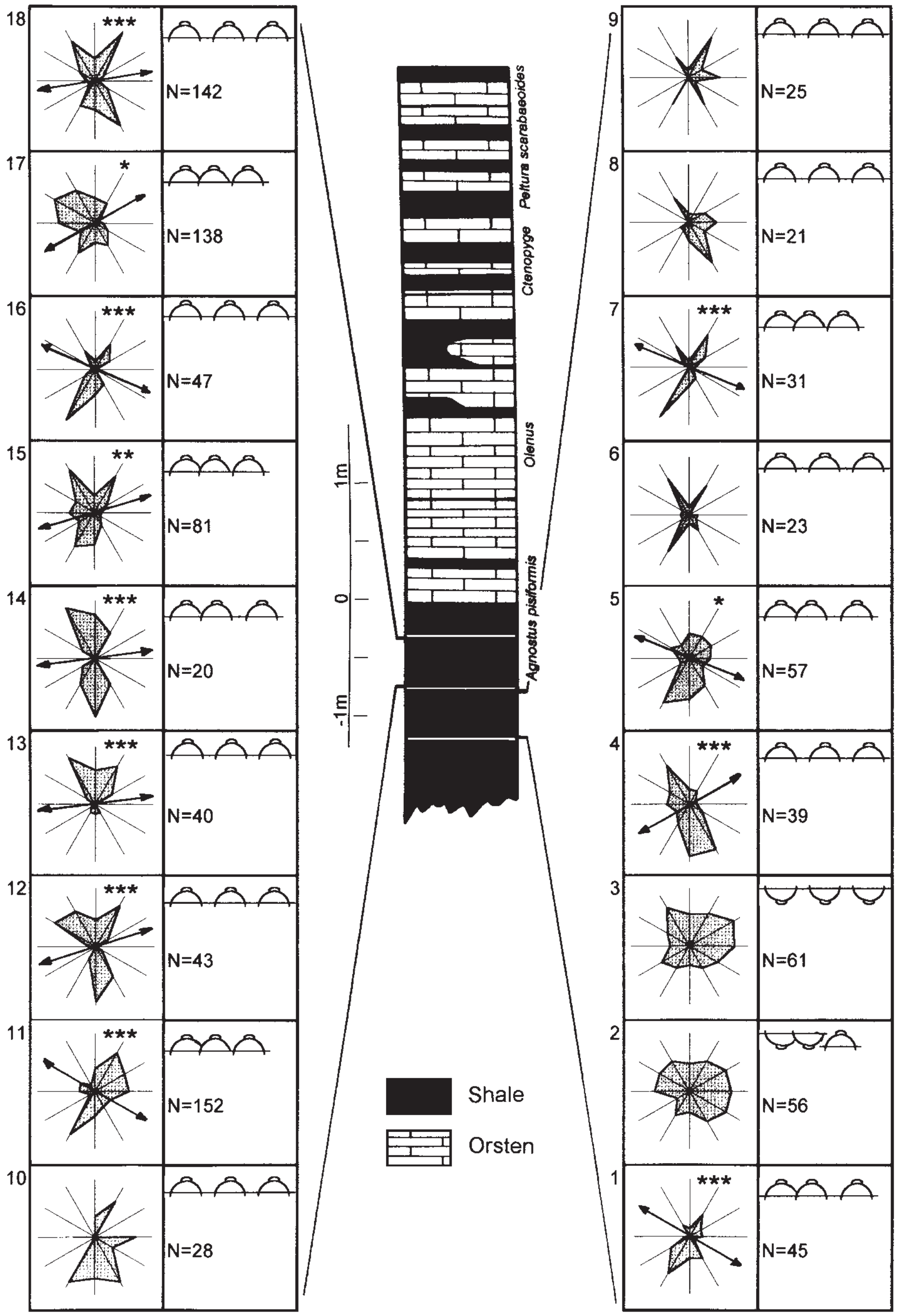

Fig. 4. Polar angle distribution (azimuth orientation) of *Agnostus pisiformis* shields in 18 shale surfaces of the Upper Cambrian Alum Shale Formation of Kakeled on Kinnekulle, Västergötland, Sweden. Asterisks denote significant bimodality in shield orientation (Rayleigh tests; statistical details in Table 1), and arrows show the likely current directions. On the metre scale, zero defines the base of the major bank of orsten with the *Olenus/Agnostus obesus* Zone. Also shown are the total number of shields (N) on each surface (225 cm^2), their prevailing vertical position (convex side up or down) as well as their density.

the convex side was up or down.

The distribution of polar angles on each surface was then tested for unimodality (*versus* random) and also for bimodality (*versus* random), using circular statistics, in the same way as for the model experiment (Rayleigh tests; Batchelet 1981). To test whether the orientation of the shields was independent of their density and packing, we used non-parametric Spearman's Rank Correlation coefficients. We employed a rejection level of P=0.05 throughout.

Table 1. Statistics of the polar angle distributions (azimuth orientations) in *Agnostus pisiformis* shields on 18 shale surfaces of the Upper Cambrian Alum Shale Formation of Kakeled on Kinnekulle, Västergötland, Sweden. The uni- and bimodality of the shield orientation (r = mean vector length, P = significance level) were analysed using circular statistics (Rayleigh tests; Batchelet 1981).

Surface no.	No. of specimens	Unimodality r	Unimodality P	Bimodality r	Bimodality P
18	142	0.064	n.s.	0.369	<0.001
17	138	0.273	<0.001	0.153	<0.05
16	47	0.204	n.s.	0.507	<0.001
15	81	0.188	n.s.	0.217	<0.05
14	20	0.094	n.s.	0.507	<0.01
13	40	0.534	<0.001	0.438	<0.001
12	43	0.102	n.s.	0.450	<0.001
11	152	0.160	<0.05	0.231	<0.001
10	28	0.357	<0.05	0.223	n.s.
9	25	0.363	<0.05	0.262	n.s.
8	21	0.350	n.s.	0.238	n.s.
7	31	0.057	n.s.	0.452	<0.01
6	23	0.136	n.s.	0.285	n.s.
5	57	0.147	n.s.	0.229	0.05
4	39	0.197	n.s.	0.339	0.01
3	61	0.166	n.s.	0.059	n.s.
2	56	0.120	n.s.	0.094	n.s.
1	45	0.235	n.s.	0.364	<0.01

Results

On two of the 18 surfaces (nos. 2 and 3) most or all of the shields were deposited with the convex side down. In these cases, as expected, distribution of the polar angles of the shields did not differ significantly from random (Fig. 4; Table 1). On the other 16 surfaces (nos. 1 and 4–18) virtually all the shields were deposited with their convex side up. On all of these surfaces, except two (nos. 6 and 8), the orientation differed significantly from random. In 12 cases (nos. 1, 4, 5, 7, and 11–18) it showed significant bipolar distributions and in five cases (nos. 9–11, 13, and 17) significantly unipolar one (Fig. 4; Table 1). Hence, three of the surfaces (nos. 11, 13, and 17) showed tendencies towards both unipolarity and bipolarity and two surfaces (6 and 8; both having relatively few shields) showed neither.

On the 12 surfaces that showed a significant bipolar distribution, the orienta-tions of the shields were always roughly north and south, or, more specifically within 45° of N and S, never east and west. Most likely this consistency did not occur by chance (P<0.001; Sign test); north–south and east–west distributions would be expected to be equally common.

The number of shields per surface varied between 20 and 152, and this variation significantly affected whether or not there was a bipolar orientation of the shields (r=0.47, N=18, P<0.05). The six surfaces on which no bipolar distribution could be detected included the two with the shields deposited upside down (nos. 2 and 3) and also four with relatively few shields (nos. 6 and 8–10). Hence, bipolar distributions were more likely in larger samples. Nevertheless, close packing of the shields did not seem to affect the orientation. There was no significant correlation neither between the occurrence of bipolarity and the extent of shield packing, i.e. the percentage of shields that were in contact with another shield ($r=0.32$, $N=18$, $P>0.05$), nor between shield density and packing ($r=0.43$, $N=18$, $P>0.05$).

Discussion

The two surfaces on which the agnostid shields were deposited with the convex side down may justify our assumption that they originated from the water column, as opposed to having been transported only along the sea floor. However, this observation should not be used to argue that the agnostids actually lived in the open water (Robison 1972) or on floating vegetation (Bergström 1973). On the contrary, the absence of articulated specimens and thoracic segments suggests that the animals did not live in the area of deposition at all. Instead they probably entered it as disarticulated exuviae, perhaps after having been stirred up from another area by a storm. At least in the associated orsten, agnostid exuviae seem to be sorted according to size (Rydell & Eklöf unpubl. observations; Clarkson et al. 1998). This provides another indication that the shields had been floating in the water for some time. The presence of thin silt laminae also indicates lateral transport (Buchardt et al. 1997).

The most common pattern observed on the bedding planes, however, was that nearly all the shields were deposited with the convex side up. This indicates that they had been affected by currents of some kind during or just after deposition. The fact that the majority of the surfaces also shows a bipolar orientation suggests that bidirectional currents such as waves or perhaps tides were responsible. In contrast, the two surfaces where shields were deposited with the convex side down (16 and 17) indicate that the deposition was sometimes unaffected by currents. This means that waves rather than tides were involved. Convex side down may simply indicate that the storm waves had waned by the time the shields came to rest on the sea bed. Overall the results are inconsistent with the hypothesis that the Upper Cambrian Alum Shales were formed below storm wave base (Berg-ström & Gee 1985; Piper 1985; Thickpenny 1987). Instead, they suggest that the deposition took place in shallow water, which was occasionally affected by waves (i.e., a depth of less than ca. 50 m).

It could be argued that the polarity of the shield orientations was a result of tight packing, causing space restrictions, rather than of currents. However, the rank correlation analysis suggested otherwise: the orientation of the shields was not significantly correlated with the degree of packing. On the other hand, the orientation seemed to be related to the total number of shields on each surface; a significant bipolar distribution was more likely on surfaces with many shields. This could indicate that the presence of many shields affected the subsequent position of new ones indirectly, perhaps by inducing turbulence in the prevailing water currents. However, on four surfaces (4, 12, 13, and 16) the orientations were strongly bipolar, although the shields were relatively few (between 20 and 47) and not densely packed. Hence, bipolar orientation was probably not a result of space restrictions, or of turbulence caused by dense packing.

The lack of significant alignment on some surfaces could have been caused by small sample sizes, i.e. by too few shields. This argument is supported by the results. The four surfaces lacking significant bipolar orientation (6, 8, 9, and 10, excluding the two surfaces where the shields were deposited convex side down) were among those with the smallest numbers of shields. Hence small sample size on some surfaces was probably the real reason behind the apparent correlation between polar angle distribution and shield density. In cases where there was a significant bipolar distribution, the orientation of the shields was always around north and south, never east and west. This is strong evidence that the polar angle distributions were caused by oscillating currents rather than high shield density or close packing. If the bipolar distribution had resulted predominantly from packing or crowding, the orientation would not have been consistent from surface to surface, but would have varied randomly.

In conclusion, the polar angle distribution of the shields was probably the result of water currents. Although packing of shields or turbulence caused by high numbers of shields could have affected the orientation on some of the densely populated surfaces, such effects could not have been responsible for the overall pattern. A predominantly north–south orientation of the shields indicates east–west oscillating currents caused by storm waves touching bottom. Hence our data indicate that the deposition of *Agnostus pisiformis* shields took place above storm wave base. The shields were already disarticulated and sorted when they entered the water column above the depositional area on the sea floor.

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Arne Strömberg