Palaeozoic evolution of animal mouthparts

CHRISTIAN KLUG, LINDA FREY, ALEXANDER POHLE, KENNETH DE BAETS & DIETER KORN

During the Palaeozoic, a diversification in modes of life occurred that included a wide range of predators. Major macroecological events include the Cambrian Explosion (including the Agronomic Substrate Revolution and the here introduced 'Ediacaran-Cambrian Mouthpart Armament'), the Great Ordovician Biodiversification Event, the Palaeozoic Plankton Revolution, the Siluro-Devonian Jaw Armament (newly introduced herein) and the Devonian Nekton Revolution. Here, we discuss the evolutionary advancement in oral equipment, *i.e.* the Palaeozoic evolution of mouthparts and jaws in a macroecological context. It appears that particularly the latest Neoproterozoic to Cambrian and the Silurian to Devonian were phases when important innovations in the evolution of oral structures occurred. • Key words: Gnathostomata, Cephalopoda, evolution, convergence, diversity, nekton, jaws.

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'Explosions' in the sense of evolutionary bursts attract attention. Correspondingly, explosive radiations such as the Cambrian explosion and those following the Big Five mass extinctions as well as these extinctions themselves rank among the most widely known macroecological and palaeobiodiversity-altering events of the Phanerozoic (Fig. 1). Logically, there were other ecological events and processes that fundamentally changed the biosphere, hydrosphere and atmosphere of our planet. Knowledge of such processes appears to be somewhat under-represented in the palaeobiological literature. With this review, we want to demonstrate that some slower (more gradual) evolutionary and macroecological processes may have been underestimated. Additionally, we will discuss the differences in impact between drastic short term events and more gradual and less spectacular processes of macroecological fluctuations, radiations of groups and cases of ecological replacement of large groups (Fig. 2; see, *e.g.* Thayer 1979, Algeo & Scheckler 1998, Bambach 1999, Seilacher 1999, Klug *et al.* 2010, Roopnarine 2010, Bush & Bambach 2011, Payne *et al.* 2014, Liow *et al.* 2015).

In addition to the Cambrian explosion and the Great Ordovician Biodiversification Event (GOBE; Harper 2006, Servais *et al.* 2016), several major mass extinctions altered global biodiversity during the Palaeozoic (Sepkoski 1984, 2002; Korn 2000; House 2002; Bambach *et al.* 2004; Lu *et al.* 2006; Alroy 2010a, b; Hannisdal & Peters 2011; McGhee *et al.* 2013; McGhee 2014; Long *et al.* 2016). Classically, Palaeozoic macroecology has been assessed by trying to quantify changes in palaeobiodiversity (Fig. 1). Still, one of the big challenges is to overcome the effects of biases in these data (*e.g.* Signor & Lipps 1982; Alroy 2010a, b; Smith *et al.* 2012) or the link between diversity and functional disparity. The main issues are likely great differences in sampling, the inhomogeneous rock record and the incompleteness of the fossil record. Functional diversity and disparity might be more appropriate measures, although not always easy to obtain, particularly for extinct invertebrates.

Inclusion of detailed diversity analyses of single groups carried out by experts and evaluating palaeoecological or morphological information has improved our ability to develop hypotheses about major macroecological changes in the marine realm during the Palaeozoic (*e.g.* Signor & Brett 1984; Vermeij 1977, 1994; Brett 2003; Nützel & Frýda 2003; Nützel *et al.* 2007; Klug *et al.* 2010, 2015a; Servais *et al.* 2016). For example, the occupation of the water column by nektonic metazoans began already in the Cambrian

(Rigby & Milsom 2000, Butterfield 2001), but the nekton became important only in the Silurian and even more so in the Devonian, at the cost of large planktonic organisms (Bambach 1999; Kröger 2005; Klug *et al.* 2010, 2015a; Dahl *et al.* 2011). We have dubbed this process the Devonian Nekton Revolution (Fig. 2). It is strongly linked with the rise of predatory jawed vertebrates, which also became more active swimmers in the same interval (from demersal to nektonic; see also Anderson *et al.* 2011). The relationships between locomotion properties (motility), feeding strategies (predation) and required mouthparts and their influence on marine diversity will also be addressed in this article.

As far as diversity is concerned, the Cambrian explosion cannot be fully separated from the GOBE (Servais *et al.* 2008, 2009, 2016); both really belong to one giant diversification cycle, interrupted by extinctions in the Cambrian and Ordovician, and subsequently followed by a (somewhat fluctuating) plateau until the Devonian and a decline that started with the Late Devonian climatic changes and mass extinctions and, depending on author and method, a diversity spike in the Permian (*e.g.* Sepkoski 1978, Alroy 2010b, Smith *et al.* 2012).

Also, looking at earlier summaries of diversity trends for the Phanerozoic (Fig. 1) like those of Valentine (1969) or Sepkoski (1978), the end-Permian extinction could also be called the late-Palaeozoic mass extinction, as the palaeobiodiversity decrease started already in the Late Devonian and climaxed at the end of the Permian. This idea of a prolonged late Palaeozoic decline is also supported by 'dead clades walking' (Jablonski 2001), such as the trilobites and pterygotid eurypterids, which both continued with a very low (*i.e.* strongly reduced) diversity and disparity after the Hangenberg Event (end-Devonian; *e.g.* Brauckmann *et al.* 1993; Korn 1993, 2000; Adrain *et al.* 1998; Lamsdell & Braddy 2010; Klug *et al.* 2015a, 2016; Korn *et al.* 2004, 2015). Recent diversity analyses (*e.g.* Korn *et al.* 2004, Stanley 2007, Alroy 2010b, Smith *et al.* 2012), however, show a moderately low diversity plateau from the Late Devonian well into the Permian, ending in a diversity maximum in the middle of the Permian. The moderate diversity of the Late Palaeozoic is classically explained by the Carboniferous to early Permian ice age (*e.g.* Stanley 2007).

It is commonly accepted that abiotic influences (meteorite impacts, volcanism, plate tectonics, climate including sea-level changes) as well as biotic factors influence marine diversity. In this article, we focus on biotic processes, such as radiations of groups and the potential importance of evolutionary novelties, including development of new organs, as well as the associated ecological properties. Accordingly, we address the questions of (i) when mouthparts and jaws in major groups of organisms originated, (ii) the timing of the evolution of metazoan mouthparts during the Palaeozoic, and (iii) how benthic diversification enabled the stepwise success of various levels of predators.

Material, Definitions and Methods

In addition to published diversity curves, we used published phylogenetic reconstructions, which were based on phylogenetic analyses (Halanych 2004, Paxton 2009, Kröger *et al.* 2011, Parry *et al.* 2014, Brazeau & Friedman 2015). We partially simplified the published phylogenies by limiting the displayed clades to those relevant to the present paper.

Various rigid, articulated structures that function to grasp, manipulate, and process food at the entrance of the animal's alimentary canal could be defined as jaws *sensu lato* (Hochberg *et al.* 2015). Research has particularly focused on vertebrates and arthropods but various other invertebrate groups also possess such structures (Hochberg *et al.* 2015, Uyeno & Clark 2015). We will herein concentrate on animal groups with a reasonable fossil record.

For our purposes, we differentiate between 'mouthparts' and 'jaws' *sensu stricto*. 'Mouthparts' refers to either radially or linearly (vertically or horizontally) arranged hardened cuticular, sclerotic or mineralized structures in the feeding apparatus (either surrounding the mouth externally or lying directly inside the oral cavity), which consist of one part ('jaws' of the Monoplacophora, Gastropoda), where they are accompanied by radulae or more than two functional units (as in the Annelida, Conodonta, Echinoidea or Radiodonta), where they are neighboured by additional mouthparts (as in the Mandibulata) or move horizontally (as in the Chelicerata). Most of these mouthparts can only process smaller food particles, in relation to body size, than jaws.

Jaws open vertically and consist of two articulated functional units (upper and lower jaw) as in the Gnathostomata and crowngroup Cephalopoda surrounding the mouth. Each of the two units can consist of one (cephalopods) or more hard parts (vertebrates). Although jaws function quite differently in cephalopods than they do in vertebrates (see Uyeno & Kier 2005, 2007; Uyeno & Clark 2015), they might still have made it possible to attack more tough and elusive prey in conjunction with their tentacles. Suction feeding is an important innovation of jawed vertebrates to draw mobile or elusive prey into the oral cavity (*e.g.* Mallat 1996, Anderson & Westneat 2007, Wainwright *et al.* 2015). In cephalopods, arms might perform this function – although these have so far not been reported from fossil externally shelled cephalopods (Ritterbush *et al.* 2014, Clements *et al.* 2017).

Dimensions of mouth parts and jaws are given in Table 1. Note that the structures herein identified as "jaws" included here always exhibits a width to body length ratios > 0.1, while those structures here dubbed "mouthparts"

have ratios below 0.1. In turn, this corroborates the hypothesis that jaws permitted the ingestion of larger food items.

Results and Discussion

What was the timing of the evolution of metazoan mouthparts?

Particularly the less heavily sclerotized or mineralized mouthparts, jaw-like structures and jaws have a reduced likelihood of preservation and thus suffer from the incompleteness of the fossil record. Bengtson (2002) as well as Bengtson & Yue (1992) discussed various steps in the evolution of predation in the Proterozoic organisms. Although fossilized mouthparts are normally missing, Neoproterozoic traces, such as boreholes in the conchs of members of the *Cloudina-Namacalathus* assemblage and radula traces (*Radulichnus*, *e.g.* Seilacher *et al.* 2003, Buatois *et al.* 2014) are documents of the earliest known macroscopic cases of predation. The radula traces were potentially produced by radulae of the stem-group mollusc or lophotrochozoan *Kimberella*. The oldest radula was described by Butterfield (2008) from the lower Cambrian Mahto Formation (Canada).

Mouthparts undoubtedly evolved independently in various groups and in very different non-homologous ways (Hochberg *et al.* 2015, Uyeno & Clark 2015). As far as ecdysozoans are concerned, sclerotized mouthparts have been recorded from the early Cambrian in several groups. For example, early chaetognath mouthpart remains have been documented from the Chengjiang biota (Vannier *et al.* 2007) and arthropods with mouthparts are quite well-known from various Cambrian Fossillagerstätten (*e.g.* Conway Morris 1985, Forchielli *et al.* 2014). By contrast, the pentameral mouthparts of echinoids originated somewhat later, in the Ordovician (*e.g.* Reich & Smith 2009). Annelid mouthparts (scolecodonts) are known from the late Cambrian and diversified rapidly in the Ordovician (Hints & Eriksson 2007, Paxton 2009), but their early evolutionary history is still poorly constrained. Phosphatic mouthparts of conodonts first appeared in the early Cambrian.

Bipartite jaws evolved from much less sclerotized precursors independently and in some respects at least convergently if not in parallel (for a discussion of parallel
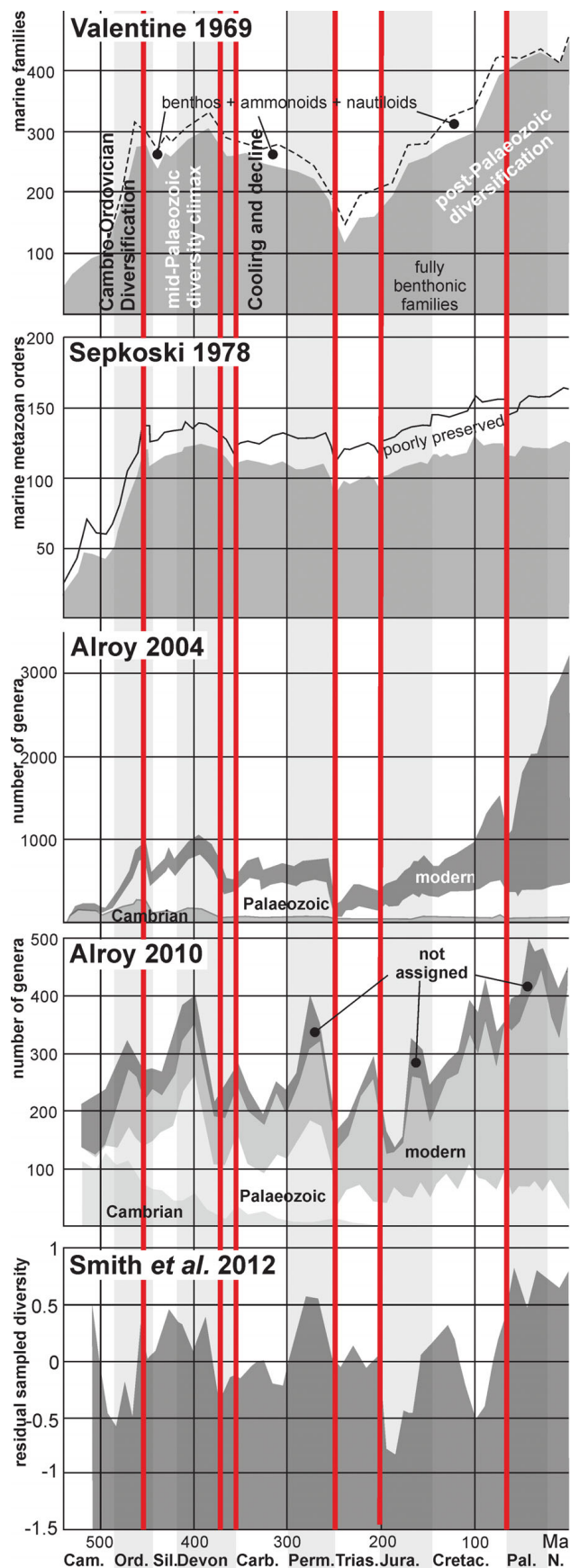

Figure 1. A short history of marine metazoan diversity in the Phanerozoic. Note that all curves share the Cambro-Ordovician diversification, the declines following the biggest mass extinctions, and the mid-Palaeozoic diversity climax (data and curves from Valentine 1969; Sepkoski 1978; Alroy 2004, 2010b; Smith *et al.* 2012). The most important mass extinctions are marked in red.

Table 1. Proportions of mouth parts and jaws in various vertebrates and invertebrates. Uncertain values are printed in bold.

Systematics	Species	width	length	width/ length	body size	number	length/size	Vert.	Source
Monoplac.	*Neopilina galatheae*	2.5	1.5	0.6	28.5	1	0.053	1	Lemche & Wingstrand (1959)
Gastropoda	*Testudinalia tesulata*	2.2	1.4	0.63	18	1	0.078	1	Vortsepneva *et al.* (2013)
Echinodermata	*Rhenechinus hopstaetteri*	2	4	2	42	10	0.095	0.5	Smith *et al.* (2013)
Malacostraca	*Nahecaris jannae*	0.9	1.5	1.67	70	2	0.021	0	Klug *et al.* (2008)
Merostomata	*Hughmilleria socialis*	5	13	2.6	220	2	0.059	0	Clarke (1912)
Merostomata	*Limulus polyphemus*	3	12	4	210	2	0.057	0	own data
Placodermi	*Qilinyu rostrata*	51	9	0.18	400	2	0.023	1	Zhu *et al.* (2016)
Placodermi	*Guiyu*	**40**	45	1.13	310	2	0.145	1	Zhu *et al.* (2009)
Chondrichthyes	*Cladoselache*	**70**	160	2.29	1120	2	0.143	1	own data
Cephalopoda	*Manticoceras orbiculum*	4.2	3.4	0.81	10.5	2	0.324	1	Clausen (1969)
Cephalopoda	*Postclymenia evoluta*	6.5	14	2.15	35	2	0.4	1	Klug *et al.* (2016)

evolution see Monnet *et al.* 2011) in early jawed vertebrates and early cephalopods. The fossil record is too poor to test these lineages for parallelism, because the less sclerotized or mineralized structures are missing and the exact timing of evolutionary events is unknown. However, convergence and parallelism in unrelated lineages are unlikely to occur in random groups with no ecological connection or functional similarity. This likely correlation leads to further questions discussed below.

When did jaws originate in vertebrates?

The origin of vertebrate jaws and teeth as well as their evolutionary implications have recently received a good deal of attention (*e.g.* Anderson *et al.* 2011, Rücklin *et al.* 2012, Brazeau & Friedman 2015, Chen *et al.* 2016, Zhu *et al.* 2016). In the past decades, the fossil record of gnathostomes has been extended backwards in time into the Ludlow Epoch (Silurian) with the discoveries of stem gnathostomes like *Entelognathus* and *Quilinyu*, as well as stem osteichthyans like *Guiyu* (Zhu *et al.* 1999, 2009). According to the phylogeny proposed in Brazeau & Friedman (2015), these facts point at an origin of gnathostomes and thus jaws before the Ludlow Epoch.

Remarkably, there appears to be an – at least superficial – convergence or even parallelism in the evolutionary transition from circum-oral reinforcements like the mouthparts in gastropods and monoplacophorans or cartilaginous structures in agnathans (*e.g.* Janvier 1996, 2007, Donoghue & Sansom 2002, Schilling 2003, Goudemand *et al.* 2011) to much more strongly mineralized or sclerotized jaws in cephalopods and gnathostomes, although the question as to whether or not these structures are necessarily homologous in agnathans and gnathostomes remains open. As in early mollusc evolution, the evolutionary increase in mouth reinforcement begins with cartilaginous structures or other non-mineralized supports,carrying tooth-like structures in

jawless vertebrates including conodonts *sensu lato* (protoconodonts; Missarzhevskij 1973, Bengtson 2002, Goudemand *et al.* 2011, Murdock *et al.* 2013). In both Mollusca and early Vertebrata, these jaw-precursors (possibly non-homologous cartilaginous or chitinous-scleroproteinaceous structures) have a low likelihood of preservation and thus are absent from the pre-Silurian fossil record, although their presence is likely, based on the extant phylogenetic brackets (Witmer 1995).

The slow increase in mouthpart reinforcement from the Cambrian to fully evolved gnathostomes in the Silurian might make it difficult to draw a clear line from jawless to jawed fish; newly discovered fossils show transitional stages in initial jaw evolution. Due to the lack of older fossil evidence and using current phylogenetic hypotheses, we suggest that the origin of vertebrate jaws occurred more or less shortly before cephalopod jaws sometime in the early Silurian (or even in the Ordovician; *e.g.* Sansom & Smith 2001, Andreev *et al.* 2016).
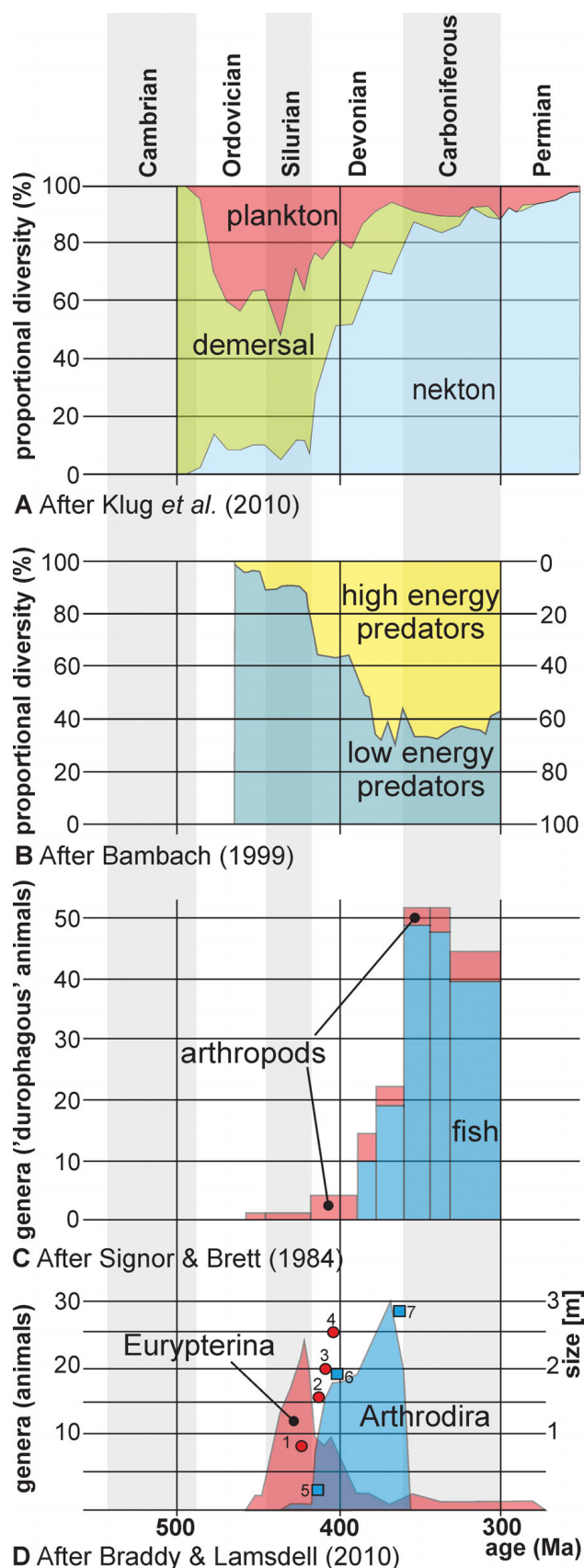
When did jaws originate in cephalopods?

This question was briefly addressed by Kröger *et al.* (2011). They suggested that jaws are limited to the cephalopod crowngroup. This interpretation is somewhat supported by the current fossil record of cephalopod jaws, which does not extend into strata older than the Late Devonian (Matern 1931; Clausen 1969; Mapes 1987; Tanabe *et al.* 2015; Klug *et al.* 2015b, 2016). There is only one older (Silurian) record of non-conch hard parts from the apertural region of cephalopods, namely *Aptychopsis*. This structure is composed of three components and was first described by Barrande (1872) and later convincingly re-interpreted by Turek (1978) and Holland *et al.* (1978) as cephalopod opercula. So far, the oldest unequivocal cephalopod jaws were recorded by Trauth (1927–1936) and Clausen (1969) from Frasnian strata of Germany (see also

Frye & Feldmann 1991). They belong to gephuroceratid ammonoids. Recently, we described new discoveries from the latest Famennian of Morocco, documenting jaws from three additional important clades of Devonian ammonoids (Klug *et al.* 2016). Combining this information, it appears most parsimonious to assume that all ammonoids possessed jaws, including the earliest forms from the Emsian.

Here, the earliest presence of jaws or mouthparts, respectively, is inferred primarily from fossil occurrences and secondarily, in the case of cephalopods and vertebrates, from phylogenetic bracketing (Witmer 1995). In terms of mollusc jaws, the picture is blurred. Polyplacophorans and bivalves lack jaws (*e.g.* Vortsepneva *et al.* 2014), while jaw-like structures are present in monoplacophorans (Lemche & Wingstrand 1959), gastropods (*e.g.* Boletzky 2007; Vortsepneva *et al.* 2013, 2014) and all Recent cephalopods (*e.g.* Boletzky 2007). An essential question is whether these structures are homologous. In gastropods and monoplacophorans, the chitinous-scleroproteinaceous structures oppose the radula, *i.e.* they represent some kind of upper jaw and thus might be homologous to the upper jaw in cephalopods. As far as the lower jaw is concerned, the situation is less clear: Boletzky (2007) stated that the "evolutionary origin of the lower jaw, which has no obvious homologue in other molluscs, remains a matter of debate". In any case, it appears reasonable that at least some kind of precursor or 'Anlagen' of jaws were present in the common ancestors of cephalopods, monoplacophorans and gastropods.

But why are cephalopod jaws absent from strata older than the Late Devonian? Answering this question becomes even more difficult in light of the fact that cephalopod radulae are known from the Late Ordovician Soom Shale Lagerstätte (South Africa; Gabbott 1999) and the Silurian Kirusillas Shale (Bolivia; Mehl 1984). Their general scarcity and the absence of cephalopod radulae between the Silurian and the Carboniferous (*e.g.* Closs 1960, 1967), however, underscores the incompleteness of the fossil record (Kruta & Tanabe 2015). In turn, this incompleteness suggests that the presence of the chitin and scleroproteins in "jaws" of monoplacophorans and gastropods on the one hand and pre-Frasnian cephalopods on the other hand was the reason for its non-preservation. In other words, it appears that jaw-like structures were already present in the

Figure 2. The respective roles of plankton versus nekton (A), energy-need in predators (B), diversity of 'durophagous' animals (C) and diversity/size of eurypterines versus arthrodires throughout the Palaeozoic (D). Data and curves from Signor & Brett (1984), Bambach (1999), Klug *et al.* (2010) and Lamsdell & Braddy (2010). Numbers in D correspond to taxon names: 1 – *Erettopterus*; 2 – *Pterygotus*; 3 – *Acutiramus*; 4 – *Jaekelopterus*; 5 – *Arctolepis*; 6 – *Eastmanosteus*; 7 – *Dunkleosteus*.

first cephalopods (as indicated by the extant phylogenetic bracket between *Neopilina* and Recent cephalopods; *e.g.* Clausen 1969; Vortsepneva *et al.* 2013, 2014) but initially with a much 'weaker' chitin and scleroproteins (thinner and maybe less resistant) with a lower preservation potential than the beaks in crown group cephalopods (Kear *et al.* 1995). Extant cephalopods jaws are made of one of the hardest and stiffest known wholly organic materials (Miserez *et al.* 2008), which probably applied to many extinct cephalopods as well. Slightly elevated structures in the Ordovician orthocones published by Gabbott (1999) might be homologous to jaws of later cephalopods; at least superficially, these structures are reminiscent of the narrow "jaws" of gastropods. A re-examination of these materials might shed more light on this issue. The lack of jaws is even more peculiar as large orthoconic nautiloids have often been interpreted as 'durophagous' predators (Brett & Walker 2002). Large paired injuries in Ordovician nautiloids might have been caused by shell-breaking predators including nautiloids and eurypterids (Kröger 2005), although the culprits are hard to pin down (Kröger 2005, 2011).

Taking these observations and inferences together, it appears that jaws evolved from weakly sclerotized structures in early molluscs to the tough chitinous-scleroproteinaceous cephalopod beaks, of which Frasnian to Recent records are known. This slow evolutionary increase in jaw reinforcement by chitin and scleroproteins appears to parallel the evolutionary change in mouthparts *sensu latu* of, *e.g.* ecdysozoans and vertebrates. We place the origin of cephalopod jaws quite conservatively in the late Silurian because the phylogenetic bracket combined with good fossil evidence points at that age (Fig. 3).

How was the Palaeozoic benthic diversification linked with the evolution of various levels of predators?

Overall, the long-term evolution of life on our planet has been characterized by an increasing occupation of habitats until their saturation, followed (or accompanied) by the conquest of new habitats and novel modes of life. Assuming that the origin of life includes the initial formation of cells near the water surface or around black smokers, life would have begun either as planktonic or benthic to demersal prokaryotic cells; 'soon' thereafter, the sessile benthic mode of life, including eukaryotic algae appeared and spread over the global oceans (*e.g.* Signor & Vermeij 1994, Schopf *et al.* 2007). In the Neoproterozoic, multicellular organisms added motile benthic modes of life including the first macroscopic predators in a broad sense (review *in* Bengtson 2002; see also Kelley *et al.* 2003). Thus, after a very long phase of Proterozoic prokaryote 'peace' (see

Porter 2016 for a different view), the escalation of the ongoing predatory arms race had begun.

During the Neoproterozoic, macroscopic life was largely limited to benthic habitats (*e.g.* Seilacher 1999); skeletons and sclerotized mouthparts began to evolve toward the end of this era. With the Cambrian success of protective skeletons (Cambrian explosion, *e.g.* Valentine *et al.* 1999), mouthparts experienced a positive selection for reinforcement, *i.e.* more strongly sclerotized or even mineralized mouthparts. An increase in motility, the reinforcement of defensive skeletal structures or the choice of an infaunal life habit ('Agronomic substrate revolution'; Seilacher & Pflüger 1994) were probably the main evolutionary responses to the rising predatory pressure. In turn, these changes led to a higher energy requirement as the predators themselves had to actually chase, catch, and kill their prey, to break the increasingly resistant protective skeletons or to dig them out of the sediment. On the one hand, prey animals were forced to escape into new habitats or behaviours, often increasing energetic requirements, or a greater investment in defence (Signor & Brett 1984; Bambach 1993, 1999; Brett & Walker 2002; Brett 2003); on the other hand, predators of most levels had to invest more energy in catching prey, overcoming the new defensive structures or excavating endobenthos (Fig. 2B). In the light of this escalatory process, it is not surprising that large demersal or even nektonic predators, as well as large filter feeders, had already evolved in the Cambrian (*e.g.* Whittington & Briggs 1985, Harvey & Butterfield 2008, Daley *et al.* 2013, Vinther *et al.* 2014, Van Roy *et al.* 2015). This arms race could proceed only by producing ever more efficient mouthparts and locomotory structures, dealing in different ways with the trade-offs between investment in these structures and physical efforts on the one side and the greater predation success on the other.

Similar conclusions were drawn by Brett & Walker (2002). According to them, several 'durophagous' groups (*sensu latu*, *i.e.* including a broad range of animals feeding on prey with hard skeletons) originated or radiated around the Mid-Palaeozoic (see Fig. 4) including cephalopods (*e.g.* ammonoids), crustaceans (phyllocarids, decapods and stomatopods) and jawed fish (Brett &Walker 2002). The radiation of phyllocarids had already started in the Early Palaeozoic (Collette & Hagadorn 2010). Cambrian anomalocaridids (Conway Morris & Jenkins 1985, Nedin 1999) as well as other basal arthropods like *Sidneyia* (Briggs *et al.* 1994) or *Utahcaris* (Conway-Morris & Robison 1986), possibly a basal chelicerate (Legg & Pates 2016), have occasionally been interpreted to be 'durophagous' predators (see also Conway Morris & Jenkins 1985) based on gut contents or more indirectly based on attributed coprolites or injuries in their prey, but this might only be true for some species like *Anomalocaris canadensis* (Daley *et al.* 2013), while some other Cambrian
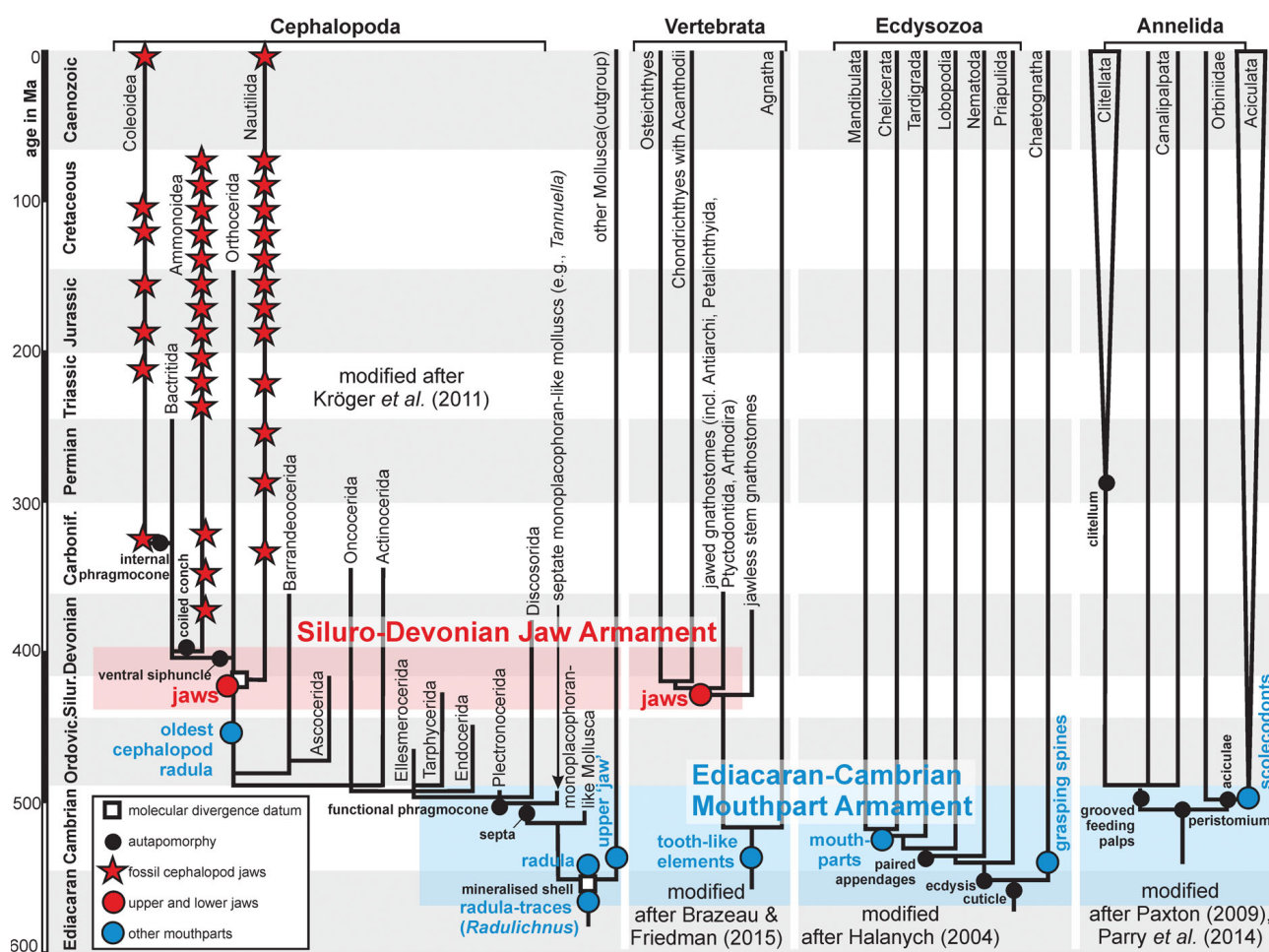
Figure 3. Cephalopod, vertebrate and ecdysozoan diversity with the origins of mouthparts and jaws. Note that many mouthparts evolved in the Cambrian, others in the Ordovician (some are not illustrated here, *e.g.* echinoid mouth parts). Interestingly, jaws (including an upper and a lower element) appear to have evolved in the Silurian both in cephalopods and in fish. Simplified cladograms based on Halanych (2004), Paxton (2009), Kröger *et al.* (2011), Parry *et al.* (2014) and Brazeau & Friedman (2015).

and Ordovician anomalocaridids were filter feeders (Vinther *et al.* 2014, Van Roy *et al.* 2015). It is more likely that anomalocaridids were mostly feeding on weakly sclerotized arthropods and other soft-bodied prey. Eurypterids are known from the Ordovician until the Permian (Tetlie 2007), but many were marginal marine. The predatory marine eurypterids (Eurypterina) diversified from the Ordovician to the Siluro-Devonian where some nektonic pterygotids reached gigantic sizes (Braddy *et al.* 2008, Lamsdell & Braddy 2010, Klug *et al.* 2015a). Eurypterina diversity waned during the Devonian, possibly because they were out-competed by jawed fishes and other predators (Fig. 2D; Lamsdell & Braddy 2010). The only known "jawed" annelids are eunicids and phyllodocids, which are closely related based on morphological and molecular evidence (see Parry *et al.* 2014 for a review). The earliest phosphatic annelid mouthparts (scolecodonts) are known from the late Cambrian strata and the Annelida radiated in the Ordovician (Hints & Eriksson 2007, Paxton

2009). Some extant annelids like bobbit worms (*Eunice aphroditois*) are vicious predators capable of cutting their prey (including fishes) in half. Mouthparts of bobbit worms used in raptorial feeding are known since the Devonian (Eriksson *et al.* 2017), but their feeding ecology is still unclear. Stem-group annelids lack phosphatic mouthparts, indicating that these only evolved later – although they probably had an eversible pharynx (Parry *et al.* 2014). Conodonts with multi-element apparatuses with phosphatic elements first appeared in the Cambrian, although their architecture varies widely and their feeding mode poorly is constrained (*e.g.* Martínez-Pérez *et al.* 2016).

The repeated macroecological 'resets' that occurred due to mass extinctions of varying intensity freed the ecospace, especially at the level of larger predators. Possibly, it is this interplay between extinctions and arms races that allowed the evolution of ever more sophisticated and thus more efficient (but possibly more expensive from an
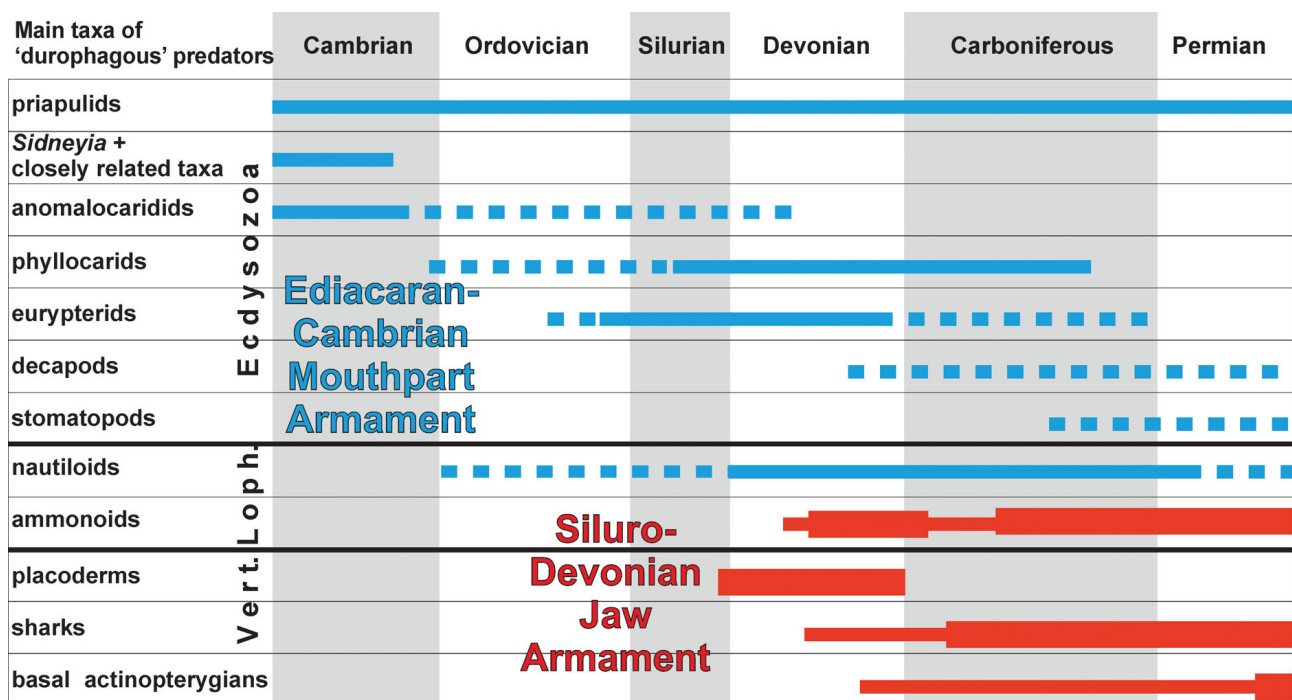
Main taxa of 'durophagous' predators		Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian
priapulids							
Sidneyia + closely related taxa							
anomalocaridids							
phyllocarids							
eurypterids							
decapods							
stomatopods							
nautiloids							
ammonoids							
placoderms							
sharks							
basal actinopterygians							

Figure 4. Ranges of major groups of Palaeozoic 'durophagous' predators (updated and modified from Brett & Walker 2002). Thin lines – present, but minor; thick lines – abundant; broken lines – possibly present but rare or difficult to interpret. Jawed groups in red. Abbreviations: Vert. – Vertebra; Loph. – Lophotrochozoa.

energetic point of view) locomotory and feeding apparatuses. Among meso- to macro-predators, a positive selection therefore occurred towards an increase in mobility (Devonian Nekton Revolution; Klug *et al.* 2010) as well as larger and stronger oral instruments (this paper). For the two main phases of mouthpart and jaw formation, we suggest the terms Ediacaran-Cambrian Mouthpart Armament and Siluro-Devonian Jaw Armament (Fig. 4; compare, *e.g.* Brett & Walker 2002, Anderson *et al.* 2011). A greater mobility at reasonable energetic costs was achieved by, *e.g.* reinforced axial skeletons and reduced body armor in vertebrates as well as tightly coiled conchs (much later also internalized or reduced) in cephalopods (*e.g.* Klug & Korn 2004, Kröger *et al.* 2011, Naglik *et al.* 2015).

As far as the evolution of jaws in cephalopods and vertebrates is concerned, we hypothesize the following scenario (taking into account the incompleteness of the fossil record and limitations in functional interpretations). In both groups, poorly sclerotized and mineralized supporting structures existed around the mouth even in Cambrian representatives, indicating that some mechanical stress was involved in the feeding process, thus hinting at a predatory mode of life. Enhancement of defensive structures in prey organisms (Signor & Brett 1984) caused a positive selection for an oral rearmament.

From the fossil record, it appears that this rearmament occurred at around the same time, though maybe somewhat earlier in vertebrates than in cephalopods. This proximity in the appearance of a functionally similar structure in two phylogenetically independent groups is suggestive of an ecological link. Nevertheless, suction feeding in cephalopods is probably limited, which instead used their arms to get prey close to their mouths. Despite the fact that jaws function quite differently in cephalopods and vertebrates, they might still have allowed both groups to attack larger or more robust prey. Accordingly, we propose the following hypotheses and discuss them:

(1) Null hypothesis: The temporal correlation is pure coincidence; an ecological link does not exist.

This lack of connection appears unlikely, because Siluro-Devonian gnathostomes and cephalopods occurred in the same habitats, both likely occupied a range of water depths, both were predators of strongly varying size and both likely used all available metazoan food sources. Therefore, a strong ecological overlap (diet, geographic distribution, water depth, motility *etc.*) is highly likely.

(2) The food sources of cephalopods were always largely different from those of fishes and thus these changes occurred completely independently.

This hypothesis appears unlikely because both cephalopods and gnathostomes occupy a broad range of marine habitats today and also have a broad range of food sources, which partially overlap. One observation from Recent ecosystems is that, for example, in pelagic habitats that have

been overfished for predatory fish (tuna, sharks), the large Humboldt squid *Dosidicus gigas* becomes more abundant and appears to adopt the role of the large gnathostomes (Zeidberg & Robinson 2007).

(3) The evolution of gnathostomes increased the predatory pressure causing a further enhancement in defensive structures (e.g. spinosity in arthropods and crinoids). In order to maintain access to these food sources, a positive selection for stronger mouthparts fostered the evolution of reinforced cephalopod jaws.

During the Silurian and Devonian interval, productivity increased, probably caused by the increaed release of nutrients from soil by rooted land plants and rising input of terrestrially derived organic matter (Algeo & Scheckler 1998). This increase in nutrient supply created a general boost in marine diversity following the Late Ordovician extinction (Fig. 1) and thus also in potential prey for gnathostomes and cephalopods. Reciprocal feedbacks between prey and their defence structures, *e.g.* in arthropods and echinoderms (see for example Reich & Smith 2009) and either group of competing jawed predators (and increasing efficiency of both locomotory structures and jaws), appear quite likely (*cf*. Vermeij 1987, 1994, 2013; Brett & Walker 2002).

(4) Cephalopods evolved jaws earlier, but the preservation potential is lower and thus, the fossil record shows an inaccurate pattern.

The preservation potential of chitin and scleroproteins is lower than that of bone and thus this possibility cannot be ruled out. Nevertheless, it does not falsify the hypothesis of escalatory feedbacks between gnathostomes, cephalopods, and prey organisms. Furthermore, in rare Ordovician and Silurian orthoconic nautiloids with preserved chitinous radulae, jaw-like structures are not preserved in sufficient quality to permit unequivocal interpretation.

Conclusions

Macroecological changes during the Palaeozoic are reflected in diversity fluctuations. Some of these changes have abiotic causes, but some were also induced by biotic processes such as major evolutionary innovations that profoundly impacted marine ecosystems. Here, we discuss the evolution of invertebrate mouthparts as well as jaws of cephalopods and vertebrates in the light of macroecological changes. Although the fossil record is quite incomplete, hampering the identification of the exact time of origin of these structures, it appears that invertebrate mouthparts mainly evolved in the late Proterozoic and early Cambrian, while the jaws of cephalopods and vertebrates appeared probably in the Silurian (based on fossils and phylogenetic

bracketing). Current evidence suggests that the jaws of vertebrates evolved before those of cephalopods. Independent of the sequence of these evolutionary events, it appears likely that the rise of jawed animals increased predatory pressure on prey organisms. In turn, the evolution of enhanced defensive structures potentially caused a positive selection for reinforced jaws in the other group (reciprocal selection; Vermeij 2013). Using Vermeij's terminology (Vermeij 1987, 1994), vertebrates would be the 'predators', cephalopods the 'competitors', and other invertebrates the 'dangerous prey'.

The evolution and radiation of jawed metazoans makes sense in the context of the increasing nutrient availability due to the spread of land plants, which likely fostered increased productivity of marine life to varying degrees (though it was likely detrimental in the Late Devonian, where it led to black shale deposition and extinctions). This increase in nutrients implies that energy was available for the addition of new trophic levels, providing ecospace for the evolution of new groups of predators. Reciprocal feedbacks between the two main groups of jawed metazoans and invertebrate prey are here suggested to have been an important evolutionary feedback loop of the Middle Palaeozoic (Brett & Walker 2002, Vermeij 2013). For the initial phase of evolution of mouthparts, we suggest the term Ediacaran-Cambrian Mouthpart Armament and for the later (Middle Palaeozoic) reinforcement, we coin the term Siluro-Devonian Jaw Armament. Much more research on the origin, functional disparity and biomechanics of these structures is needed, particularly in invertebrates, to test their evolutionary relevance and degree of convergence.

Acknowledgements

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