The Devonian nekton revolution

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LETHAIA

Traditional analyses of Early Phanerozoic marine diversity at the genus level show an explosive radiation of marine life until the Late Ordovician, followed by a phase of erratic decline continuing until the end of the Palaeozoic, whereas a more recent analysis extends the duration of this early radiation into the Devonian. This catch-all approach hides an evolutionary and ecological key event long after the Ordovician radiation: the rapid occupation of the free water column by animals during the Devonian. Here, we explore the timing of the occupation of the water column in the Palaeozoic and test the hypothesis that ecological escalation led to fundamental evolutionary changes in the mid-Palaeozoic marine water column. According to our analyses, demersal and nektonic modes of life were probably initially driven by competition in the diversity-saturated benthic habitats together with the availability of abundant planktonic food. Escalatory feedback then promoted the rapid rise of nekton in the Devonian as suggested by the sequence and tempo of water-column occupation. □ *Devonian, diversity, ecology, food webs, nekton, plankton, radiation.*

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Metazoans successively occupied various marine macroecological niches during the Early Palaeozoic (Sepkoski 1984; Stanley 2007; Servais *et al.* 2008, 2009). Metazoan benthos existed as early as the Neoproterozoic and with the beginning of the Phanerozoic, a benthic tiering evolved with forms extending into water levels above and below the sediment surface (Signor & Brett 1984; Seilacher 1999; Dornbos & Bottjer 2000; Dzik 2005; Bush *et al.* 2007). This includes the origin of the demersal mode of life, i.e. swimming animals that live close to the seafloor. Although small planktonic predators (i.e. passively drifting or migrating vertically) occurred already in the Cambrian (Butterfield 2001; Hu *et al.* 2007), it was not before the Ordovician that a vast number of planktonic metazoans (Bambach 1999; Rigby & Milsom 2000; Servais *et al.* 2008) conquered the higher parts of the water column. The first active pelagic swimmers, i.e. true nekton, also occurred in this interval together with the Early Phanerozoic phytoplankton diversity maximum (Servais *et al.* 2008, 2009).

One of the first authors to discuss and analyse the Devonian 'faunal turnover' was Bambach (1999, p. 135). Instead of grouping the metazoans into benthic, demersal, planktonic and nektonic animals, he used the units 'Low Energy' and 'High Energy' Predators (p. 136), which show a similar change to the groups considered here, but he restricted his analyses to six groups: nautiloids, eurypterids and asteroids were placed within the 'Low Energy' Predators *versus* ammonoids, malacostracans and jawed fish, which he placed within the 'High Energy' Predators. On the one hand, his analyses already reflected the macroecological changes displayed by our analyses but on the other hand, he used quite different ecological aspects to classify his faunas. While Bambach's (1996, p. 136) approach focused on 'biomass, general physical activity, metabolic rates and the concomitant need for a level of food consumption sufficient for the support of metabolic needs', we included only non-benthic organisms according to habitat as well as swimming activity, and we included all well-documented groups

with a non-benthic mode of life; we thus analysed a much larger data-set including substantial new information. The approach of Bambach *et al.* (2002) had again a different focus: They grouped the organisms 'as either passive (nonmotile) or active (motile)' (p. 6854). As we excluded, the motile benthos (e.g. gastropods and hyoliths) from our study, their results and conclusions also differ from those presented here.

Our aims were, accordingly, (1) to analyse this Devonian macroecological turnover using new data and new approaches as well as (2) to discuss the results of these analyses in the light of global ecological changes during the Palaeozoic.

Methods

We first grouped all higher-ranked taxa of non-benthic metazoans according to their assumed dominant mode of life into demersal, plankton and nekton (Table 1; a discussion of the assignment to ecological megaguilds can be found below). We did not include cnidarian plankton such as scyphozoans and ctenophores because of their low diversity in the Devonian (probably because of a preservational bias). We then analysed the stratigraphical ranges of all genera comprising these ecological megaguilds based on Sepkoski's compendium (Sepkoski 2002) to assess their diversity trajectories at the stage level. Data from the Paleobiology Database (PaleoDB, http://paleodb.org/) were used to test if the patterns were matched by abundance data estimated from the number of occurrences of each megaguild. Although both Sepkoski's compendium and the PaleoDB contain taxonomic errors, these are unlikely to affect large-scale diversity patterns (Wagner *et al.* 2007). Sampling problems are largely taken into account by focussing on proportional rather than raw data (Madin *et al.* 2006) or by applying rarefaction analyses when detailed occurrence counts were available.

In addition to Sepkoski's compendium (Sepkoski 2002), unpublished or new databases were available on acritarchs (not included in Sepkoski's data) and several invertebrates and vertebrates (see below). These data are partially derived from our own investigations and were used to evaluate detailed ecological changes among Palaeozoic marine metazoans. Based on these data, we performed simple diversity analyses including counts of boundary-crossing genera of all groups. As we included rapidly evolving groups such as acritarchs, dacryoconarids and cephalopods in our study, we also tabulated diversity with taxa known from only one stratigraphical interval (singletons).

Table 1. Assignment of animal groups to ecological megaguilds.

Demersal megaguild		Plankton megaguild		Nekton megaguild	
Taxon	Explanation	Taxon	Explanation	Taxon	Explanation
Ascocerida Discosorida Oncocerida	Coiled or curved shell, position of hyponome, occur in shallow water facies, actualistic comparison	Orthocerida	Orthoconic to slightly curved shells, secondary deposits in phragmocone rare, vertical migrants (undiff. muscle attachment), occur in black shales	Ammonoidea Nautilida Tarphycerida	Differentiated muscle attachment, coiled shell, occur also in black shales
Ellesmerocerida Plectronocerida Protactinocerida Yanhecerida	Usually breviconic with short body chamber, occur in shallow water facies	Dacryoconarida Homoctenida	Abundant in black shales, occur in all facies, too small for active swimming		
Actinocerida Endocerida Intejocerida	Usually large orthocones with expanded siphuncles, in shallow water deposits, often ventrally flattened or depressed shell				
Radiodonta Eurypterida	Walking and swimming appendages				
Cephalochordata Agnatha	Flat body, mouth orientation, actualistic comparison with lancelet	Graptoloidea	Occur in black shales, too small for active swimming, global distribution	Acanthodii Chondrichthyes Osteichthyes, Placodermi	Occur in black shales, actualistic comparison

Demersal zone

We assume that the following major taxa lived in demersal habitats: Among the nautiloids, all nautiloids originating during the Cambrian, the Actinocerida, Ascocerida, Discosorida, Ellesmerocerida, Endocerida, Lituitida and Oncocerida are here considered demersal (Table 2); this inference is based on the facies they occur in and morphological features such as coiling and position of hyponomic sinuses (Chen & Teichert 1983; Stridsberg 1985; Westermann 1999; Kröger &

Mutvei 2005). Most of the Radiodonta and Eurypterida are also thought to have lived in the demersal zone because of the presence of what probably were swimming and walking appendages. Agnathans (Galeaspida, Osteostraci and Pteraspidomorphi; Tables 3–5) most likely shared this habitat because of their usually dorsoventrally flattened body (Janvier 1996). Cephalochordata were probably demersal like their modern relative, the lancelet (*Branchiostoma*). Some Devonian fish traces provide evidence for a demersal habitat for the jawless fishes (Morrissey *et al.* 2006). As far as thelodont genera in the Devonian are concerned, they

Table 2. Diversity of mid-Palaeozoic Discosorida, Nautilida, Oncocerida and Tarphycerida. The data compilation was performed by B.K. (Kröger 2003, 2005, 2008), largely based on Sepkoski's raw data (2002).

	Ludlow	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Taxa	84	60	71	59	84	107	88	69	78
Crossing lower boundary	57	55	45	48	45	45	54	34	19
Crossing only lower boundary	15	12	9	7	7	13	28	19	
Crossing only upper boundary	13	2	12	3	7	22	8	4	
Crossing both boundaries	42	43	36	41	38	32	26	15	
Singletons	14	5	13	7	28	40	27	30	
FADs	23	5	25	10	38	58	34	34	56
LADs	30	15	23	14	36	50	54	46	
Mean standing diversity	56	50	46.5	46	45	49.5	44	26.5	
Mean standing diversity + singletons∕3	60.7	51.7	50.8	48.3	54.3	62.8	53	36.5	
Occurrences of species	209	80	99	87	94	204	192	135	133
Species diversity at 70 occurrences (rarefied)	42	38	41	29	49	48	41	40	49

Table 3. Diversity of Devonian Pteraspidomorphi (heterostracans). The compilation was performed by B.K. (Kröger 2003, 2005), largely based on Sepkoski's (2002) raw data.

	Wenlock	Ludlow	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian
Genera per stage	13	11	21	29	13	5	3	6	4
Crossing lower boundary	2	7	8	12	2	4	0	1	2
Crossing only lower boundary	0	2	3	11	1	4	0	1	2
Crossing only upper boundary	5	3	7	1	3	0	1	2	0
Crossing both boundaries	2	5	5	1	1	0	0	0	0
Singletons	6	1	6	16	8	1	2	3	2
FADs	11	4	13	17	11	1	3	5	2
LADs	6	3	9	27	9	5	2	4	4
Mean standing diversity	4.5	7.5	10	7	3	2	0.5	1.5	1
Mean standing diversity + singletons∕3	6.5	7.8	12	12.3	5.7	2.3	1.2	2.5	1.7

Table 4. Diversity of Devonian Cephalaspidomorphi. P. Janvier (Paris) kindly provided us with an unpublished personal data base which we were allowed to evaluate.

	Wenlock	Ludlow	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	8	13	3	28	17	15	3	1	2	0
Bottom-boundary crossers	0	5	1	4	7	8	0	0	0	0
Crossing only lower boundary	0	5	0	3	3	1	0	0	0	0
Crossing only upper boundary	5	1	2	7	4	0	0	0	0	0
Crossing both boundaries	0	0	1	0	4	0	0	0	0	0
Singletons	3	7	0	21	6	7	3	1	2	0
FADs	8	8	2	25	10	4	3	1	2	0
LADs	3	12	0	21	9	15	3	1	2	0
Mean standing diversity	2.5	3	2	5	7.5	0.5	0	0	0	0
Mean standing diversity + singletons∕3	3.5	5.3	2	12	9.5	2.8	1	0.3	0.7	0

Table 5. Diversity of Devonian Galeaspida. P. Janvier (Paris) kindly provided us with an unpublished personal data base which we were allowed to evaluate and literature data (Zhu 2000; Zhu *et al.* 2000) were also included.

	Llandovery	Wenlock	Ludlow	Pridoli	Lochkovian	Pragian	Emsian	Eifelian
Genera per stage	9	6	1	5	16	16	46	1
Bottom-boundary crossers	9	3	1	1	5	3	1	0
Crossing only lower boundary	6	3	0	0	4	3	0	0
Crossing only upper boundary	3	1	0	1	2	0	0	0
Crossing both boundaries	0	0	1	1	1	0	0	0
Singletons	6	1	0	3	9	13	6	1
FADs	9	3	0	4	11	13	6	1
LADs	6	5	0	3	16	16	6	1
Mean standing diversity	4.5	2	1	1.5	15	1.5	6	1
Mean standing diversity + singletons/3	6.5	2.3	1	2.5	18	19	8	1.3

Table 6. Diversity of Devonian Thelodonti. Data from Märss *et al.* (2007).

	Lochkov	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	23	7	5	5	1	2	0
Bottom-boundary crossers	8	5	3	5	1	1	0
Crossing only lower boundary	7	4	0	4	0	1	0
Crossing only upper boundary	4	2	2	0	0	0	0
Crossing both boundaries	1	1	3	1	1	0	0
Singletons	11	0	0	0	0	1	0
FAD	15	2	2	0	0	1	0
LAD	18	4	0	4	0	1	0
Turnover	33	6	2	4	0	2	0
Mean standing diversity	6.5	4	4	3	1	0	0
Mean standing diversity + singletons/3	11.9	2	0	3.5	0.5	0.8	0

essentially show the pattern discussed but only one genus extends through the Frasnian-Famennian boundary into the lower-middle Famennian (Märss *et al.* 2007). At present we include it in *Turinia* but this has become a waste basket taxon and will probably change. Thelodontidid and turiniid thelodont global distribution is different from other agnathans which might reflect larvae in the plankton, but as adults, many had a demersal and some possibly a nektobenthic mode of life (Table 6).

Plankton

We included graptoloids, dacryoconarids, homoctenids, orthocerids and bactritids as plankton (Tables 7–

10). Many members of these groups occur frequently in black shales and thus certainly lived in the water column. Most orthocerids were probably capable of minor horizontal movements but they were ineffective swimmers and migrated predominantly vertically and/or drifted passively (Hewitt & Watkins 1980; Westermann 1999; Mutvei 2002; Kröger 2003, 2005; Kröger & Mutvei 2005; Mutvei *et al.* 2007). This is suggested by their poorly differentiated muscle-attachment structures, the absence of significant endosiphonal or endocameral deposits and, in some cases, also shell morphology. Dacryoconarids and homoctenids (small conical shells of unclear systematic affinity) were too small to have been part of the nekton (Li 2000; Berkyová *et al.* 2007). Graptoloids simply had a colony-morphology unsuitable for active swimming

Table 7. Diversity of mid-Palaeozoic acritarchs. Data from G.L.M.'s database.

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian	Tournaisian
Species per stage max.	220	120	180	137	165	289	251	128
Bottom-boundary crossers	89	43	61	55	64	65	144	66
Crossing both boundaries	31	40	41	53	43	41	56	3
Singletons	65	4	23	6	39	93	74	15
FADs	86	29	41	16	59	202	90	16
LADs	123	7	43	8	60	117	162	78
Mean standing diversity	70.5	54	60	59	63.5	107.5	108	35
Mean standing diversity + singletons/3	92.2	55.3	67.7	61	76.5	138.5	132.7	40

Table 8. Diversity of Devonian radiolarians.

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian	Tournaisian
Genera per stage	8	8	8	9	10	12	25	26
Genera per stage + singletons	8	8	8	9	10	15	31	27
Bottom-boundary crossers	8	8	8	8	9	10	12	24
Singletons	0	0	0	0	0	3	6	1
Mean standing diversity + singletons/3	8	8	8	8	9	12	20	22.3
Mean standing diversity	8	8	8	8	9	11	18	22.0

Table 9. Diversity of Devonian dacryoconarids and homoctenids. Most of the data (Li 2000; Berkyová *et al.* 2007) were collected by S. Berkyová.

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	13	23	23	15	10	5	2
Bottom-boundary crossers	0	13	15	11	9	5	2
Crossing only lower boundary	0	4	9	4	4	3	2
Crossing only upper boundary	12	7	5	2	0	0	0
Crossing both boundaries	0	8	6	7	5	2	0
Singletons	1	4	3	2	1	0	0
FADs	13	11	7	4	1	0	0
LADs	0	8	11	6	5	3	2
Mean standing diversity	6	13.5	13	10	7	3.5	1
Mean standing diversity + singletons/3	6.3	14.8	14	10.7	7.3	3.5	1

Table 10. Diversity of Devonian orthocerids and bactritids (Kröger 2005).

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	26	22	26	27	21	12	4
Bottom-boundary crossers	19	19	18	20	15	11	4
Crossing only lower boundary	3	2	3	8	7	7	0
Crossing only upper boundary	3	1	5	3	3	0	
Crossing both boundaries	16	17	15	12	8	4	
Singletons	3	0	2	3	1	1	
FADs	5	1	7	6	5	1	0
LADs	5	2	5	10	9	8	
Mean standing diversity	19	18.5	19	17.5	13	7.5	
Mean standing diversity + singletons/3	20	18.5	19. 7	18.5	13.3	7.8	
Occurrences of species	33	41	34	60	46	31	10
Species diversity at 10 occurrences (rarefied)	8.1	5.8	7.8	7.4	7.2	4.7	4

but have been shown convincingly to have lived as vertical migrants (Finney 1979; Rigby & Rickards 1989).

The rich phytoplanktonic nutrient reservoir that existed from the Cambrian until at least the Late Devonian is reflected in the Early Devonian rise and extraordinary abundance of dacryoconarids and homoctenids which persisted until the Givetian (Middle Devonian; Li 2000; Berkyová *et al.* 2007) as well as in the high radiolarian diversity (new data) which increased from the Givetian until the Early Carboniferous.

Nekton

Here, we included the ammonoids, cartilaginous and bony jawed fishes, and most coiled nautiloids in the nekton (Tables 11–15). Ammonoids and coiled nautiloids are considered nektonic organisms because of their differentiated muscle-attachment structures and buoyancy devices, their occurrences in black shale facies, and actualistic comparisons (Doguzhaeva & Mutvei 1991, 1996; Klug & Korn 2004; Kröger *et al.* 2005). Recent studies have convincingly falsified the classical arguments against the high mobility of the ammonoids (Jacobs & Chamberlain 1996) such as the absence of retractor muscles (see also Klug *et al.* 2008b) and the closer phylogenetic relationship to the coleoids than to the nautilids utilizing different musculature for propulsion. The presence of muscle attachments in ammonoids comparable with those of the nautilids has now been shown for various ammonoids (Doguzhaeva & Mutvei 1991, 1996; Kröger *et al.* 2005;

Table 11. Diversity of Devonian ammonoids (Korn & Klug 2002; Korn & Ilg 2007).

	Early Emsian	Late Emsian	Eifelian	Givetian	Frasnian	Early Famennian	Middle Famennian	Late Famennian
Genera per stage	22	20	23	27	46	31	54	59
Crossing lower boundary	0	6	6	4	3	5	2	7
Crossing upper boundary	6	6	4	3	5	2	7	2
Crossing only lower boundary	0	5	6	4	2	5	2	7
Crossing only upper boundary	6	5	4	3	5	2	7	2
Crossing both boundaries	0	1	0	0	1	0	0	0
Singletons	16	9	12	20	40	24	45	50
FADs	22	7	17	24	45	26	52	52
LADs	16	14	19	24	42	29	47	57
Turnover	38	21	36	48	87	55	99	109
Mean standing diversity	3	6	5	3.5	4.5	3.5	4.5	4.5
Mean standing diversity + singletons/3	8.3333	9	9	10.17	17.833	11.5	19.5	21.17

Table 12. Diversity of Devonian acanthodians. The data of this table were extracted from Denison (1979).

	Lochkov	Prag	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	16	18	15	11	13	6	
Crossing only lower boundary	8	9	8	12	10	6	5
Crossing only upper boundary	9	7	12	10	6	5	4
Crossing both boundaries	6	5	7	7	5	3	3
Singletons	5	6	1	1	1	6	0
FADs	8	8	5	4	1	5	1
LADs	7	11	1	3	5	8	2
Mean standing diversity	9	9	9	10	7	4	5
Mean standing diversity + singletons/3	10	11	9	10	7	6	5

Table 13. Diversity of Devonian placoderms. The data of this table were extracted from Denison (1978) and Carr (1995).

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	31	50	55	53	66	94	32
Crossing lower boundary	0	20	20	8	33	20	17
Crossing upper boundary	20	20	8	33	20	17	4
Crossing only lower boundary	0	8	16	3	21	14	13
Crossing only upper boundary	20	9	5	32	7	12	0
Crossing both boundaries	0	10	3	4	13	6	4
Singletons	11	17	27	15	25	62	14
FADs	31	26	32	47	32	74	14
LADs	11	25	43	18	46	76	27
Mean standing diversity	10	18.5	13.5	21.5	27	19	10.5
Mean standing diversity + singletons/3	13.67	24.17	22.5	26.5	35.33	39.67	15.167
Occurrences	12	41	49	97	104	236	93

Table 14. Diversity of Devonian sharks. M. Ginter (Warszawa) allowed us to use his unpublished database on the occurrences of sharks (Ginter *et al.* 2008). We also used data from Zangerl (1981) and from S.T.

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	2	0	2	1	8	10	21
Bottom-boundary crossers	0	0	0	1	1	4	6
Top-boundary crossers	0	0	1	1	4	6	12
Crossing only lower boundary	0	0	0	0	1	2	4
Crossing only upper boundary	0	0	1	0	4	4	10
Crossing both boundaries	0	0	0	1	0	2	2
Singletons	1	0	1	0	3	2	5
FADs	2	0	2	0	7	6	14
LADs	2	0	1	0	4	4	9
Mean standing diversity	0	0	0.5	1	2.5	5	8.5
Mean standing diversity + singletons/3	0.3	0	1	1	4	6	11

Table 15. Diversity of Devonian bony fish. The data compilation was performed by B.K. (Kröger 2005) based on Sepkoski's raw data (2002). In Fig. 2 of the main text, two curves of Carr (1995) are reproduced showing the diversity of sarcopterygian and actinopterygian genera per stage.

	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Genera per stage	3	4	5	11	15	21	14
Bottom-boundary crossers	0	1	2	4	9	11	8
Top-boundary crossers	1	2	4	9	11	8	1
Crossing only lower boundary	0	1	0	1	4	4	7
Crossing only upper boundary	1	2	2	6	6	1	0
Crossing both boundaries	0	0	2	3	5	7	1
Singletons	2	1	1	1	0	9	6
FADs	3	3	3	7	6	10	6
LADs	2	2	1	2	4	13	13
Mean standing diversity	0.5	1.5	3	6.5	10	9.5	4.5
Mean standing diversity + singletons/3	1.2	1.8	3. 3	6.8	10	12.5	6.5

Klug *et al.* 2008b) and the idea that a coleoid mantle was hidden in an ammonoid shell is not supported for phylogenetic reasons since the body chamber was reduced long after the ammonoids had evolved from the bactritoids (Fuchs 2006; Kröger & Mapes 2007).

The coiled Tarphycerida and Nautilida are interpreted as nektobenthic or nektoplanktonic based on actualistic comparision of the shell form, muscle-attachment structures and position of the hyponome (Westermann 1999; Kröger & Mutvei 2005).

Among Devonian cephalopods, several striking evolutionary inventions are apparent. During the Early Devonian, the ammonoids, one of the most important groups of fossil marine invertebrate metazoans, evolved from bactritoids (Kröger & Mapes 2007) which had, in turn, just evolved from the orthocerids (Hewitt & Watkins 1980; Sepkoski 2002; Kröger & Mutvei 2005; Kröger & Mapes 2007; Kröger 2008). While the diversity and abundance of most cephalopods with straight conical or incompletely coiled shells decreased significantly towards the end of the Devonian, groups with adaptations to active, horizontal swimming life modes began to diversify in the Early Devonian. In addition to the bactritids and ammonoids, the coleoids (squids and octopods: Fuchs 2006; Kröger & Mapes 2007), or at least their ancestors, evolved. While the nautiloids produced conch morphologies strikingly similar to the earliest ammonoids, the coleoids embarked on a differing strategy by later forming internal shells, the only successful strategy with respect to modern cephalopods. Interestingly, shell coiling or an increase in shell coiling occurred in such different groups as in dacryoconarids, gastropod larvae, bactritoids and ammonoids, both juvenile and adult. This can be interpreted as a reaction to the increasing predation pressure (Nützel & Frýda 2003).

Early Palaeozoic marine vertebrate remains belong predominantly to the agnathans (jawless fishes). Early jawed fishes (Gnathostomata) are rarely documented from strata older than the Silurian (Gagnier 1989; Janvier 1996; Sansom & Smith 2001). Marine gnathostome diversity increased explosively in the Mid Devonian with the radiations of placoderms, cartilaginous and bony fishes (Denison 1978, 1979; Zangerl 1981; Cloutier & Forey 1991; Ginter *et al.* 2008). Remarkably, these evolutionary patterns coincided with some crucial morphological and ecological alterations (Long *et al.* 2008). Laterally compressed and thus nektonic body forms became more prevalent than the dorsoventrally flattened forms adapted to a predominantly demersal to benthic mode of life (Janvier 1996). Diversification trends can be grouped according to life habits: (1) demersal forms that display a clear diversity decrease, and in some cases extinction, towards the end of the Devonian (many jawless fishes); (2) nektonic forms, which exhibit low diversity in the Early Devonian, became highly diverse towards the end of the Devonian, and survived the end-Devonian extinctions with little or no loss (most jawed fishes) and (3) intermediate forms which were neither clearly demersal nor truly independent from the seafloor (acanthodians and placoderms). The data presented here require new analyses in the future which incorporates latest publications and results from research in progress (e.g. placoderm data are currently being revised by M. Rücklin, Bristol; reasonably new data were published by Long 1993; Carr 1995 and Blieck & Turner 2000 and were included in our analyses).

The diversity curves of the acritarchs, ammonoids, placoderms, bony and cartilaginous fish track roughly parallel throughout the Devonian with maxima in the Late Devonian, whereas the diversity of jawless fishes and acanthodians fluctuated in different ways.

Additional groups

Diversity data of the radiodonts, the eurypterids and graptoloids were extracted from Sepkoski's compendium (2002) and the Paleobiology Database. Gastropods with openly coiled protoconchs formed a considerable, sometimes even dominant, part of Ordovician and Silurian gastropod communities. During the Early Devonian, their number rapidly decreased and their embryonic shells became on average smaller (Nützel & Frýda 2003; Nützel *et al.* 2007; Frýda *et al.* 2008). These macroevolutionary trends were followed by the Late Palaeozoic radiation of Neritimorpha, Caenogastropoda and Heterobranchia. Thus, the Devonian was the period which determined the composition of all post-Palaeozoic gastropod faunas.

Results and discussion

Both the diversity and abundance data suggest an initial scarcity of macroplankton and nekton, an Ordovician plankton radiation and a Devonian nekton revolution (Figs 1, 2); this is in accordance with the results of Bambach (1999). Although there seems to be a greater proportion of plankton in the early Palaeozoic according to abundance data (Fig. 1B), this may largely reflect differences in the documentation of demersal and planktonic groups in the PaleoDB.

The diversity of acritarchs was clearly lower in the Devonian than in the Ordovician but still high compared with the late Palaeozoic (Servais *et al.* 2008). During the Late Devonian, acritarchs experienced a last radiation prior to the subsequent strong decline ('phytoplankton blackout'; Mullins & Servais 2008). Most important groups of Devonian invertebrate

meso- and macro-zooplankton are not only morphologically similar (bactritoids, dacryoconarids, homoctenids, orthocerids) but also declined synchronously in diversity towards the end of the Devonian, similar to jawless fish diversity (e.g. Janvier 1996; Märss *et al.* 2007). Some nektonic groups with a close affinity to the benthos such as many nautiloids, acanthodians and placoderms behaved differently (e.g. Long 1993; Bambach 1999). They underwent minor extinctions and radiations during the Devonian but, except for the placoderms, persisted much longer than the end-Devonian. Taken together, the nektonic groups display a rising diversity through most of the Devonian. Although they suffered during the Late Devonian mass extinctions to a varying degree, they continued to radiate and became highly diverse in the Late Devonian and Early Carboniferous. Remarkably, the Mid- to Late Devonian generic diversification of the nekton was delayed compared with the origins of most of the higher taxa.

After the Cambrian explosion (Seilacher 1999; Butterfield 2001; Hu *et al.* 2007) and the Great Ordovician diversification (Turner *et al.* 2004; Harper 2006; Servais *et al.* 2008, 2009), all nektonic organisms display a steep diversity increase from the Late Silurian to the Early Carboniferous at the expense of demersal and planktonic forms (compare Bambach 1983, 1999). This is accompanied by the radiation of radiolarians and various mollusc clades with planktotrophic juveniles or larvae (cephalopods, gastropods and perhaps bivalves).

For the explanation of the simultaneous explosive diversification of the nekton at the cost of various planktonic and demersal benthic groups, three hypotheses are available:

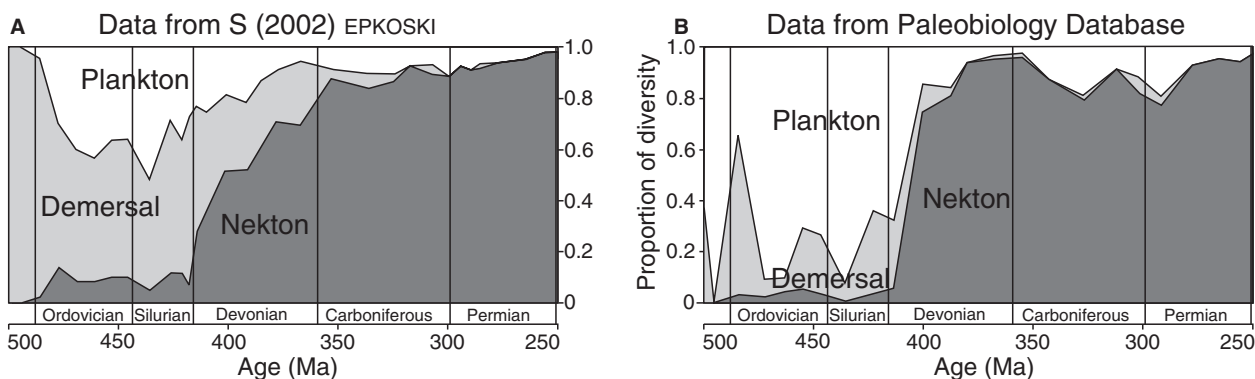1. Eutrophication by increasing organic input because of the steady rise of land plants (Algeo

Fig. 1. Patterns of diversity and proportional abundance of demersal organisms, plankton and nekton in the Palaeozoic. A, diversity based on Sepkoski's data resolved to geological stages (Sepkoski 2002). B, occurrence counts from the Paleobiology Database resolved to 10 myr intervals.
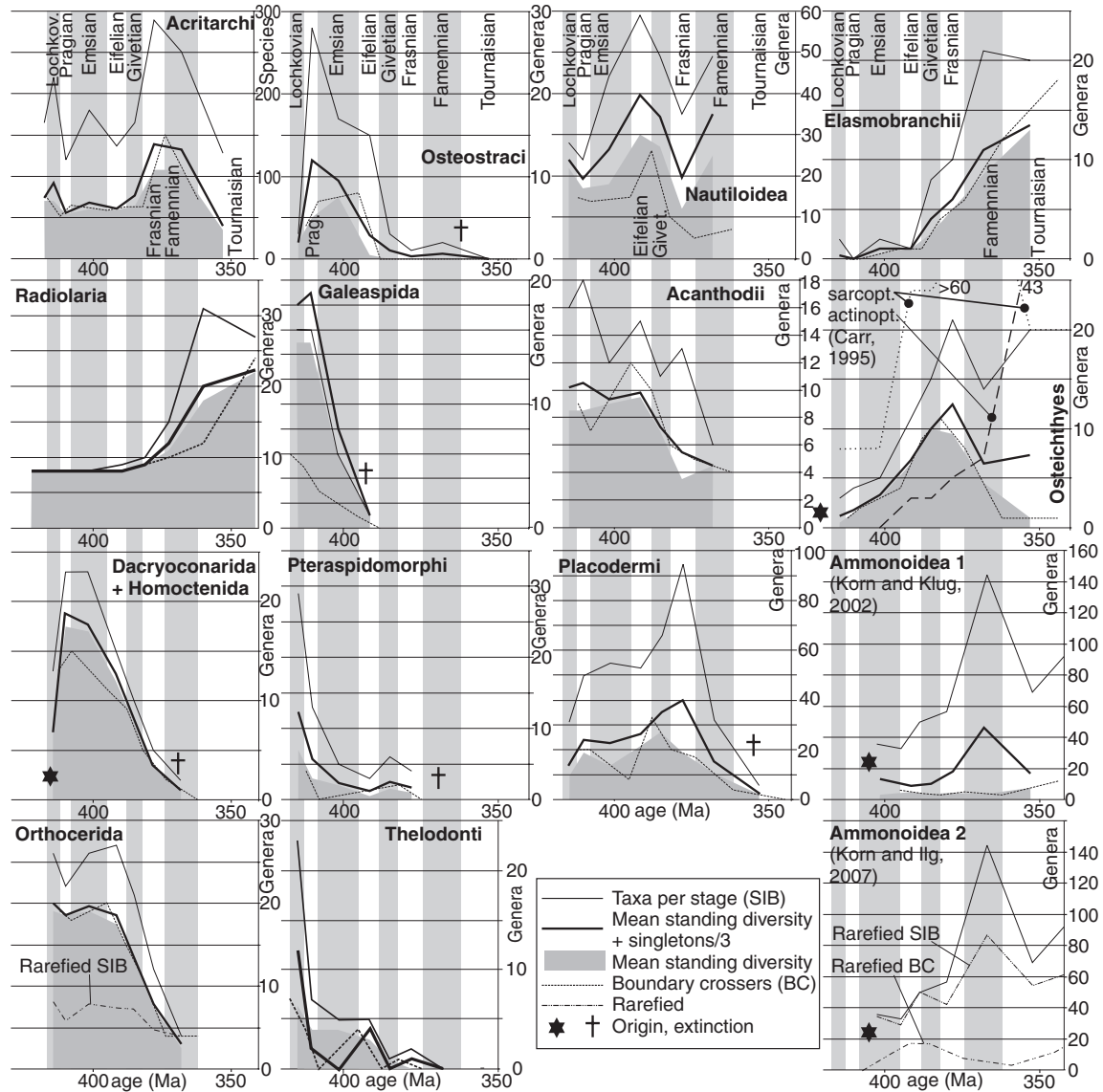
Fig. 2. Diversification of various higher rank taxa of phytoplankton, zooplankton, demersal and pelagic nekton in the Devonian and Early Carboniferous (for data see Tables 2–15).

et al. 1998), which induced a plankton bloom. The continuously high abundance of primary producers and the radiation of radiolarians (Fig. 2) fostered the diversification and radiation throughout marine food webs. Because of increasing competition in all habitats, the mobility increased simultaneously in various groups: nektonic ammonoids evolved via bactritoids from planktonic orthocerids (Klug & Korn 2004), gnathostomes replaced demersal agnathans and nektonic nautilids from demersal oncocerids. Assuming this hypothesis is correct, one would expect a parallel diversification of nektonic groups and a subsequent plankton decrease.

2. Repeated and lasting anoxia throughout the Silurian and Devonian, caused by organic input (Algeo *et al.* 1998), caused selection in favour of non-benthic and -demersal life styles. If correct, mainly benthic and demersal groups should decline in diversity while nekton and plankton are less affected.
3. The free water column served as refuge from benthic and demersal predation pressure (Signor & Vermeij 1994) and the Devonian Nekton Revolution (compare Vermeij's 1977) can be interpreted as reflecting an escalation at the bottom, forcing an invasion of benthic or demersal organisms into the free water column. Especially,

the radiation of gnathostomes then increased predatory pressure on cephalopods, selecting for higher mobility (Klug & Korn 2004; Kröger 2005). Assuming this hypothesis is correct, an initial high diversity in the demersal zone, followed by a radiation of some transitional demersal to pelagic-nektonic predators, again followed by a nekton diversification and a plankton decrease, would be expected.

The first hypothesis is corroborated by the radiation of molluscs with planktotrophic larvae and juveniles; profound changes in larval morphology and thus, reproductive and larval strategies among many molluscs began in the latest Cambrian and intensified during the Devonian (House 1996; Nützel & Frýda 2003). Morphological adaptations of gastropod larvae and juvenile ammonoids to changes in the planktonic habitat are indicated by the closure of a larval or early juvenile umbilical opening, size-decrease of the larval or embryonic shell and occurrences of their shells in anoxic environments (Nützel & Frýda 2003). Regional faunal analyses of the Moroccan Lower Devonian (Klug *et al.* 2008a) have shown that bivalve associations change from palaeotaxodont-dominated towards pteriomorph-dominated with perhaps planktotrophic larvae (Jablonski & Lutz 1983). Therefore, an increasing proportion of larvae and juveniles from many important mollusc groups fed probably on plankton during the Devonian (Jablonski & Lutz 1983). There is, however, no cross-correlation between originations and extinctions of phytoplankton and the zooplankton ($R = 0.2$ and 0.38, respectively, not significant) and thus, the first hypothesis is insufficient to explain the observed diversity fluctuations.

Lasting and repeated anoxic episodes are well-documented for the Devonian (Joachimski & Buggisch 1993; Algeo *et al.* 1998). The main prediction drawn from the second hypothesis would be an extinction of all forms that lived close to the seafloor and were unable of escaping into higher, well-oxygenated water levels. Phytoplankton, zooplankton and nekton should be less affected by anoxia-induced extinctions. Nevertheless, this hypothesis fails to explain why the nekton radiation begins clearly before the most significant anoxia of the end-Givetian and -Frasnian.

The third hypothesis implies an initially high abundance and diversity of organisms in the demersal zone, followed by a selection for a mobility increase, ultimately leading to the rise of descendants of demersal organisms. This is in accordance with the observed diversity and occurrence fluctuations. Around the Silurian-Devonian boundary, the predominantly demersal jawless fish were rather diverse (Janvier 1996). In general, nektonic organisms with some

demersal affinity such as several groups of nautiloids, acanthodians, placoderms and thelodonts display repeated minor diversifications and extinctions. The acanthodians have their maximum diversity in the Early Devonian, followed by a long-term decline. Many placoderms had thick bony armour and are morphologically intermediate between dorsoventrally flattened agnathans and laterally compressed bony fish, indicating a demersal to nektonic habitat (Janvier 1996). These mobile predators possibly suppressed many demersal animals (such as some cephalopods). The placoderm diversity peak (Fig. 2) predates the diversity and abundance maxima of the perhaps more meso- to epipelagic nekton such as some derived nautiloids (Kröger 2005), ammonoids (Klug & Korn 2004), chondrichthyans (sharks and relatives; Miller *et al.* 2003; Ginter *et al.* 2008) and bony fish. Potentially, the nektonic predators subsequently suppressed representatives of the zooplankton, causing a partial zoo- and phytoplankton extinction (graptoloids, dacryoconarids, homoctenids, 'phytoplankton blackout') or at least profound changes. Simultaneously, the proportional diversity of benthos decreased relative to that of inhabitants of the water column (Fig. 3).

Tests

We tested our conclusions by plotting the proportional diversity of benthic animals *versus* those inhabiting the water column (Fig. 3). The resulting graph clearly shows that diversity changes among taxa inhabiting the water column cannot be explained simply by a general increase in the diversity of marine taxa.

Additionally, we produced regressions for boundary crossers, genera with and without singletons for all marine genera, benthos only and nekton only (Fig. 4). The regressions support our conclusions that the diversity of nekton increases at the cost of other marine genera including benthos and plankton.
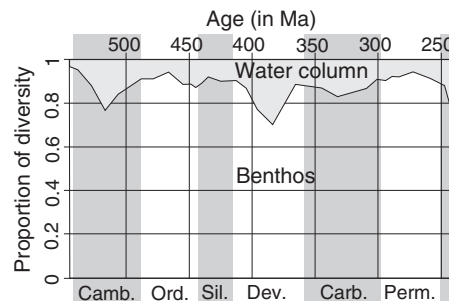

Fig. 3. Proportional diversity of benthic animals *versus* those inhabiting the water column throughout the Palaeozoic (Sepkoski 2002).
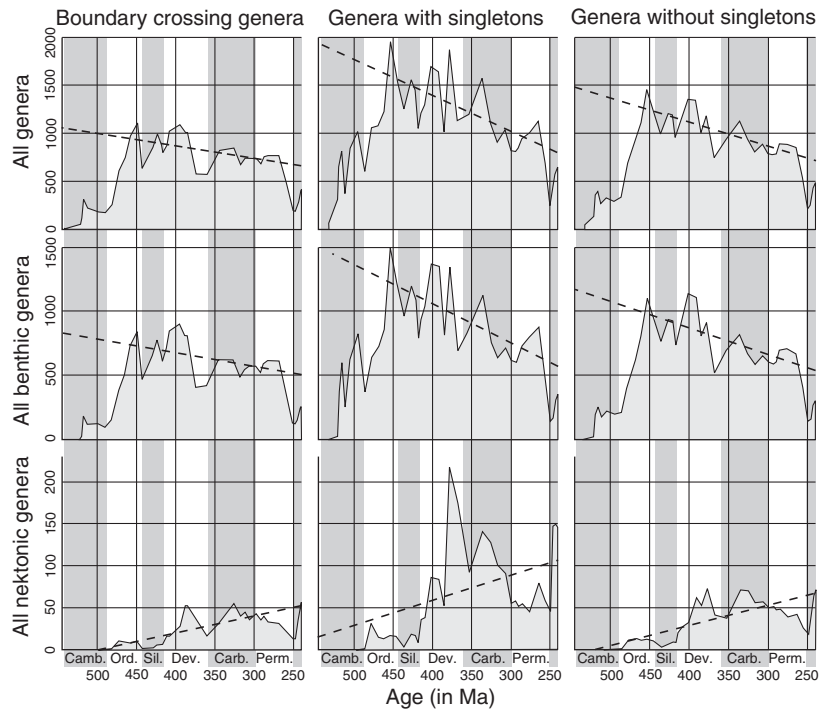
Fig. 4. Boundary-crossing marine genera throughout the Palaeozoic with the regression from the Caradoc to the Guadalupian (Sepkoski 2002). Boundary crossers, all genera with and without singletons of all marine genera, of all benthic genera and all nektonic genera are shown.

Conclusions

Major macroecological changes usually require some kind of trigger: The appearance of early mobile predators induced the evolution of skeletons and thus the Cambrian radiation, the Ordovician abundance of microplankton formed the basis for the radiation of larger plankton, the Ordovician to Devonian radiation of land plants enabled animals to follow on land. The
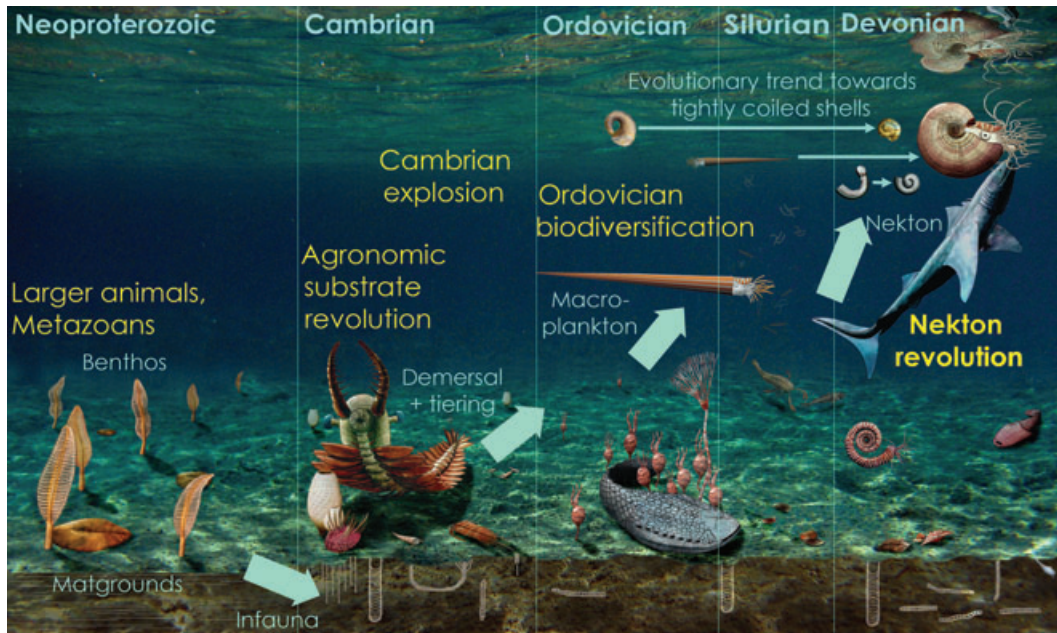
Fig. 5. Macroecological steps in the evolution of Palaeozoic marine food webs.

evolutionary acquisition of the capability to swim actively in the pelagic realm thus followed the evolution of demersal and planktonic innovations, which occurred in several groups of macroscopic metazoans more or less simultaneously in the Cambrian and Ordovician (e.g. various arthropods, early cephalopods and graptoloids). The timing of diversification of various demersal and nektonic groups suggests that the Devonian Nekton Revolution was initiated by an escalation in the benthic and demersal zones (Fig. 5). The synchronous decline of benthic animals (Fig. 3) might be sufficient to explain why the overall diversity is not strongly affected. Increasing nutrient supply from the increasing terrestrial biomass probably supported the diversification of microplankton, organisms with planktotrophic larvae (Cambrian pelagic predators are here considered as parts of the plankton because of their small size; compare Butterfield 2001 and Hu *et al.* 2007) and nekton, which suppressed many demersal organisms and the macroplankton from their habitats. Consequently, among the marine metazoans, almost only nektonic predators of most scales and the diverse benthos remained following the explosive nekton radiation in the Early Devonian while the proportion of demersal and planktonic taxa decreased dramatically.

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