

FAUNAL DYNAMICS IN THE MIDDLE ORDOVICIAN (VIRUAN) OF BALTO-SCANDIA

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ABSTRACT. Faunal dynamics, that is, changes of faunas in time and space, are analysed in the epicontinental Viruan (Middle Ordovician) of Balto-Scandia. The study is based mostly on ostracodes in northern Estonia and the central Balto-Scandian *confacies belt* of Sweden since little pertinent information is available for other groups and other Balto-Scandian areas. Distinction is made between *immigrations* (entry of species not known in earlier beds within the region) and *faunal shifts*, caused by shifts of habitats within the region and mostly associated with lithological change. Models of immigrations, simulated by using a table of random numbers, have shown that data in faunal logs are strongly density dependent and should be interpreted with caution.

The results indicate that in Upper Viruan strata the relative intensity of some main faunal changes of immigration type in northern Estonia has no contemporaneous counterpart in the central *confacies belt*, and vice-versa, suggesting that some *confacies belts* were affected by environmental changes which influenced the benthonic fauna of other belts only slightly or not at all. The horizons of several major changes in the graptolite faunas of Scania (used to define zonal boundaries) evidently correspond to levels at which no distinct change can be recognized in the shelly fauna, suggesting that factors affecting planktonic graptolite faunas were largely different from those affecting the benthonic faunas. An interesting faunal shift, associated with the change from calcilitites to calcarenites in the lowermost Dalby Limestone, introduced into central Sweden a fauna of sedentary organisms that includes many taxa which are widely distributed in earlier beds or northern Estonia. These factors have important consequences for the practice of biostratigraphical classification and correlation.

RÉSUMÉ. L'auteur analyse la dynamique des faunes, c'est-à-dire leurs changements dans le temps et dans l'espace, dans le Viruan (Ordovicien Moyen) épicontinental de la Balto-Scandinavie. L'étude se base principalement sur les ostracodes de l'Estonie septentrionale et de la *ceinture de confacies* de la Balto-Scandinavie centrale en Suède, les autres groupes et les autres régions balto-scandinaves ne fournissant que peu d'informations utilisables. Une distinction est faite entre les *immigrations* (introduction d'espèces inconnues dans les couches plus anciennes de la région) et les *déplacements* fauniques dus à la modification des habitats dans la région et généralement associés à un changement lithologique. Des modèles d'immigration, simulés en utilisant une table de nombres au hasard, montrent que les données concernant les distributions (logs) fauniques dépendent étroitement de l'abondance (density) et doivent être interprétés avec prudence.

Les résultats indiquent que dans les couches du Viruan Supérieur de l'Estonie septentrionale l'intensité relative de certains changements fauniques principaux—du type immigration—n'a pas de contrepartie dans la partie centrale contemporaine de la ceinture de *confacies* et vice-versa; ceci suggère que certaines de ces ceintures sont affectées par des changements de milieu exerçant une influence légère ou nulle sur la faune benthique d'autres ceintures. Les horizons de plusieurs changements majeurs dans les faunes graptolithiques de Scandie (utilisés pour définir les limites des zones) correspondent de toute évidence à des niveaux auxquels aucun changement notable ne peut être reconnu dans la faune coquillière; ceci suggère que les facteurs affectant les faunes graptolithiques planctoniques sont très différents de ceux qui affectent les faunes benthiques. Un déplacement faunique intéressant, associé à un passage de calcilitites à des calcarénites dans la partie la plus inférieure du Calcaire de Dalby, introduit en Suède centrale une faune sédentaire incluant de nombreux taxa largement répandus dans des couches plus anciennes de l'Estonie septentrionale. Ces facteurs ont des conséquences importantes en classification et en corrélation biostratigraphique.

ZUSAMMENFASSUNG. Faunendynamik, das heisst, Veränderungen von Faunen in Zeit und Raum, wird hier für die epikontinentale Viru-Serie (Mittelordovizium) innerhalb der baltoskandischen Region analysiert. Die Untersuchung gründet sich hauptsächlich auf Ostrakoden aus dem nördlichen Estland und der zentralen baltoskandischen *Confazieszone* Schwedens, da wenig Information für andere Gruppen und aus anderen baltoskandischen Gebieten vorliegt. Es wird zwischen *Einwanderung* (Eintreten von Arten, die in älteren Lagern derselben Region nicht bekannt sind) und *Faunenverschiebungen*, deren Ursache Umweltsveränderungen innerhalb der Region waren und die meistens mit lithologischen Veränderungen verbunden sind, unterschieden. Einwanderungsmodelle, die mit Hilfe von einer Tabelle von Zufallsziffern simuliert wurden, haben gezeigt,

dass Angaben über die vertikale Verbreitung der Arten in den Profilen stark von der Dichte der Exemplaren in einzelnen Proben abhängig sind und daher mit Vorsicht zu interpretieren sind.

Die Ergebnisse zeigen, dass im oberen Teil der Viru-Serie die relative Intensität der Einwanderungen in nördlichen Estland und in der zentralen Confazieszone verschieden ist, welsches darauf hindeutet, dass die Umweltsveränderungen die benthonische Fauna der verschiedenen faziellen Zonen ungleichmässig beeinflusst haben. Einige Einwanderungen in einer Fazieszone scheinen in anderen Fazieszonen überhaupt keinen gleichzeitigen Gegenspieler aufzuweisen. Die Horizonte mehrerer grösserer Veränderungen in der Graptolithenfaunen von Schonen fallen in der Kalksteinslagerfolge auf Horizonte, wo keine deutliche Veränderung in der benthonischen Fauna nachzuweisen ist. Das deutet darauf, dass die Faktoren, die die planktonische Graptolithenfauna beeinflussen, verschieden waren von denen, die die benthonischen Faunen beeinflussen. Eine interessante Faunaverschiebung, die mit dem Wechsel von Calcilutiten in Calcareniten im untersten Dalby-Kalkstein verbunden ist, führte in Mittelschweden eine Fauna von sessilen Organismen ein, die viele Taxa enthält, die in älteren Sedimenten in nördlichen Estland weite Verbreitung haben. Die beschriebene Faktoren haben grosse Bedeutung in der Praxis der biostratigraphischen Klassifikation und Korrelation.

EARLY studies by the writer in the Middle Ordovician (Viruan) sequence of northern Estonia indicated that the fauna had not changed continuously or randomly with time, but that a period of change was normally followed by a much longer period during which the taxonomic composition of the fauna remained fairly stable. It was therefore suggested (Jaanusson 1945) that during Viruan times there had been a number of successive immigrations into the area. The pattern of immigrations, based mostly on 'bag-stratigraphical' data, was illustrated diagrammatically (Jaanusson 1945; see also Männil 1966, fig. 40). The term 'bag-stratigraphical' is used here to designate information on vertical ranges of taxa given only in terms of stratigraphical units (formations, members, zones, etc.), and alludes to the frequent field practice of gathering fossils from a stratigraphical unit in a bag without noting the precise level of occurrence of individual specimens.

In the comparable part of the Swedish sequence, most exposures proved too small for detailed studies on changes in the macrofauna; attention was then focused on ostracodes and small macro-organisms, which could be obtained from densely spaced samples or cores (Jaanusson 1960a, 1962, 1963b, 1965, and unpublished data). The sequence under consideration consists predominantly of carbonate rocks. In order to study the relationship of faunal changes to change in lithology (substrate), a method for determining grain size of limestone was elaborated (Jaanusson 1952) that proved to be useful.

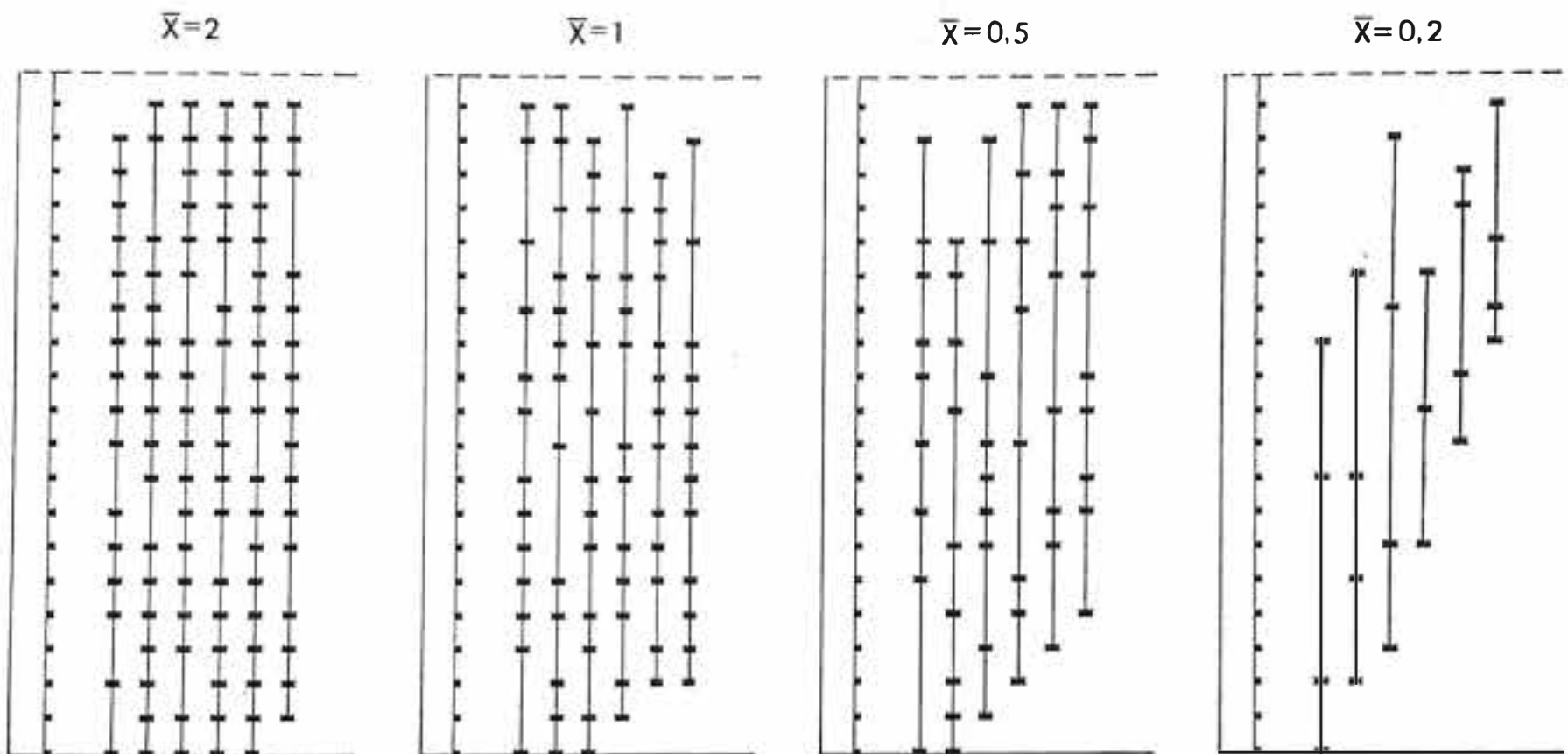
The term *faunal dynamics* as applied in this paper refers to faunal changes in time and space relative to characteristics of the sedimentary record, that is, to environmental conditions reflected in lithology. During early stages of studies on faunal dynamics in Viruan strata the following working hypothesis was formulated. There are two main types of faunal changes: (1) those which are due to changes in local conditions such as the change from carbonate mud bottom to skeletal sand bottom (*faunal shift*) and (2) those which are caused by environmental changes, such as temperature, of at least regional scale, or by elimination of a distributional barrier between two areas with the same ecological conditions (*immigrations*). Biostratigraphical correlation implies basically a correlation of physical events which are reflected in the fauna but not always in the sedimentary record (the fauna is a much more subtle tool for recognizing environmental changes than the process of deposition). If the succession of faunal changes in different regions is worked out and compared with the lithological record, there should be a possibility for inter-regional correlations based on a comparison of

immigrations, provided that some of the physical events causing immigrations affected different regions at about the same time.

Confrontation of this working hypothesis with the faunal and sedimentary record, as well as with various methodological difficulties for obtaining necessary data, showed faunal dynamics to be much more complicated and more difficult to decipher than was originally believed.

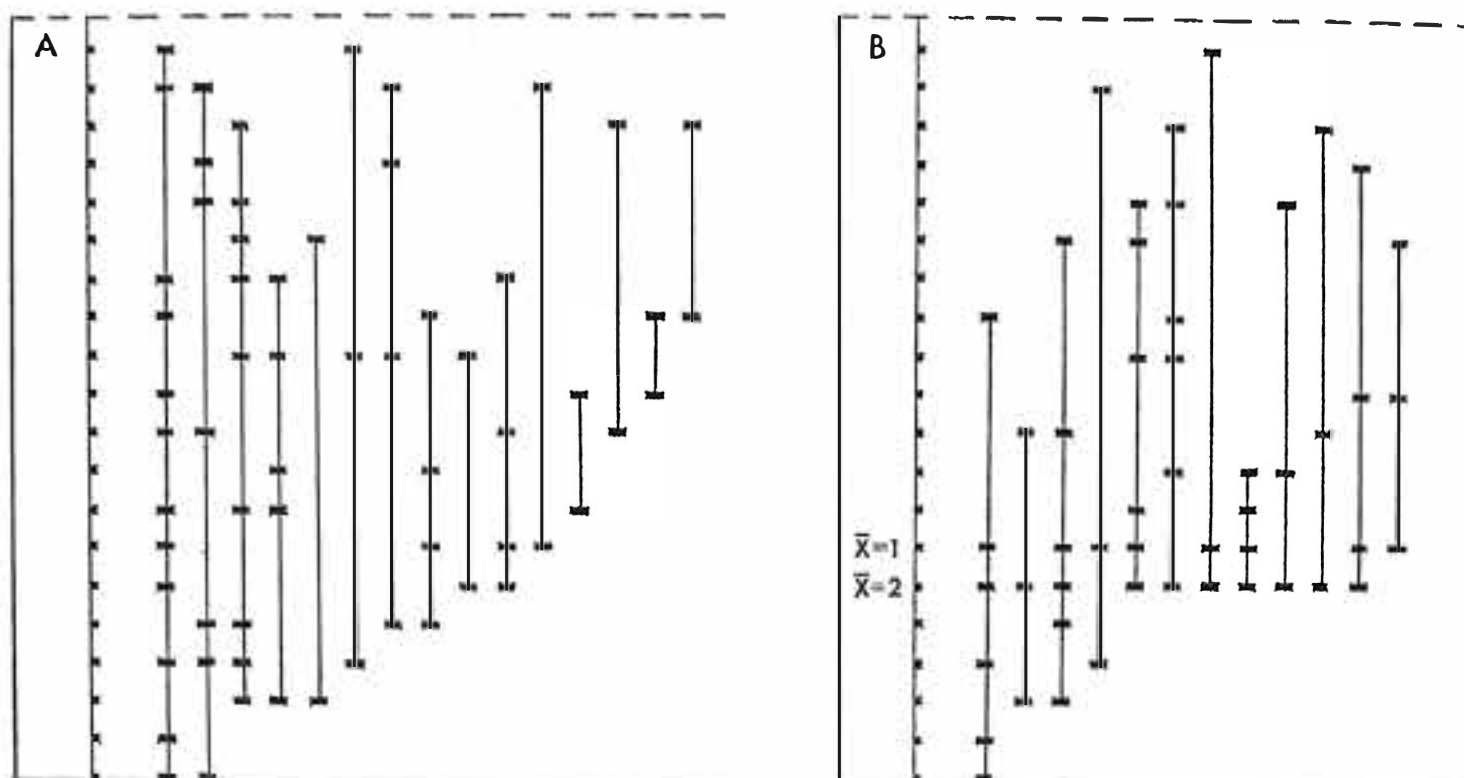
INTERPRETATION OF DATA IN FAUNAL LOGS

At an early stage in the assembly of data the problem arose as to how to recognize an immigration from data in *faunal logs*, that is, in charts showing the observed vertical range of various species within a sequence. For example, species seldom seemed to enter the sequence at the same level, and the order of appearance of successive species was not always the same in different localities. A study of statistical models proved to be helpful in understanding some of the problems.



TEXT-FIG. 1. Effect of different densities (\bar{X}) on faunal logs. Four models of immigrations simulated using a table of random numbers, assuming that the distribution of specimens within the section is random. A horizontal bar represents the occurrence of at least a single specimen of a species. The density (\bar{X}) varies from model to model but is the same for all species within a model. All species are assumed to enter the sequence at the level of the lowermost sample. Sample density $S = 0.2$.

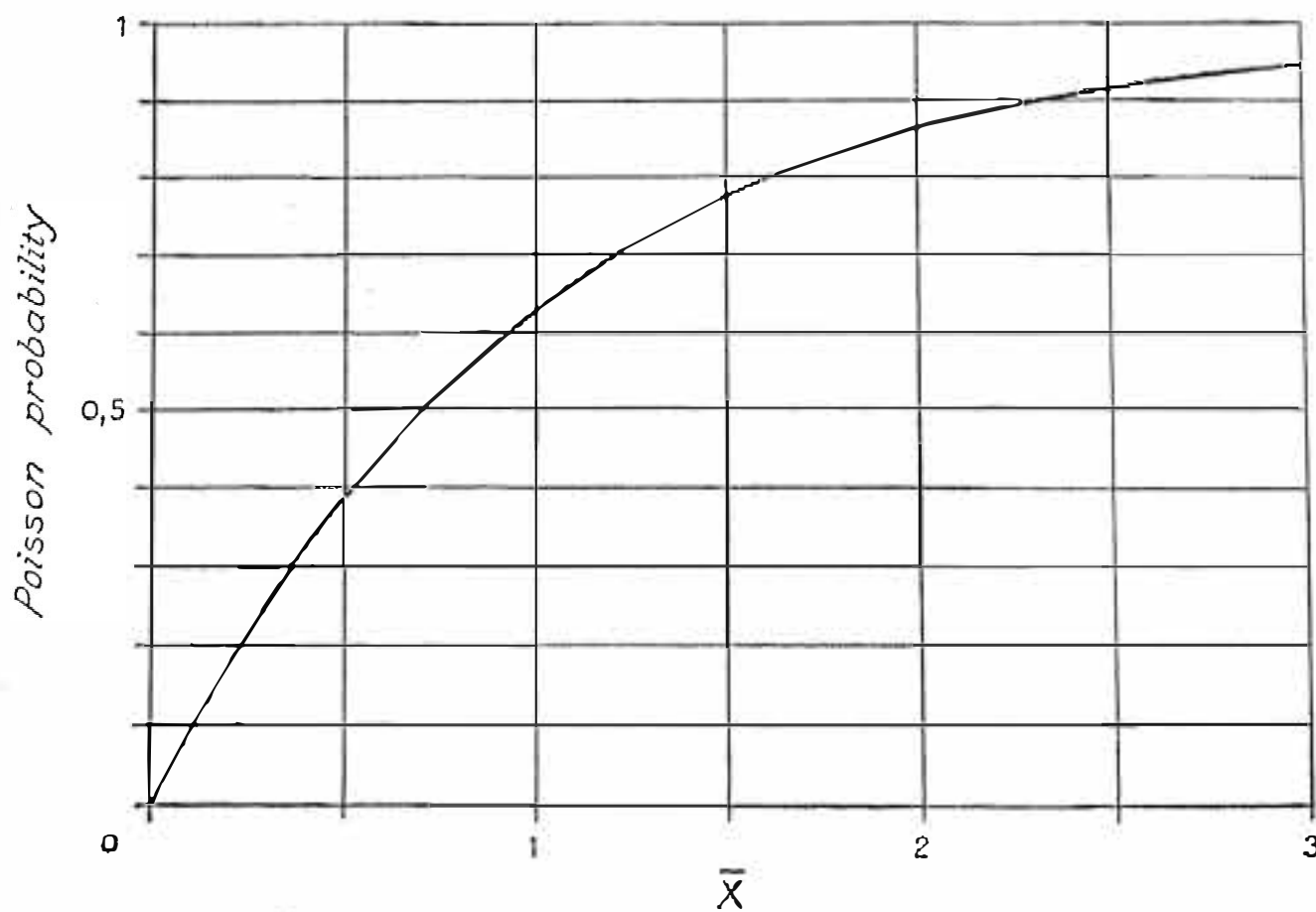
Faunal logs were simulated using a table of random numbers. The assumptions were made that the distribution of specimens within the section is random and that the size of sample is constant throughout the section. The plotted data were tested for randomness by means of the chi-square test of homogeneity and compared with a Poisson distribution. *Density* as used in this paper refers to number of individuals per unit sample size (either volume or weight of the rock, or area of a quadrat). It is dependent on sample size. What is dealt with in practice is not necessarily the real density of specimens of a species in a sample, but what can be termed *operational density*. For example, the best method of obtaining ostracodes from limestone samples of the Fjäckå section is to crush the rock into small pieces and to scan the pieces under a binocular microscope. Not all specimens contained in the rock can be found but, as the pieces of rock are of about the same size, and thus the scanned area roughly the same from sample to sample of about equal weight, the operational density of a species is roughly comparable throughout the section. *Sample density* refers to the total thickness of sampled individual beds within a section or a core, divided by the thickness of the sampled unit.



TEXT-FIG. 2. A, model of an immigration comprising species with various densities ($\bar{X} = 1$ to 0.1). B, model of a 'density dependent immigration' with all species having the density $\bar{X} = 0.25$ except at two levels where the density increases to $\bar{X} = 1$ and $\bar{X} = 2$, respectively, for all species. The models are simulated using a table of random numbers, assuming that the distribution of specimens within the section is random. All species are assumed to enter the sequence at the level of the lowermost sample. Sample density $S = 0.2$.

Various models were produced by varying the density of species or sample density (for selected examples see text-figs. 1, 2A, 4). Models in which density of species varied not only from species to species but also along the section within a species could also be produced easily (text-fig. 2B).

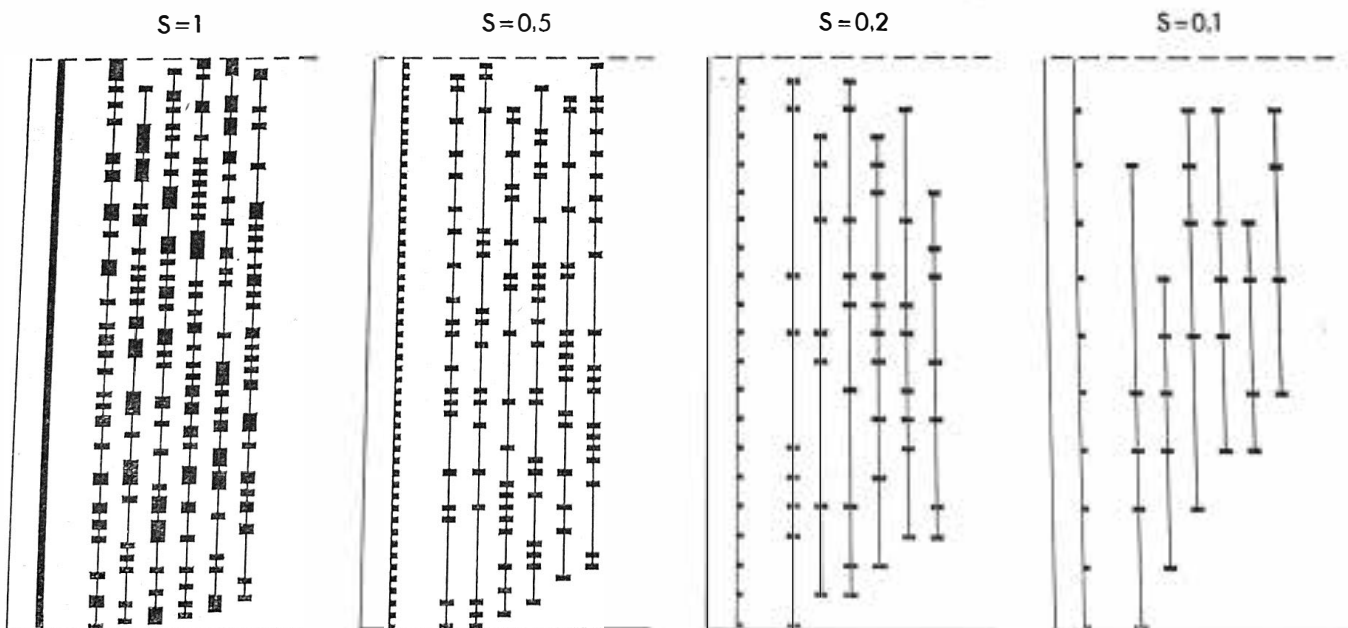
The simulations show that, as may be expected, information on vertical ranges of various species within a section is strongly density dependent and also show how various densities affect a faunal log



TEXT-FIG. 3. Poisson probability that a species occurs in a unit sample, calculated from the equation $p(\bar{X}) = e^{-\bar{X}} \left(\frac{\bar{X}^k}{k!} \right)$, for different densities (\bar{X}) of the species, expressed as $\bar{X} = \frac{\sum f X}{N}$, where N = number of specimens.

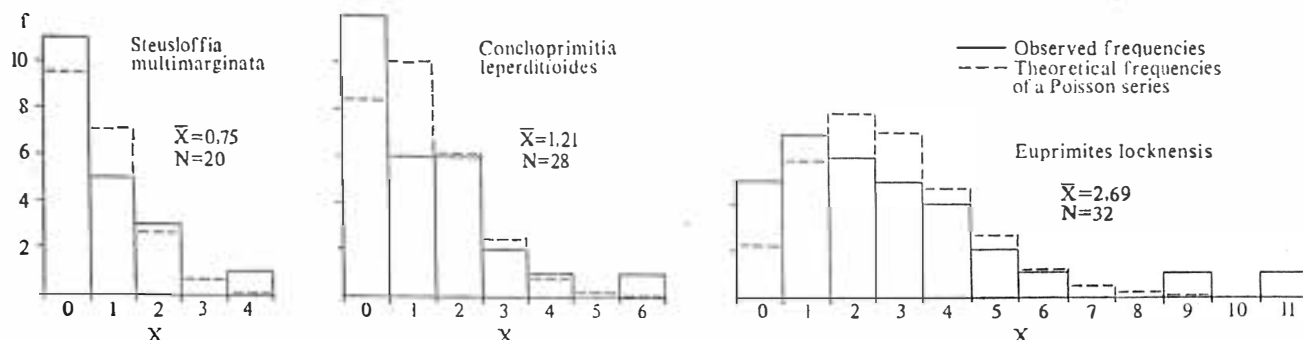
(text-fig. 1). Even with an average density as high as 1 (the species occurs, on average, with one specimen per unit sample), the probability that the species will be found in a sample is not higher than 0.63 (the species is missing at this level, on average, in every third sample, text-fig. 3). With still lower densities the probability of finding the species decreases still more (text-fig. 3). Thus, even if all species had appeared contemporaneously, the faunal log may show a successive appearance of species. In fact, for species with an average density, say, of less than 0.25, determination of their real level of appearance is difficult. Density can be increased by increasing the sample size but normally only to a certain limit, since the amount of rock that is available or can be processed is limited. Information on the appearance of species in a section is also strongly dependent on sample density (text-fig. 4). Widely spaced samples may give an unrealistic picture of the vertical ranges of different species.

In locating what may have been periods of immigrations within a faunal succession, one is thus faced with serious difficulties. Reliable data come only from species with relatively high densities, provided that these high densities prevailed from the time of appearance of the species into the area. Densities are seldom constant but in many sections change from bed to bed or according to slight changes in lithology. Different sections with the same assemblage of species may show different species to be involved in the same immigration because slight ecological differences may have caused different species to be dominant. A sudden increase of either the general density, or densities of a number of species that were rare previously easily gives the impression of an immigration, although most or all of these species may exist with low densities at lower levels ('density-dependent immigration', text-fig. 2B). Occasionally the occurrence of such species at lower levels can be proved in other sections where they have been found either because of higher densities or by chance. Species involved in a faunal immigration seldom invade an area at the same time. They normally appear successively throughout a period, although in a sequence with a very low rate of sedimentation that period, if relatively short, may be represented by a thin stratum where the order of appearance of species is difficult to determine. If the period of immigration is longer relative to the rate of sedimentation, it is difficult to distinguish, in a faunal log, between the real level of appearance of a species and an apparent appearance due to chance. All this shows that data on vertical ranges of species must be interpreted with caution.



TEXT-FIG. 4. Effect of different sample densities (S) on faunal logs. Four models of immigrations simulated by using a table of random numbers, assuming that the distribution of specimens within the section is random. All species in all models have the density $\bar{X} = 0.5$ whereas sample density varies from model to model. All species are assumed to enter the sequence at the level of the lowermost sample.

Whether the distribution of a species within a section is random or not can be checked by test of fit to the Poisson distribution, provided that the unit sample size is constant and the number of specimens per sample is known. Such tests were applied to all common species shown in the faunal log (text-fig. 9) of the main section at Fjäckå (for examples see text-fig. 5). The histograms show the observed distributions to be not very different from the theoretical Poisson distributions. Noteworthy in each case is the considerable frequency of samples that also lack the species in the random distribution. Chi-square tests reveal that for $N=2$ degrees of freedom the observed distribution of *Steusloffia multimarginata* has a satisfactory agreement with the expected distribution (probability between 0.75 and 0.50) whereas the distributions of the other species do not agree with the Poisson distribution (probability less than 0.50). The observed distributions of these species are a result of a combination of random and non-random factors.

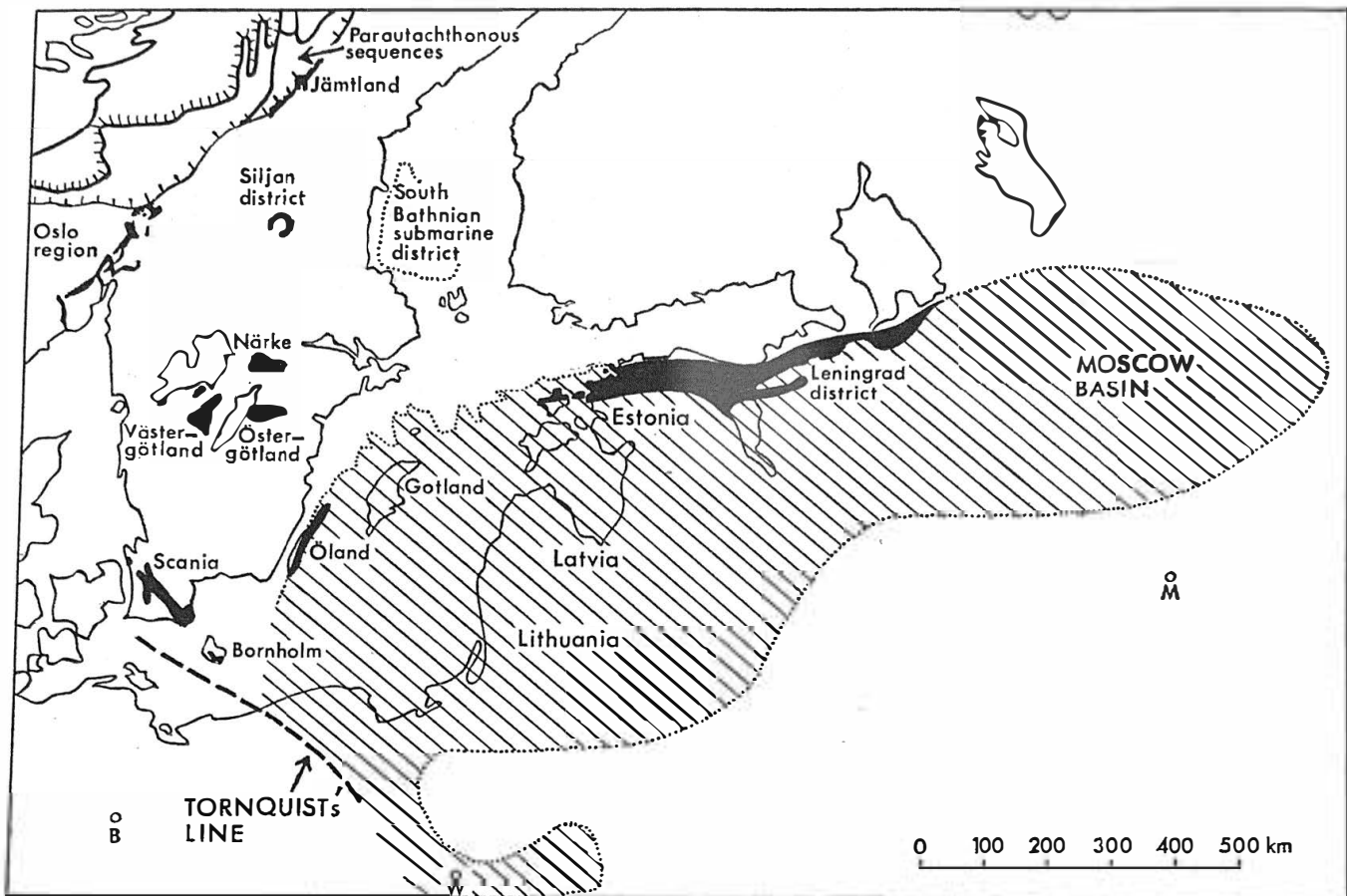


TEXT-FIG. 5. Comparison between expected distribution of a species with theoretical Poisson distribution and observed distribution of three species. X = number of specimens per sample, f = frequency of samples, \bar{X} = mean of specimens per sample (operational density), and N = number of samples. The observed data are from a series of samples from the Dalby Limestone of the main Fjäckå section (text-fig. 9); for *Steusloffia multimarginata* 12.50 to 17.80 m, for *Conchoprimitia leperditioides* 10.20 to 16.75 m, and for *Euprimites locknensis* 1.50 to 9.50 m below the lower boundary of the complex of bentonite beds.

ORDOVICIAN DEPOSITS OF BALTO-SCANDIA

The Ordovician epicontinental sea covered a large area east and south-east of the Caledonian geosyncline of Scandinavia. Accumulation in that sea was characterized by a very low net rate (some 2 to 3 mm per 1000 years) and by a preponderance of carbonate sediments. The total thickness of Ordovician rocks rarely exceeds 200 m.

The main central part of the area is currently termed the Balto-Scandian region. To the north-west it is bordered by the Caledonian geosyncline of Scandinavia. To the west the nature of the boundary is unclear. The Jutland Peninsula in Denmark and some adjoining areas seem to lack Ordovician deposits, but whether this is due to erosion or non-deposition is not clear. The south-west boundary of the area is known as the Tornquist Line, separating two depositionally as well as tectonically different regions in Europe. What is known of Ordovician strata south-west of this line (Wendean Basin, proposed in this paper) provides evidence of terrigenous deposits, largely greywackes, with a thickness measurable in kilometres and thus of geosynclinal nature (Jaeger 1967; Modlinski 1973). In the general direction of the south-eastern continuation of the line, Ordovician epicontinental deposits crop out in the Holy Cross Mountains of central Poland. Ordovician deposits of Balto-Scandian type can be traced farther south-east into Podolia and Moldavia where they are very thin and presumably of littoral type. Otherwise on the Russian Platform the eastern and northern margins of

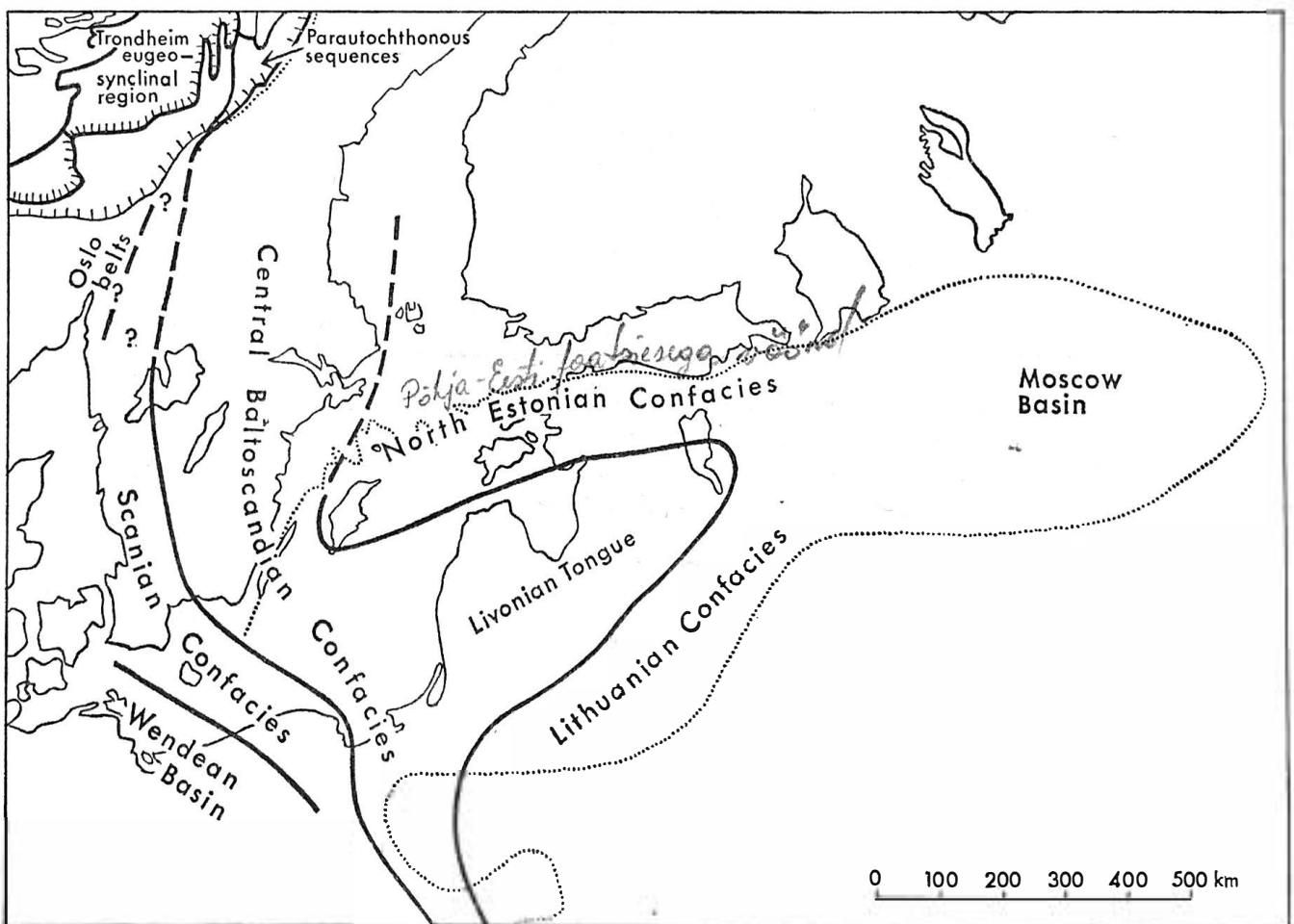


TEXT-FIG. 6. Map showing outcrop areas of Ordovician deposits in Balto-Scandia (black) and the extent of subsurface and submarine Ordovician on the Russian Platform (diagonal shading). On the mainland of Sweden the whole outcrop area of the Cambro-Silurian outliers is shown, of which Ordovician rocks occupy only a minor part. B, Berlin; W, Warszawa; M, Moscow.

Ordovician deposits are erosional and the original extent of the Ordovician sea is difficult to reconstruct. To the east the Balto-Scandian region merges in the subsurface into the Moscow Basin (text-fig. 6).

Within the Balto-Scandian region Ordovician deposits crop out discontinuously along the north-western and western margin of the Russian Platform, from the Leningrad district to Öland (text-fig. 6). The lithology and faunas of Ordovician subsurface deposits on the Russian Platform are now known from numerous borings. On the mainland of Sweden Ordovician rocks are preserved in a number of outliers, from the Siljan district and the submarine South Bothnian district in the north to Scania in the south. A further outlier is on the Danish island of Bornholm. Furthermore, autochthonous Ordovician deposits crop out in front of the Caledonian thrusts as a narrow belt which is widest and best studied in the Jämtland Province. In the parautochthonous sequences in front of the main Caledonian thrusts, faulted and folded Ordovician rocks, mainly terrigenous and including greywackes in the west, are exposed in several areas along the eastern margin of the Caledonian range, again particularly in the Jämtland Province. The westernmost Balto-Scandian epicontinental Ordovician is exposed in the Oslo region, Norway, in a graben some 220 km long.

In the epicontinental area various lithofacies are arranged mainly in belts directed almost meridionally on the mainland of Sweden (Jaanusson 1963*a*; Männil 1966), and thus at an angle to the direction of the Caledonian front (Jaanusson 1973). Männil (1966) distinguished what he termed 'facies zones' that include one or several lithofacies belts, or even only part of one belt, characterized by common biofacies trends and certain recurrent lithofacial features. Although within each major facies unit lithology as well as fauna changes with time, the unit retains its individuality and can be distinguished in roughly the same geographical position throughout most of the Ordovician. There does not seem to exist an appropriate term for such a category of facies, that is, belts defined by a combination of litho- and biofacial characteristics and with a fairly stable relative position within the depositional area. The term 'structural-facial belt' (Põlma 1973) is not particularly recommendable. In the present paper the term *confacies belt* is coined for major composite facial units of this type.



TEXT-FIG. 7. Map showing approximate boundaries of the Ordovician confacies belts in the Balto-Scandian region.

The approximate boundaries of Ordovician confacies belts in Balto-Scandia are shown in text-fig. 7. However, the position of the boundaries was not static but changed with time, mostly as a result of slight shifts in the extent of lithofacies belts. Moreover, between adjacent belts a transitional zone of varying width is frequently developed (Põlma 1967). The central Balto-Scandian confacies belt (the Swedish-Latvian facies

zone of Männil 1966) occupies most of the mainland of Sweden and has a varied lithology (in the Viru Series predominantly carbonates, calcilutites as well as calcarenites, red in the lower part of the sequence). South of Gotland the belt continues eastwards, extending as a tongue-like projection (Livonian Tongue, Jaanusson 1973) into Latvia and southern Estonia (Männil 1964, 1966), as well as southwards far into Poland (Modlinski 1973). The Livonian Tongue is bordered in the north by the North Estonian confacies belt (predominantly calcarenites), which extends from Gotland and the Swedish island of Gotska Sandön to the Leningrad district (Ingermanland), and in the south by the Lithuanian confacies belt (Männil 1966) which continues southward into eastern Poland, east of the central confacies belt (Modlinski 1973). To the southwest the central confacies belt is bordered by the Scanian confacies belt where graptolitic shales are predominant. The north-western continuation of the Scanian belt is not yet clear because of the absence of outcrops. The Oslo belt (Størmer 1953, 1967) may be a composite unit, parts of which possibly belong to a belt that extends along the Caledonian front to the parautochthonous sequence of Jämtland. Along a confacies belt stratigraphical units tend to have a remarkable spatial continuity, whereas correlation from belt to belt frequently imposes problems since not only lithology but also fauna changes.

Sedimentological problems related to confacies belts have been discussed by Männil (1966), Jaanusson (1973) and Põlma (1973). The central confacies belt was, in general, deposited in deeper water than the eastern confacies belts. However, this was not without exceptions (Jaanusson 1973) since the belt includes rocks that were deposited in upper, sublittoral to supralittoral environments but whose lithological and faunal characteristics are otherwise close to those of the rest of the belt. For example, in the Lockne area of the autochthonous sequence of Jämtland the middle Dalbyan Limestone, with a polymict conglomerate at the base, rests on Precambrian or various Ordovician limestones (Thorslund 1940). The Middle Ordovician beds underlying the conglomerate have desiccation cracks and stromatolitic algal mats (Larsson 1973), indicating recurrent subaerial exposure. However, the fauna in all these beds is characteristic of the central confacies belt. Thus the relationship of confacies belts to marine depth zones is by no means simple.

The method of classifying the Viruan sequence varies somewhat from one confacies belt to another. In the North Estonian belt, where the sequence is fairly uniform lithologically and moderately to richly fossiliferous throughout, the classification is by tradition (Schmidt 1858, 1881) basically biostratigraphical, based on faunal assemblages without preference for any particular group (for a summary see Rõõmusoks 1970). Boundaries are normally drawn at the level of changes in the fauna. Some of the faunal changes are not well defined and then frequently a lithological index horizon is chosen for defining the position of a boundary. In the Upper Viruan, bentonite beds are used for this purpose. The level of bentonite beds does not coincide exactly with the level of the beginning of a faunal change but, despite this, index horizons have proved to be useful as boundaries from a practical point of view. The problem is that in areas where a particular index horizon is not developed the corresponding level cannot be recognized by criteria other than those provided by the fauna.

In the central confacies belt lithological differentiation is far greater than in northern Estonia and portions of the sequence are poorly fossiliferous, so that a consistent

classification of the type used in northern Estonia is difficult to apply. In order to obtain a practical classification a special type of stratigraphical category ('topostratigraphical') was introduced (Jaanusson 1960a). For definition of such a unit both faunal and lithological criteria were used, biostratigraphical for one boundary at which the level of faunal change is easily recognizable, and lithostratigraphical for the other boundary where lithological change is conspicuous but faunal change cannot be used for various reasons to define the boundary. The aim was a classification in which stratigraphical units have the widest possible spatial extent, with boundaries that remain as synchronous as possible. It has now been shown that many of the subdivisions so defined can be followed from the autochthonous sequence of Jämtland in the north (Larsson 1973) to southern Estonia (Männil 1966), a distance of more than 1500 km along the belt. The units were originally termed formations, but because toposstratigraphical units can then be confused easily with strictly lithostratigraphical units, the term *topoformation* is here introduced for the former units. Examples of topoformations are the Segerstad Limestone, Furudal Limestone, Dalby Limestone, Skagen Limestone and Moldå Limestone. The term Moldå Topoformation (introduced without definition by Jaanusson 1973, fig. 3) is defined as the stratigraphical division between the entry of the *Chasmops extensa* fauna and the base of the Slandrom Limestone (corresponding to what previously has been termed the *Macrourus* Limestone in the nodular limestone lithofacies of the central confacies belt; type locality is the main section of Fjäckå at Moldå, 0 to 5.75 m below the base of the Slandrom Limestone). Other divisions such as the Skärlov Limestone, Folkeslunda Limestone, and Gullhögen Formation are normally defined by strictly lithostratigraphical criteria.

IMMIGRATIONS

Faunal changes discussed under this heading are characterized by the appearance of taxa not known from older beds elsewhere in the Balto-Scandian region. Moreover, the taxa enter at levels that lie within a lithologically almost uniform sequence, so that at present it is difficult to associate the faunal change with a change in lithology.

Within the region there are also numerous examples of species that appear in a confacies belt earlier or later than in another belt, or even enter the sequence at different levels in different areas of the same belt. Such differences in vertical ranges may in part be density dependent. A species may have appeared at the same time in different areas, but in some of the areas has not yet been found in the lower part of its true range because of its very low density there. In other cases metachronous appearance of a species within the region may be real, and its later appearance in any one area may have been associated with a shift in environmental conditions that moved the habitat of the species into the area. It should be stressed that appearance of a species in an area at a higher level than elsewhere within the region is not considered here to constitute an immigration. Geographically the Balto-Scandian region is small and wherever suitable ecological conditions existed a species would probably have been able to spread there. Future studies may show the existence of persistent gradients of biogeographical nature in the distribution of species within the region. Until such distribution patterns, independent of local ecological conditions, are known, it is preferable to regard faunal differentiation within the region as having been controlled by ecological and not distributional factors.

What appears to be one of the most pronounced faunal changes in the Ordovician carbonate sequence of Balto-Scandia takes place at the boundary between the Kunda and Aseri stages (base of the Viru Series) (text-fig. 8). In the central confacies belt this level corresponds to the boundary between the *Gigas* and Segerstad limestones, whose faunas are dominated by cephalopods and trilobites, with few sedentary organisms (Jaanusson & Mutvei 1953; Jaanusson 1960a; Larsson 1973). The macrofaunal change is marked by the disappearance of a number of trilobite genera, such as *Megistaspis*, *Niobe*, *Celmus*, *Pliomera* and *Cyrtometopus*, which were characteristic elements of the Balto-Scandian fauna during Kundan time. In the ostracode fauna *Aulacopsis*, *Glossomorphytes*, *Pinnatulites procera* and *Conchoprimitia erratica* disappear at this level. The new fauna appearing in the Segerstad Limestone has a low taxonomic diversity, and most of the new species belong to genera that occur in the Kunda Stage. At many places the change in fauna is not associated with a change in lithology; in fact, in many districts the boundary can scarcely be drawn on strictly lithological evidence.

In northern Estonia the Upper Kundan (Aluoja) macrofauna is more diverse than in the central belt and includes also sedentary organisms such as articulate brachiopods and bryozoans. The sedentary groups were also affected by extinction (*Antigonambonites*, *Gonambonites*, *Progonambonites*, *Ahtiella*, *Ingria* and *Productorthis* among articulate brachiopods). Again, the new fauna in the lower part of the Aseri Stage contains only a few genera that are truly new to the Balto-Scandian region.

The pronounced faunal change at the boundary between the Kunda and Aseri stages can be followed in the carbonate sequence throughout the region. The level may be close to the boundary between the *Didymograptus bifidus* and *Didymograptus murchisoni* zones of the graptolitic sequence in Scania (Jaanusson 1960b), but how precisely the two levels match is unknown. An interesting feature is that it is extinction rather than immigration of new faunal elements that characterizes the faunal change. As a result of the extinction, the fauna of the region became less provincial than before.

Series	Northern Estonia Standard stages	Central belt (Siljan district) Topostratigraphic classification	Graptolitic succession (Scania)
Viru	Kukruse	Dalby (lower part)	Nemagraptus gracilis
	Uhaku	Furuådal	Glyptograptus teretiusculus
	Lasnamägi	Folkeslund	Didymograptus murchisoni
		Seby Skärlöv	
Aseri	Segerstad		
Onniska	Kunda	Kunda	Didymograptus "bifidus"

TEXT-FIG. 8. Correlation of Lower and Middle Viruan sequences of northern Estonia, the central confacies belt (Siljan district), and Scania.

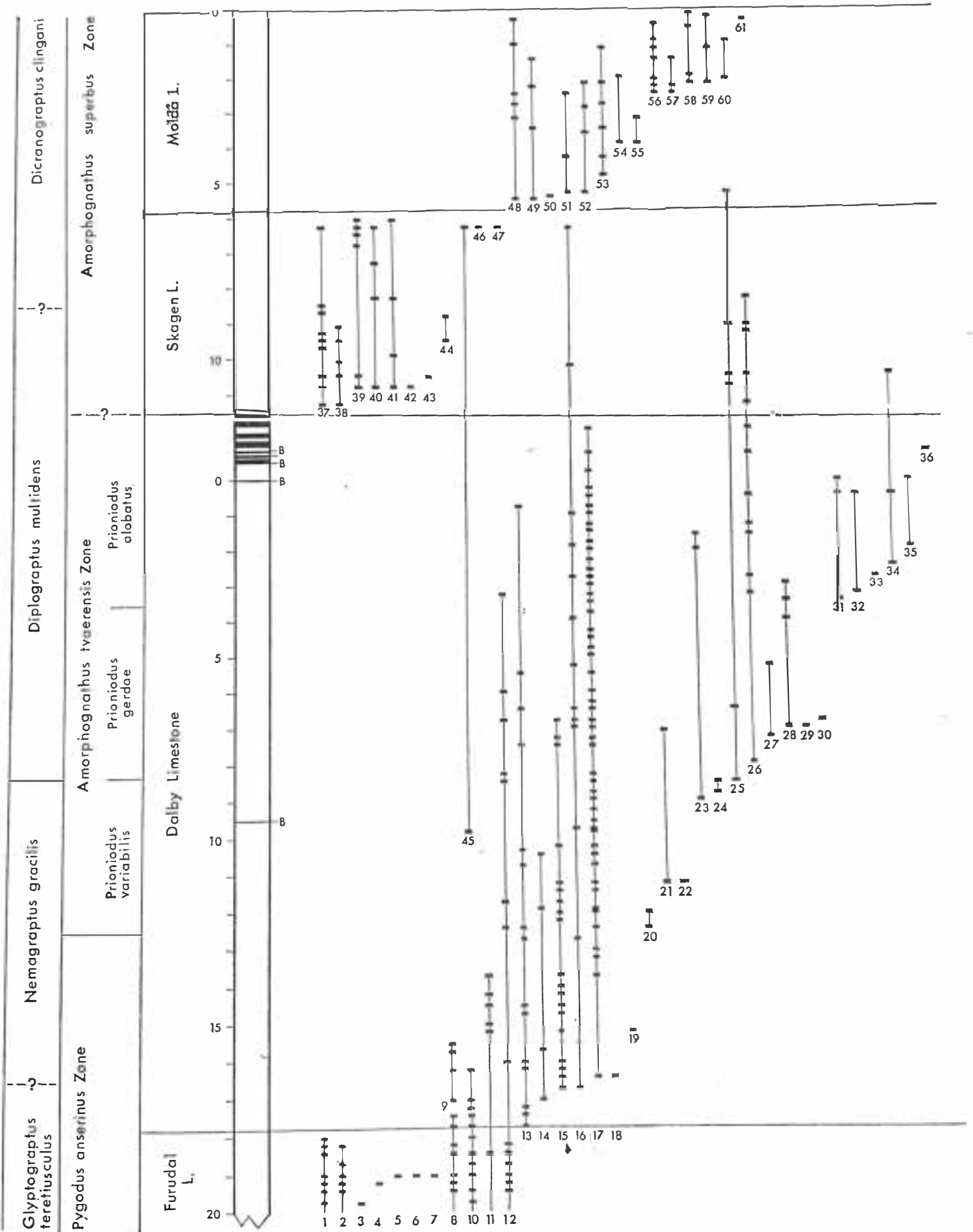
The faunal change is also associated with a considerably increased faunal differentiation between confacies belts.

Upper Aserian, Lasnamägian and Lower Uhakuan faunal changes are at present difficult to analyse. In Sweden the sequence includes divisions that are poor in macrofossils and in which ostracodes tend to be poorly preserved (much of the Lower Segerstad Limestone and Skärlov Limestone). In the macrofauna at least three faunal changes can be recognized (at the base of the Vikarby, Seby and Folkeslunda limestones). A prominent faunal change appears to take place in the boundary region between the Aseri and Lasnamägi stages but in the central belt this part of the sequence lies within the poorly fossiliferous Skärlov Limestone in which the level of the change is difficult to recognize.

In the central belt the boundary between the Lasnamägi and Uhaku stages is associated in many places with a faunal shift from calcarenites, with a mainly transported assemblage of motile organisms (trilobites, cephalopods, gastropods), to calcilitites that are poor in fossils. It is notable that where this part of the sequence is continuously in a calcilitite or mudstone lithofacies (Gullhögen Formation in Västergötland), the faunal change from Lasnamägi to Uhaku is poorly defined or not recognizable at all (Jaanusson 1965). This gives the impression that organisms associated with a mud substrate were only slightly affected by the factors that caused the faunal change elsewhere.

In northern Estonia the faunal succession in the Aseri, Lasnamägi and Uhaku stages has not yet been worked out in detail and most of the available information is 'bag-stratigraphical'.

TEXT-FIG. 9. Faunal log of the main Fjäckå section, Siljan district, Sweden. A horizontal bar represents the occurrence of at least a single specimen of a species. Sample density is about 0.2. B, bentonite beds. 1, *Sigmoopsis perpunctata* (Öpik); 2, *Steusloffia linnarssoni* (Krause); 3, *Estoniops* sp. nov.; 4, *Oepikium* sp.; 5, *Phillipsinella* sp. nov.; 6, *Uhakiella periacantha* Jaanusson; 7, *U. labrosa* (Krause); 8, *Laccochilina (Laccochilina) paucigranosa* Jaanusson; 9, *Laccochilina (L.)* cf. sp. C Jaanusson, may fall in the range of *L. (L.) paucigranosa*; 10, *Euprimites* sp. (non *locknensis*), may include two species; 11, *Uhakiella kohtlensis* Öpik; 12, *Tallinnella angustata* (Krause); 13, *Steusloffia multimarginata* Öpik; 14, *Baltonotella kuckersiana* (Bonnema); 15, *Conchoprimitia leperditioides* Thorslund; 16, *Pandera parvula* (Holm); 17, *Euprimites locknensis* (Thorslund); 18, *Uhakiella coelodesma* Öpik; 19, *Euprimites* cf. *suecicus* (Thorslund); 20, *Polyceratella kuckersiana* (Bonnema); 21, *Euprimites* sp. nov.; 22, *Sigmoopsis platyceras* (Öpik); 23, *Uhakiella granulifera* (Ulrich & Bassler); 24, *Platybolbina kapteyni* (Bonnema); 25, *Hesperidella esthonica* (Bonnema); 26, *Steusloffia costata* (Linnarsson); 27, *Bolbina* sp. nov.; 28, *Brevibolbina* sp. nov.; 29, *Oecematobolbina* sp. A; 30, *Sigmoopsis obliquejugata* (Schmidt); 31, *Platybolbina* sp. A; 32, *Tvaerenella carinata* (Thorslund); 33, *Laccochilina (Prochilina) decumana* (Bonnema); 34, *Lomatobolbina mammillata* (Thorslund); 35, *Sigmoopsis sigmoopsoides* Schallreuter; 36, *Oecematobolbina* sp. B.; 37, *Henningsmoenia gunnari* (Thorslund); 38, *Sigmobolbina cyclopa* Schallreuter; 39, *Baltonotella* sp. nov.; 40, *Platybolbina* sp. B; 41, *Ampletochilina swantia* Schallreuter; 42, *Balticella binodis* (Krause); 43, *Unisulcopleura* sp. nov. A; 44, *Ceratobolbina* sp.; 45, *Sigmoopsis rostrata* (Krause); 46, *Unisulcopleura* sp. B; 47, *Distobolbina pinna* Schallreuter; 48, *Chasmops extensa* (Boeck); 49, *Taphrorthis dalarnaensis* Hints; 50, *Oepikium flagelliferum* (Krause); 51, *Pandera migratoria* Bruton; 52, *Sigmobolbina tuberculata* Jaanusson; 53, *Pelycobolbina pelycoidea* Jaanusson; 54, *Steusloffia neglecta* Sarv; 55, *Platybolbina* sp. C; 56, *Howellites wesenbergensis* (Wysogorski); 57, *Onniella longa* Hints; 58, *Sigmobolbina camarota* Jaanusson; 59, *S. tropeota* Jaanusson; 60, *Piretella oepiki* Thorslund; 61, *Platybolbina temperata* Sarv.



The succession of faunas in post-Uhakuan Viruan beds of the central confacies belt is best exemplified by the faunal log of the main section of Fjäckå (text-fig. 9). The log is based mainly on two series of limestone samples (Jaanusson 1963*b*), one of which was also used for defining the Balto-Scandian conodont zones and subzones between the *Pygodus serrus* and *Amorphognathus ordovicicus* zones (Bergström 1971; the main Fjäckå section is the reference section for this part of the conodont zonation) as well as for description of chitinozoans (Laufeld 1967). Both sets of samples were processed for ostracodes and other fossils with a carbonate skeleton. In addition, a series of samples of calcareous mudstone intercalations between the limestone beds was processed and searched for fossils. Many of the samples yielded small articulate brachiopods (some material has been described by Hints 1973) and bryozoans but were astonishingly poor in ostracodes, while others were almost barren (particularly in the Dalby Limestone below 6 m from the complex of bentonitic beds, and in most of the Skagen Limestone). The information in the log on the vertical range of brachiopods in the Moldå Topoformation is mainly from samples of calcareous mudstone. Although the limestone samples were of appreciable size (up to 2 kg or more) the density of most macrofossils was too low to yield satisfactory information on vertical ranges from the samples alone. For this reason, this information has been complemented by a search for macrofossils, bed by bed, over many years. However, several parts of the section are poorly exposed and the amount of rock accessible to a search for macrofossils is limited. For this reason the available information on the range of large fossils is still incomplete. *Chasmops extensa* (Boeck) is the only large species included in the log.

The log shows three successive main changes in the fauna, which are here termed, in ascending order, the basal Dalbyan, the basal Skagenian, and the basal Moldån immigrations (text-fig. 12). Between the periods of faunal change occasional species do appear but they are mainly those with a low operational density. There is a cluster of species that appear in the Dalby Limestone between 7 and 9 m below the bentonitic beds, but most of these species are known from lower levels elsewhere. *Uhakiella granulifera* (Ulrich & Bassler) and *Steusloffia costata* (Linnarsson) occur in Västergötland in beds comparable to the zone of *Pygodus anserinus* (text-fig. 13; Jaanusson 1964). *Sigmoopsis obliquejugata* (Schmidt) appears in northern Estonia in the Uhaku Stage and *Hesperidella esthonica* Öpik as well as *Platybolbina kapteyni* (Bonnema) were originally described from the lower part of the Kukruse Stage (the latter has also been found in the lowermost Dalby Limestone on Öland; Jaanusson 1960*a*). The absence of these species from the lower part of the Dalby Limestone of the Fjäckå section may depend on their very low density in that portion of the section. On the other hand they may have been introduced by a faunal shift into the Siljan district later than into some other areas. A similar but somewhat less pronounced cluster of species with a low operational density appears in the Dalby Limestone between 2.0 and 3.5 m below the complex of bentonitic beds. The assemblage is dominated by species described from the Dalby beds of the Brunflo-Lockneare a in Jämtland [*Tvaerenella carinata* (Thorslund), *Laccochilina decumana* (Bonnema), *Lomatobolbina mammillata* (Thorslund)] and the Tvären area in Södermanland (*T. carinata*, *L. decumana*). The Tvären fauna includes a representative assemblage of the *Prioniodus variabilis* Subzone although a minor part of the material may be derived from the next younger subzone (Bergström 1971). In northern Estonia *L. decumana* has been reported only from the Uhaku Stage and the

lower substage of the Kukruse Stage (Sarv 1959). Thus in the Fjäckå section the appearance of these species in beds corresponding to the *Prioniodus alobatus* Subzone is due either to chance or a faunal shift.

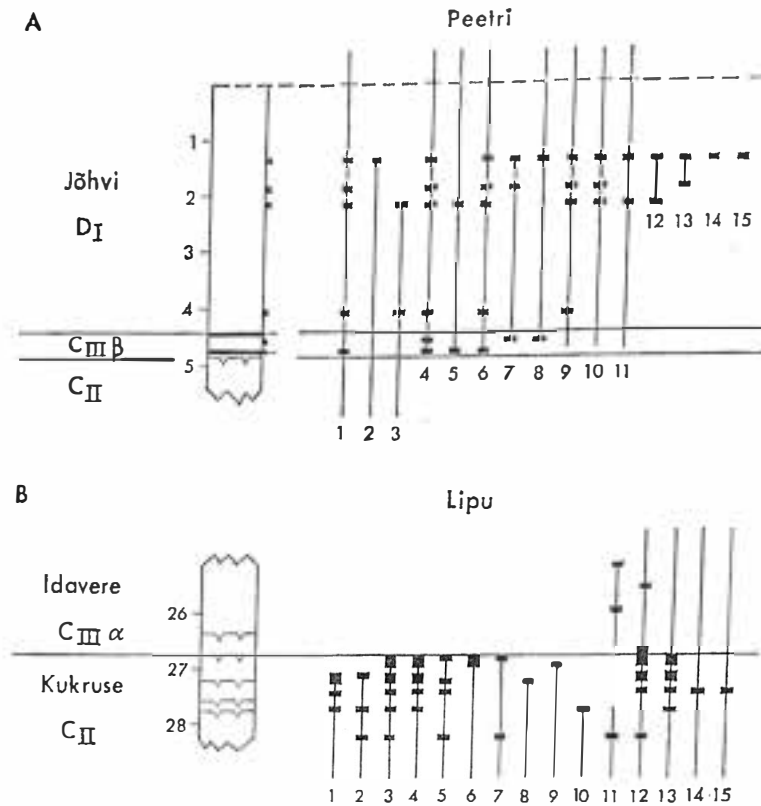
The pattern of faunal changes as exemplified by ostracodes agrees fairly well with what is known about vertical ranges of macrofossils. However, there are two exceptions. About 7 to 8 m above the base of the Dalby Limestone several new macrofossil taxa appear, most notably the plectambonitacean brachiopods *Bimuria* and *Eoplectodonta*. These two genera have a relatively high density throughout the rest of the Dalby Limestone and are not known at a lower level anywhere in the Balto-Scandian region. This mid-Dalbyan faunal change does not seem to be reflected in the ostracode faunas. About 2.5 m from the top of the Moldå Topoformation several new brachiopod taxa appear, most notably *Howellites wesenbergensis* (Wysogorski) (Linda Hints pers. comm.). This mid-Moldån faunal change also appears to be reflected weakly in the ostracode fauna (text-fig. 9). The information on post-Uhakuan Viruan faunal changes in the Siljan district agrees with what is known from the other Cambro-Silurian districts within the central confacies belt of Sweden. There the information on vertical ranges is mainly from bore-hole data (Jaanusson 1960a, 1962, 1965, and unpublished) and less complete owing to the small sample size.

The base of the Dalby Topoformation appears to correspond roughly to the base of the Kukruse Stage in northern Estonia. However, in contrast to the central belt, the faunal change at this level in northern Estonia is blurred and not easy to define. Many species of ostracodes and articulate brachiopods cross the boundary between the stages, and species appearing in the Kukruse Stage commonly have low densities. The trilobite species are mainly different in the Uhaku and Kukruse stages but, as most of these occur with low densities, their exact vertical range is difficult to determine. No detailed faunal log is available from the boundary region between these stages in northern Estonia.

In the post-Kukrusean Viruan strata faunal development is very different between northern Estonia and Sweden. The differences are so great that despite the short geographical distance serious problems in correlating the strata still exist. No uniform chronostratigraphical classification at the stage level can be applied at present.

In northern Estonia the succeeding conspicuous faunal change takes place at the base of the Idavere Stage (CIII). In the macrofauna the change is well defined, particularly with regard to trilobites and articulate brachiopods. Of the seventeen trilobite species known from the Upper Kukruse Stage (CII β) only three continue into the Lower Idavere Stage (Ojamaa Beds, CIII α) and of the thirty-one species of articulate brachiopods in CII β only four (subspecies included) are common to CII and CIII. In the Ojamaa Beds seventeen species of trilobites and twenty species of articulate brachiopods appear. Rõõmusoks (1956) emphasized the importance of the faunal change at the boundary between the Kukruse and Idavere stages by drawing a subserial boundary at that level.

The majority of ostracode species known from the Kukruse Stage disappear at the boundary with the overlying Idavere Stage (text-fig. 10B; Nölvak 1972) but the lower Idavere Stage is extremely poor in palaeocope ostracodes and its ostracode fauna is therefore almost unknown. The ostracodes became abundant again in beds associated with bentonites in the upper part of the upper Idavere Stage (text-fig. 11; Sarv 1960).



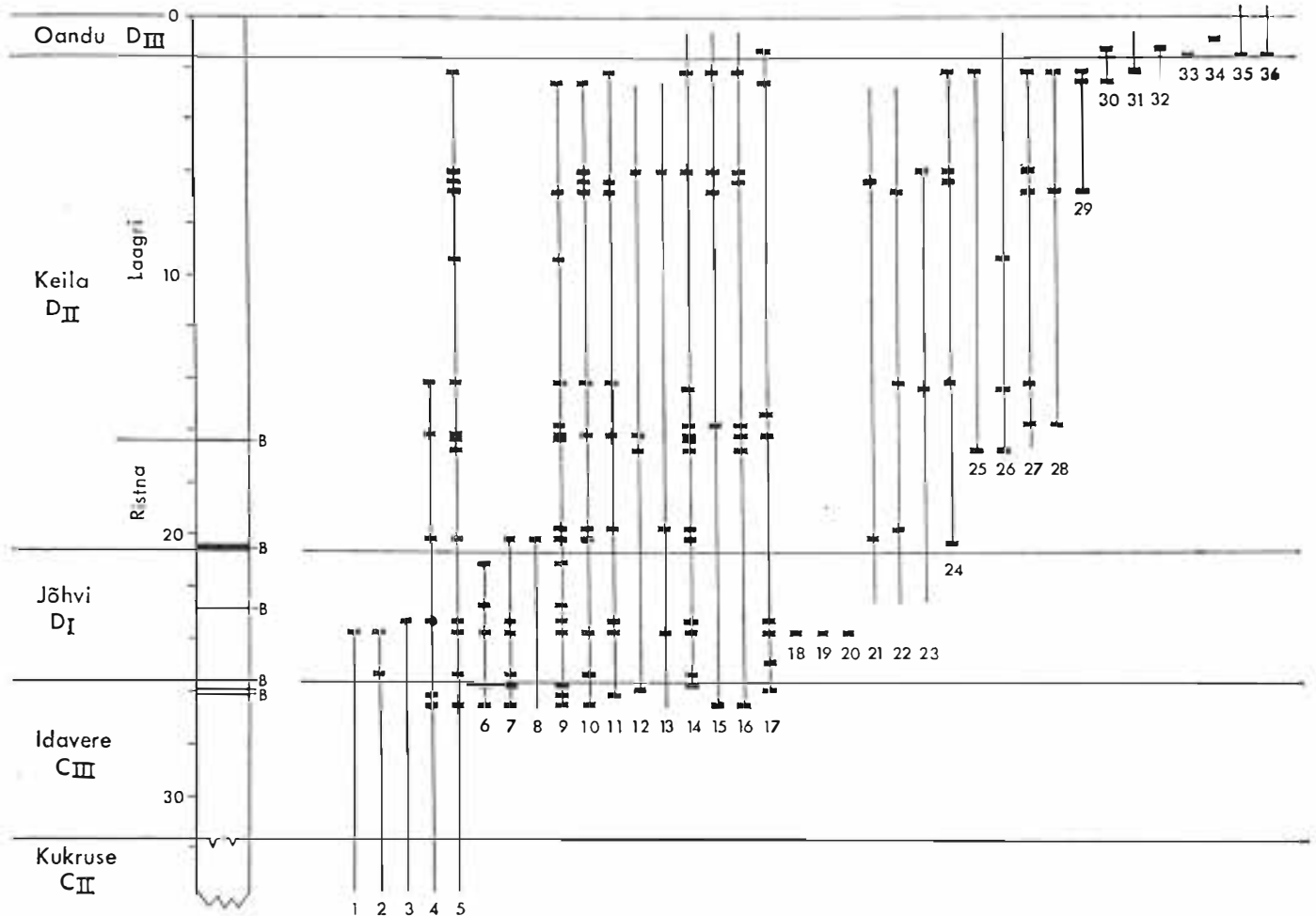
TEXT-FIG. 10. A, faunal log (ostracodes) of the upper Idaverean and lower Jõhviaan strata at Peetri, northern Estonia. In that section the lower Idaverean Ojamaa Beds (C_{III}α) are missing. B, bentonite beds. 1, *Sigmoopsis rostrata* (Krause); 2, *S. cornuta* (Krause); 3, *Sigmobolbina variolaris* (Bonnema); 4, *Tetrada memorabilis* (Neckaja); 5, *Bichilina prima* Sarv; 6, *Polyceratella aluverensis* Sarv; 7, *Severobolbina severa* (Sarv); 8, *Pentagona prominescã* (Sarv); 9, *Henningsmoenia? auricularis* (Krause); 10, *Pedomphalella egregia* (Sarv); 11, *Pseudostrepula asymmetrica* (Neckaja); 12, *Disulcina indeterminata* Sarv; 13, *Ceratobolbina allikuensis* (Sarv); 14, *Henningsmoenia? reticulata* (Sarv); 15, *Piretella* sp. indet.

B, faunal log (ostracodes) of the uppermost Kukrusean and lower Idaverean (Ojamaa Beds) in the Lipu bore-hole, north-eastern Estonia, based on data in Nõlvak 1972. 1, *Conchoprimitia sulcata* (Krause); 2, *Tallinnopsis perplana* (Neckaja); 3, *Ceratobolbina monoceratina* (Jaanusson); 4, *Sigmoopsis platyceras* (Öpik); 5, *S. obliquejugata* (Schmidt); 6, *Polyceratella bicornis* (Neckaja); 7, *Platybolbina kapteyni* (Bonnema); 8, *Carinobolbina estona* (Öpik); 9, *Pseudostrepula kuckersiana* (Bonnema); 10, *Chilobolbina dentifera* (Bonnema); 11, *Polyceratella kuckersiana* (Bonnema); 12, *Sigmobolbina* cf. *variolaris* (Bonnema); 13, *Brevibolbina amabilis* (Neckaja); 14, *Tallinnopsis calkeri* (Bonnema); 15, *Hesperidella esthonica* (Bonnema).

There the ostracode fauna (the *Bichilina prima*–*Tetrada memorabilis* assemblage; cf. also Schallreuter 1969) has only eight species in common with the Kukruse Stage. In these beds sixteen species appear and many range through most of the rest of the Viruan sequence in northern Estonia. None of the species and only some of the genera have been found in the central confacies belt of Sweden.

In the central belt the level of the boundary between the Kukruse and Idavere stages falls somewhere within the Dalby Limestone, but there no faunal change of a comparable magnitude has been recognized. Männil (1966) suggested that in the main Fjäckå section the level corresponding to the Kukruse–Idavere boundary is about 6.5 m below the bentonitic complex. He found further support for this suggestion from the ranges of chitinozoan species (Männil 1972; see also Nõlvak 1972). In the central confacies belt of Sweden no clear faunal change can be recognized at this level, neither in the

macrofauna nor in the ostracodes. Bergström (1971) suggested that the level of the Kukruse–Idavere boundary is within the middle part of the *Prioniodus variabilis* Subzone (that is, about 10·0 to 10·5 m below the bentonitic complex in the main Fjäckå section). This suggestion was based on an examination of conodonts in some samples from northern Estonia, including those from the Ojamaa Beds of Idavere quarry. This level may not be very different from the level of mid-Dalbyan macrofaunal change; if so, *Eoplectodonta* appeared roughly contemporaneously in northern Estonia and Sweden.



TEXT-FIG. 11. Composite faunal log (ostracodes) for north-central Estonia based on information from the Seljaküla, Mustla, Atla and Äiamaa bore-holes (Rõõmusoks 1970), the section at Peetri (text-fig. 10A), and some other sources, projected into the section of the Atla bore-hole. B, bentonite beds. 1, *Sigmoopsis cornuta* (Krause); 2, *Sigmobolbina* cf. *variolaris* (Bonnema); 3, *Sigmoopsis* sp. nov.; 4, *Hesperidella esthonica* (Bonnema); 5, *Sigmoopsis rostrata* (Krause); 6, *Severobolbina severa* (Sarv); 7, *Tetrada memorabilis* (Neckaja); 8, *Bolbilithis altonoda* (Sarv); 9, *Bichilina prima* Sarv; 10, *Henningsmoenia? auricularis* (Krause); 11, *Pentagona prominesca* (Sarv); 12, *Kiesowia frigida* Sarv; 13, *Pseudostrepula asymmetrica* (Neckaja); 14, *Polyceratella aluverensis* Sarv; 15, *Consonopsis consona* (Sarv); 16, *Tallinnopsis iewica* (Neckaja); 17, *Pedomphalella egregia* (Sarv); 18, *Disulcina indeterminata* Sarv; 19, *Ceratobolbina allikuensis* (Sarv); 20, *Henningsmoenia? reticulata* (Sarv); 21, *Carinobolbina carinata* (Krause); 22, *Pseudotallinnella scopulosa* Sarv; 23, *Ctenonotella bidens* (Krause); 24, *Bolbina major* (Krause); 25, *Tallinnopsis grandis* Sarv; 26, *Leperditella? prima* Sarv; 27, *Tallinnopsis ovalis* Sarv; 28, *Neotsitrella longata* (Sarv); 29, *Polyceratella spinosa* Sarv; 30, *Bichilina? posterovelata* Sarv; 31, *Pseudostrepula estona* Sarv; 32, *Platybolbina temperata* Sarv; 33, *Moeckowia rava* (Sarv); 34, *Uhakiella oanduensis* Sarv; 35, *Bolbina rakverensis* Sarv; 36, *Sigmoopsis granulata* Sarv.

No detailed faunal log is available from the upper part of the Viru Series of northern Estonia except for that from the Äiamaa boring (Sarv 1960). As a partial compensation, a faunal log is presented here based on six samples of argillaceous beds collected by the writer from the Upper Idavere and Jõhvi beds in the exposure at Peetri, west of Tallinn (text-fig. 10A). Moreover, a composite ostracode log (text-fig. 11) has been compiled from various information and projected into the section of the Atla boring, north-central Estonia (data from the Äiamaa boring, published by Sarv in 1960, could not be used because the precision of published vertical ranges was considered to be unsatisfactory). Bentonite beds could safely be used as index horizons. The value of such a combined log is questionable and it should be stressed that no single core or exposure will show exactly this pattern of vertical ranges. However, the log seems to convey a fairly realistic picture of faunal changes within this part of the sequence. One of its advantages compared with an ordinary 'bag-stratigraphical' presentation of data is that it also gives an impression of relative densities of species.

The composite log (text-fig. 11) shows that many of the ostracode species that enter in the Idavere Stage not only range through the Jõhvi and Keila stages but, together with *Sigmoopsis rostrata* (Krause), belong to the species with highest density throughout this part of the sequence. This puts a fairly uniform imprint on the ostracode fauna of much of the Upper Viruan sequence of northern Estonia.

The faunal change in the Jõhvi Stage takes place somewhat above the lower boundary of the stage as currently defined (1.5 to 2.0 m above the base according to Männil 1963 and Rõõmusoks 1970). At about this level nine species of ostracodes appear but these species mostly have low densities, making it difficult to recognize the faunal change in cores (Sarv 1960). Among the twenty-four species of ostracodes recorded from the upper Idavere Stage as many as seventeen have been found in the Jõhvi Stage. Twenty-eight species of articulate brachiopods are known from the upper Idavere Stage and seventeen of these continue also into the Jõhvi Stage (Rõõmusoks 1970). The faunal change is better defined in the macrofauna than in the ostracodes, mainly because of the appearance of the large fossils *Clinambon anomalus* (Schlotheim) and *Chasmops maximus* (Schmidt), which occur with moderate densities. On the whole, the magnitude of the faunal change between the Idavere and Jõhvi stages is much less than that at the base of the Idavere Stage.

None of the species entering the Jõhvi Stage in northern Estonia is known from the central Swedish confacies belt. Männil (1966) suggested that if the thickest bentonite in the main Fjäcka section is comparable to the main bentonite bed in Västergötland and on the Baltic islands, then the probable equivalents of the Jõhvi Stage at Fjäcka are within the bentonitic complex and have a maximum thickness of 0.4 m. This correlation was influenced strongly by his solution of the intricate problem of how to correlate individual beds of bentonite within Sweden as well as between Sweden and north-western Estonia. Later Männil (1972), on the evidence of vertical ranges of chitinozoan species, suggested that in the Fjäcka section the level corresponding to the base of the Jõhvi Stage is about 4 m below the bentonitic complex. In this case, according to him, the portion of the section corresponding to the Idavere Stage is only about 2.5 m thick (4.0 to 6.5 m below the bentonitic complex at Fjäcka). At about 4 m below the bentonites no clear faunal change can be recognized at Fjäcka.

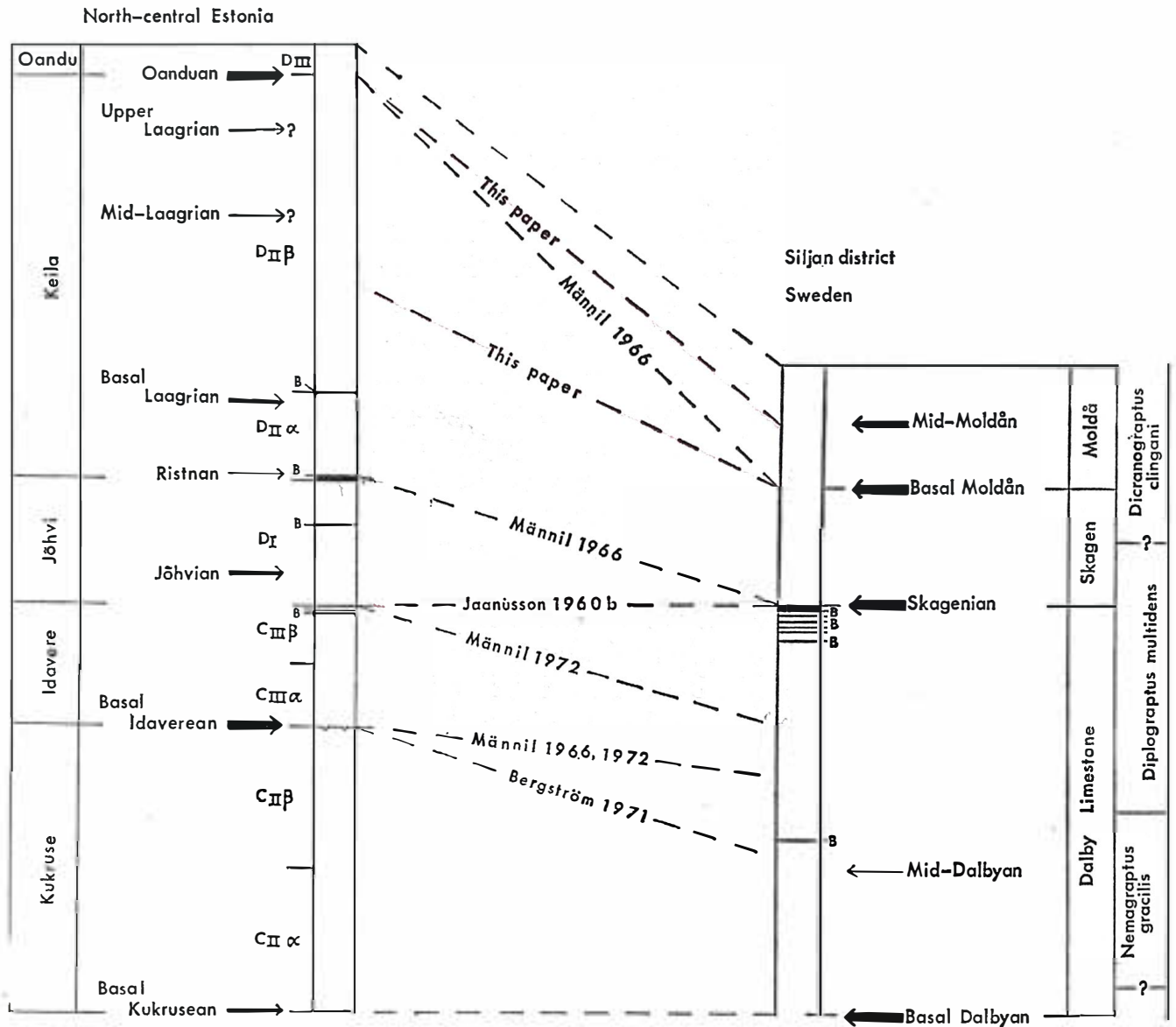
The basal Skagenian change in the ostracode fauna can be followed in the whole

central Balto-Scandian confacies belt. In the Livonian Tongue a level possibly somewhat above the entrance of the Skagenian ostracodes was considered by Männil (1966) as that of the lower boundary of the Jöhvi Stage. This correlation is based on a comparison of the sequence in bore-holes from northern to southern Estonia. Thus the interesting situation arises that, if the correlations proposed by Männil are correct, the entrance of the Skagenian fauna takes place at two different levels—at the upper boundary of the Jöhvi Stage in the central Swedish confacies belt and at about the base of the Jöhvi Stage in the Livonian Tongue. That the basal Skagenian invasion reached the Livonian Tongue a stage earlier than central Sweden is of course possible and then of great theoretical interest. However, as the correlation is still uncertain both between northern Estonia and central Sweden, as well as between northern and southern Estonia, a contemporaneous appearance of the basal Skagenian fauna is not excluded.

Männil (1958) suggested that in the Keila Stage three periods of immigrations can be distinguished: (1) at the base of the Stage, (2) at the base of the upper (Laagri) Substage, and (3) somewhere in the middle of the upper Substage. The faunal change at the base of the Keila Stage (here termed the Ristnan faunal change) is poorly reflected in the ostracode faunas (text-fig. 11) and is not particularly well defined even in the macrofauna (Männil 1963). The base of the Stage is probably difficult to recognize in areas where the index bentonite bed is missing (Männil 1963). The faunal change at the base of the upper Substage (the basal Laagri immigration; according to evidence from ostracodes probably somewhat below the index bentonite bed, cf. text-fig. 11) is defined in the ostracode fauna as well as in the macrofauna. However, the change in the fauna is not particularly pronounced and may be difficult to recognize in areas in which the incoming species have low densities. The level and nature of the faunal change within the upper Substage of the Keila Stage is at present difficult to define. There may exist two separate faunal changes instead of one, the first at some level in the middle of the Substage (the mid-Laagri faunal change) and the second in the upper part of the Substage (the upper Laagri faunal change). The first change may be associated with the appearance of *Horderleyella kegelensis* (Alichova) but does not seem to be reflected in the ostracode fauna. The uppermost part of the Keila Stage is marked by the appearance of several ostracode species, most of which continue into the Oandu Stage. This change appears to be poorly reflected in the macrofauna. These faunal changes within the Keila Stage give the impression of successive appearances of species rather than of well-defined immigrations; the general picture is also blurred by regional differences in the density of species within the belt.

Männil (1966) suggested that the main bentonite bed at the boundary between the Dalby and Skagen limestones of Sweden corresponds to the index bentonite bed at the base of the Keila Stage. In this case the Skagen Limestone is of Keilan age and the faunal change at the base of the Keila Stage is comparable to the basal Skagenian immigration. However, this does not agree with the horizon of the basal Skagenian immigration in the Livonian Tongue where the faunal change is supposed to occur close to the base of the Jöhvi Stage (Männil 1966).

In northern Estonia a major faunal change takes place at the base of the Oandu Stage. This immigration introduces a great number of taxa into the area and affects all phyla. Of particular interest is the appearance of *Chasmops extensa*, which is a common species in the central confacies belt as well as in the Oslo region, and has been recorded



TEXT-FIG. 12. Proposed correlations in Middle and Upper Viruan strata between northern Estonia and the central confacies belt of Sweden (exemplified by the Siljan district). Relative intensity of faunal changes is indicated by thickness of arrows. B, bentonite beds. For vertical scale see text-fig. 11.

also from Shropshire (Dean 1961) and possibly from the central Urals (*Chasmops* aff. *maxima* of Anzygin 1970). In the central confacies belt of Sweden this species appears at the base of the Moldå Topoformation (text-fig. 9). Männil (1963) first suggested that the base of the Moldå ('*Macrourus*') Beds might correspond to that of the upper (Laagri) Substage of the Keila Stage. Later (1966) he tentatively correlated the base of the Moldå Beds with that of the Oandu Stage, in which case the basal Moldån immigration would correspond to the immigration at the base of the Oandu Stage. The latter immigration is normally best characterized by the appearance of *Howellites wesenbergensis*, which is an abundant species in most sections and cores through the Oandu Stage in northern and southern Estonia as well as in Lithuania. In the main Fjäckå section *H. wesenbergensis* and *Onniella* sp. nov. (restricted to the Oandu Stage in southern Estonia and Lithuania) occur only in the upper part of the Moldå Topo-

formation (text-fig. 9; Linda Hints pers. comm.), which suggests that the Oandu immigration may be roughly contemporaneous with the mid-Moldån faunal change. A hint on a possible correlation of the basal Moldån immigration is given by the faunal log from the Pajavonys bore-hole in Lithuania (Männil *et al.* 1968, fig. 3). In that core *C. extensa* enters the sequence far below *H. wesenbergensis* and other species characteristic of the Oandu Stage, at a level now regarded as lying within the upper part of the Keila Stage, indicating that it spread to northern Estonia later than to the central belt.

The approximate levels of the beginning of faunal changes in the Middle and Upper Viruan sequence of northern Estonia and the central Swedish confacies belt (Fjäckå section) are shown in text-fig. 12. The correlation is still uncertain in many points, to such a degree that the writer is not prepared to present a formal correlation table. Additional detailed faunal logs are needed, particularly from areas transitional between the confacies belts, and much additional taxonomic work is required on various groups.

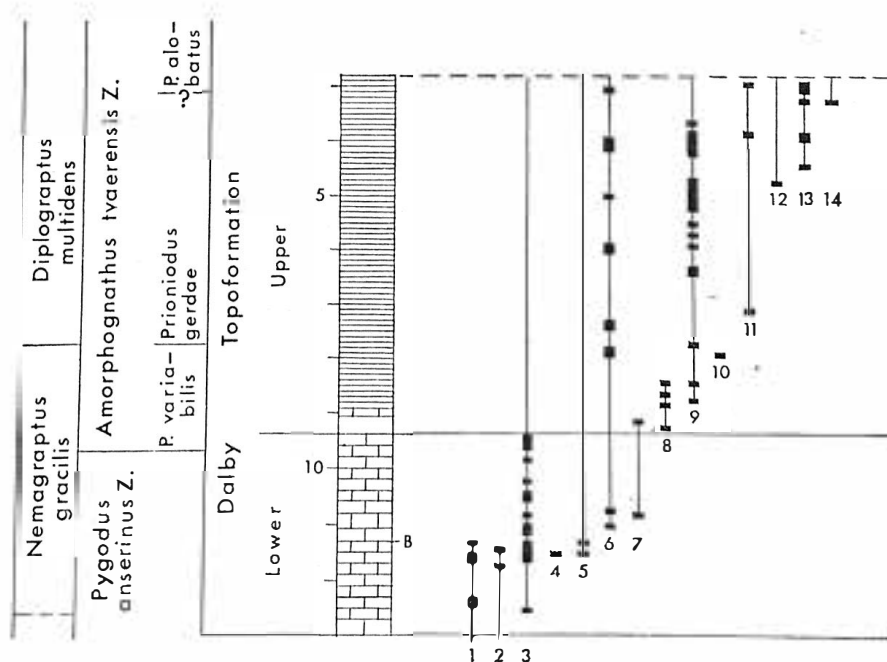
It is evident that the relative intensity of some main faunal changes in the central confacies belt has no contemporaneous counterpart in northern Estonia, and vice-versa. Indeed, some major faunal changes in one belt do not seem to be reflected at all in the other. It is possible that in this case the intensity of the faunal change is too low to recognize the horizon of the change; that is, the faunal change may have affected only species with very low densities. In any case, the evidence presented indicates that in benthonic faunas changes of immigration type are not always comparable even within a region. This in turn suggests that each confacies belt was occasionally affected by changes in environmental factors that were specific to the belt and scarcely influenced the fauna of the other belts.

In Scania the Middle Ordovician graptolitic succession is one of the most complete in the world and has been studied in detail by Ekström (1937), Hede (1951), Nilsson (unpublished data) and others. The known data suggest a number of successive immigrations separated by periods during which the taxonomic composition of the graptolite fauna was fairly stable. Correlation of the levels of changes in the faunas with those in the shelly sequence cannot be expected to be exact. However, for some horizons the correlation between the graptolitic and shelly sequences is approaching reasonable precision (for a summary see Bergström 1973). Some changes in the shelly faunas do not seem to be reflected in the graptolites, e.g. the basal Lasnamägian and the Skagenian immigrations. The boundary between the *Glyptograptus teretiusculus* and *Nemagraptus gracilis* zones may correspond roughly to the base of the Dalby Topoformation (Bergström 1971, 1973) but how exactly these two levels match is difficult to say because of a break at the base of the *gracilis* Zone in Scania. The boundary between the *gracilis* and *Diplograptus multidentis* zones, on the other hand, falls within the shelly sequence at a level about 9.5 m below the complex of bentonitic beds in the Fjäckå section (Bergström 1971), where no changes in shelly faunas can be recognized in the central confacies belt, nor in northern Estonia. The level of the boundary between the *multidentis* and *Dicranograptus clingani* zones is probably somewhere within the Skagen Limestone (Bergström & Nilsson 1974). If this is so, neither the basal Moldån nor the mid-Moldån faunal change has any distinct counterpart in the graptolite faunas. Thus it seems that in general the levels of change in graptolite faunas do not correspond

to those in shelly faunas. The environmental events that caused planktonic graptolite faunas to change were apparently largely different from those that affected benthonic faunas.

FAUNAL SHIFTS

Distinction between immigrations and faunal shifts is not always sharp. An environmental change that causes an immigration of species into a region may introduce species that previously lived in another part of the region. Likewise, a change in the physical environment that causes a shift of the habitats within the region may be associated with immigration of species into the region. The latter is particularly true if the environmental change introduces habitats that did not previously exist in the region. However, the source of taxa involved in immigration is normally in areas outside the region, whereas that of taxa introduced by a faunal shift is in other areas within the region, provided that the region is biogeographically homogeneous. This distinction can be illustrated by the following example. At present the central part of



TEXT-FIG. 13. Faunal log from the Dalby Topoformation of the Norra Skagen bore-hole, Västergötland, Sweden, showing a faunal shift associated with change in lithology from limestones of the lower member to mudstones of the upper member. B, bentonite bed. 1, *Tallinnella angustata* (Krause); 2, *Laccochilina* (*Laccochilina*) sp.; 3, *Euprimites locknensis* (Thorslund); 4, *Conchoprimitia* cf. *leperditoides* Thorslund; 5, *Steusloffia* cf. *costata* (Linnarsson); 6, *Conchoprimitia* cf. *conchoides* (Hadding); 7, *Uhakiella granulifera* (Ulrich & Bassler); 8, *Nileus* sp. nov.; 9, *Parapyxion subovatum* (Thorslund); 10, *Hippula cetona norra* Schallreuter; 11, *Pyxion kinnekullensis* Thorslund; 12, *Actinochilina suecica* (Thorslund); 13, *Parapyxion* sp. nov.; 14, *Spinopleura spiniger* (Lindström).

the North Sea lacks a littoral fauna because it lacks a littoral environment. If a littoral environment were to appear there, for instance along the coast of a small island, it would soon become inhabited by the general littoral fauna of the region such as that existing in neighbouring areas. In fact, such a process is probably already in progress on pillars of the off-shore drilling platforms. The process is comparable to a faunal shift as here understood. If, on account of an increase in temperature, Lusitanian species should move into the North Sea (as happened during a short period of the Quaternary Epoch), the faunal change would involve immigration as defined in this paper. In Ordovician deposits the insufficient knowledge of ranges, spatial as well as vertical, of various taxa imposes problems when analysing faunal changes. For this reason it was found useful to use the term faunal shift provisionally for all changes in benthonic faunas that are demonstrably associated with a change in lithology. A change in physical properties of the substrate is, apart from change in depth, the most common environmental factor causing faunal shifts in benthonic faunas.

In several areas of the central Balto-Scandian confacies belt the basal Dalbyan immigration is associated with a conspicuous faunal shift, which roughly follows the change from calcilitites to calcarenites as defined by the present writer; that is, from less to more than about 20% skeletal sand grains in thin section (Jaanusson 1952; in terms of soft sediment this value possibly corresponds to about 40% skeletal sand grains by weight, Jaanusson 1972). The basal Dalbyan immigration itself is largely independent of lithology. It is within a calcilititic sequence in the Siljan district (Jaanusson 1963*b*) and Västergötland (Jaanusson 1965) and in a uniform calcarenitic sequence on northern Öland (Jaanusson 1960*a*). In the Siljan district the change from calcilitites to calcarenites takes place about 2.5 to 2.7 m above the appearance of the first elements of the Dalbyan fauna (Jaanusson 1963*b*). The change is associated with the appearance of numerous cystoids (in particular *Echinosphaerites*), relatively large articulate brachiopods, and trepostomate bryozoans. Carbonate mud was evidently too soft a substrate for sedentary organisms of some size, particularly those with a recumbent mode of life. When the content of sand grains increased, the physical properties of the bottom became suitable for large sedentary organisms. The composition of the macrofauna changed accordingly, from an assemblage dominated by trilobites to one dominated by cystoids. In northern Estonia, assemblages dominated by articulate brachiopods and bryozoans developed in Lasnamägian time or even earlier. The faunal shift in the Dalby Limestone introduced a similar assemblage to central Sweden. As a result, many taxa appear in the Dalby Limestone of the Siljan district that existed much earlier in northern Estonia, at least since Uhakuan time (*Oepikina*, *Oxoplecia*, *Paucicrura*, *Platystrophia*, *Hesperorthis*, *Orthisocrania* and others). Without a thorough taxonomic study it is difficult to say how many of these taxa are identical at the species level to those in the Uhaku Stage of northern Estonia. However, some such species do occur [e.g. *Oxoplecia dorsata* (Hisinger), *Platystrophia dentata* (Pander)].

Another example of a faunal shift is from the base of the upper member of the Dalby Topoformation in parts of Västergötland. On Kinnekulle and Mösseberg the lowermost part of the Topoformation is dominantly calcilititic and is overlain by a sequence of dark mudstones (Jaanusson 1965). The limestone contains an assemblage that is not very different from that of the Dalby Limestone in many other Cambro-

Silurian districts of Sweden. In the mudstones new ostracodes appear (text-fig. 13) that are unknown in the Dalby Topoformation outside Västergötland but which are present in contemporaneous shales and mudstones of Scania. The shift in the ostracode fauna largely follows the change in lithology and is accentuated by the almost complete disappearance of the normal Dalbyan assemblage prevailing in the limestone below. This assemblage reappears close to the top of the Dalby Topoformation where the carbonate lithology also reappears (Jaanusson 1965, fig. 1).

CONCLUSIONS

The composition of marine faunas has changed with time but, although faunal successions have been widely used for stratigraphical purposes, few attempts have been made to analyse faunal changes in detail. Normally a fauna does not change continuously or randomly with time. In many instances a short period of faunal change, characterized by immigration of species not known in earlier beds within a region, is followed by a much longer period during which the taxonomic composition of the fauna remains fairly stable. In routine biostratigraphical correlations it is usually assumed that such a faunal change is roughly contemporaneous within a region. This is true in many cases, and such a faunal change—a response to a widespread event in the physical environment—is an important biostratigraphical tool. Evidence presented in this paper indicates that in regions with a strong spatial zonation, probably of ecological nature, benthonic faunas changed independently at times within each zone, suggesting that each major zone was then affected by environmental changes that were specific to the zone. In such cases correlation between environmental zones (confacies belts) presents great problems.

Typical faunal changes of immigration type are not clearly associated with a change in lithology. Faunal changes which are dependent on lithological change, and thus on physical properties of substrate among other factors, mostly reflect a shift of habitats within a region. Such a faunal change (faunal shift) is frequently more radical than a faunal change of the immigration type, and it also presents problems in correlation if not properly understood.

The main tool for studying faunal dynamics (faunal changes and associated processes) is the faunal log. The effectiveness of the tool depends mainly on the state of taxonomic knowledge of the taxa involved, the size of the samples and the sample density. A reconstruction of faunal dynamics should normally be one of the first steps in a palaeoecological analysis of a faunal sequence.

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DISCUSSION

M. Kay. Dr. Jaanusson referred to the Moscow Basin on his maps. It may be of interest that the North American plate in the Palaeozoic seemed to be distinctive in bearing basins which subsided much more deeply in a constant position through much or all of the Era than those on other plates. Palaeomagnetic evidence appears to confirm this. The Michigan Basin, the type autogeosyncline, exemplifies this, for it subsided about 5 km. I have been led to believe that such basins are lacking in the Palaeozoic of other plates. This has been interpreted to mean that the North American plate was linked to the mantle during the Era, and that other plates moved towards it (*Nature, Lond.*, 24 June 1974).