

Biotic effects of the Ordovician Kinnekulle ash-fall recorded in northern Estonia

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The Late Ordovician (455 Ma) Kinnekulle volcanic ash-fall represents one of the largest ash eruptions known in Phanerozoic history. The dynamics of ostracodes, polychaete annelids and some shelly macrofauna across the Kinnekulle Bed in the Pääsküla section, northern Estonia indicate some significant faunal changes. The ostracod assemblage underwent major reorganization, including the replacement of predominant forms, a drop in taxon frequency and species diversity, and the probable extinction of some species following the ash-fall. The abrupt response of ostracodes indicates that the sediment surge and the resulting seafloor environment significantly affected the ostracodes. Jaw-bearing polychaetes (as represented by scolecodonts) display changes in their diversity curve and in the abundance of individual species above the altered ash layer. This change occurred after some delay indicating that polychaetes were not affected directly by the sediment influx but indirectly, probably by a change in their relationships with other biotas during a gradual rearrangement of seabed communities triggered by the ash-fall. Macrofaunal data also contains some evidence of the possible direct effects of the ash-fall. Thus, the biotic effects of the Kinnekulle ash-fall were probably larger than previously suggested. Many benthic organisms were strongly affected and the influence of this event persisted some time after the ash-fall.

Key words: Ordovician, K-bentonites, volcanic ash-falls, biotic effects, ostracodes, scolecodonts.

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Material of volcanic origin may be recognized thousands of kilometers from its source and may often be preserved in sedimentary successions. Altered volcanic ash layers are widespread in the Ordovician, where they are frequently referred to as K-bentonites or metabentonites. These beds are of great interest to geologists not only because they are useful stratigraphical markers, but also, they provide material for mineralogical and geochemical studies and radiometric age determinations. The occurrence of volcanogenic layers in fossiliferous successions also provides an opportunity to investigate how the past biota responded to catastrophic events.

Intense volcanic activity was typical during the early Late Ordovician within and around the closing Iapetus Ocean. More than 150 individual volcanogenic beds, altered to potassium-rich clays (K-bentonites) or feldspathites, are known from the Ordovician sequences of Baltoscandia and nearly 50 occur in northern America (Huff *et al.* 1992). The thickest bed in Baltoscandia, the Kinnekulle Bed of Bergström *et al.*

(1995), is more than two meters thick in southern Sweden and can be traced for more than 1000 km eastward to the western part of the St. Petersburg region in Russia.

Even though the hypothesis of a single gigantic volcanic eruption producing two widespread K-bentonites, the Kinnekulle Bed in Baltica and Millbrig Bed in Laurentia (Huff *et al.* 1992), has now been rejected by some workers (Min *et al.* 2001), the Kinnekulle event still remains one of the largest known eruptions in the Earth's geological history (Huff *et al.* 1996). Following Jaanusson & Martna (1948) and Männil (1958) the Kinnekulle Bed has been widely used in stratigraphy as the marker of the lower boundary of the Keila Regional Stage in the Baltic region (e.g. Männil 1966; Rõõmusoks 1970; Nõlvak 1997).

Although the possible biotic effects of volcanic ash-falls are generally known and documented in a number of cases (e.g. Harper *et al.* 1995; Heikoop *et al.* 1997; Botting 1999), the influence of the Kinnekulle ash-fall on fossil communities has gained relatively little at-

tention. However, Huff *et al.* (1992) argued that there is no evidence for major extinctions in main fossil groups and the marine biota, if it had been strongly affected, must have recovered very rapidly.

The initial task of this study was to obtain some new quantitative data from a fossiliferous exposure, to record the succession of different fossil groups and identify any changes in the associations, even if they do not embody an extinction, which could be related to the ash-fall.

Eighteen samples were taken from a 7.5 m interval of limestone from the Pääsküla outcrop, northern Estonia. The samples were divided into two parts, one (300g) processed with sodium-hyposulphite for calcareous fossils (mainly ostracodes), and the other (300–800g) dissolved with acetic acid to study phosphatic- and organic-walled microfossils. The distribution of scolecodonts and ostracodes, two common benthic groups that easily provide quantitative data, were recorded and analyzed. In addition, macrofossils (brachiopods, bryozoans, echinoderms, trilobites, gastropods and algae), represented mainly by fragments or particles of skeleton of different size (dominantly less than 10 mm) were collected from ostracod sample residues.

Geological setting and locality

The main configuration of the Late Ordovician sedimentary basin in Baltoscandia has been described by Männil (1966), Jaanusson (1976), and Nestor & Einasto (1997). In general, northern Estonia was characterized by relatively shallow-water shoal to open shelf facies, the Marginal Confacies. These conditions contrast with the deeper-water environments in Latvia and Sweden, which make up the westward deepening Central Confacies (Fig. 1; see Nestor & Einasto 1997). The Kinnekulle ash was deposited geologically simul-

taneously at the beginning of the Keila time in different parts and in different facies of this palaeobasin.

The Haljala–Keila stage boundary interval is present in numerous boreholes of the East Baltic area, however, there are very few surface outcrops that expose the Kinnekulle Bed. An extensive exposure at Pääsküla Hill on the southern limit of Tallinn, northern Estonia, provides the best opportunity for studying the Kinnekulle Bed and the under- and overlying limestones. This outcrop has been recently described by Hints *et al.* (1997), and was proposed as the boundary stratotype for the Keila Regional Stage (Hints & Nölvak 1999). A continuous section at Pääsküla Hill exposes a more than 8 m thick succession of limestones that contains two volcanogenic beds, the Kinnekulle Bed and a bed from the Grimstorp complex (Bergström *et al.* 1995). In the Baltic region, these beds have also been referred to as bed 'd', and bed 'e', respectively (Jürgenson 1958). The sampled section (Fig. 1) is highly fossiliferous, except for the topmost part, which lacks organic-walled microfossils due to the effect of weathering.

The Kinnekulle Bed is nearly 30 cm thick in the Pääsküla section. Its basal and upper parts are hard, rich in K-feldspar whilst the middle part of the bed usually contains plastic clay that can be easily disintegrated in water (see Hints *et al.* 1997 for details of the mineralogical composition). It has a flat and sharp lower boundary, and, primarily as a result of bioturbation, a transitional and often unclear upper boundary.

Faunal succession

Ostracodes

The distribution of ostracodes in the Haljala–Keila interval of Estonia was first discussed by Sarv (1959). More detailed information on the ostracod succession across the Kinnekulle Bed was given by Sarv (1960)

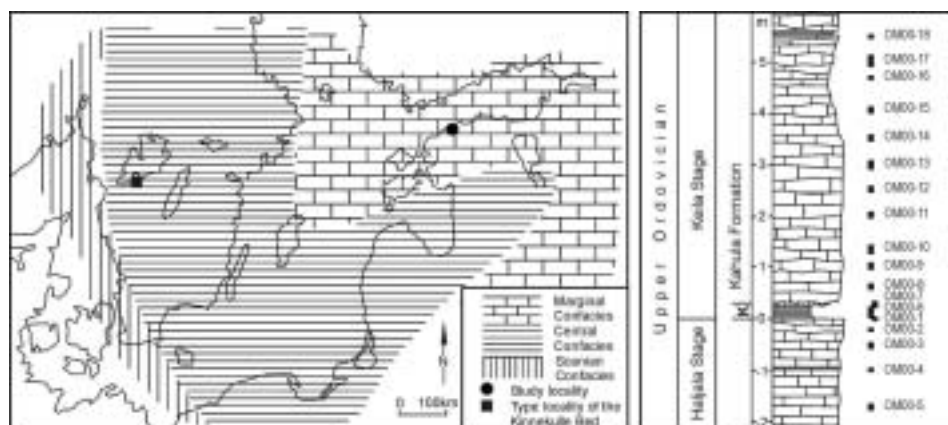
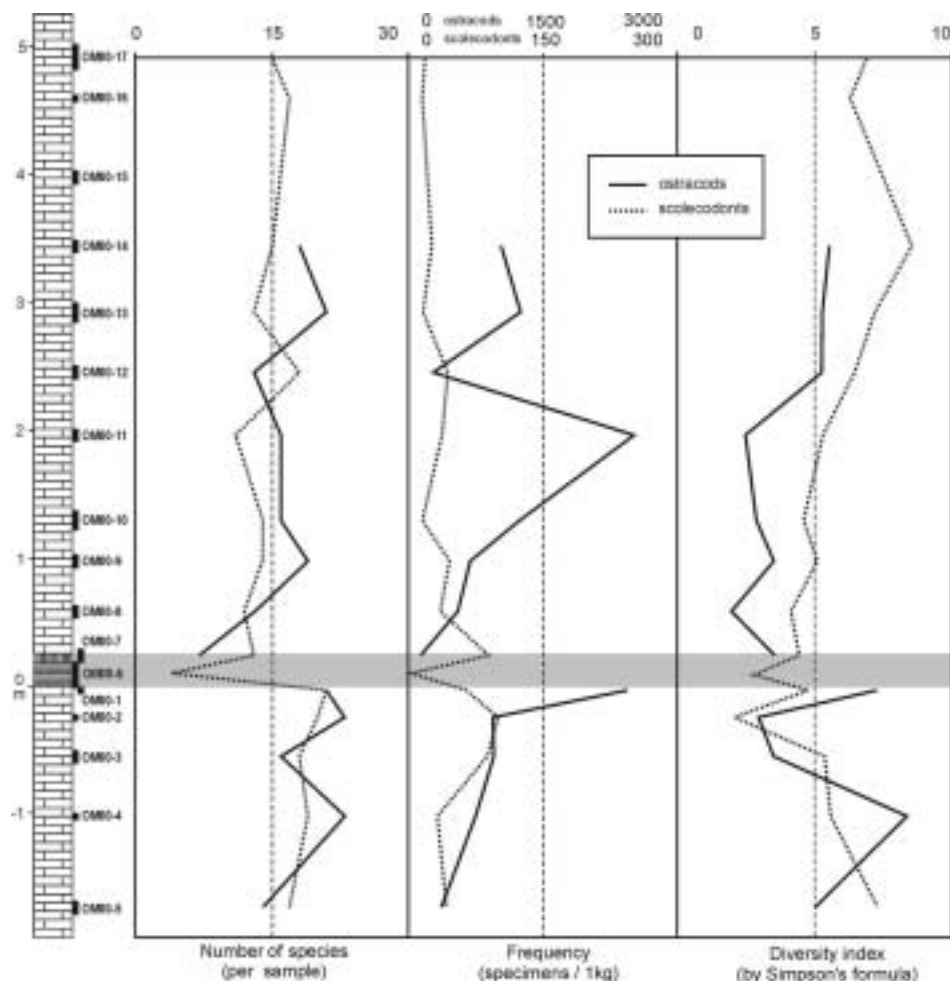


Fig. 1. Sketch map of the study locality and stratigraphy of the Pääsküla section. K – Kinnekulle Bed.

Fig. 2. Frequency and diversity patterns of ostracodes and scolecodonts in the Haljala-Keila transition of Pääsküla section. Light grey ornament marks the Kinnekulle Bed.



and Sarv in Põlma *et al.* (1988). The latter paper argued that the lower boundary of the Keila Stage is characterized by disappearance of the ostracod assemblage typical of the Haljala interval, including *Pseudorakverella optata* Sarv, *Disculcina interminata* Sarv, *Scrobisylthis reticulatus* (Sarv), *Tetrada memorabilis* (Neckaja) and *Cytherellina cf. jonesi* Bonnema. Ostracod logs of the Keila, Rummu and Pagari drill cores (all located in northern Estonia) show that distributions of some of the other species may also have been affected by the Kinnekulle ash-fall. The possibility that this faunal change could reflect the effect of the volcanic ash-fall was nevertheless not discussed by Põlma *et al.* (1988).

During the present study, 65 species of ostracodes (among these several tentatively identified) were documented from the Pääsküla section. The frequency and diversity patterns of the ostracod assemblage are illustrated in Figure 2. At the level of altered volcanic ash, notable changes in frequency and species diversity are recorded. The frequency increases upwards below the Kinnekulle Bed but drops strikingly at the

level of the altered ash bed, so that the number of specimens in sample OM00-7 is several times lower than that in the underlying sample. Above sample OM00-7, the frequency begins to increase again and in sample OM00-11 it achieves the level of sample OM00-1 just below the Kinnekulle Bed (Fig. 2). This trend is controlled by five samples, and is therefore most probably not coincidental. It could be an indication that a natural, continuous frequency trend in the ostracod community was disrupted by the deposition of the ash. Alternatively, this could be explained by the increased rate of sedimentation just above the Kinnekulle Bed causing a 'dissolution effect' amongst the ostracods.

The taxonomic diversity of ostracodes (number of species per sample) displays a drop following, and possibly resulting from, the ash-fall (samples OM00-7 and OM00-8). Otherwise the average for below and above the Kinnekulle Bed is relatively similar, with a slightly higher number below it.

The diversity index calculated by Simpson's formula has been successfully applied to ostracod data

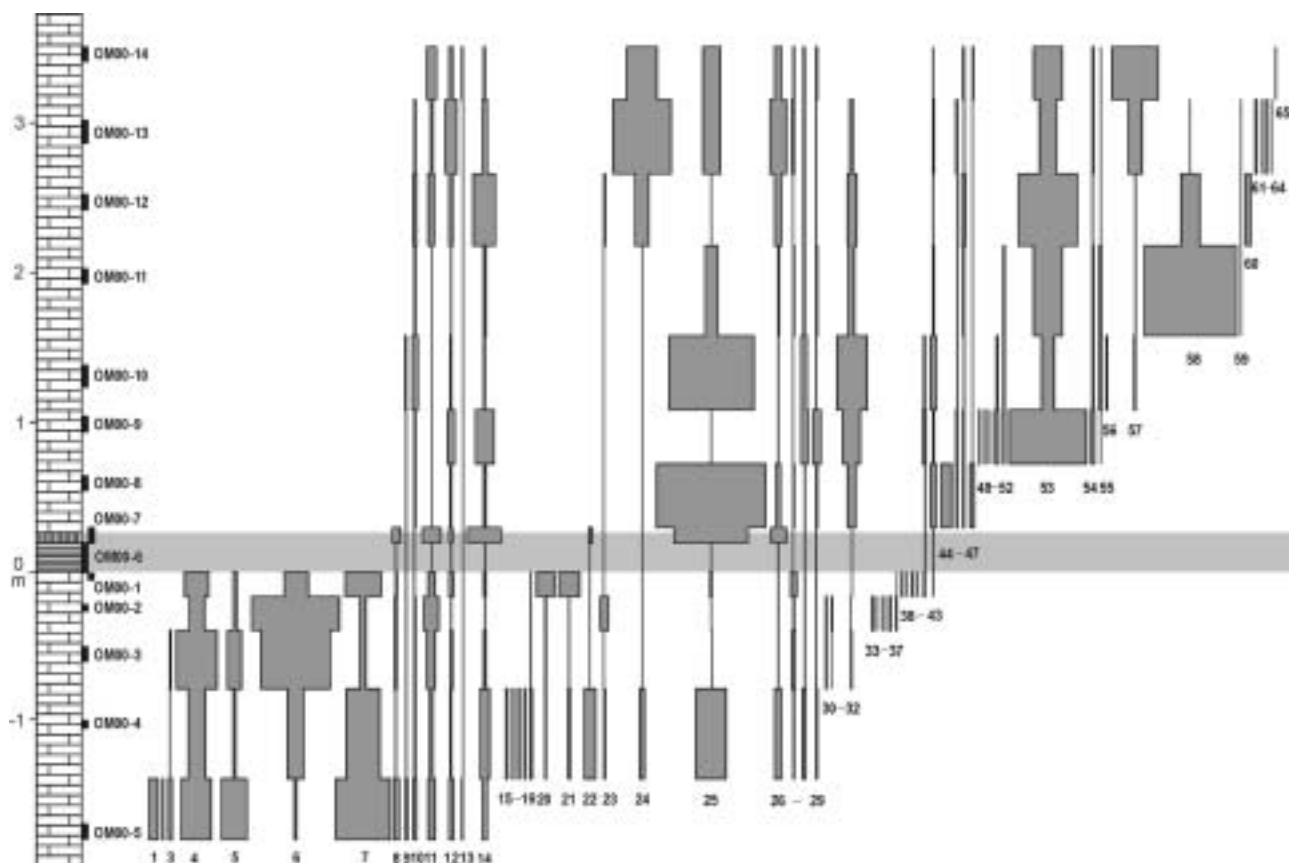


Fig. 3. Succession of ostracodes in the Pääsküla section. Width of the bar represents relative frequency (%) of species, light grey marks the Kinnekulle Bed. 1 – *Pseudorakverella optata*; 2 – *Sigmoopsis cornuta*; 3 – *Severobolbina elliptica*; 4 – *Tetrada memorabilis*; 5 – *Kiesowia* (*Carinobolbina*) *carinata*; 6 – *Cytherellina* cf. *jonesi*; 7 – *Olbianella braderupensis*; 8 – *Miehlkella*? sp.; 9 – *Bolbina ornata*; 10 – *Pentagona pentagona*; 11 – *Tetrada krausei*?; 12 – *Sigmoopsis rostrata*; 13 – *Homeokiesowia frigida*; 14 – *Braderupia asymmetrica*; 15 – *Ceratobolbina* sp.; 16 – *Disulcinoides auricularis*; 17 – *Syllthis interminata*; 18 – *Eolomatella bicuspidata*; 19 – *Platybolbina temperata*; 20 – *Eurocyamus posterobicarinatum*; 21 – *Sigmobolbina*? *wennigstedensis*; 22 – *Seviculina* sp.; 23 – *Longiscula* sp.; 24 – *Pedomphalella egregia*; 25 – *Airina amabilis*; 26 – *Rectella* sp.; 27 – *Easchmidtella fragosa*; 28 – *Krauselloides* sp.; 29 – *Circulina fimbriata*; 30 – *Tetrada longata*; 31 – *Baltonotella* sp. n.; 32 – *Bolbina major*; 33 – *Rectella inaequalis*?; 34 – *Oepikium* sp.; 35 – *Piretella* sp.; 36 – *Sudon*? *nussi*; 37 – *Bolbina plicata*; 38 – *Oepikella canaliculata*; 39 – *Unisulcopleura weitschati*; 40 – *Ardennea tricostrata*; 41 – *Kiesowia* (*Quadrilia*) *quadrifurcata*; 42 – *Scrobisyllthis reticulatus*; 43 – *Bilobatia bidens*; 44 – *Ningulella*? sp.; 45 – *Unisulcopleura* sp.; 46 – *Fallaticella bulbata*; 47 – *Leperditella prima*?; 48 – *Hippula serra*; 49 – *Snaidar radians*; 50 – *Moekovia*? sp.; 51 – *Longiscula parrectis*; 52 – *Kiesowia* (*Pseudotallinnella*) *moles*?; 53 – *Pariconchoprimitia coniqua*; 54 – *Polyceratella aluversensis*; 55 – *Tvaerenella* sp.; 56 – *Uthoernia longofrenatorum*; 57 – Gen. et sp. n.; 58 – *Tetrada harpa*; 59 – *Karinutatia* sp.; 60 – *Ceratobolbina obliqua*?; 61 – *Pyxion nitidum*?; 62 – *Vaiguva* sp.; 63 – *Platybolbina* sp.; 64 – *Sigmobolbina* sp.; 65 – *Sigmobolbina*? sp.

(Pokorny 1971). It is the inverse of dominance, that is, the higher value of the index, the more evenly the species are represented in the assemblage.

The diversity index curve calculated here for the ostracod succession at Pääsküla fluctuates, and the current sampling density does not allow for an unambiguous interpretation (Fig. 2). It seems, however, that the average diversity index is somewhat higher just below the Kinnekulle Bed. Following the altered ash bed, the index displays rather low values with low variability until the sample OM00-11, above which it nearly doubles.

The raw numeric data on individual ostracod species (as well as scolecodonts; see below) provided in this study were recalculated as relative frequencies (%), and as absolute frequency (specimens / 1kg sample). Relative frequency best characterizes the assemblage structure whilst the absolute frequency better describes the dynamics of individual taxa. It was found, however, that the difference between the two approaches is not significant (that is, the trends are not reverse) so only the per cent calculation is illustrated in Figure 3.

Considering the individual species that account for

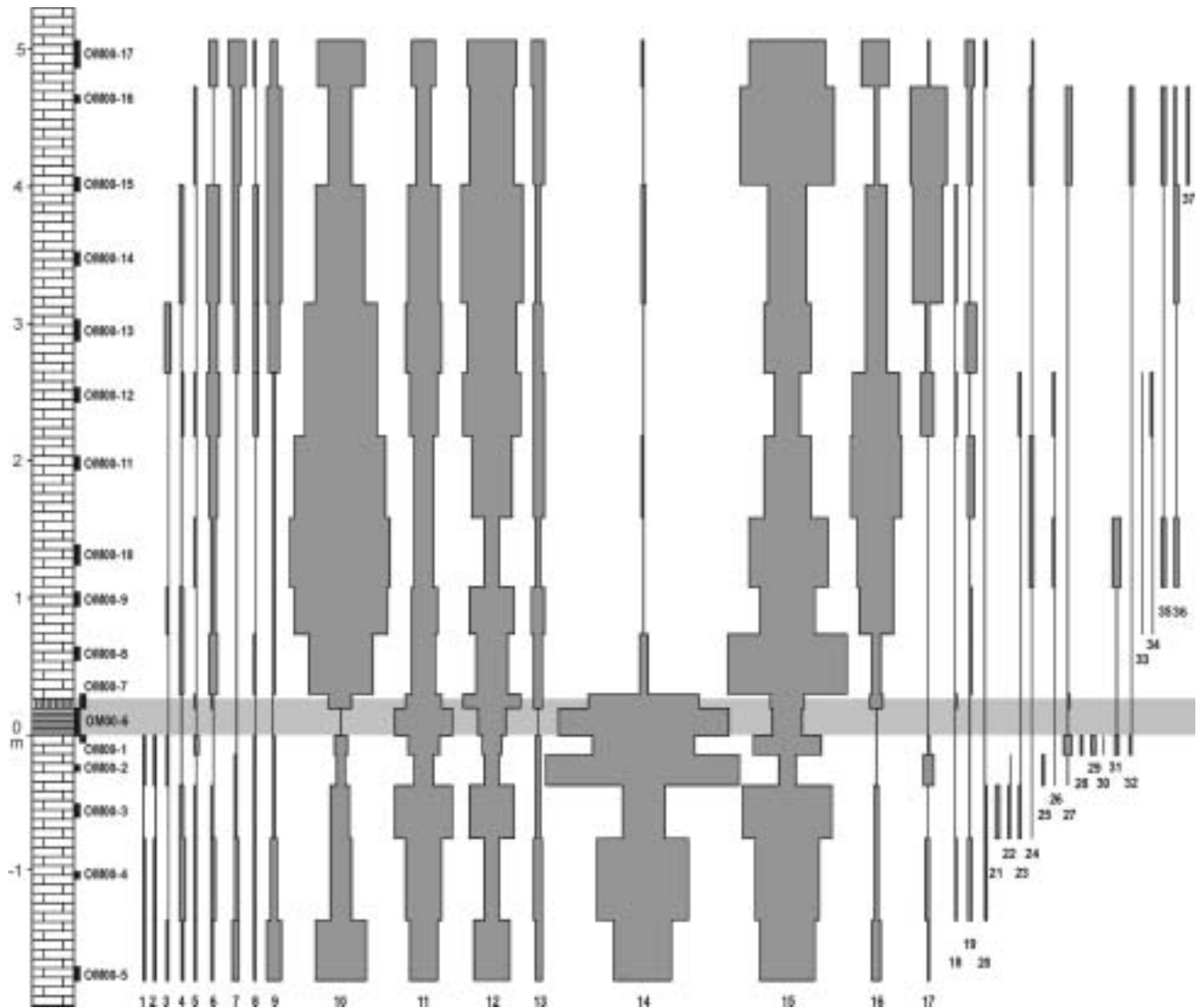


Fig. 4. Succession of scolecodonts in the Pääsküla section. Width of the bar represents relative frequency (%) of species, light grey marks the Kinnekulle Bed. 1 – *Estoniopriion maennili*; 2 – *Pteropelta kielanae*; 3 – *Mochtyella duplicidentata*; 4 – *Oenonites varsoviensis*; 5 – *Xaniopriion* sp. B; 6 – *Incisipriion incisus*; 7 – *Kozlowskipriion breviaulatus*; 8 – *Leptopriion* sp.; 9 – *Lunopriinella symmetrica*; 10 – *Mochtyella cristata*; 11 – *Oenonites gadomskae*; 12 – *Oenonites* sp.; 13 – *Oenonites tuberculatus*; 14 – *Pistopriion transitans*; 15 – *Pteropelta gladiata*; 16 – *Tetrapriion pozaryskae*; 17 – *Vistulella kozlowskii*; 18 – *Ramphopriion*? sp.; 19 – *Atraktopriion* sp.; 20 – *Ramphopriion bialatus*; 21 – *Oenonites latus*; 22 – *Mochtyella* sp. B; 23 – *Ramphopriion* sp.; 24 – *Kallopriion* sp.; 25 – *Mochtyella fragilis*; 26 – *Mochtyella* sp. A; 27 – *Oenonites* sp. A; 28 – *Mochtyella* sp. B; 29 – *Mochtyella* sp. C; 30 – *Xaniopriion* sp. C; 31 – *Atraktopriion cornutus*; 32 – *Tetrapriionidae*? gen. et sp. n.; 33 – *Conjungaspis* sp.; 34 – *Incisipriion edentulus*; 35 – *Ramphopriion* cf. *staufferi*; 36 – *Tetrapriion*? sp.; 37 – *Pararamphopriion* sp.

the majority of specimens, the most striking change in the ostracod succession occurs at the level of the Kinnekulle Bed. Four species that dominate the assemblage below the ash layer, *Tetrada memorabilis*, *Kiesowia* (*Carinobolbina*) *carinata* (Krause), *Cytherellina* cf. *jonesi* and *Olbianella braderupensis* (Schallreuter) disappear. Their position is taken over by e.g. *Airina amabilis* (Neckaja), *Bolbina major* (Krause), *Pariconcho-primitia coniqua* Schallreuter, *Tetrada harpa* (Krause). There are a few other species that occur only below

the Kinnekulle Bed in the Pääsküla section, but these are of low frequency.

Two of the disappearing species, *Tetrada memorabilis* and *Cytherellina* cf. *jonesi*, have never been found above the Kinnekulle Bed. Sarv in Põlma *et al.* (1988) reported that the last local occurrence of these species is, in some sections, within the Kinnekulle Bed. In the Pääsküla section, the altered ash bed was barren of ostracods.

Olbianella braderupensis (= *Olbia* sp. of Sarv in Põlma

et al. 1988) also disappears just below the Kinnekulle Bed. *Kiesowia* (*Carinobolbina*) *carinata* has in some other sections been recovered from the Keila Stage, but even so it seems to display a strong decrease in frequency above the Kinnekulle Bed (Põlma *et al.* 1988).

Ostracod species that range through the sequence studied [e.g., *Sigmoopsis rostrata* (Krause), *Pentagona pentagona* Jaanusson, *Braderupia asymmetrica* (Neckaja), *Circulina fimbriata* (Neckaja), *Rectella* sp., *Easchmidtella fragosa* (Neckaja)] have in most cases low frequencies and do not provide sufficient material to serve as a basis for statistical conclusions.

Jawed polychaetes (scolecodonts)

Jaw-bearing polychaetes of the Baltic Late Ordovician have been dealt with in several papers (Kielan-Jaworowska 1966; Szaniawski 1970; Hints 1998, 1999, 2000). Hints *et al.* (1997) also reported the occurrence of scolecodonts in the Kinnekulle Bed and in directly under- and overlying limestones of the Pääsküla outcrop. The section studied by Hints *et al.* (1997) is located a few hundred meters from the one described herein. In that section, the polychaete assemblage changes close to the ash bed, but as most data were from the Kinnekulle Bed itself, no further conclusions were presented.

In the present study, 37 species of jaw-bearing polychaetes are documented from the Pääsküla section (Fig. 4). Most of them are typical of this stratigraphical interval (Hints 1998), but a few new species, which are yet to be described, were also found. The most common species are *Mochtyella cristata* Kielan-Jaworowska, *Oenonites gadomskae* (Kielan-Jaworowska), *Oenonites* sp., *Oenonites tuberculatus* (Kielan-Jaworowska), *Pistoprion transitans* Kielan-Jaworowska, *Pteropelta gladiata* Eisenack, *Tetraprion pozaryskae* Kielan-Jaworowska and *Vistulella kozlowskii* Kielan-Jaworowska.

The number of species per sample of jawed polychaetes is comparable with that of ostracodes but fluctuates less (note that ostracod samples were smaller than those of scolecodonts and of standard weight). Compared with the species diversity in the lower strata, the number of species decreases above the Kinnekulle Bed (Fig. 2). This characteristic is dependent on the sample size (total specimens counted). As shown in the frequency chart in Figure 2, the samples within the higher diversity assemblage partly coincide with the interval of highest frequency. However, considering the sample mass and the recorded frequency, the samples directly above the Kinnekulle Bed (OM00-7, OM00-8, OM00-9) would have been ex-

pected to yield a few more species. Moreover, the Margalef diversity measure, which is normalized against the sample size (total specimens), gives a result that is in a good accordance with the curve presented in Figure 2. Therefore the drop in the taxonomic diversity following the ash-fall might be related to this event. However, since the species diversity remains rather low until the top of the section, some other factors have probably been involved.

Below the Kinnekulle Bed, the diversity index for jawed polychaetes shows a generally decreasing trend, which can be regarded as a normal background pattern for the assemblage. Above the altered ash layer this trend is reversed showing a very gradual increase until the sample OM00-14 (see Fig. 2). It is possible that the coincidence of the change in the diversity pattern and the ash-fall is circumstantial. Alternatively, the shape of the curve could be due to some sort of relationship between the ash-fall and the change of polychaete assemblage structure.

The distribution pattern of scolecodonts shows that many of the 37 species cross the Kinnekulle Bed. Only two species, *Estonioprion maennili* Hints and *Pteropelta kielanae* (Hints), occur in most samples below the altered ash bed, but not above it. *P. kielanae*, however, has been recovered from the upper part of the Keila Stage in other sections (Hints 1998). *E. maennili* has not been found in the Keila Stage thus far, but bearing in mind the relative rarity of this species, its distribution pattern may not yet be adequately documented. There are also few other species restricted to the pre-Keila strata of the Pääsküla locality (see Fig. 4), but since they are represented by very few specimens occurring in one or two samples only, they will not be discussed further here.

The frequency data for individual species shows that the assemblage structure changed slightly above the Kinnekulle Bed (Fig. 4). Most remarkable is the drop in frequency of *Pistoprion transitans* between samples OM00-7 and OM00-8. The dominance of *P. transitans* below the ash layer was substituted mainly by *Mochtyella cristata*, *Pteropelta gladiata* and *Tetraprion pozaryskae* above the Kinnekulle Bed.

P. transitans is known to be an environmentally controlled species showing preference for shallow-water conditions (Hints 2000). On the other hand, *Pteropelta gladiata*, which is also facies dependent and typical of shallower-water facies, shows only a minor frequency change close to the altered ash layer. Therefore, *P. transitans* seems to have suffered from the ash-fall more than other species. There are also several other species, e.g., *Oenonites gadomskae*, *Oenonites tuberculatus*, and *Oenonites* sp. that show almost no change in frequency (absolute or relative) across the Kinnekulle Bed and they can therefore be

interpreted as tolerant to the environmental changes induced by ash-falls.

Remarkably, sample OM00-7 from the upper transitional part of the ash bed and the limestones just above, still contains an assemblage similar to that of sample OM00-1 below the ash bed. Unless those specimens represent a redeposited assemblage, the change in the jawed polychaete assemblage must have been gradual, occurring some time after the ash-fall. Abiotic transportation is nevertheless very improbable as the ostracodes would have a similar distribution pattern which is not the case (see above).

Hints *et al.* (1997) described the occurrence of scolecodonts within some parts of the Kinnekulle Bed, with abundances similar to that of adjacent limestones. The Kinnekulle Bed of the section studied herein contained only a few specimens confirming that the distribution of scolecodonts in the altered ash layer is uneven within a limited area. This may be an indication of post-depositional displacement of material inside the Kinnekulle Bed caused by glaciotectonics at the Pääsküla locality.

Macrofauna

Bryozoans, brachiopods, and echinoderms are the three most common groups encountered. The data on their frequency are illustrated (Fig. 5) as the number of fragments of colonies or valves or stem columnals per sample. In spite of the fact that the absolute numbers are largely tentative, the relative trends provide some information on the macrofossil succession across the Kinnekulle Bed.

The bryozoans show rather low absolute frequencies (fragments per sample) in the beds underlying the Kinnekulle Bed, representing 10–45% of all fragments encountered. Just above the level of the ash, the absolute frequency of bryozoans increases several times and it is also considerably more variable higher up in the sequence than below the Kinnekulle Bed (Fig. 5). The relative frequency of bryozoan fragments across the Kinnekulle Bed does not significantly change, however, the relative numbers of bryozoans seems to increase upwards from sample OM00-9 expanding to 75% of encountered fragments.

Brachiopods display a slight increase (both in absolute and relative frequency) in the upper transitional part of the Kinnekulle Bed (sample OM00-7), where the occurrence of abundant *Sowerbyella* sp. has been documented in our residues and also in the field (noted also by Rõõmusoks 1970, p. 258). Põlma *et al.* (1988) showed that in some sections (e.g. the Keila drill core) this brachiopod is very common above the Kinnekulle Bed, and rare or absent just below it. In

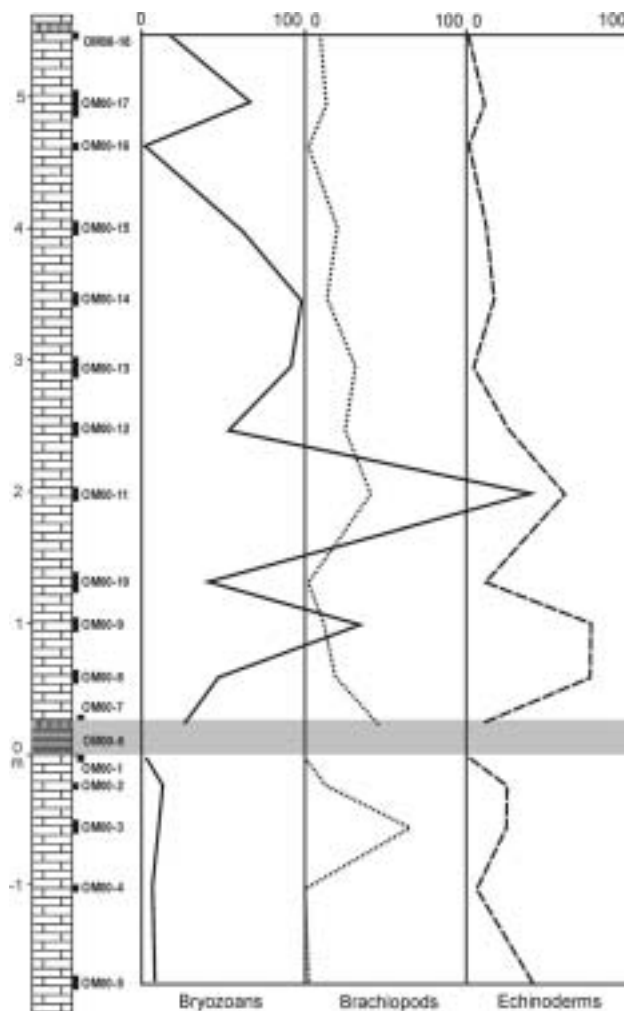


Fig. 5. Absolute frequency (number of fragments in 300g sample) of bryozoans, brachiopods and echinoderms in the Pääsküla section. Light grey marks the Kinnekulle Bed.

the Pääsküla section, *Sowerbyella* is also common in some samples below the Kinnekulle Bed (e.g., OM00-3). Its frequency changes, like that in the sample OM00-7, and may reflect storm accumulations and is probably not dependent on the volcanic event. It is nevertheless interesting that similar brachiopod accumulations are also found in, or close to the 'e' (Grimstorp) K-bentonite (Rõõmusoks 1970, p. 253).

The present data on echinoderms, represented mostly by stem columnals, show highly variable frequencies. Above the Kinnekulle Bed (above the sample OM00-7), there is a notable increase in the abundance of the crinoid *Ristnacrinus*.

Discussion and conclusions

The biotic effects of volcanism are generally well known and a number of studies deal with different volcanic ash-falls. It is known that plankton is much less affected than benthos and the near-shore and hard-substrate communities show more susceptibility than those in offshore and soft-substrate environments.

Among the most commonly described effects resulting from volcanic ash-falls are mass mortality events (Harper *et al.* 1995; Heikoop *et al.* 1997). In the present case, the benthic community colonized a soft-substrate environment in shallow to moderate depth on the open shelf. Resulting taphocoenoses contain sporadically distributed macrofossils and their fragments. Brachiopods, bryozoans, echinoderms and others are common but no large sessile epifauna like corals or stromatoporoids is present. The nature of the Pääsküla section precluded the possibility to easily expose a large surface of the base of the Kinnekulle Bed for examination, and also the sampling density was rather low. For these reasons, a mortality event could not be documented, although it is very likely that the taxa, which could not escape burial died after deposition of the ash.

The most obvious effect of the Kinnekulle ash-fall was the turnover in the ostracod assemblage. Abrupt drop in species diversity and frequency, and change in the dynamics of individual species, some of which disappeared after the ash-fall, indicate that most ostracods suffered strongly from the direct effects of the ash-fall. Probably the changed characteristics of the substrate due to sediment surges and the alteration of water chemistry played an important role. Influences through change in the food chains are also very likely.

A decrease in species diversity and frequency, and perhaps also the diversity index of ostracodes, indicate strong stress on the assemblage after the ash-fall. The following increase in these characteristics seems to correspond to the reorganization and stabilization of a new assemblage. It is disputable how long it took for the fauna to recover, but possibly at the time represented by sample OM00–9, the assemblage was more or less stable.

It is interesting to note that the frequency curve of ostracods across the Kinnekulle Bed at Pääsküla corresponds rather well to the curve illustrated by Botting (1999, fig. 3), who studied faunal dynamics across Ordovician tuffs in Central Wales. In both cases, the general trend of upwards increasing frequency is disrupted by the volcanogenic layer, causing a significant drop, after which another continuous increase with a clear peak occurs. Botting (1999) did not com-

ment on the increase in ostracod frequency before the ash-fall but argued that the post ash-fall bloom might have been the result of upwelling nutrients initiated by the descent of surface waters enriched in ash particles. However, the sedimentological regimes of Central Wales and northern Estonia were quite different, making it doubtful that the same mechanism might be applicable in both cases. Also the sampling scale used by Botting was much finer. Thus it is uncertain whether this similarity is by chance or resulted from analogous environmental processes.

Jaw-bearing polychaetes were not as harshly affected as the ostracods, their distribution pattern in the Pääsküla section was less variable and irregular, especially above the Kinnekulle Bed. Only a few species show significant changes in frequency close to the altered ash bed. Hence, polychaetes in general can be considered less sensitive to the ash-falls than ostracods.

The change in the polychaete assemblage was not sudden. Unlike the ostracod faunas, sample OM00–7 has a similar polychaete faunal composition as the samples below the Kinnekulle Bed indicating that a different type of influence must have affected the polychaetes, and the change occurred after some delay. That is, faunal changes could not be directly related to sediment influx and accompanying changes in substrate properties. Instead it seems that polychaetes were affected via their relationships with other biota during a gradual rearrangement of bottom communities triggered by the ash-fall.

Bryozoan, brachiopod and echinoderm frequency also displayed some change close to the ash bed, which might have partly been associated with the ash-fall. Following the fall, the increase in the number of bryozoans is significant. More definitive conclusions cannot be drawn without further taxonomic study.

Finally, it cannot be entirely excluded that the above described distribution patterns do not result from the ash-fall but are instead related to some other event or process, or a gap in the sedimentary record. However, since no evidence for these have been found, we conclude that a biotic event, larger than previously suggested, was associated with the Kinnekulle ash-fall. Some components of the benthic fauna were strongly affected and the influence of this event persisted some time after the ash-fall.

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