Cretaceous-Palaeogene incumbent replacement of associations of mollusc plankton and giant filter feeders (#20400)

First submission

Important notes

Editor and deadline

Kenneth De Baets / 22 Oct 2017

Files	3 Figure file(s) 3 Other file(s) Please visit the overview page to **download and review** the files not included in this review PDF.
Declarations	**Involves vertebrate animals.**

Review guidelines

Please read in full before you begin

How to review

When ready **submit your review online**. The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

To finish, enter your editorial recommendation (accept, revise or reject) and submit.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to **PeerJ standards**, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see **PeerJ policy**).

EXPERIMENTAL DESIGN

- ✓ Original primary research within **Scope of the journal**.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ Data is robust, statistically sound, & controlled.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.
- ✓ Speculation is welcome, but should be identified as such.

The above is the editorial criteria summary. To view in full visit **https://peerj.com/about/editorial-criteria/**

7 Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that your international audience can clearly understand your text. I suggest that you have a native English speaking colleague review your manuscript. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Give specific suggestions on how to improve the manuscript	*Line 56: Note that experimental data on sprawling animals needs to be updated. Line 66: Please consider exchanging "modern" with "cursorial".*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Cretaceous-Palaeogene incumbent replacement of associations of mollusc plankton and giant filter feeders

Amane Tajika [1] , **Alexander Nützel** [2] , **Christian Klug** Corresp. [1]

[1] Palaeontologisches Institut und Museum, University of Zurich
[2] Bayerische Staatssammlung für Paläontologie und Geologie, Ludwig-Maximilians-Universität München, München, Germany

Corresponding Author: Christian Klug
Email address: chklug@pim.uzh.ch

Owing to their great diversity and abundance, ammonites and belemnites represented key elements in Mesozoic food webs. Because of their extreme ontogenetic size increase by up to three orders of magnitude, their position in the food webs likely changed during ontogeny. Here, we reconstruct the number of eggs laid by adult females of these cephalopods and discuss these developmental shifts in their ecologic roles. Based on similarities in conch morphology, size, habitat and abundance, we suggest that juvenile ammonites and belemnites were ecologically replaced by holoplanktonic gastropods after the Cretaceous/ Palaeogene mass extinction. As primary consumers, these extinct cephalopod groups were important constituents of the plankton and a principal food source for planktivorous organisms. As victims or, respectively, profiteers of this case of ecological replacement, filter feeding chondrichthyans and cetaceans likely filled the niches formerly occupied by large pachycormid fish during the Jurassic and Cretaceous.

Cretaceous-Palaeogene incumbent replacement of associations of mollusc plankton and giant filter feeders

Amane Tajika[1], Alexander Nützel[2] and Christian Klug[1]

[1]Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland. [2]SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Department of Earth and Environmental Sciences, Palaeontology & Geobiology, GeoBio-Center LMU, Richard-Wagner-Str. 10, 80333 München, Germany

Corresponding author Christian Klug, chklug@pim.uzh.ch

ABSTRACT

Owing to their great diversity and abundance, ammonites and belemnites represented key elements in Mesozoic food webs. Because of their extreme ontogenetic size increase by up to three orders of magnitude, their position in the food webs ~~likely~~ changed during ontogeny. Here, we reconstruct the number of eggs laid by adult females of these cephalopods and discuss these developmental shifts in their ecologic roles. Based on similarities in conch morphology, size, habitat and abundance, we suggest that juvenile ammonites and belemnites were ecologically replaced by holoplanktonic gastropods after the Cretaceous/ Palaeogene mass extinction. As primary consumers, these extinct cephalopod groups were important constituents of the plankton and a principal food source for planktivorous organisms. As victims or, respectively, profiteers of this case of ecological replacement, filter feeding chondrichthyans and cetaceans likely filled the niches formerly occupied by large pachycormid fish during the Jurassic and Cretaceous.

Subjects Palaeontology, Developmental Biology, Evolutionary Studies, Marine Biology, Zoology

Keywords Ammonoidea, Belemnitida, Pachycormiformes, Holoplanktonic Gastropoda, Fecundity, Mass Extinctions, Cretaceous, Palaeogene, Filter Feeders

INTRODUCTION

The fate of individual groups of marine organisms at mass extinction intervals is ~~often~~ well-studied (*Jablonski & Raup, 1994; Jablonski, 2008*). By contrast, the disappearance of entire communities or ecological associations or food webs or important parts of any of these structures from the geologic past still requires ~~a lot of~~ palaeontological research (*Hautmann, 2014; Hoffmann et al., 2014; Roopnarine & Angielczyk 2015*). Extinctions of entire communities or ecosystems are most conspicuous during the great mass extinctions, when usually vast new ecospace was freed and thereby, ~~new ecological niches could form,~~

Although it is not the most severe of the Big Five, the end-Cretaceous mass extinction is likely the most famous among those with the greatest severity (*McGhee et al., 2013*). This fame ~~roots~~ in the fact~~s~~ that popular groups of organisms such as dinosaurs (*Sloan et al., 1986; Archibald & Fastovsky, 2004*) and ~~ammonites~~ (*Goolaerts, 2010; Kennedy, 1993; Landman et al., 2015*) were erased by the consequences of an impact in Mexico and flood-basalt-eruptions in India (*Keller et al., 2009; Miller et al., 2010; Schulte et al., 2010; Tobin et al., 2012*).

Marine communities were heavily affected as reflected in the partial or total disappearance of major groups such as ammonoids and belemnites (*Doyle, 1992; Marshall & Ward, 1996; Iba et al., 2011; Olivero, 2012; Landman et al. 2014*) as well as foraminifers (*Alvarez et al., 1980; Smit, 1982*) and bivalves (*Jablonski & Raup, 1994*). Ammonoids were both highly diverse and evolved a great disparity in the course of the Cretaceous (*Ward & Signor, 1983; Ward, 1996*); some of the most bizarre forms such as *Nipponites*, *Diplomoceras* and *Didymoceras* appeared. Additionally, the largest ammonoids of all times, members of the family Puzosiidae, also lived during Cretaceous times (*Landois, 1895; Olivero & Zinsmeister, 1989; Kennedy & Kaplan, 1995*). Puzosiids are not only gigantic but they also occurred worldwide and in great numbers.

The great abundance, wide geographical distribution, extreme diversity, ~~middle~~ to giant size in combination with the likely high fecundity of ammonites raises questions (i) for Cretaceous marine food webs that partially relied on the adults as planktotrophic consumers, but particularly on their minute offspring as food source and (ii) what groups might have replaced ammonites, belemnites and their predators or had similar ecological roles ~~including their positions~~ in post-Cretaceous food webs.

METHODS

We estimated the fecundity of large Cretaceous ammonites such as *Parapuzosia seppenradensis* using the following ~~facts,~~ assumptions ~~and measurements.~~ (i) We know that the major part of egg-development happened in the body chamber (*De Baets et al., 2015; Mironenko & Rogov, 2015*); (ii) there is good evidence that the ammonitella represents the embryonic part of the conch (*De Baets et al., 2015*); (iii) we suggest that egg~~-~~size only slightly exceeded ammonitella~~-~~size because of their dense packing in fossils with embryos preserved in the body chamber (*De Baets et al., 2015; Mironenko & Rogov, 2015*); and (iv) we followed the proportion of 8% of the soft body volume being occupied by the gonads ~~according to~~ the proportions known from Recent *Nautilus* (*Tanabe & Tsukahara, 1987; Korn & Klug, 2007; De Baets et al., 2015*). As far as (iv) is concerned, there is some uncertainty because the proportions of the ovaries are poorly known

~~from~~ ammonoids due to the extremely rare and fragmentary preservation of soft parts (*Mironenko & Rogov, 2015; Lehmann, 1981; Lehmann, 1985; Klug & Lehmann, 2015; Klug et al., 2012*). ~~When regarding the~~ specimens figured by *Mironenko & Rogov (2015)*~~, one tends to assume~~ that the gonads filled a much larger portion of the body chamber. This hypothesis finds further support in symmetric bulges in the posterior body chamber in mature *Pachydesmoceras* (Fig. 1) and scaphitid conchs (*Kennedy, 1989*). These bulges may have offered space for the growing ovaries. ~~Owing to~~ these ~~materials~~ and morphological adult modifications of ammonoid conchs, we calculated alternative maximum egg-numbers using a body chamber volume proportion occupied by gonads of 30%.

The largest specimen of the largest ammonite species *Parapuzosia seppenradensis* is incomplete (*Landois, 1895; Kennedy & Kaplan, 1995*). We estimated the adult body chamber volume and the surface area of the terminal aperture assuming a body chamber length of about 180 degrees ~~because of~~ shell traces of the missing conch part along the umbilical seam. Accordingly, the maximum diameter dm can be reconstructed to have reached 2200 mm with a whorl height wh of about 800 mm and a whorl width ww of about 500 mm. The radiuses would then measure 1250 mm (r_1) at the terminal aperture and 950 mm (r_2) on the opposite side. Using the wh and ww values, we reconstructed a whorl cross section in CorelDraw and measured the area; accordingly, the cross section area K amounts to almost 320’000 mm^2.

As demonstrated by *De Baets et al. (2012)*, derived ammonoids likely had a high fecundity. This is corroborated by the great differences between embryo size and adult conch size. For example, in the largest specimen of *Parapuzosia seppenradense* from the Late Cretaceous of Germany, the embryonic conch measured about one millimeter in diameter at hatching, while the adult conch exceeded two meters in diameter (*Kennedy & Kaplan 1995; De Baets et al., 2012;*

De Baets et al., 2015; Korn & Klug, 2007; Landman et al., 1996; Tanabe et al., 2008). This implies a factor of at least 2000 in diameter increase between embryos and adult macroconchs. Embryonic conch size (ammonitella size) is well documented for most ammonoid clades (*De Baets et al., 2015*). In Cretaceous ammonoids, ammonitella size ranges between 0.5 and 1.5 mm with the average being smaller than 1 mm (*De Baets et al., 2015*).

In order to estimate the absolute gonad volume, we determined the body chamber volume VBC, which can be achieved by applying an equation introduced by *Raup & Chamberlain (1967)* and also used by *De Baets et al. (2012)*:

$$(1)\ V_{BC} = 2 / 3 * \pi * (K * Ra / \ln W) * (1 - W^{-3\theta/2\pi})$$

with K − area of the last aperture, Ra − distance coiling axis to center of mass (estimated 200 mm based on comparisons with species with similar conch shape: *Tajika et al. 2015; Naglik et al., 2016*), θ − angular length of the body chamber in radians (equals π here, because the body chamber is about 180° long), the whorl expansion rate for this particular body chamber length

$$(2)\ W = (r_1 / r_2)^{2\pi / \theta}$$

with r_1 − maximum conch diameter and r_2 – conch diameter 180° behind the aperture.

RESULTS

Estimating ammonoid fecundity

Applying the data and calculations ~~listed~~ in the methods section to the lectotype of *Parapuzosia seppenradense*, we obtain a whorl expansion rate W of 1.73 and then ~~an according~~ body chamber volume V_{BC} of 137’075’470 mm^2. Depending on the ~~proportion~~ of the gonads (between 8 and 30%; see discussion in methods), we obtain gonad volumes varying between about 10’000’000 mm^2 and 40’000’000 mm^2. Assuming an egg-volume of 1 mm^2, we obtain numbers of

10’000’000 to 40’000’000 eggs per adult female *Parapuzosia seppenradensis* if they were semelparous. If we assume iteroparity, these numbers increase by the factor of the number of reproductive cycles. Also, if we assume that the eggs and embryos continued to grow after they were laid, ammonoid fecundity would further increase, but evidence for this is missing in ammonoids (*Mironenko & Rogov, 2015*). For an adult female of half the diameter, we would obtain egg-numbers of between 3’000’000 (8% gonad volume) and 10’000’000 eggs (30% gonad volume) at semelparity. Puzosiids and other large Cretace~~a~~ous ammonoids in the size range between 500 and 1000 mm are quite common worldwide (e.g. *Pachydesmoceras*).

The role of r-strategy in ammonite and belemnite ecology

Depending on the proportional gonad size and whether or not ammonites were semelparous or iteroparous, it appears likely that adult females of the largest puzosiid ammonites such as *Parapuzosia seppenradensis* laid between ~~10’000’000 and 100’000’000~~ eggs and ammonoids about half the size still over ~~1’000’000~~ eggs. ~~The~~ simple calculation ~~above itself~~ highlights the likelihood that derived ammonites were extreme r-strategists~~, which~~ produced vast amounts of offspring, likely contributing an important part of the plankton in size ~~at the limit from~~ micro- to macroplankton. High fecundity corresponded with high mortality and it is likely that hatchlings and juveniles of ammonites formed a major source of food in the marine realm.

As far as belemnites are concerned, their global abundance had decreased in the Late Cretaceous already, freeing ecospace for, e.g., other coleoids (*Iba et al., 2011*). Nevertheless, coleoids with conical phragmocones such as belemnites, diplobelids, *Groenlandibelus* ~~or~~ *Naefia* share a small initial chamber and likely small embryonic conchs (*Bandel et al., 1984*). Accordingly, we can assume that their fecundity was also high, although much lower than those of the puzosiid ammonites because of the much lower size difference between adults and embryos (about 100 to 1000 eggs per female).

Which animals ate ammonites?

Evidence for successful and unsuccessful predation on medium to large-sized ammonites is not rare but identifying the actual predator is possible only in very few cases (*Keupp, 2012; Hoffmann & Keupp, 2015*). Additionally, most hard parts of ammonites (conch and lower jaw) were likely crushed by the predators and quickly dissolved in the digestive tract, making ammonites as fossilized stomach contents improbable, although a few cases have been reported where juvenile ammonoid remains are preserved in stomachs of Jurassic ammonites (*Klug & Lehmann, 2015*). It is even more difficult to find evidence for predators that fed on hatchlings and neanic juveniles of ammonites (dm < 10 mm), which must have occurred in vast numbers in the world's oceans of the Mesozoic. These early post-hatching developmental stages probably lived in the water column because their conchs already had functional phragmocones and they are often found in black shales, which were deposited under hypoxic to anoxic bottom water conditions and therefore, a strictly benthic mode of life was impossible (*Nützel & Mapes, 2001; Mapes & Nützel, 2008*). Thus, pelagic nektonic animals (including older growth stages of ammonites) are the likeliest candidates as predators feeding on these young ammonites (Fig. 2). For abundant and easy prey like juvenile ammonites, a broad range of predators can be hypothesized. Like plankton today, these masses of juvenile ammonites represent perfect food sources for medium-sized to large suspension feeders (invertebrates and vertebrates). ~~From~~ the Cretaceous, giant planktivorous bony fishes (pachycormids: *Friedman et al., 2010*) have been suggested to be nektonic suspension feeders, which might have fed on plankton comprising a wealth of juvenile ammonites. In the SOM of their paper, *Friedman et al. (2010)* show a fragment of the gill rakers; their filaments have a spacing of about 1 mm, which is suitable to filter out hatchlings and juvenile ammonites with conchs of a few millimeter diameter (Fig. 3). This trophic relationship is further corroborated by the extinction of ~~this group~~ synchronous with the demise of the Ammonoidea and Belemnitida ~~but direct evidence is missing~~. Taking the direct fossil evidence from the Jurassic into account, it appears likely that ammonites also played a role as micropredators feeding on early juvenile ammonite offspring (*Klug & Lehmann, 2015; Keupp, 2012; Kruta et al. 2011*).

The extreme differences in size (up to three orders in magnitude) between adults and juveniles in large ammonites indicate that the range of potential predators changed significantly throughout the life history of these cephalopods. As hatchlings and small juvenile planktonic forms, moderate-sized to large suspension feeders and small predators likely used them as a food source but for adult puzosiids, only large predators such as mosasaurs, pliosaurs and large fishes can be considered, although the seeming direct evidence for such a trophic relationship is still under debate (*Kauffman & Kesling 1960*). Late Cretaceous ammonites were probably not the primary food source of ichthyosaurs since the latter ~~became~~ extinct ~~already~~ in the Cenomanian whereas ammonites persisted ~~to be~~ diverse and abundant; ~~in~~ spite of a better link of ~~their~~ demise with the extinction of belemnites in the North Pacific near the end of the Early Cretaceous (*Iba et al. 2011*), belemnite decline in the Tethys at the CTB (*Doyle, 1992; Christensen, 2002*) and direct evidence for a trophic relationship between phragmocone-bearing coleoids and ichthyosaurs (*Kear et al., 1995*, and references therein), *Acikkol (2015)* suggested that a link between the severe reduction of belemnite diversity and ichthyosaur extinction is unlikely.

Which groups filled the ecospace freed by the extinction of ammonite hatchlings and planktivorous actinopterygians?

Association of the extinctions of large marine reptiles, large planktivorous fish and ~~those of~~ ammonites suggest trophic relationships between these groups; their extinction freed ecospace for both small zooplankton and suspension feeders. This association coincides with other major changes in the planktonic realm, especially the rise of holoplanktonic gastropods. Although a few Early Jurassic to Cretaceous heteropods are known (*Bandel & Hemleben, 1995; Nützel, 2014; Teichert & Nützel, 2015; Nützel et al. 2016*), the major expansion of heteropods and ‘pteropods’ falls in~~to~~ the Cenozoic (*Tracey et al., 1993*).

In size and their coiled form, many fossil Limacinidae (Thecosomata, planktonic opisthobranch gastropods) resemble ammonites. Similarly, the conchs of fossil Creseidae morphologically and in size (at least roughly) correspond to hatchlings of belemnites, diplobelids and other phragmocone-bearing coleoids of the Cretaceous (*Bandel et al., 1984; Lokho & Kumar, 2008*). In addition to these morphologic similarities, these groups shared the planktonic habitat. According to *Janssen & King (1988, 2013)*, ‘pteropods’ were already present as early as the latest Palaeocene. A number of Eocene pteropod occurrences is known worldwide (*Bristow et al., 1980; King, 1981; Curry, 1982; Zorn, 1991; Hodgkinson et al., 1992; Janssen et al., 2007; Lokho & Kumar, 2008; Ando et al., 2009; Cahuzac & Janssen, 2010*). An early Palaeogene origin is supported by a combination of palaeontological and molecular clock data published by *Corse et al. (2013)*. The latter authors even compare the uncoiling of the conch of Thecosomata with the coiling of ammonites, but they did not discuss macroecological implications. As far as abundance of these fossils is concerned, pteropods are much less frequent than subadult to adult ammonites and belemnites, while their hatchlings are similarly rare. This is probably due to the combination of their small body size as well as their thin and fragile aragonitic shells (*Janssen & King, 1988*), which did not provide a high fossilization potential. The great majority of these thin aragonitic shells ~~was~~ undoubtedly rapidly dissolved during early diagenesis and as a consequence not fossilized. Nevertheless, the fact that quite a few pteropods have been reported from the Eocene implies that they were abundant and widely distributed since that ~~period of~~ time.

Similarities in size, overall morphology, habitat, abundance as well as the timing of their respective extinction and origination suggest that hatchlings and small individuals of ammonites as well as belemnites were ecologically replaced by planktonic opisthobranchs (Thecosomata) and other holoplanktonic gastropods. In turn, the ecological ~~instalment~~ of the Thecosomata contributed to the dietary basis for the evolution of new groups of large planktivorous suspension feeders. As suggested by *Friedman et al. (2010)*, the Cretaceous ~~‘~~giant planktivorous bony fishes~~’~~ found an ecological replacement in both large suspension-feeding chondrichthyans and baleen whales. Several of these groups are known to take in important amounts of planktonic gastropods, although not exclusively. Today, thecosomes may contribute up to 50% of the zooplanktonic biomass and thus are ecologically important (*Mackas & Galbraith, 2012*). ~~However~~, ~~today’s Manta~~ rays (Mobulidae) are known to feed predominantly on small ~~Crustaceans~~ and the same holds true for several baleen whales. ~~Nevertheless,~~ it is somewhat unclear what ~~these~~ early Palaeogene suspension feeders ate, ~~but at least~~ the filter mesh spacing of both planktivorous chondrichthyans and several baleen whales fits well with the size range of thecosomes.

CONCLUSIONS

Large late Cretaceous ammonites such as puzosiids reached sizes exceeding two meters in diameter. Their offspring ~~has~~ a conch size that is in stark contrast to the adult size; the embryonic conchs of many Cretaceous ammonites measure only about 1 mm in diameter at the time of hatching. This size relationship, conch geometry and anatomical proportions allow estimates of the number of offspring per female. Accordingly, the largest females might have laid between 10’000’000 (semelparity, small gonads) and 100’000’000 eggs (iteroparity, large gonads). Apart from this extreme example, the great abundance of ammonites, many of them of considerable size as adults, throughout the Mesozoic and the generally small size of their offspring implies that juvenile ammonites and belemnites played a fundamental role near the base of Mesozoic food webs, both as primary consumers and as food source for secondary consumers. We assume that Mesozoic oceans were full of small hatchlings and juveniles of ammonites and belemnites in the mm to cm size range. This part of the planktonic food chain vanished with the extinction of ammonites and belemnites but may have enabled the evolutionary and ecological rise of holoplanktonic gastropod, which occupy a similar size range, conch morphologies (coiled and straight) and trophic role. This underlines the importance of ecological differentiation between different ontogenetic stages. Gill raker filament spacing in huge pachycormids correspond in size to these juvenile ammonites, suggesting a trophic link in the light of the synchronous extinction at the end of the Cretaceous.

Here, we suggest that the ecospace formerly occupied by ammonite and belemnite juveniles was filled during the post-Mesozoic rise of holoplanktonic gastropods like, e.g., the Palaeocene expansion of the Thecosomata (holoplanktonic heterobranchs). ~~As far as the~~ incumbent replacement of the pachycormids is ~~concerned, it is a bit~~ more difficult. During the early Palaeogene, three important large planktivorous lineages of chondrichthyans occur; however, modern mobulids (~~M~~anta rays), for instance, are known to feed on planktonic ~~C~~rustaceans. ~~Perhaps, stomach~~ contents of exceptionally preserved specimens of Palaeogene planktivorous chondrichthyans ~~will~~ shed more light on the suspension feeders that, at least in their function as primary consumers, profited from the thecosomes that ecologically replaced juvenile ammonites. Independent of the filter feeder-side, we conclude that in r-strategists, the young offspring can play a more important ecological role than their large adults. This case of incumbent replacement underlines the significance of differences at which developmental stage the acme in ecological importance of an organism occurs.

Acknowledgements

The Swiss National Science Foundation SNF (project No. 200021_149119) kindly supported this study. Jakob Vinther (Bristol) generously provided an illustration, which was a valuable basis for one of our illustrations. We thank C. Steinweg, L. Schöllmann and J.-O. Kriegs (all Münster), Kishor Kumar (Uttarakhand, India), Kazushige Tanabe (Tokyo), and Klaus Bandel (Hamburg) for providing illustrations and allowing us to use them.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This study is supported by the Swiss National Science Foundation SNF (project number 200021_149119). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:

Swiss National Science Foundation SNF 200021_149119.

Competing Interests

All authors confirm that there are no competing financial interests.

Author contributions

- Amane Tajika wrote much of the first version and produced parts of the illustrations.
- Christian Klug formulated the initial hypotheses, contributed to the first draft and produced parts of the illustrations.
- Alexander Nützel provided data and information related to gastropods and wrote parts of the final version.
- All authors were included in several rounds of revisions of the manuscript.

REFERENCES

Acikkol, N. 2015. Testing the Cretaceous diversity of ichthyosaurs and their extinction Hypotheses using a quantitative approach. *Degree project at the Department of Earth Sciences.* 40 pp. Uppsala University, Uppsala.

Alvarez, L.W., Alvarez, W., Asaro, F. & Michel, H.V. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* **208**: 1095–1108.

Ando, Y. Ujihara, A. & Ichihara, T. 2009. First occurrence of Paleogene pteropods (Gastropoda; Thecosomata) from Japan. *Jour. Geol. Soc. Japan* **115**: 187–190.

Archibald, D & Fastovsky, D. 2004. Dinosaur Extinction. In: Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd ed.). 672–684. Berkeley: University of California Press.

Bandel, K., Engeser, T. & Reitner, J. 1984. Embryonic development of *Hibolithes* (Belemnitida, Cephalopoda). *N. Jahrb. Geol. Paläont., Abh.* **167**: 275-303.

Bandel, K. & Hemleben, C. 1995. Observations on the ontogeny of thecosomatous pteropods (holoplanktic Gastropoda) in the southern Red Sea and from Bermuda. *Marine Biology* **124**: 225–243.

Bristow, C.R., Ellison, R.A., & Wood, C.J. 1980. The Claygate Beds of Essex. *Proc. Geol. Assoc.* **91**: 261-277.

Cahuzac, B. & Janssen, A.W. 2010. Eocene to Miocene holoplanktonic Mollusca (Gastropoda) of the Aquitaine Basin, southwest France. *Scripta Geologica* **141**: 1-193.

Christensen, W.K. 2002. Palaeobiology, phylogeny and palaeobiogeography of belemnoids and related coleoids. *Berliner paläobiol. Abh.* **1**: 18-21.

Corse, E., Rampal, J., Cuoc, C., Pech, N., Perez, Y. & Gilles, A. 2013. Phylogenetic analysis of Thecosomata Blainville, 1824 (holoplanktonic Opisthobranchia) using morphological and molecular data. *PLOS ONE* **8, e59439** : 1-20.

Curry, D. 1982. Ptéropodes éocènes de la tuilerie de Gan (Pyrénées–Atlantiques) et de quelques autres localités de SW de la France. *Cahiers de Micropaléontologie* **4**(for 1981): 35–44.

De Baets, K., Klug, C., Korn, D. & Landman, N.H. 2012. Early evolutionary trends in ammonoid embryonic development. *Evolution* **66**:1788-1806.

De Baets, K., Landman, N.H. & Tanabe, K. 2015. Ammonoid embryonic development. In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds), *Ammonoid paleobiology: from anatomy to paleoecology.* 113-205 Dordrecht: Springer.

Doyle, P.A. 1992. Review of the biogeography of Cretaceous belemnites: *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **92**: 207–216.

Friedman, M., Shimada, K., Martin, L.D., Everhart, M.J., Liston, J., Maltese, A. & Triebold, M. 2010. 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. *Science* **327**: 990-993.

Goolaerts, S. 2010. Late Cretaceous ammonites from Tunisia: chronology and causes of their extinction and extrapolation to other areas. *Aardkundige Mededelingen* **21**: 1-220.

Hautmann, M. 2014. Diversification and diversity partitioning. *Paleobiology* 40, 162-176.

Hodgkinson, K.A., Garvie, C.L. & Bé, A.W.H. 1992. Eocene euthecosomatous Pteropoda (Gastropoda) of the Gulf and eastern coasts of North America. *Bull. Am. Paleontol.* **103**: 5–62.

Hoffmann, R. & Keupp, H. 2015. Ammonoid Paleopathology. In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds), *Ammonoid paleobiology, Volume I: from anatomy to ecology.* *Topics in Geobiology* **43**: 877-926 Dordrecht: Springer.

Hofmann, R., Hautmann, M., Brayard, A., Nützel, A. Bylund, K.G., Jenks, J.F., Vennin, E., Olivier, N. & Bucher, H. 2014. Recovery of benthic marine communities from the end-Permian mass extinction at the low-latitudes of Eastern Panthalassa. *Palaeontology* **57**: 547-558.

Hönisch, B., Ridgwell, A., Schmidt, D.N., Thomas, E., Gibbs, S.J., Sluijs, A., Zeebe, R., Kump, L., Martindale, R.C., Greene, S.E., Kiessling, W., Ries, J., Zachos, J.C., Royer,

D.L., Barker, S., Marchitto Jr., T.M., Moyer, R., Pelejero, C., Ziveri, P., Foster, G.L. & Williams, B. 2012. The geological record of ocean acidification. *Science* **335**: 1058-1063. DOI: 10.1126/science.1208277

Iba, Y., Mutterlose, J., Tanabe, K., Sano, S., Misaki, A. & Terabe, K. **2011.** Belemnite extinction and the origin of modern cephalopods 35 m.y. prior to the Cretaceous−Paleogene event. *Geology* **39**: 483–486.

Jablonski, D. 2008. Extinction and the spatial dynamics of biodiversity. *Proc. Natl. Acad. Sci. USA* **105**: 11528–11535.

Jablonski, D. & Raup, D.M. 1994. Selectivity of end-Cretaceous marine bivalve extinctions. *Science* **268**: 389–391.

Janssen, A.W. & King, C. 1988. Planktonic mollusks (Pteropods). In: Vinken, R. (ed), *The Northwest European Tertiary Basin, Results of the International Geological Correlation Programme Project no. 124*. *Geol. Jahrb.* **100**: 356–368.

Janssen, A.W. & Peijnenburg, K.T.C.A. 2013. Holoplanktonic Mollusca: development in the Mediterranean Basin during the last 30 Ma and their future. In: Goffredo, S. & Dubinsky, Z. (eds), *The Mediterranean Sea. Its history and present challenges.* 341–362. Dordrecht: Springer.

Janssen, A.W., Schnetler, K.I. & Heilmann-Clausen, C. 2007. Notes on the systematics morphology and biostratigraphy of fossil holoplanktonic Mollusca, 19. Pteropods (Gastropoda, Euthecosomata) from the Eocene Lillebaelt Clay Formation (Denmark, Jylland). *Basteria* **71**: 157–168.

Jarman, S.N. 2001. The evolutionary history of krill inferred from nuclear large subunit rDNA sequence analysis. *Biological Journal of the Linnean Society* **73**: 199–212.

Kauffman, E.G. & Kesling, R.V. 1960. An Upper Cretaceous ammonite bitten by a mosasaur. *Contr, Michigan Univ, Mus, Paleont,* **15**: 193–248.

Kear, A.J., Briggs, D.E.G. & Donovan, D.T. 1995. Decay and fossilization of non-mineralized tissue in coleoid cephalopods. *Palaeontology* **38**: 105–131.

Keller, G., Abramovich, S., Berner, Z. & Adatte, T. 2009. Biotic effects of the Chicxulub impact, K-T catastrophe and sea level change in Texas. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **271**: 52–68.

Kennedy, W.J. 1989. Thoughts on the evolution and extinction of Cretaceous ammonites. *Proc. Geol. Assoc.* **100**: 251–279.

Kennedy, W.J. 1993. Ammonite faunas of the European Maastrichtian; diversity and extinction. In: House, M. R. (ed) *The Ammonoidea: environment, ecology, and evolutionary change*. *System. Assoc. Spec. Vol.* **47**: 285–326.

Kennedy, W.J. & Kaplan, U. 1995. *Parapuzosia* (*Parapuzosia*) *seppenradensis* (Landois) und die Ammonitenfauna der Dülmener Schichten, unteres Unter-Campan, Westfalen. *Geologie und Paläontologie in Westfalen* **33**: 1–127.

Keupp, H. 2012. Atlas zur Paläopathologie der Cephalopoden. *Berliner paläobiol. Abh.* **12**: 1–390.

King, C. 1981. The stratigraphy of the London Clay. *Tertiary Research Spec. Pap.* 6: 1–158.

Klug, C. & Lehmann, J. 2015. Soft part anatomy of ammonoids: reconstructing the animal based on exceptionally preserved specimens and actualistic comparisons. In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R. H. (eds): *Ammonoid paleobiology, Volume I: from anatomy to ecology. Topics in Geobiology* **43**: 539–552. Dordrecht: Springer.

Klug, C., Riegraf, W. & Lehmann, J. 2012. Soft-part preservation in heteromorph ammonites from the Cenomanian-Turonian Boundary Event (OAE 2) in the Teutoburger Wald (Germany). *Palaeontology* **55**: 1307–1331.

Korn, D. & Klug, C. 2007. Conch form analysis, variability, and morphological disparity of a Frasnian (Late Devonian) ammonoid assemblage from Coumiac (Montagne Noire, France). In: Landman, N. H., Davis, R. A., Manger, W. & Mapes, R. H. (eds), *Cephalopods – Present and Past*. 57–86. Dordrecht: Springer.

Kruta, I., Landman, N.H., Rouget, I., Cecca, F. & Tafforeau, P. 2011. The role of ammonites in the marine Mesozoic food web revealed by jaw preservation. *Science* **311**: 70–72.

Landman, N.H., Goolaerts, S., Jagt, J.W.M., Jagt-Yazykova, E.A., & Machalski, M. 2015. Ammonites on the brink of extinction: diversity, abundance, and ecology of the Order Ammonoidea at the Cretaceous/Paleogene (K/Pg) boundary. In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds), *Ammonoid paleobiology: from ~~macroevcolution~~ to paleogeography. Topics in Geobiology* **44**: 497–553. Dordrecht: Springer.

Landman, N.H., Goolaerts, G., Jagt, J.W.M., Jagt-Yazykova, E.A., Machalski, M., Yacobucci, M.M. 2014. Ammonite extinction and nautilid survival at the end of the Cretaceous. *Geology* **42**: 707–710.

Landman, N.H., Tanabe, K. & Shigeta, Y. 1996. Ammonoid embryonic development. In: Landman, N.H., Tanabe, K. & Davis, R.A. (eds), Ammonoid Paleobiology. New York: Plenum.

Landois, H. 1895. Die Riesenammoniten von Seppenrade, *Pachydiscus* Zittel *seppenradensis* II. Landois. *Jahresbericht der Zoologischen Section des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst* **23**: 99–108.

Lehmann, U. 1981. Ammonite jaw apparatus and soft parts. In: House, M. R. & Senior, J. R. (eds), *The Ammonoidea. Syst. Ass. Spec. Pap.* **18**: 275–287.

Lehmann, U. 1985. Zur Anatomie der Ammoniten: Tintenbeutel, Kiemen, Augen. *Paläontol. Z.* **59**: 99–108.

Lokho, K. & Kumar, K. 2008. Fossil pteropods (Thecosomata, holoplanktonic Mollusca) from the Eocene of Assam-Arakan Basin, northeastern India. *Current Science* **94**: 647–652.

Mackas, D.L. & Galbraith, M.D. 2012. Pteropod time-series from the NE Pacific. *ICES Journal of Marine Science* **69**: 448–459.

Mapes, R.H. & Nützel, A. 2008. Late Palaeozoic mollusc reproduction: cephalopod egg-laying behavior and gastropod larval palaeobiology. *Lethaia* **42**: 341–356.

Marshall, C.R. & Ward, P.D. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous in western European Tethys. *Science* **274**:1360–1363.

McGhee, G.R. Jr., Clapham, M.E., Sheehan, P.M., Bottjer, D.J. & Droser, M.L. 2013. A new ecological-severity ranking of major Phanerozoic biodiversity crises. *Palaeogeogr., Palaeoclim., Palaeoeco.* **370**: 260–270.

Miller, K.G., Sherrell, R.M., Browning, J.V., Field, M.P., Gallagher, W., Olsson, R.K., Sugarman, P.J., Tuorto, S. & Wahyudi, H. 2010. Relationship between mass extinction and iridium across the Cretaceous-Paleogene boundary in New Jersey. *Geology* **38**: 867–870.

Mironenko, A.A., & Rogov, M.A. 2015. First direct evidence of ammonoid ovoviviparity. *Lethaia*, DOI: 10.1111/let.12143.

Naglik, C., Rikhtegar, F.N. & Klug, C. 2016. Buoyancy in Palaeozoic ammonoids from empirical 3D-models and their place in a theoretical morphospace. *Lethaia* **49**: 3–12.

Nützel, A. 2014. Larval ecology and morphology in fossil gastropods. *Palaeontology* **1**: 1–25.

Nützel, A. & Mapes, R.H. 2001. Larval and juvenile gastropods from a Carboniferous black shale: palaeoecology and implications for the evolution of the Gastropoda. *Lethaia* **34**: 143–162.

Nützel, A., Schneider, S., Hülse, P., Kelly, S.R.A., Tilley, L. & Veit, R. 2016. A new Early Jurassic gastropod from Ellesmere Island, Canadian Arctic – an ancient example of holoplanktonic gastropods. *Bulletin of Geosciences* **91**: 229–242.

Olivero, E.B. 2012. Sedimentary cycles, ammonite diversity and palaeoenvironmental changes in the Upper Cretaceous Marambio Group, Antarctica. *Cret. Res.* **34**: 348–366.

Olivero, E.B. & Zinsmeister, W.J. 1989. Large heteromorph ammonites from the Upper Cretaceous of Seymour Island, Antarctica. *J. of Paleont.* **63**: 626–636.

Raup, D.M. & Chamberlain, J.A. Jr. 1967. Equations for volume and center of gravity in ammonoids shells. *J. Paleontol.* **41**: 566–574.

Roopnarine, P.D. & Angielczyk, K.D. 2015. Community stability and selective extinction during the Permian-Triassic mass extinction. *Science* **350**: 90–93.

Schulte, P., Alegret, L., Arenillas, I., Arz, J.A., Barton, P.J., Bown, P.R., Bralower, T.J., Christeson, G.L., Claeys, P., Cockell, C.S., Collins, G.S., Deutsch, A., Goldin, T.J., Goto, K., Grajales-Nishimura, J.M., Grieve, R.A.F., Gulick, S.P.S., Johnson, K.R., Kiessling, W., Koeberl, C., Kring, D.A., MacLeod, K.G., Matsui, T., Melosh, J., Montanari, A., Morgan, J.V., Neal, C.R., Nichols, D.J., Norris, R.D., Pierazzo, E., Ravizza, G., Rebolledo-Vieyra, M., Reimold, W.U., Robin, E., Salge, T., Speijer, R.P., Sweet, A.R., Urrutia-Fucugauchi, J., Vajda, V., Whalen, M.T. & Willumsen, P.S. 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene Boundary. *Science* **327**: 1214–1218.

Seilacher, A. 1998. Mosasaurs, limpets or diagenesis: How *Placenticeras* shells got punctured. *Mitt. Mus. Naturkde .Berlin. Geowiss. Reihe* **1**: 93–102.

Sloan, R.E., Rigby, K., Van Valen, L.M. & Diane, G. 1986. Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek formation. *Science* **232**: 629–633.

Smit, J. 1982. Extinction and evolution of planktonic formaninifera after a major impact at the Cretaceous/ Tertiary boundary. *GSA Spec. Pap.* **190**: 329–352.

Tajika, A., Naglik, C., Morimoto, N., Pascual-Cebrian, E., Hennhöfer, D.K. & Klug, C. 2015. Empirical 3D-model of the conch of the Middle Jurassic ammonite microconch *Normannites*, its buoyancy, the physical effects of its mature modifications and speculations on their function. *Historical Biology* **27**: 181–191.

Tanabe, K., Kulicki, C. & Landman, N.H. 2008. Development of the embryonic shell structure of Mesozoic ammonoids. *American Museum Novitates* **3621**: 1–19.

Tanabe, K. & Tsukahara, J. 1987. Biometric analysis of *Nautilus pompilius* from the Philippines and the Fiji Islands. In: Saunders, W.B. & Landman, N.H. (eds), *Nautilus*. 105–113. New York: Plenum Press.

Teichert, S. & Nützel, A. 2015. Early Jurassic anoxia triggered the evolution of the oldest holoplanktonic gastropod *Coelodiscus minutus* by means of heterochrony. *Acta Palaeont. Pol.* **60**: 269–276.

Tobin, T.S., Ward, P.D., Steig, E.J., Olivero, E.B., Hilburn, I.A., Mitchell, R.N., Diamond, M.R., Raub, T.D. & Kirschvink, J.L. 2012. Extinction patterns, δ^{18}O trends, and magnetostratigraphy from a southern high-latitude Cretaceous-Paleogene section: Links with Deccan volcanism. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **350-352**: 180–188.

Tracey S., Todd, J.A., & Erwin, D.H. 1993. Mollusca: Gastropoda. In: Benton, M. J. (ed), *The Fossil Record.* 131–167. London: Chapman and Hall.

Vinther, J., Stein, M., Longrich, N.R. & Harper, D.A.T. 2014. A suspension-feeding anomalocarid from the Early Cambrian. *Nature* **507**: 496–497.

Ward, P.D. & Signor, P.W. III 1983. Evolutionary tempo in Jurassic and Cretaceous ammonites. *Paleobiology* **9**: 183–198.

Ward, P.D. 1996. Ammonoid extinction. In: Landman, N. H., Tanabe, K. & Davis, R. A. (eds), *Ammonoid Paleobiology*. Plenum, New York.

Yacobucci, M.M. 2015. Macroevolution and paleobiogeography of Jurassic-Cretaceous ammonoids. In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds): *Ammonoid paleobiology, Volume I: from anatomy to ecology. Topics in Geobiology* **43**: 539–552. Dordrecht: Springer.

Zorn, I. 1991. A systematic account of Tertiary Pteropoda (Gastropoda, Euthecosomata) from Austria. *Contributions to Tertiary and Quaternary Geology* **28**: 95–139.

Figure Captions

Figure 1 Adult ammonites (A-C), juvenile ammonites (D, E), and an embryonic belemnite (F) compared to fossil conchs of Thecosomata from the Eocene of India (G-J). 0.1 mm-scale ~~bare~~ applies to figures D to J. Photo in A courtesy C. Steinweg, L. Schöllmann and J.-O. Kriegs (all Münster); D and E from *Tanabe et al. (2008)*; F from *Bandel et al. (1984)*; G to J from *Lokho & Kumar (2008)*. A. *Parapuzosia seppenradensis*, Campanian, Seppenrade. B, C. *Pachydesmoceras* sp., Campanian, Hokkaido, diameter 1.3 m, D. Aiba (Mikasa) for scale. Note the symmetrical bulges in the posterior body chamber in C. D, juvenile conch of *Scaphites whitfieldi*, AMNH 44833, Turonian, U.S.A. E, embryonic conch of *Aconeceras* cf. *trautscholdi*, UMUT MM 29439–4, Aptian, Russia. F, embryonic conch of *Hibolithes* sp., GPIT Ce 1599, Callovian, Lithuania. G to J, Upper Disang Formation, Phek District, Nagaland. G, H, Limacinidae spp. I, J, Creseidae spp.

Figure 2 Occurrences, extinctions, originations and diversity changes in plankton and large planktotrophic suspension feeders from the Cretaceous to the Palaeogene (mass extinction marked by red bar). Data from *Friedmann et al. (2010)*, *Bristow et al. (1980)*, *Corse et al. (2013)*, *Yacobucci (2015)* and *Jarman (2001)*.

Figure 3 Zooplankton size ranks and filter mesh spacing of planktivorous filter feeders. Modified after *Vinther et al. (2014)*, using data from *Lokho & Kumar (2008)*, *Friedman et al. (2010)* and *De Baets et al. (2015)*.

Figure 1(on next page)

Adult ammonites (A-C), juvenile ammonites (D, E), and an embryonic belemnite (F) compared to fossil conchs of Thecosomata from the Eocene of India (G-J).

Figure 1 Adult ammonites (A-C), juvenile ammonites (D, E), and an embryonic belemnite (F) compared to fossil conchs of Thecosomata from the Eocene of India (G-J).

0.1 mm-scale bare applies to figures D to J. Photo in A courtesy C. Steinweg, L. Schöllmann and J.-O. Kriegs (all Münster); D and E from *Tanabe et al. (2008)*; F from *Bandel et al. (1984)*; G to J from *Lokho & Kumar (2008)*. A. *Parapuzosia seppenradensis*, Campanian, Seppenrade. B, C. *Pachydesmoceras* sp., Campanian, Hokkaido, diameter 1.3 m, D. Aiba (Mikasa) for scale. Note the symmetrical bulges in the posterior body chamber in C. D, juvenile conch of *Scaphites whitfieldi*, AMNH 44833, Turonian, U.S.A. E, embryonic conch of *Aconeceras* cf. *trautscholdi*, UMUT MM 29439–4, Aptian, Russia. F, embryonic conch of *Hibolithes* sp., GPIT Ce 1599, Callovian, Lithuania. G to J, Upper Disang Formation, Phek District, Nagaland. G, H, Limacinidae spp. I, J, Creseidae spp.

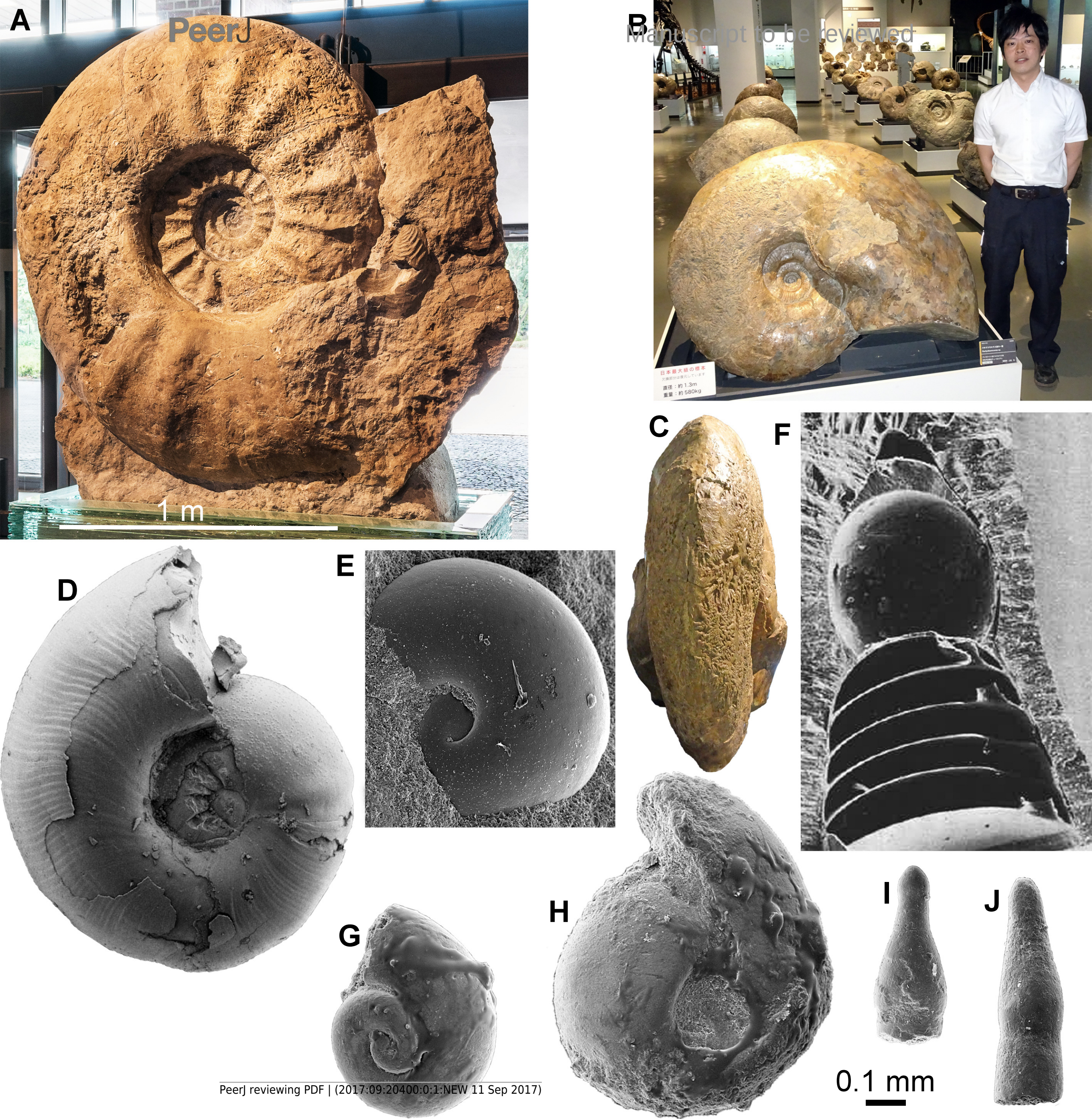

A
1 m
B
日本最大級の標本
欠損部分は復元しています
直径：約 1.3m
重量：約 580kg
C
F
D
E
G
H
I
J
0.1 mm

Figure 2(on next page)

Zooplankton size ranks and filter mesh spacing of planktivorous filter feeders.

Figure 3 Zooplankton size ranks and filter mesh spacing of planktivorous filter feeders. Modified after *Vinther et al. (2014)*, using data from *Lokho & Kumar (2008)*, *Friedman et al. (2010)* and *De Baets et al. (2015)*.

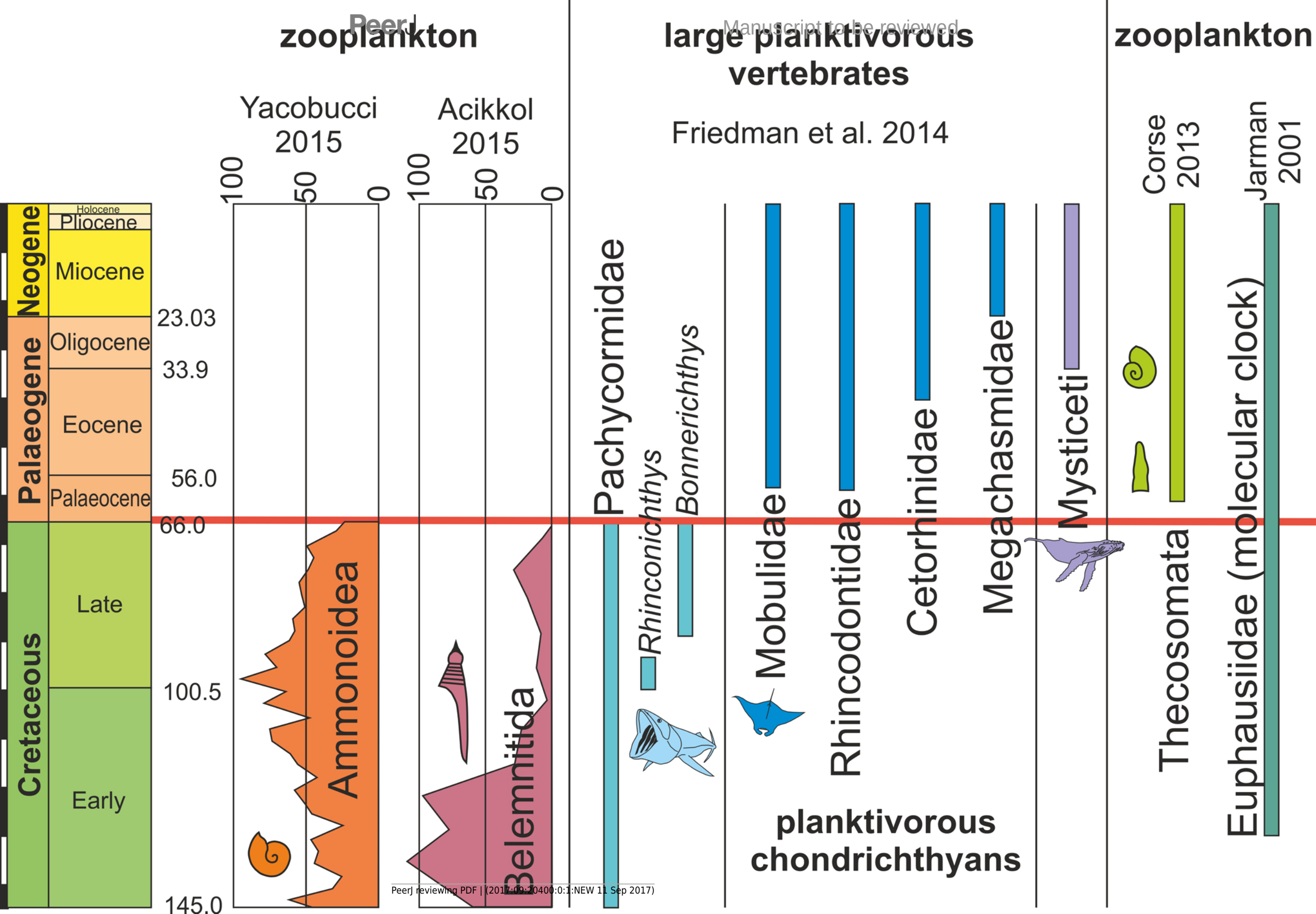
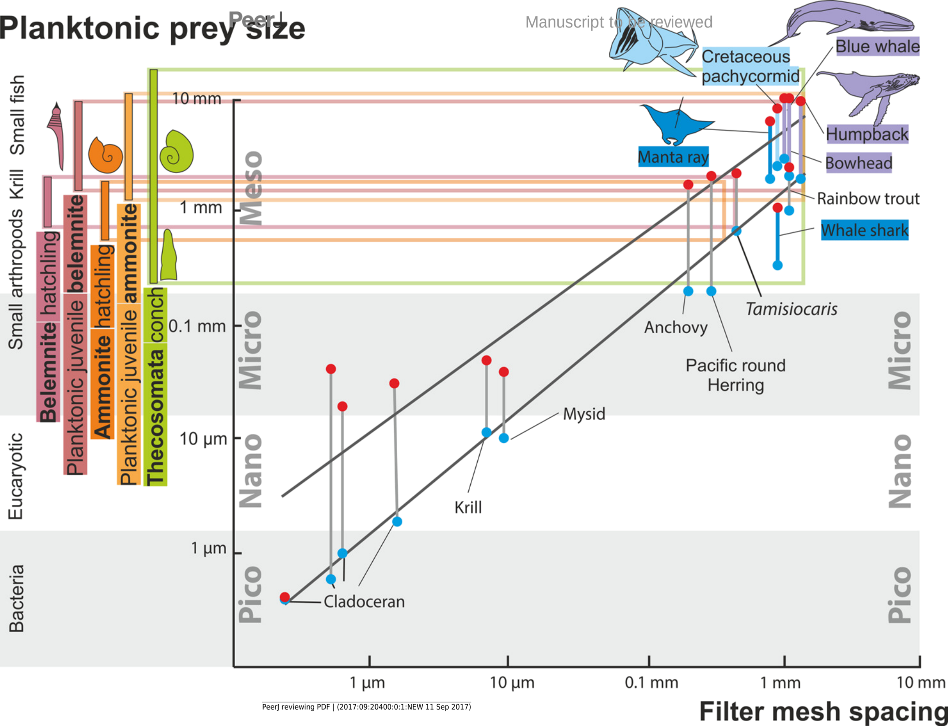

zooplankton
Yacobucci 2015
100
50
0
Acikkol 2015
100
50
0
large planktivorous vertebrates
Friedman et al. 2014
zooplankton
Corse 2013
Jarman 2001
Neogene
Holocene
Pliocene
Miocene
23.03
Palaeogene
Oligocene
33.9
Eocene
56.0
Palaeocene
66.0
Cretaceous
Late
100.5
Early
145.0
Ammonoidea
Belemnitida
Pachycormidae
Rhinconichthys
Bonnerichthys
Mobulidae
Rhincodontidae
Cetorhinidae
Megachasmidae
Mysticeti
Thecosomata
Euphausiidae (molecular clock)
planktivorous chondrichthyans

Figure 3(on next page)

Occurrences, extinctions, originations and diversity changes in plankton and large planktotrophic suspension feeders from the Cretaceous to the Palaeogene

Figure 2 Occurrences, extinctions, originations and diversity changes in plankton and large planktotrophic suspension feeders from the Cretaceous to the Palaeogene (mass extinction marked by red bar).

Data from *Friedmann et al. (2010)*, *Bristow et al. (1980)*, *Corse et al. (2013)*, *Yacobucci (2015)* and *Jarman (2001)*.


Planktonic prey size
Small fish
Krill
Small arthropods
Eucaryotic
Bacteria
Belemnite hatchling
Planktonic juvenile belemnite
Ammonite hatchling
Planktonic juvenile ammonite
Thecosomata conch
10 mm
1 mm
0.1 mm
10 µm
1 µm
Meso
Micro
Nano
Pico
Cretaceous pachycormid
Blue whale
Humpback
Bowhead
Manta ray
Rainbow trout
Whale shark
Tamisiocaris
Anchovy
Pacific round Herring
Mysid
Krill
Cladoceran
1 µm
10 µm
0.1 mm
1 mm
10 mm
Filter mesh spacing