

Diversification patterns in the clitambonitoid brachiopods of the Ordovician of Baltoscandia

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Two intervals of clitambonitoid diversification followed by major extinctions have been recorded in the Ordovician rocks of Baltoscandia, one during the Arenig and a second in the mid Caradoc. The Arenig radiation was characterized by high origination and extinction rates of both genera and species associated with the development of carbonate environments across the region. In addition the migration of numerous stocks of clitambonitoids out of Baltica to a number of other palaeocontinents occurred during this diversity peak during the Arenig, together with the spread of the majority of genera into a range of more local environments. A marked extinction in the Early Llanvirn coincided with shifts in sedimentation patterns whereas the diversity hike in the Mid Caradoc reflects the diversification of clitambonitoid species in both inner and outer shelf environments. The later Caradoc extinction coincided with an extensive eustatic regression event and the major restructuring of the ecosystem and brachiopod fauna. The final extinction of Baltic clitambonitoids in the late Ashgill was gradual and probably reflected an increasing dependence on more restricted niches.

Key words: Brachiopods, Ordovician, Baltoscandia, Clitambonitoidea, biodiversity.

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The Clitambonitoidea is one of the most characteristic groups of Baltic fossils (Jaanusson 1973a; Williams 1973), participating in a spectrum of brachiopod-dominated associations within the various confacies belts across Baltica during the Ordovician (Jaanusson 1973b). The clitambonitoids were widely distributed across many different environments in the Baltoscandian region, occurring, for example, in the shales of the deeper-water facies of the Oslo Basin, Norway, in the red-coloured carbonates of Latvia, northern Russia and Sweden, and most abundantly in the grey-coloured shallow-water facies carbonate rocks of Estonia. Although changes in the diversity of the Baltic brachiopod fauna as a whole are relatively well studied (Rõõmusoks 1967, 1970; Jaanusson 1973a, 1976, 1979, 1984), the diversification patterns of the clitambonitoid brachiopods are poorly known despite their high profile at many horizons and their excellent stratigraphical record across the entire region. The present study addresses the diversification of this group of predominantly Baltic Ordovician brachiopods, tracking their development in the Baltoscandian region through time and space.

Data and methods

The Ordovician superfamily Clitambonitoidea comprises two families, the Clitambonitidae and the Gonambonitidae. Both families attained their greatest diversity in Baltoscandia. The oldest known clitambonitoids, with the exception of *Atelelasmoidea* from the Arenig of South China (Rubel & Wright 2000), occur in Baltoscandia. During a rapid diversification during the early Arenig in Baltica (Fig. 1), several clitambonitoids migrated to North America, Avalonia and Siberia (Rubel & Wright 2000). The present study is based mainly on published data on the Ordovician of the Baltic (Öpik 1930, 1932, 1934, 1939; Alikhova 1953, 1969; Rõõmusoks 1970; Rubel 1963; Spjeldnæs 1978; Harper 1986; Rubel & Popov 1994; Hints & Rõõmusoks 1997; Tinn 1998; Vinn & Spjeldnæs 2000; Harper & Hints 2001; Hints & Harper 2003). The known stratigraphical distributions of all genera and species have been plotted within a framework that includes the 16 Baltic regional chronostratigraphical intervals (Baltic stages) from the lower Arenig to the upper Ashgill (Figs 1, 2). The correla-

Ashgill	Porkuni
	Pirgu
	Vormsi
Caradoc	Nabala
	Rakvere
	Oandu
	Keila
	Johvi
	Idavere
	Kukruse
Llanvirn	Uhaku
	Lasnamägi
	Aseri
Arenig	Kunda
	Volkhov
	Latorp

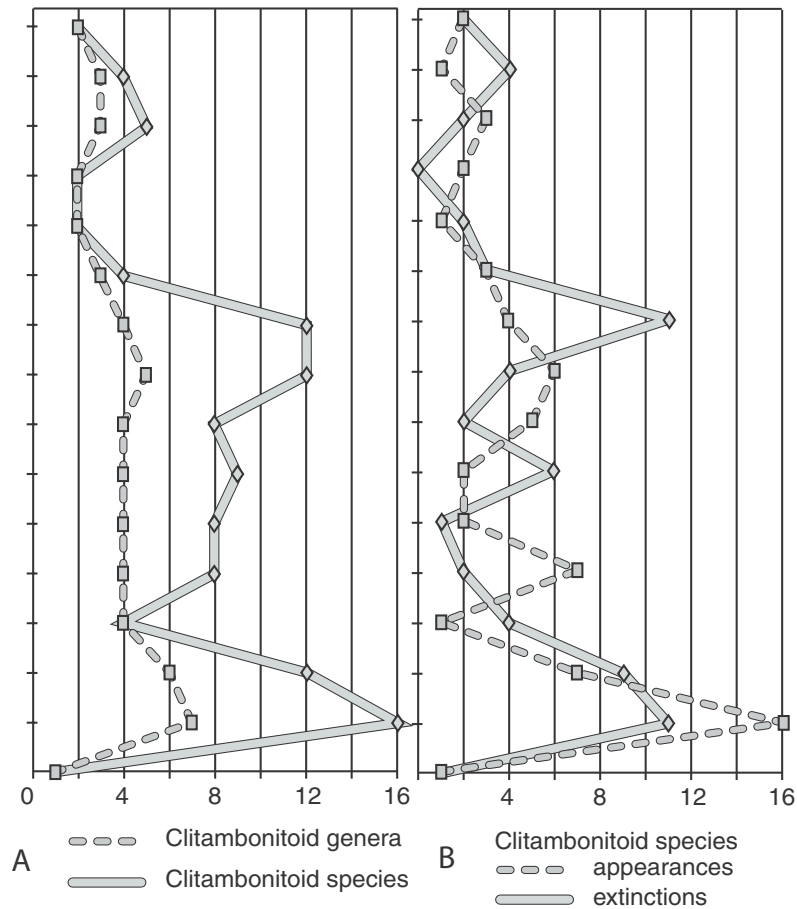


Fig. 1. Diversity of Baltic Ordovician clitambonitoids: A. Standing diversity counts of genus and species diversity. B. Appearances and extinctions of clitambonitoid species.

tions of Baltic stages with the British standard follow Fortey *et al.* (2000).

The systematic framework is mainly that of the revised Treatise (Rubel & Wright 2000), with the exception of the genus *Lacunarites* which is considered here to belong to the gonambonitids on the basis of its pseudopunctuation and radiate dorsal adductor field. The representatives of the genera *Antigonambonites* and *Raunites* are not included within clitambonitoids because of a possible origin within the Billingselloidea rather than the Protorthoidea (see Vinn & Rubel 2000; Popov *et al.* 2001). For the purposes of frequency counts, all valid subspecies are considered here as separate taxa. In addition, *Kullervo* species from the Caradoc (Jõhvi-Keila stages) of the Oslo Region (Vinn & Spjeldnæs 2000), described as *cf.* or *aff.* are regarded here as separate taxa as they are clearly not conspecific with stratigraphically-older taxa (Uhaku-Jõhvi stages) from Estonia.

The basin profiles used in the illustrations (Fig. 3) are generalizations based on Jaanusson (1973b) with some details of the North Estonian confacies belt

based on the model of Nestor & Einasto (1997); the latter represents a simplistic basin profile developed in terms of depth gradients. There is no doubt the environmental seascape was much more complex with the interaction of many integrated factors including both depth and substrate; the template presented here is a first approximation to aid the understanding of clitambonitoid distribution during the Ordovician Period. Six generalized brachiopod associations corresponding to a spectrum of different environments are used to illustrate clitambonitoid distributions across the Baltoscandian basin. The nearshore tidal environment (A1) and deep water basin (A6) environment have no records of clitambonitidines. However the corresponding sediments are rarely preserved or commonly absent in the Baltoscandian region. The environments A2-A3 correspond to the North Estonian confacies belt, whereas A4 corresponds to the Central Baltoscandian confacies belt (Jaanusson 1973b), and A5 to the basin slope. The subtype A3-1 has been used to indicate more specific environments and brachiopod faunas associated with

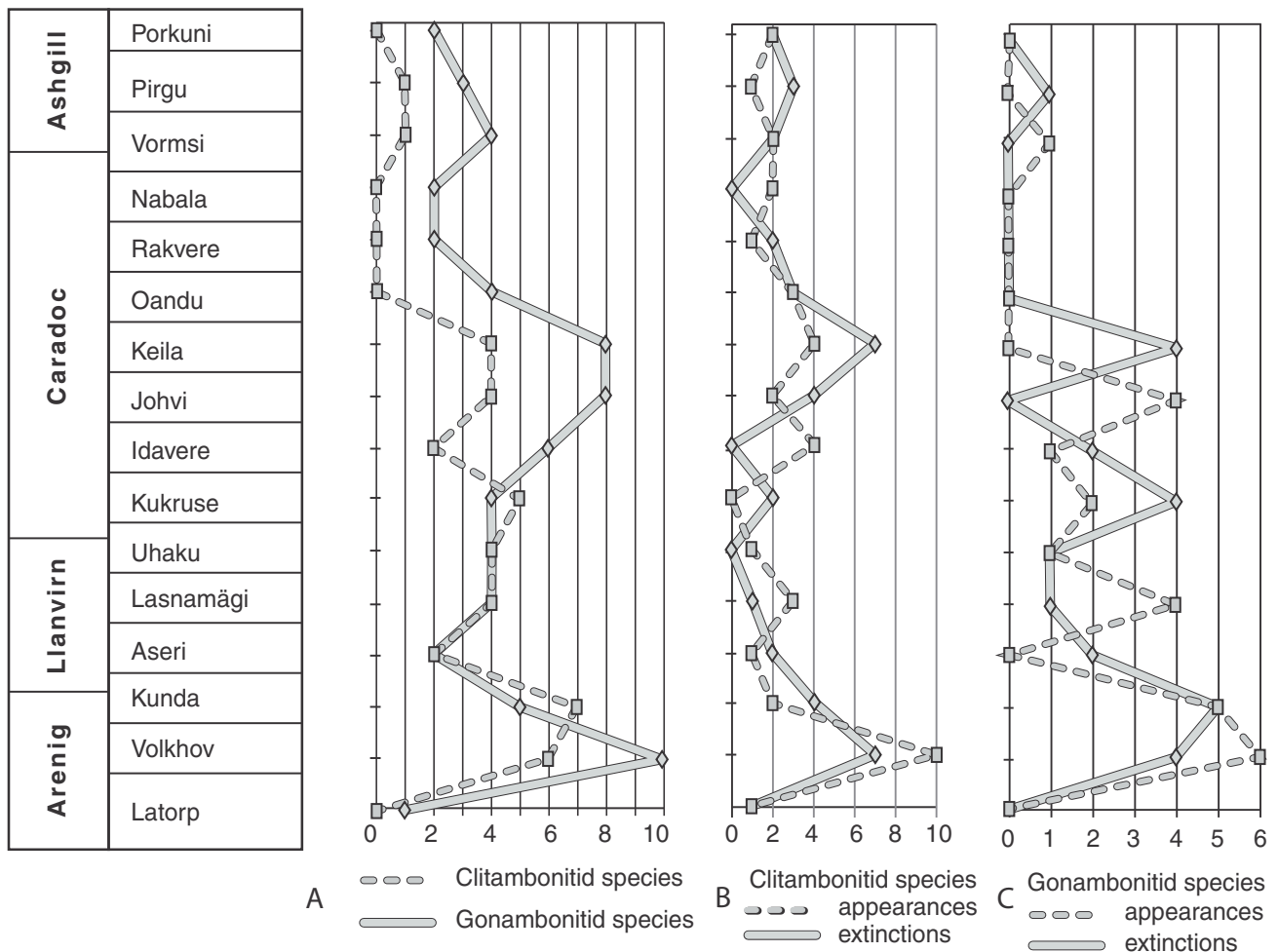


Fig. 2. Diversity of Baltic Ordovician clitambonitids and gonambonitids: A. Standing diversity counts of species of clitambonitid and gonambonitid brachiopods. B. Appearances and extinctions of clitambonitid species. C. Appearances and extinctions of gonambonitid species.

the carbonate build-ups after the mid Caradoc interval.

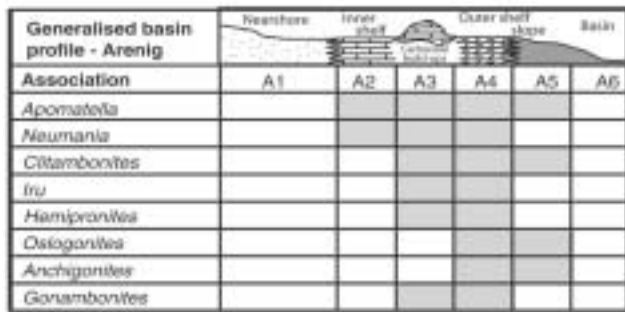
Diversification of clitambonitoids in the Ordovician of Baltoscandia

The appearance of large numbers of clitambonitoid taxa during the early Arenig coincided with the establishment of predominantly carbonate sedimentation in shallow-water parts of Baltoscandian basin (Fig. 1). During the Arenig the clitambonitids slightly exceeded the diversity of the gonambonitids (Fig. 2A) while during the Llanvirn (Kunda–Uhaku stages) and at the beginning of Caradoc (Kukruse Stage) the number of gonambonitids and clitambonitids taxa was more or less equal. During the Caradoc, however, from the Idavere Stage onwards, the numbers of

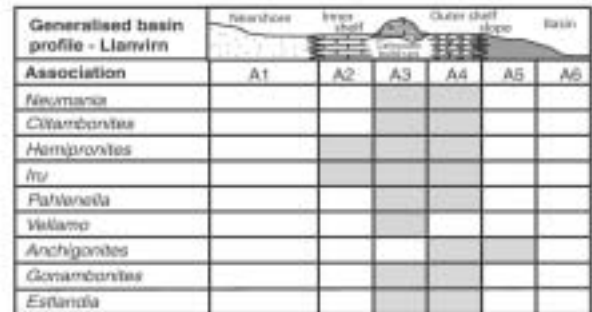
gonambonitids remained a relatively minor component of the group as a whole until their first wave of extinction in Baltica (late Caradoc, Oandu Stage) and the recolonization of the region in the Ashgill, prior to their final extinction.

The initial rapid diversification, high diversity and extinction in the Arenig

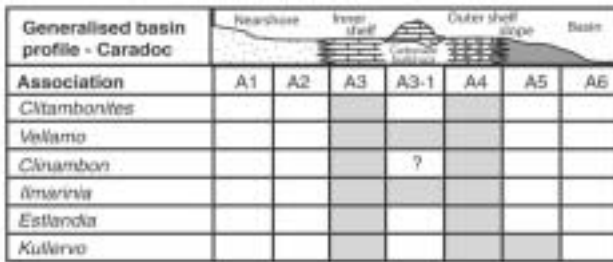
The mid to late Arenig was characterized by a large number of short-lived genera and species (Figs 1, 2). Nevertheless, some taxa remained rare (e.g., *Anchigonites* and *Neumania*) while others were present in large numbers (*Hemipronites* [= *Ladogiella*], *Clitambonites* and *Gonambonites*). A maximum of sixteen clitambonitoid species belonging to seven genera are known from the Volkhov Stage. The diversification rate was extremely high in the mid Arenig, when these new spe-



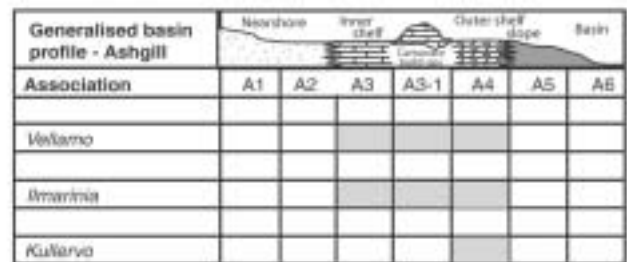
A



B



C



D

Fig. 3. The distribution of Baltic clitaubonitoid genera across generalized environmental gradients in the Baltoscandian region. The A1 association corresponds to tidal zone environments; A2 to the nearshore part of the inner shelf, with a high content of glauconite; A3 is the offshore part of the inner shelf (carbonate sediments with little glauconite); A3-1 equates with carbonate build-ups; A4 corresponds to the outer shelf (purple-coloured sediments) [Central Baltoscandian confacies belt of Jaanusson 1973]; A5 slope facies, (mainly dark shales and mudstones) [Scanian Confacies belt of Jaanusson 1973]; A6 corresponds to the basin plain environment: A, Arenig; B, Llanvirn; C, Caradoc; D, Ashgill.

cies and new genera appeared during the Volkhov Stage (Late Arenig) (Nestor & Einasto 1997), which was followed by rapid transgression, creating a range of shallow-water carbonate environments dominated by storm-generated sediments deposited below seasonal-normal wave base. These sea-level changes were probably eustatic (Nielsen in press) although this interval was also characterised by tectonic events in the adjacent Caledonides together with the rapid northward translation and rotation of Baltica as a whole. The progressive development of a range of relatively shallow-water environments may have helped trigger the initial diversifications of clitaubonitoids, concluding with their extinction at the end of the Arenig, comprising a cycle of radiation and extinction.

Low diversity interval at the beginning of the Llanvirn

The widespread extinction of the clitaubonitoids at the end of the Arenig was followed by an interval of extremely low numbers of taxa (Fig. 1). Only four species, each belonging to a different genus are known. Numbers dropped to 25% of the maximum

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diversity reported in the Volkhov Stage. The Aseri was preceded by a massive extinction of species and genera. This pattern is repeated after a second wave of extinction in the Oandu, when again each genus was reduced to a single species. Extinction was thus much more intense at the species level; the number of genera remained more stable during these ecological crises. This may be explained by the differences in the ecology of taxa at the species level. Generic extinctions occurred only when critical changes took place involving all species habitats of given genera. The Aseri Stage is also characterized by very low species origination rates, while extinction rates were relatively high (Fig. 2B, C). The drastic environmental change from the less stable environmental conditions of the Arenig to the more uniform carbonate milieu of the Llanvirn did not favour the development of the varied, high diversity faunas typical of the early Ordovician.

Recovery and moderate diversity interval during the Llanvirn and early Caradoc

Diversity recovered in the Lasnamägi Stage, when the clitambonitoids attained a moderate diversity (Fig. 1). On average, eight species belonging to four different genera occur. The recovery interval is characterized by high origination rates in the Lasnamägi Stage, while the extinction rate of clitambonitoid species continued to decrease (Fig. 2), reaching its minimum in the Uhaku Stage (end of the Llanvirn). A consistent decrease in the species extinction rate through the Volkhov to Uhaku stages probably tracks the gradual changes in environments in the marginal and central parts of the basin as carbonate facies became dominant (see Nestor & Einasto 1997, pp. 195–197). The initially high-species origination rates during the Lasnamägi Stage (Fig. 2) may be explained by the appearance of taxa taking advantage of the stable environmental conditions in the marginal and central parts of the Baltoscandian basin, where bioclastic argillaceous-calcareous muds accumulated (Nestor & Einasto 1997).

During the Kukruse, the species extinction rate suffered a short-term increase (Fig. 2), coincident with the spread of kukersite (Nestor & Einasto 1997) in some marginal parts of the basin (North Estonia and western part of Ingria, Russia).

Mid Caradoc diversity peak and extinction

The Mid Caradoc diversity peak (Jõhvi–Keila stages) contains on average 12 species belonging to four gen-

era (Fig. 1). This increased Mid Caradoc diversity (Jõhvi and Keila stages) was achieved by the acceleration of diversification rates of the clitambonitids during the Idavere to Keila stages (Fig. 2A), with the addition of a variety of new and more favourable niches in the marginal parts of the Baltoscandian palaeobasin. The development of carbonate facies was much more varied with a significantly larger range of lithofacies than those of the Lower Ordovician. The number of clitambonitid species (Fig. 2A) doubled when compared with the faunas of the moderate diversity interval of the Late Llanvirn (Lasnamägi Stage) to Early Caradoc (Kukruse Stage); the number of gonambonitid species does not show an increase but rather a short, low diversity interval in the Idavere Stage (Fig. 2C). The increased diversification of the gonambonitids (see Fig. 2A) during the Mid Caradoc (Jõhvi Stage) is possibly related to the migration of Avalonian *Kullervo* species into the offshore regions of Baltica (see Vinn & Spjeldnæs 2000).

The regression event in the late Mid Caradoc (Keila Stage) is coincident with a significant turnover of the brachiopod fauna at the Keila–Oandu transition (Hints & Rõõmusoks 1997). Most clitambonitoid brachiopod species and many genera disappeared at the end of the Keila Stage (see Rõõmusoks 1970). The clitambonitoid species extinction rate reached levels (11 species) comparable to those in the Arenig (see Fig. 1B); only one genus became extinct.

The clitambonitoid recovery in the Late Caradoc and final extinction at the end of the Ashgill

The Late Caradoc (Oandu, Rakvere, Nabala stages) was an interval of extremely low diversity (Fig. 1) with on average two to four different clitambonitids, belonging to 2–3 genera (Fig. 4). The remarkable difference between the interval (Aseri Stage) following the Early Arenig extinction and that after the Mid Caradoc is the relatively long temporal extent and slow species diversification rates of the latter (see Figs 1, 2). Thus, it is possible that the extinction in transition between the Keila–Oandu stages may have been caused by more profound crises in the ecosystem for clitambonitoids than those driving extinctions at the end of Arenig.

The Ashgill (Vormsi, Pirgu, Porkuni stages) is characterized by low diversity clitambonitoid faunas (Fig. 1) and ends with the final extinction of this stock of exclusively Ordovician brachiopods. This final extinction in Baltica cannot be directly correlated with the any particular event as their species number started

a steady decline from the beginning of Ashgill, after brief maximum in Vormsi Stage.

Migration and distribution of the clitambonitoids across different environments

Possibly the highest migration potential of clitambonitoids occurred during their rapid diversification in the dynamic Arenig environments of Baltica. Many of the ancestors of the non-Baltic genera (e.g. *Atelasma*, *Jaanussonites* and *Fistulogonites*) as well as the majority of Arenig-Early Llanvirn cosmopolitan or widespread taxa (*Neumania*, *Anchigonites*, *Clitambonites* and *Gonambonites*) are probably migrants from Baltoscandia originating during the high diversification interval in the Arenig. This is supported by the fact that most clitambonitoid genera (80%) and species in Baltica covered a relatively wide range of environments (A2–A5) in the Arenig (Fig. 3A). By the end of the Arenig clitambonitids became largely extinct in deeper-water environments (A5) across Baltica (Fig. 3).

During the Late Llanvirn (Lasnamägi Stage) to Mid Caradoc (Keila Stage), the majority of the clitamboni-

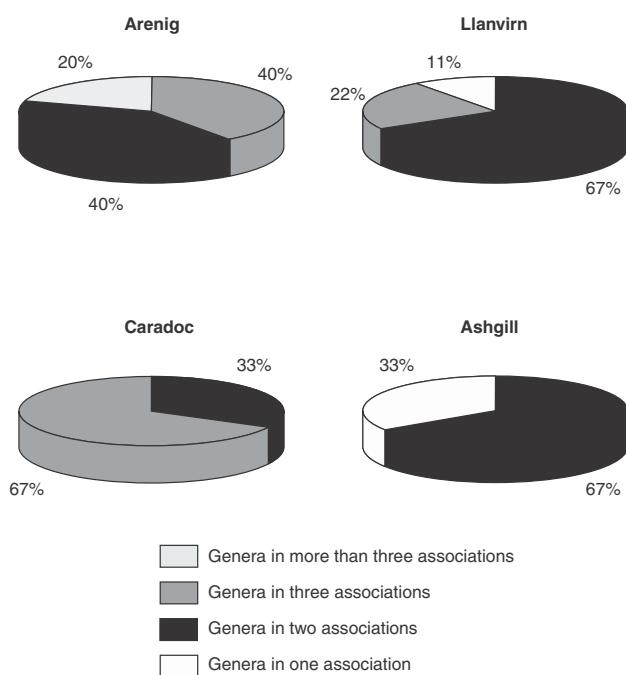


Fig. 4. Comparison of the distribution of Baltic Ordovician clitambonitoid genera in different environments: Percentages of genera occurring in one, two, three and four different environments during the Arenig, Llanvirn, Caradoc and Ashgill.

toids were probably well adapted to the relatively stable environmental conditions in the shallow epicontinental sea of Baltica. A high number of genera had restricted distributions (78%), and their main diversifications mostly occurred in the marginal (A3) and central parts (A4) of the Baltoscandian basin (Fig. 3B) where calcareous muds accumulated (see Nestor & Einasto 1997). The Baltic endemic stocks such as *Estlandia*, *Lacunarites*, and *Pahlenella*, but possibly also ancestors of *Clinambon* and *Ilmarinia*, may have originated in these environments during the Llanvirn.

During the Caradoc the clitambonitoids colonized, on average, a larger number of different environments than those in the Llanvirn, mainly due to the development of various types of carbonate build-ups (see Fig. 3C). The majority of genera (67%) occurred in three different environments (Fig. 4) and only two, *Estlandia* and *Clitambonites* occurred in both environments, A3 and A4. During the Caradoc the development of organic build-ups (A3–1) (see Rõõmusoks 1970; Nestor & Einasto 1997) played a major part in the diversification of the genera *Vellamo* and *Ilmarinia*, and possibly also *Clinambon*. The deeper-water slope environment was characterized by the *Kullervo* fauna (Fig. 3C), which at least partially was of Avalonian origin (see Vinn & Spjeldnæs 2000). However, the migration with time of these taxa from the shelf environments (A3 and A4) to the slope can not be excluded because the phylogenetic relationships of these *Kullervo* species with earlier Baltic taxa is unknown. By the end of the Caradoc the clitambonitids had virtually disappeared from deep-water environments (A5) and were less common in outer shelf environments (A4) (Fig. 3).

During the Ashgill the clitambonitids in Baltica had very restricted distributions in terms of different environments (Fig. 3D). Two genera, *Vellamo* and *Ilmarinia*, are known from the inner shelf environment (A3) and specifically reef environments, while *Kullervo* occurs only in carbonate environments. The North American *Kullervo* species group (*K. complectens*) migrated into Baltica following the near closure of the Iapetus Ocean. The final extinction of the group in Baltica at the end of the Ashgill coincided with their more restricted distribution in narrower, shallow-water niches.

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