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Distribution of the order Proetida (Trilobita) in Baltoscandian Ordovician strata

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Abstract. The trilobite order Proetida forms a minor but important faunal element within the Ordovician strata of Baltoscandia. This review follows the current systematic, taxonomic, and stratigraphical usage and discusses the distribution of these trilobites within the context of the Confacies Belt model. A database of species-level information was derived from numerous publications relating to the Scandinavian and Baltic states and relevant neighbouring regions. Important additional information on stratigraphical occurrences of genera has been derived from glacial erratic boulders (geschiebe) from northern Germany and adjacent areas. The representatives from Baltoscandia of three superfamilies, Bathyuroidea, Aulacopleuroidea, and Proetoidea, are listed. The genus level was chosen as the most practicable to plot on the maps, one showing the time interval for the Kukruse Regional Stage (or Global Stage Slice Sa1), the other that for the Pirgu and Porkuni stages (or stage slices Ka4 and Hi1–Hi2). These intervals each show a diversity peak within the ranges of about 30 genera of Proetida and over 70 species from the Ordovician successions of Baltoscandia. Out of these a total of nine genera cross the Ordovician–Silurian boundary.

The regional comparisons from within Baltoscandia show differences in facies dependency of certain genera, with possibly also a latitudinal component. During the late Ordovician the faunal resemblance appears to be closest to the neighbouring palaeocontinent Avalonia, suggesting a faunal exchange between or pathways to both continents from elsewhere. Besides climatic and geographical proximity of palaeocontinents, sea-level changes also have to be considered in explaining the distribution of Proetida in Baltoscandia.

Key words: Ordovician, Baltoscandia, geschiebe, Trilobita, Proetida, distribution, biodiversity.

INTRODUCTION

The trilobite order Proetida Fortey & Owens, 1975, comprises at least 470 Early Ordovician to Permian genera worldwide. In its original definition it included the families Aulacopleuridae Angelin, Bathyuridae Walcott, Brachymetopidae Prantl & Přibyl, Celmidae Jaanusson, Dimeropygidae Hupé, Glaphuridae Hupé, Otariionidae Richter & Richter, and Proetidae Salter. New data, especially on the ontogeny and morphology of early representatives of the group, have generated considerable discussion on the concept and composition of its component families and on the classification of the order (e.g. Bergström 1977; Lütke 1980, 1990; Owens & Hammann 1990; Adrain & Chatterton 1994, 1996; Chatterton 1994; Ahlberg 1995a, b; Edgecombe et al. 1997; Chatterton et al. 1998, 1999; Adrain et al. 2001; Jell & Adrain 2003; Owens 2004; Bergström & Suzuki 2005; Fortey 2006; Yuan et al. 2006). This has been taken into account in our review on the Baltoscandian Proetida. We here follow the revised edition of *Treatise on Invertebrate Paleontology* (Fortey 1997, p. 300), with

modifications by Jell & Adrain (2003), and include three superfamilies – Proetoidea Salter, Aulacopleuroidea Angelin, and Bathyuroidea Walcott in the order.

There is a long history of research into the Proetida of the Baltic area, dating from Angelin (1851, 1854) for Scandinavia and Nieszkowski (1857, 1859) for the Baltic states. Thereafter, the work of Schmidt (1894, 1907; see also Bruton et al. 1997) was a major milestone. Descriptions of individual genera and species are scattered through monographic works from the late 19th and early 20th centuries (e.g. Eichwald 1861; Linnarsson 1869; Törnquist 1884; Olin 1906; Warburg 1925; Öpik 1925, 1927, 1928, 1937). A large number of later publications include or deal specifically with Ordovician Proetida: Hadding (1913), Asklund (1936), Thorslund (1940), Jaanusson (1956), Balashova (1961), Männil (1963), Nikolaisen (1963), Owens (1970, 1973, 1974, 1979, 1981, 2004), Rõõmusoks (1970, 1997), Bruton & Owen (1979), Owen & Bruton (1980), Owen (1981, and in Owen & Harper 1982; Harper & Owen 1984; Harper et al. 1984), Bruton (1983), Wandås (1984), Ahlberg (1995a, b), Suzuki & Bergström (1999), Bergström &

Suzuki (2005), Bruton & Høyberget (2006), Pärnaste (2006), Popp & Pärnaste (2008a, b), Hansen (2008, in press). Important monographic works on faunas (which include Proetida) from glacial erratic boulders (geschiebe) were published by Roemer (1861, 1885), Steinhardt (1874), and Pompeckj (1890). More recent contributions on geschiebe faunas are those by Neben & Krueger (1971, 1973, 1979), Schöning (1982), Rudolph (1997), Schimmelpfennig & Schneider (1997), Bilz (2001), Popp & Schöning (2001, 2006), Rhebergen (2001), Krueger (2004), and Popp (2007). Data derived from these sources were used to compile Table 1.

Initially, a simple database was established for entering species-level information, but due to different levels of data quality and confidence it was decided that it would be more appropriate to use genus level. Today, almost 30 genera of Proetida with more than 70 species are known from the Ordovician successions of Baltoscandia, including glacial erratic boulders (geschiebe) from Northern Europe (Table 1). The locality data are organized according to the Confacies Belt structure of the basin (Männil 1966; Jaanusson 1982a), to demonstrate the facies distribution of different genera. It is obvious that the pattern is rather uneven, biased towards areas of outcrop (e.g. Oslo Region, Siljan District) compared to those where material has been collected only from borehole cores (e.g. Latvia, Lithuania). Because of their relatively small size these trilobites can be found in small rock samples (borehole cores, geschiebe), offering the possibility of a high biostratigraphical potential. Although data from geschiebe cannot be plotted on palaeogeographical maps, they reveal important information for genus level presence in various stratigraphical levels within the Ordovician of Baltoscandia. Proetida are relatively minor components of most Ordovician trilobite faunas, but representatives of all three superfamilies occur across all confacies belts (here modified after Jaanusson 1982a, 1995).

BATHYUROIDEA

Two families, Telephinidae Marek and Dimeropygidae Hupé, are represented in the Ordovician of Baltoscandia. These families include the earliest Proetida known from this region.

Telephinidae

The family Telephinidae is represented in the Lower Ordovician by *Carolinites* Kobayashi, the type species of which, *C. genacinaca* Ross, is the most widely distributed trilobite species known, according to McCormick & Fortey (1999). The broad palaeogeographical distribution

of this genus is explained by its pelagic life style. Balashova (1961) described *C. popovkiensis* from calcareous glauconite sandstones belonging to the Mäeküla Member (Leetse Formation) of the St Petersburg region, which she believed to be of Tremadoc age. This unit is now correlated with the lower part of the Billingen Stage (B₁β) (Pärnaste 2006) and time slice 2b (Nölvak et al. 2007) or stage slices F11–F12 (Bergström et al. in press). Another closely related taxon determined as komaspidid (Nikolaisen 1962; Hansen 2008) or aff. *Carolinites* (Wandås 1984) is known from the uppermost Stein Formation of the Kunda Stage on Helgøya, Oslo Region (Hansen in press). In general, *Carolinites* is more common outside Baltica, for example in Laurentia (Adrain et al. 2004, fig. 24. 4) and in South China Plate (Turvey & Zhou 2004), and is also known from Siberia, Australia, France (Montagne Noire), Turkey (see references in McCormick & Fortey 1999), and Iran (Bruton et al. 2004).

Telephina Marek is another genus adapted to pelagic habits. It was reviewed by Ahlberg (1995a, b), who documented its occurrence in the Oslo Region, Norway (see also Nikolaisen 1963; Bruton & Høyberget 2006; Hansen in press), Jämtland (see also Thorslund & Asklund 1935), Dalarna, Västergötland, Öland, and Scania in Sweden (see also Angelin 1854; Månsson 1995), in Bornholm, and in Latvia (Blidene Marls) (Ahlberg 1995b). Whilst most species occur in shales and/or intercalated dark grey limestones, two are known from pure limestone facies. *Telephina bicuspis* occurs in the Folkeslunda Formation of Öland, the Uhaku Stage (C₁c) of western Latvia, the Elnes Formation in the Oslo Region (Bruton & Høyberget 2006), and in the Andersö Shale in Jämtland (Ahlberg 1995a, b). *Telephina bicuspis* is the most common species of *Telephina* from geschiebe of the Upper Grey *Orthoceratite* Limestone, which belong to the Lasnamägi Stage (C₁b) (*Schroeteri*-Kalk, Rudolph 1997, p. 34). *Telephina wegelini*, as interpreted by Ahlberg (1995a, pp. 272–273), occurs in the Fjäcka Shale Formation and is represented by a single specimen in the Boda Limestone Formation (Warburg 1925, p. 90), thus being the youngest known *Telephina* in Baltoscandia. This occurrence of *Telephina* is unusual, because it is neither a typical inhabitant of carbonate mound environments, nor has it been recognized elsewhere in Baltica during this time interval, although another single specimen that may be conspecific has been recorded from the Kildare Limestone Formation, eastern Ireland (Dean 1971, p. 46). Outside Baltoscandia it is known from approximately coeval deposits in Bohemia and Kazakhstan (Dean 1978, p. 112). Before they arrived in Baltica, *Telephina* species inhabited a range of environments in the Precordillera from the Arenig *evae* Biozone (F12) to the Caradoc, and in Laurentia from the Llanvirn to the

Super-family	Family	Global stage slices	Fl1-3	Dp1-3	Dw1	Dw2	Dw3			Sa1	Sa2		Ka1			Ka2	Ka3	Ka4	Hi1-2	Silurian
			Regional stages	B _I	B _{II}	B _{III}	C _a	C _b	C _c	C _{II}	C _{III} -D _I	D _{II}	D _{III}	E	F _a	F _b	F _c	F _{II}		
		Genus																		
Bathyruloidea	Dimeropygidae	1. <i>Celmus</i>	[Timeline bars for Celmus]																	
		2. <i>Dimeropyge</i>	[Timeline bars for Dimeropyge]																	
		3. <i>Paratoernquistia</i>	[Timeline bars for Paratoernquistia]																	
		4. <i>Toernquistia</i>	[Timeline bars for Toernquistia]																	
		5. <i>Mesotaphraspis</i>	[Timeline bars for Mesotaphraspis]																	
		6. <i>Solariproetus</i>	[Timeline bars for Solariproetus]																	
	Telephinidae	7. <i>Carolinites</i>	[Timeline bars for Carolinites]																	
		8. <i>Telephina</i>	[Timeline bars for Telephina]																	
		9. <i>Phorocephala</i>	[Timeline bars for Phorocephala]																	
Aulacopleuroidea	Scharyiidae	10. <i>Niuchangella</i>	[Timeline bars for Niuchangella]																	
		11. <i>Panarchaeogonus</i>	[Timeline bars for Panarchaeogonus]																	
	Aulacopleuridae	12. <i>Scharyia</i>	[Timeline bars for Scharyia]																	
		13. <i>Harpidella</i>	[Timeline bars for Harpidella]																	
	Rorringtoniidae	14. <i>Cyamella</i>	[Timeline bars for Cyamella]																	
		15. <i>Madygenia</i>	[Timeline bars for Madygenia]																	
		16. <i>Rorringtonia</i>	[Timeline bars for Rorringtonia]																	
17. <i>Isbergia</i>		[Timeline bars for Isbergia]																		
Proetoidea	Tropidocoryphidae	18. <i>Decoroproetus</i>	[Timeline bars for Decoroproetus]																	
		19. <i>'Eremiproetus'</i>	[Timeline bars for 'Eremiproetus']																	
		20. <i>Dalarnepeltis</i>	[Timeline bars for Dalarnepeltis]																	
		21. <i>Stenoblepharum</i>	[Timeline bars for Stenoblepharum]																	
		22. <i>Paraproetus</i>	[Timeline bars for Paraproetus]																	
		23. <i>Ogmocnemis</i>	[Timeline bars for Ogmocnemis]																	
		24. <i>Parvigena</i>	[Timeline bars for Parvigena]																	
	Proetidae	25. <i>Ascetopeltis</i>	[Timeline bars for Ascetopeltis]																	
		26. <i>Astroproetus</i>	[Timeline bars for Astroproetus]																	
		27. <i>Xenocybe</i>	[Timeline bars for Xenocybe]																	
		28. <i>Cyphoproetus</i>	[Timeline bars for Cyphoproetus]																	
Number of genera per stage			2	1	3	2	3	1	6	6	8	7	6	1	4	22	21	9		

Caradoc. Chatterton et al. (1999) described a surprising radical metamorphism that occurs late in the meraspid period in *Telephina* and suggests that they changed their lifestyle from benthic to pelagic mode (usually the change is in the opposite order). This might explain why *Telephina* had a preference for particular areas or benthic conditions, or facies, and was restricted to one confacies belt in Baltoscandia.

Dimeropygidae

The earliest confirmed dimeropygid, which appears in the Kunda Stage (B_{III}), is *Celmus* Angelin (Jaanusson 1956; Bruton 1983), but two possible representatives, *Celmus? insolita* (Tjernvik) from Sweden and *C.? longifrons* Poulsen from Bornholm, Denmark, appeared even earlier, respectively in the Hunneberg (B_{Iα}; F11) and Volkhov (B_{II}; Dp1) stages (Pärnaste 2006). Adrain et al. (2004, p. 235) note that *Celmus* is a member of those Baltic Arenig–Llanvirn trilobite faunas that are common to Laurentia. It is one of the few trilobite genera that cross the Kunda–Aseri (B_{III}–C_{1a}) boundary, and has been found in limestones in Östergötland, Öland, St Petersburg region, and in geschiebe in Germany. Bergström & Suzuki (2005) concluded that *Celmus* was a cheirurid, but we do not accept this view.

Dimeropyge Öpik appears in oil shale (Öpik 1937) belonging to the Kukruse (C_{II}) Stage of Estonia and at an equivalent horizon of the lower *Chasmops* Limestone in Jämtland (Thorslund 1940). Whittington & Evitt (1954) revised *Dimeropyge minuta* Öpik, which was established on a pygidium, and associated it with the cranidium attributed by Öpik (1937) to *Toernquistia? minuta* (Nieszkowski).

Mesotaphraspis Whittington & Evitt and *Toernquistia* Reed are both known from the Upper Ordovician, the former from the Oslo district, Norway (Owen & Bruton 1980; Owen 1981), and the latter from Sweden (Jämtland and the Siljan District). *Toernquistia* occurs mainly in carbonate mudmounds, and the type species, *T. nicholsoni* (Reed), is known from the Boda Limestone Formation, the Keisley Limestone Formation, northern England (type stratum), and from the Kildare Limestone Formation, eastern Ireland (Dean 1974, p. 65). *Solariproetus* Qu

occurs in the Lindegård Mudstone Formation in Scania, and in the ‘*Dalmanitina* Beds’ of Bornholm. *Mesotaphraspis* and *Toernquistia* were placed in a revived Toernquistiidae Hupé by Chatterton et al. (1998) and *Solariproetus* was added by Owens (2004), but Dr J. M. Adrain (pers. comm. to RMO, September, 2005) has prepared a revised phylogenetic analysis of the Dimeropygidae which places toernquistiids in synonymy with them. We follow this classification here.

AULACOPLEUROIDEA

Three family-level taxa are present in Baltoscandia, viz. Aulacopleuridae Angelin, Rorringtoniidae Owens, and Scharyiidae Osmólska. The last-named has been regarded by some authors as a subfamily, by others as a family (see Owens & Fortey in press). Herein, it is treated as a family.

Aulacopleuridae

Aulacopleurid trilobites from Baltoscandia and from geschiebe have been assigned variously to *Harpidella* M’Coy, *Otarion* Zenker, and *Cyphaspis* Burmeister. Following their revision by Adrain & Chatterton (1994, 1996), the latter two are restricted to Silurian and Devonian strata, with only *Harpidella* being represented in the Ordovician. Until these Ordovician species are fully revised, they are placed in *Harpidella* (s.l.), following Owen (1981) and Owen & Bruton (1980). This genus occurs in small numbers throughout much of the Upper Ordovician succession.

Rorringtoniidae

Four genera are present in the Ordovician of Baltoscandia: *Rorringtonia* Whittard, *Cyamella* Owens, *Isbergia* Warburg, and *Madygenia* Petrunina. The first-named occurs at two horizons: in the lower *Chasmops* Shale (Owens 1970, p. 329), now termed as the Arnestad Formation in the Oslo district (Owen et al. 1990), and in the Lindegård Formation in Scania (Owens 2004). *Cyamella* is confined almost exclusively to the Boda

Table 1. Stratigraphical distribution of genera of Proetida, for which the locality data are divided into five Baltoscandian Confacies Belts (Jaanusson 1982a, 1995), from top to bottom, for each genus: 1, Oslo Confacies Belt; 2, Scanian Confacies Belt; 3, Central Baltoscandian Confacies Belt; 4, geschiebe (most material probably originating from the previous belt); 5, North Estonian Confacies Belt. Continuation into the Silurian, marked with the plus sign, relates to genera worldwide. Correlation within Baltoscandia is based on Nölvak et al. (2007), Ebbestad & Högström (2007), and Owen et al. (1990), and with global stage slices on Bergström et al. (in press). Note that the range bars show the presence on unit level and are not limited to show on a more precise level. Abbreviations for regional stages: B_I, Hunneberg–Billingen; B_{II}, Volkhov; B_{III}, Kunda; C_a, Aseri; C_{1b}, Lasnamägi; C_{1c}, Uhaku; C_{II}, Kukruse; C_{III}–D_I, Haljala; D_{II}, Keila; D_{III}, Oandu; F_{1a}, Nabala; F_{1b}, Vormsi; F_{1c}, Pirgu; F_{II}, Porkuni; and for global stage slices: Fl, Floian; Dp, Dapingian; Dw, Darriwilian; Sa, Sandbian; Ka, Katian; Hi, Hirnantian

Limestone Formation, where it has been found in vast numbers in cavities (Owens 1979; Suzuki & Bergström 1999; Popp & Pärnaste 2008a), with a single earlier record from a limestone erratic of the Moldå Formation from Öland. *Isbergia* occurs in the Boda Limestone Formation (Warburg 1925; Owens 1979) and in the Bønsnes Formation in Ringerike, Oslo district, Norway (Owens 1979; Owen 1981). *Madygenia* is restricted to one cranidium from the Hirnantian Loka Formation, Alleberg, Västergötland (Owens 2004).

Scharyiidae

The earliest confirmed species of *Scharyia* Přibyl, *S. heothina* Owens, occurs in the Boda Limestone Formation (see Owens 1974). *Panarchaeogonus parvus* Öpik and *P. atavus* Öpik from the Kukruse Stage, Estonia, were synonymized by Owens (1979), who also included Öpik's *Otarion* sp. a (Öpik 1937, p. 29, pl. 3, fig. 7). This synonymy is followed here. The pygidium figured by Öpik (1937, pl. 4, figs 1, 2, 6) as *Toernquistia? minuta* (Nieszkowski), which occurs together with cephalae of *P. parvus*, may prove to belong to this species. *Panarchaeogonus phylzaci* Owens from the lower *Chasmops* Shale and Limestone (Owens 1979), or from the Arnestad and Frognerkilen formations, respectively, in the Oslo district (Owen et al. 1990) and *P. holmi* (Warburg) from the Boda Limestone Formation were transferred to the closely related scharyiid *Niuchangella* W Chang by Adrain & Chatterton (1993, p. 1636). *Panarchaeogonus* Öpik and *Niuchangella* both have been recorded from outcrops of the Boda Limestone Formation and also from Upper Ordovician geschiebe at Hulterstad on Öland (Owens 1979, p. 206). One cranidium of *Panarchaeogonus* has been collected by the second author of this paper in a geschiebe of the so-called 'brick-limestone' (Backsteinkalk), Darriwilian (Popp 2007). It is the oldest representative of the family known from Baltoscandia.

PROETOIDEA

This superfamily includes the 'typical proetids', which morphologically have a rather conservative style. Owens (1973) listed 29 species, of which 17 are known from the carbonate mound facies (Kullberg Limestone, Boda Limestone) and 12 from other facies. All were included in the Proetidae Salter, mostly in the subfamilies Proetinae Salter and Tropicocoryphinae Přibyl. It is now apparent that the latter should be accorded family-level status. Thus restricted, the Proetidae are represented by a comparatively small number of taxa, whilst Tropicocoryphidae are more widespread, and

with a far greater number of species. Many of the latter have been attributed to *Decoroproetus* Přibyl, but this genus has been used in a very broad sense, and certainly includes a number of different taxa (Owens 2004). Some of these are placed in the Cornuproetinae Richter, Richter & Struve. We here follow Jell & Adrain (2003) in placing this subfamily in the Tropicocoryphidae Přibyl.

Proetidae

Three genera of Proetidae occur in the Upper Ordovician (Ka4): *Astroproetus* Begg in the Boda Limestone Formation, *Xenocybe* Owens in late Upper Ordovician strata in the Oslo district, Norway, and *Cyphoproetus* Kegel in both (Owens 1973).

Tropicocoryphidae

Decoroproetus (*s.l.*) is widespread, being present in small numbers throughout much of the Upper Ordovician, and is common in the Fjäckå Shale Formation and in pockets in the Boda Limestone Formation (Owens 1973; Suzuki & Bergström 1999). It is included in the Tropicocoryphinae. *Stenoblepharum* Owens, *Ogmocnemis* Kielan, *Ascetopeltis* Owens, *Paraproetus* Přibyl, and *Parvigena* Owens are all attributed to the Cornuproetinae. *Stenoblepharum* includes the earliest tropidocoryphids (and Proetoidea) from Baltoscandia, being present in geschiebe of Red *Orthoceratite* Limestone, of late Darriwilian age, from northern Germany (Popp & Schöning 2006). It is represented in the Viivikonna Formation (Sa1), Kullberg Limestone Formation (Ka1), Langåra Formation (Ka4–Hi1), and is especially abundant in the Boda Limestone Formation (Ka4–Hi1). The earliest *Ogmocnemis* occur in the Nakkholmen and Furuberget formations (Ka1) in the Oslo district and range up to Ka4 in Baltoscandia. '*Proetus*' *kertelensis* from the Vormsi Stage (F_{1b}; Ka3), Hiiumaa, belongs to an undescribed cornuproetine genus. *Ascetopeltis* and *Paraproetus* are mostly restricted to the late Upper Ordovician, stage slice Ka4, although the former is also present in the Porkuni Stage (F₁₁), Hi1–Hi2. '*Proetus*' *ramisulcatus* Nieszkowski, which belongs to a second undescribed cornuproetine genus, is restricted to this stage.

DISTRIBUTION AND DIVERSITY PATTERNS

The first summary of trilobite distribution in Baltoscandia was that of Schmidt (1907). Ralf Männil (1962) published a table showing the distribution of 13 genera that occur in the Upper Ordovician and Lower Silurian succession of northern Estonia, with gradual increase from 7 genera

in the Oandu Stage (D_{III}) to 13 in the Porkuni Stage (F_{II}) (only 2 of them are Proetida); there is a sudden decrease to 3 genera at the Silurian boundary. Later, Reet Männil (1992) published a revised version which also included genera from other facies belts. She showed that the terminal Ordovician extinction was stepwise, starting from the late Caradoc through the Ashgill, and that it was different in two adjacent facies belts in the East Baltic. In the northern Estonian near-shore facies, the diversity decrease was insignificant, with two out of three genera crossing the Pirgu–Porkuni boundary, but in the Latvian Depression most genera disappeared and were replaced by the low-diversity, cosmopolitan *Mucronaspis* [*Dalmanitina*] fauna. Species-level trilobite diversity through the Ordovician shows two major increases, one in the Aseri Stage (C_{Ia}) and the other in the Kukruse Stage (C_{II}) (Männil 1966; Männil et al. 1966). The same peaks are traced when including data from Sweden and Norway (Hammer 2003; Hammer in Adrain et al. 2004). Similar trends can be followed in the genus level compilation of Rõõmusoks (1997).

These diversity changes are reflected in the Proetida from the point at which they appeared, when one to two (possibly 3) genera per stage occurred in the basin. Then from the Kukruse (C_{II}) to Rakvere (E) stages (or Sa1–Ka1, or Caradoc), 6 to 8 genera occurred and after a short reduction to one and four genera from the Nabala (F_{Ia}; Ka2) and Vormsi (F_{Ib}; Ka3) stages there was a sudden increase to 22 genera in the Pirgu–Porkuni (F_{IC}–F_{II}; Ka4–Hi2) interval (Table 1). Interestingly, the brief reduction in the number of genera in the Nabala Stage involves only the Proetida; the total number of trilobite genera (including Proetida) is 20 for the Rakvere Stage, 18 for the Nabala Stage, and 19 for the Vormsi Stage (see Rõõmusoks 1997, pp. 236–237, table 38). Against a background of an essentially stable level of diversity of Proetida, with two stepwise rises (at Sa1 and Ka4), a few new genera appeared, whilst some became extinct. Of the 22 genera present in the late Pirgu–late Rawtheyan, excluding those in the Boda Limestone, five (two bathyuroids, three cornuproetines) do not occur in later Ashgill strata. Assuming that the ranges of all 14 genera recorded from the Boda Limestone extend into the uppermost, Hirnantian part of the formation, nine disappear at the HA regression (for Lowstand HA see Bergström et al. 2006). Nine genera of Proetida that occur in Baltoscandia survive into the Silurian. The end Ordovician mass extinction resulted in the trilobites losing about half their global taxonomic diversity (Adrain et al. 2004); this is reflected broadly in the case of Baltoscandian Proetida. Of these, the Bathyuroidea became extinct, whilst Aulacopleuroidea lost three out of eight genera, and the Proetoidea seven out of eleven. This general pattern is repeated in other areas.

In conjunction with Avalonia

Owen (2007) analysed changes in trilobite diversity through the Ordovician of Avalonia and showed that in contrast to elsewhere, it reached a peak immediately prior to the Hirnantian extinction event, rather than in the Caradoc or earlier. His data (Owen 2007, fig. 1A) record five genera of Proetida in the Cautleyan–Rawtheyan stages (Ka4) that have an earlier history in Avalonia. Of these, *Dimeropyge*?, *Toernquistia*, and *Panarchaeogonus* occur in the lower Caradoc (first in Sa1, two others in Sa2), but are absent from the intervening upper Caradoc and lower Ashgill. Other genera in this category, *Ogmocnemis* (included in the range of *Decoroproetus* by Owen 2007) and *Harpidella* (*s.l.*), occur sporadically throughout the succession. Other genera of Proetida, for example *Ascetopeltis*, *Paraproetus*, and *Stenoblepharum*, in Avalonia do not have a pre-mid Ashgill history in the region.

In Baltoscandia Proetida show an increase in diversity similar to that in Avalonia. There are similar gaps in the records of, for example, *Toernquistia* (assuming that the closely related *Paratoernquistia* is synonymous), which occurs in the Lower *Chasmops* Limestone (Sa1–Sa2) of Jämtland and the Kullberg Limestone Formation (Ka1) of Dalarna and recurs in the Boda Limestone Formation (Ka4–Hi2). The scharyiids *Panarchaeogonus* and *Niuchangella* show a similar pattern, but are more widespread geographically. The latter occurs in the Arnestad and Frognerkilen formations of the Oslo Region and the former in the Estonian oil shale (Viivikonna Formation, Sa1). Both disappear from the record until the Rawtheyan and lower Hirnantian stages (the upper part of Ka4 and Hi1), but do not range up to the Ordovician–Silurian boundary.

Ascetopeltis occurs in the mid-Ashgill (Cautleyan Stage, the lower part of Ka4) of Avalonia. If ‘*Proetus*’ *kertelensis* from the Vormsi Stage (F_{Ib}; Ka3) belongs to its ancestral stock, this genus might have immigrated into Avalonia from Baltica. Owen (2007, p. 267), however, referred to a Laurentian origin for *Ascetopeltis*. His suggestion that *Ascetopeltis* may have had a Laurentian ancestry arose from the comment by Owens (1973) that its origins may lie in *Cyphoproetus*. That genus had an earlier history in the Girvan district, which was located on a terrane that lay on or close to the Laurentian margin during the Ordovician (Dr A. W. Owen pers. comm., November, 2008). A Laurentian source is thought to be most likely for *Dimeropyge*, made possible by a narrowing Iapetus during the Ordovician (Chatterton 1994, p. 545; Yuan et al. 2006, p. 541). The earliest *Dimeropyge* from Baltoscandia (from the Kukruse and Haljala stages, C_{II}–C_{III}–D_I; Sa1–Sa2) are of about the same age as those from Avalonia, and the presence of *Dimeropyge*?

ericina Adrain & Fortey in the Arenig Tourmakeady Limestone of western Ireland indicates a Laurentian origin for the genus. The same applies to *Celmus*, which appears in the Kunda (B_{III}) and Aseri (C_I) stages of the Middle Ordovician in Baltoscandia and is also present in the Tourmakeady Limestone (Adrain & Fortey 1997).

DISTRIBUTION WITHIN THE CONFACIES BELTS

When genera are plotted according to their stratigraphical occurrence (Table 1), two time intervals show levels of stepwise rise to a higher diversity of Proetida. In Fig. 1A, B these were plotted on distribution maps in order to illustrate facies dependence and areas of preference.

Six genera are recorded in the early Upper Ordovician (Kukruse Stage, C_{II}, *gracilis* Biozone, Sa1) (Fig. 1A). *Telephina*, a genus adapted to an epipelagic lifestyle (Fortey 1975), is common in the deeper-water areas of the Oslo and Central Baltoscandian confacies belts (abbreviated CB hereafter). Ahlberg (1995a) concluded that in Baltica and Laurentia at least, *Telephina* is restricted to the periphery of the continental plates, and so far, there are no known occurrences from nearshore sequences. *Dimeropyge* is known from the offshore Central Baltoscandian CB and nearshore North Estonian CB. If the pygidium figured by Öpik (1937, pl. 4, figs 1, 2, 6) as *Toernquistia? minuta* (Nieszkowski) belongs to *Paratoernquistia* Chatterton et al., then this genus is also known from both areas. *Harpidella* (*s.l.*) and *Stenoblepharum* are recorded only from the Northern Estonian CB during the Kukruse Stage. However, the latter is known from both older and younger beds from *geschiebe*, suggesting that it was present in a range of environments. The most favourable area for Proetida during the Kukruse Age was in algal-rich shallow-water carbonates in the Northern Estonian CB.

The second time interval (Fig. 1B) comprises the Pirgu Stage (F_{1c}; equivalent to the Cautleyan–Rawtheyan stages and Ka4) and the Porkuni Stage (F_{II}; equivalent to the Hirnantian and Hi1–Hi2). Note that here the Boda Limestone Formation includes strata of Pirgu and Porkuni age following e.g. Jaanusson (1982b), Ebbestad & Högström (2007), and Schmitz & Bergström (2007). However, there are ongoing discussions on the upper limit of this formation. Suzuki & Bergström (1999) suggest it possibly reaches into the Silurian. Other authors argue that findings of the brachiopod *Holorhynchus* Kiaer in the flank deposits of the upper part of the Boda Limestone in Osmundsberget (Jaanusson 1982b) with low carbon isotope values prove it is pre-Hirnantian (Brenchley et al. 1997). In contrast to the previous

interval, it shows different centres of diverse trilobite occurrences: the Lake Siljan area and the Oslo Region. Of the 28 Ordovician genera of Proetida identified in Baltoscandia, 14 (*Astroproetus*, *Cyamella*, *Dalarnepeltis* Přibyl & Vaněk, *Decoroproetus*, *Isbergia*, *Niuchangella*, *Panarchaeogonus*, *Parvigena*, *Scharyia*, *Stenoblepharum*, *Toernquistia*, *Cyphoproetus*, ‘*Eremiproetus*’, and *Telephina*) have been recorded from the Boda Limestone Formation in Siljan. These carbonate mudmounds can be subdivided into a so-called core facies (see Suzuki & Bergström 1999; Ebbestad & Högström 2007), containing different types of ‘pockets’, and a ‘flank facies’ (here taken as synonymous to ‘off reef’ of Owens 1973; see Suzuki & Bergström 1999; Ebbestad & Högström 2007) characterized by marly limestones. Of the genera listed above, *Decoroproetus* and *Stenoblepharum* are abundant in the ‘core facies’ (see Owens 1979, table 2) and *Cyamella* occurs very abundantly in so-called pockets (see Suzuki & Bergström 1999) within the ‘core facies’. Only *Stenoblepharum warburgae* Přibyl is reported from both facies types from the Boda Limestone. Elsewhere *Ascetopeltis bockeliei* Owens is found within the ‘flank facies’ of the Boda Limestone in Dalarna and also in Östergötland (Jonstorp Formation) and the Oslo district (Langåra Formation), with a similar, unnamed species (Owens 1973, pp. 129–130) in the Ärina Formation, Porkuni Stage, Estonia.

The algal-rich carbonates of the Langåra and Bønsnes formations in the Oslo district share several taxa with the Boda Limestone Formation, for example *Stenoblepharum*, *Cyphoproetus*, ‘*Eremiproetus*’, and *Isbergia*. In the two last-named genera the same species is represented. A number of taxa are also shared with the Keisley Limestone Formation of northern England and the Kildare Limestone Formation of eastern Ireland, both carbonate mudmound deposits (see Dean 1978). This facies has yielded the most diverse faunas of Proetida from the Ordovician anywhere. *Paraproetus*, *Ogmocnemis*, and *Harpidella* (*s.l.*) occur more sporadically in the Central Baltoscandian and Oslo confacies belts, but are absent from carbonate mudmounds.

Representatives of the Proetoidea are the dominant element on this map. Of these *Ascetopeltis* is present in all three major confacies belts (Oslo, Central Baltoscandian, and North Estonian CBs), indicating perhaps a latitudinal rather than a facies-bound distribution. *Ascetopeltis* appears to be the most widely distributed genus of the Proetoidea during that time in Baltoscandia. Records of the genus from *geschiebe* (Neben & Krueger 1979, pl. 139) and erratic boulders (Rhebergen 2001, p. 41) point to a probable wider distribution than indicated by data from existing outcrops. *Ascetopeltis* also occurs in Avalonia (see above).

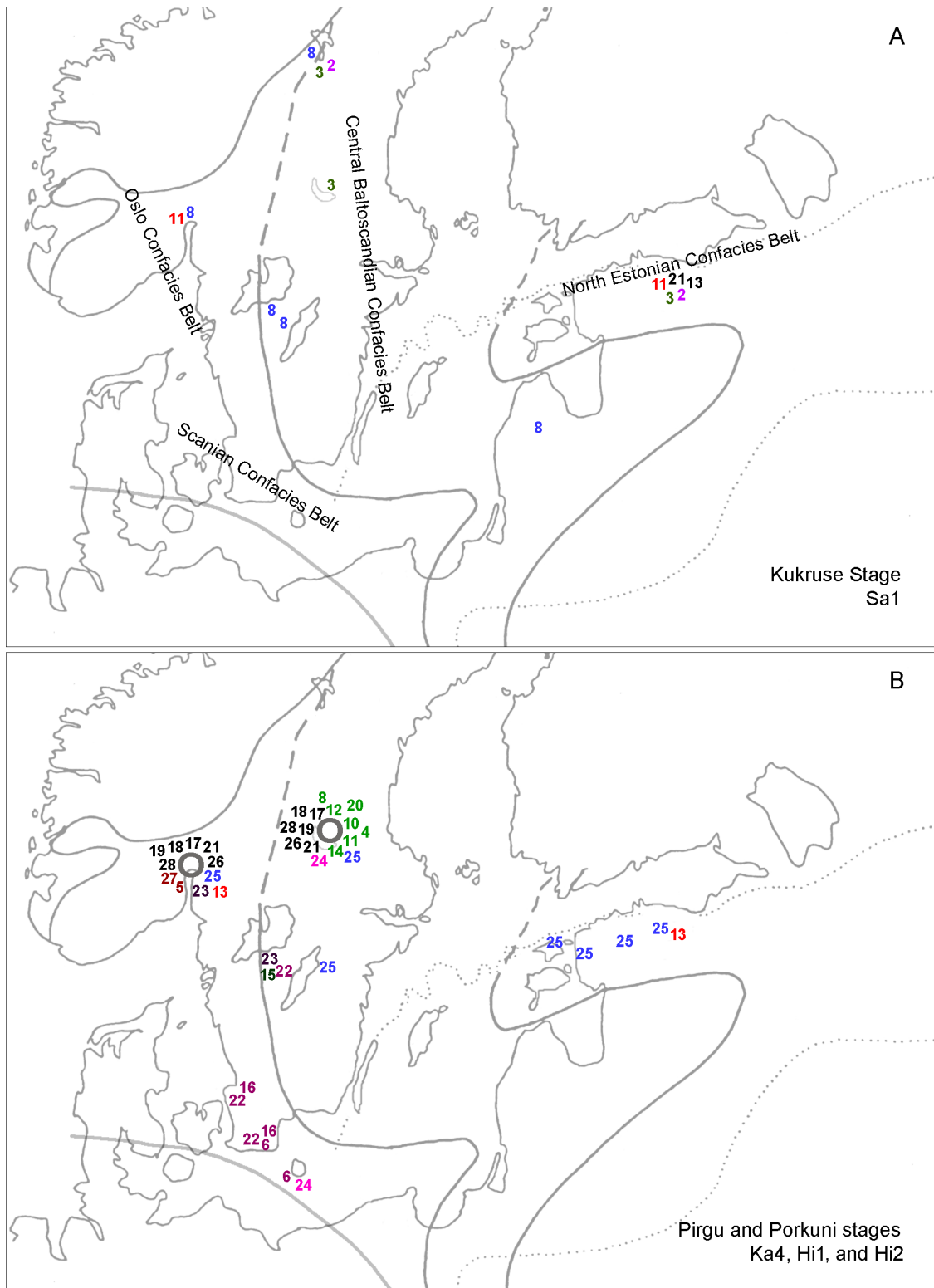


Fig. 1. Distribution maps of genera (numbering follows that in Table 1) on the Baltoscandian Confacies Belt map (modified after Jaanusson 1982a, 1995), showing facies preferences of different genera. (A) Kukuruse Stage (C_{II} ; or Global Stage Slice Sa1); (B) Pirgu and Porkuni stages (F_{Ic} and F_{II} ; or stage slices Ka4 and Hi1–Hi2) (see Bergström et al. in press). The Pirgu and Porkuni stages are taken together, considering that the Boda carbonate mounds accumulated throughout most of that period (Jaanusson 1982a, b; Suzuki & Bergström 1999) and the precise interval of occurrences is often unknown.

Stenoblepharum seemingly made a shift from its former more restricted occurrence within the North Estonian CB (Fig. 1A) to a wider distribution within the Central Baltoscandian CB and the Oslo CB. But its occurrence in mid-Darriwilian geschiebe of Red *Orthoceratite* Limestone (Popp & Schöning 2006) indicates its presence at that time within the Central Baltoscandian CB. As in the case of *Ascetopeltis*, there may be a latitudinal trend (Fig. 2B), but this might also be related to the presence of *Stenoblepharum* in (different) carbonate facies (Owens 1979, table 2). This idea is supported by observations by Owen (2007, fig. 1), who included *Stenoblepharum* in immigrant taxa restricted to pure carbonates in Avalonia.

Rorringtonia and *Solariproetus* seem to be restricted to the Scanian CB, being collected from the deeper-water Lindegård Mudstone Formation. The first appears in the Shelve Inlier, Shropshire, in the lower Caradoc (Sa1), with younger Ordovician species from the *Staurocephalus* Beds in Scania; the second occurs in the late Ashgill of the Holy Cross Mountains, Poland, and the English Lake District (Owens 2004). A third genus, *Paraproetus*, is recorded from the same areas in the late Ashgill, as well as in Västergötland in the Central Baltoscandian CB. These genera occur in the most offshore environment.

Madygenia is interesting in its palaeogeographical occurrence. Its origin appears to be in the late Caradoc–early Ashgill of the northern Alai Ridges, Uzbekistan–Kyrgyzstan borders. In the early Ashgill *Madygenia* occurred in South China. Thereafter it reached Sardinia by the late Ashgill (Rawtheyan) and soon afterwards Baltoscandia, together with other globally dispersed Hirnantian fauna. One specimen has been recorded from the *Dalmanitina* Beds (Loka Formation, Porkuni Stage, Hirnantian). *Madygenia* survived the end-Ordovician extinction event and is known from the Silurian of northern England (Owens 2004).

CONCLUSIONS

Diversity patterns of about 30 genera with more than 70 species of Proetida in Baltoscandia studied over 150 years have been analysed. The first representatives of this trilobite order in the region appeared in the Billingen Stage (B_{1β}–B_{1γ}), or possibly earlier in the Arenig. In the background of stepwise increase in genera, two diversity peaks occurred in the Ordovician, the first in the Kukruse Stage (C_{II}), and the second in the Pirgu–Porkuni stages (F_{1c}–F_{II}). Nine proetide genera out of 21 occurring in the Pirgu Stage (F_{1c}) survived the

end-Ordovician extinction event. In the background of the global extinction of Bathyporoidea, the survivors included Proetoidea and Aulacoplauroidea.

The influx of pelagic genera into Baltoscandia was possibly related to eustatic events. The common palaeogeographical occurrence of *Carolinites* in the Ordovician tropical regions is explained by their epipelagic and active surface swimming lifestyle (Fortey 1975). Rare occurrences of this genus in higher latitudes, like in Baltica, and even farther towards the South Pole, in the Montagne Noire, France, and in Turkey, have been explained by gyres originating from the equatorial current that moved southwards (McCormick & Fortey 1999). An additional factor could be the Evae Drowning Event (see Nielsen 2004) (F12), supporting the widespread migration and arrival of new faunal elements. The second arrival of pelagic Proetida (*Telephina*) came with the Furudal Highstand during the Uhaku Age (C_{1c}). The largest Phanerozoic eustatic highstand, in Caradoc times (Hallam 1992) (starting from the Kukruse Age; C_{II}), introduced a new wave of benthic immigrants.

The most diverse fauna of trilobites and other organisms occurs in the Boda mudmounds. This environment provided a wide range of habitats, coupled presumably with a rich food supply, and supported 14 genera of Proetida, some of which are restricted to it. Opinions on the climatic conditions under which the Boda Limestone Formation was deposited vary from global warming (the ‘Boda Event’; see Fortey & Cocks 2005) to a general cooling (Cherns & Wheelley 2007). The top of the formation is of early Hirnantian age, following Jaanusson (1982a, b) and Schmitz & Bergström (2007, p. 135), when carbonate deposition continued at the latitudes (30° S and less) of Baltica, Avalonia, and eastern Laurentia. Although general cooling is indicated by the Hirnantian isotopic carbon excursion (HICE; see Schmitz & Bergström 2007), this environment continued to support diverse faunas. The Ärina Formation in northern Estonia, although contemporaneous with the upper part (Hirnantian) of the Boda Limestone Formation, yields a different fauna of Proetida, dominated by ‘*Proetus*’ *ramisulcatus* and *Ascetopeltis* sp. Neither of these species is represented in the Boda Limestone, although the latter occurs in the flank facies. No Proetida have been recorded in the Saldus and Kuldiga formations of southern Estonia, which have yielded a typical *Hirnantia* association (Kaljo et al. 2008), with *Mucronaspis* Destombes and *Brongniartella* Reed. Only one genus of Proetida, *Madygenia*, is recorded from later Hirnantian strata in Baltoscandia (Owens 2004). With the termination of carbonate mound deposition by the HA regression that resulted from the first of the Hirnantian

glacial episodes (Schmitz & Bergström 2007), the rich fauna of Proetida disappeared from the region, and many genera became extinct.

During the Ordovician Baltica moved progressively closer to the tropics, and lay about 30° S by the end of the period (Cocks & Torsvik 2002). Its anticlockwise rotation led to approximate latitudinal alignment of the points corresponding to the present-day sampling sites in the Oslo, Central Baltoscandian, and N Estonian confacies belts, all of which were located in a 'belt' about 300 km wide, oriented in a north–south direction, corresponding to 2°–3°. The distribution of genera of Proetida shows a pattern of occurrences seemingly limited by latitude. Some genera pass through (W–E) all confacies belts and some only adjacent ones, but do not occur in much higher or lower latitudes. This may show a possible adaptation to very restricted, temperature-related environmental conditions, which might have been prevalent in the area due to global cooling. However, because of the very sparse coverage of data over the sample area, this assumption must remain provisional.

In general, understanding of the global palaeogeographical distribution and migrations of Proetida during the Ordovician needs further study, with careful checks of systematic identifications and stratigraphical information, although it is well known that the Boda Limestone Formation, the Keisley Limestone Formation, northern England, and the Kildare Limestone Formation, eastern Ireland, share common faunas (e.g. Dean 1978) including Proetida, and all three were deposited at a similar latitude (e.g. Fortey & Cocks 2005). In addition, this study confirms that there was some influx of pelagic proetide taxa that are common in the Laurentian Bathyrud Province during the Floian. At this time connection with Laurentian faunas is also apparent in some trilobites belonging to other orders (Hoel 1999; Pärnaste 2006), planktic acritarch assemblages (Servais et al. 2005), and epipelagic graptolites (Cooper et al. 1991). During the later Ordovician ever increasing numbers of faunal exchanges between Baltica and Avalonia occurred, due to the progressive narrowing of the Tornquist Sea, leading up to its ultimate closure and the soft docking of the two.

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Trilobiidiseltsi Proetida levik Baltoskandia Ordoviitsiumi läbilõikes

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Trilobiidiselts Proetida moodustab väikese, kuid mitte vähetähtsa faunaelemendi Baltoskandia Ordoviitsiumi läbilõikes. Suure hulga antud regiooni trilobiite käsitleva publikatsiooni põhjal on kogutud liigi tasemel andmebaas. Lisaks Skandinaavia ja Baltimaade andmetele on liidetud ka andmed Põhja-Saksamaal ning selle ümbruskonnas levivatest glatsiaalsetest rändpangastest ehk nn *geschiebe*'dest. Järgides tänapäevast süstemaatikat, taksonoomiat ja stratigraafilist baasi, on antud ülevaade nende trilobiitide eri perekondade levikust erinevas settekeskkonnas läbi Ordoviitsiumi.

Nimetatud piirkonnas on esindatud Proetida kõigi kolme ülemsugukonna esindajad (Bathuroidea, Aulacopleuroidea ja Proetoidea) kokku üle 70 liigiga umbes 30 perekonnast. Nad ilmusid Billingeni eal (või isegi veidi varem) ja enamasti mõne perekonna kaupa lademe kohta, vahetades välja mõne varasema, nii et mitmekesisus püsis enam-vähem stabiilne. Erandiks olid kaks taset, Kukruse ja Pirgu iga, kus toimus hüppeline mitmekesisuse suurenemine. Kõige rikkalikuma proetiidifaunaga Pirgu ja Porkuni eal elanud 21 perekonnast vaid 9 elasid üle Ordoviitsiumi lõpu jäätumise ning on esindatud Siluri läbilõikes. Samas suri ülemsugukond Bathuroidea välja. Selles levikupildis on sarnasusi proetiidide levikupildiga Avalonias, mis näitab kas otsest või kaudset ühendust selle piirkonnaga.

Neid kaht ülalmainitud taset settekeskkonda iseloomustava fatsiaalvööndite mudeli taustal võrreldes selgub, et proetiidide levikupildid on neis erinevad. Kui esimesed proetiidid, mis Balti paleobasseini jõudsid, olid globaalse levikuga pelaagilise elustiiliga ja nende ilmumine langeb kokku globaalse meretaseme tõusuga – *evae*-sünnimusega, siis bentiliste proetiidide esimene hüppeline mitmekesisustumine langeb kokku Fanerozoikumi suurima eustaatilise kõrgtasemega Kukruse eal. Seejuures esineb suurim mitmekesisus eelkõige Põhja-Eesti fatsiaalses vööndis, kus põlevkivide settealal oli tõenäoliselt rikkalik toiduallikas vetikate ja muu elustiku näol selle üheks faktoriks. Suurim Ordoviitsiumi ajastu proetiidide mitmekesisus on aga teada Oslo ja Kesk-Baltoskandia (Siljani piirkond) fatsiaalvööndeist Pirgu eal, kui regioon paiknes paleoekvaatori lähedal ning kus globaalsele jahenemisele vaatamata kihis äärmiselt rikkalik elustik, mis kajastub praegu Boda litohermis.