Available online at www.sciencedirect.com
SCIENCE DIRECT®

C. R. Palevol 4 (2005) 501–515

COMPTES RENDUS
PALEVOL

http://france.elsevier.com/direct/PALEVO/

Systematic Palaeontology (Invertebrate Palaeontology)

Recovery of gastropods in the Early Triassic

Alexander Nützel

Institut für Paläontologie, Universität Erlangen-Nürnberg, Loewenichstr. 28, 91054 Erlangen, Germany

Received 28 July 2004; accepted after revision 14 February 2005

Available online 18 April 2005

Written on invitation of the Editorial Board

Abstract

Gastropod rebound from the end-Permian mass extinction event initiated in the Olenekian and diversification continued until the Carnian. The most diverse and abundant Early Triassic gastropod faunas are from the Moenkopi Formation (Utah) and the Upper Werfen Formation (Europe, Alps), which contribute as much as 50% to the reported global gastropod diversity of the Early Triassic. Gastropod faunas with more than 10 to 15 species are unknown from the Induan. However, the Olenekian fauna from the Sinbad Limestone (Moenkopi Formation) comprises 26 species. Faunas with more than 100 gastropod species have not been reported prior to the Late Anisian. The number of reported gastropod taxa continues to rise until the Carnian. Several caenastropod groups and the opisthobranchs have their first occurrence in the Olenekian, which indicates a major turnover within the Gastropoda. Typical Palaeozoic gastropod groups were rapidly replaced and Early Triassic gastropod faunas are distinct form Late Palaeozoic faunas. *Zygopleura rugosa* Batten and Stokes is transferred to the genus *Ampezzopleura* and its diagnostic larval shell is reported for the first time. It corroborates the view that the highly diverse pseudozygopleurids became extinct at the end-Permian mass extinction event and were replaced by the superficially similar Mesozoic Zygopleuridae. ***To cite this article: A. Nützel, C. R. Palevol 4 (2005)***.

Résumé

Reconquête par les gastéropodes au Trias inférieur. La récupération des gastéropodes consécutive à la crise biologique de la fin du Permien débute à l'Olenekien. La diversification du groupe se poursuit jusqu'au Carnien. Les faunes de gastéropodes les plus riches du Trias inférieur, à la fois par leur diversité et par leur abondance, proviennent de la formation Moenkopi (Utah) et de la formation supérieure de Werfen (Europe, Alpes) qui contribuent pour 50% à la biodiversité globale des gastéropodes du début du Trias. L'Indusien n'a pas livré de faunes de gastéropodes comportant plus de 10 à 15 espèces. Cependant, la faune olenekienne du « Sinbad Limestone » (formation Moenkopi) comprend 26 espèces. Des faunes comptant plus de 100 espèces de gastéropodes n'ont pas été rencontrées avant l'Anisien tardif. Le nombre de taxons recensés continue de croître ensuite jusqu'au Carnien. Les premiers représentants de plusieurs groupes de caenogastéropodes et d'opisthobranches apparaissent à l'Olenekien, une époque qui marque un renouvellement majeur parmi les gastéropodes. Des groupes de gastéropodes typiquement paléozoïques sont rapidement remplacés et les faunes du début du Trias sont différentes de celles de la fin du Permien. *Zygopleura rugosa* Batten et Stokes est rapporté au genre Ampezzopleura et la diagnose de sa coquille larvaire est décrite pour la première fois. Ceci conforte l'opinion que les pseudozygopleuridés hautement diversifiés s'éteignent lors de la crise biologique de la fin

E-mail address: nuetzel@pal.uni-erlangen.de (A. Nützel).

1631-0683/$ - see front matter © 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.
doi:10.1016/j.crpv.2005.02.007

du Permien et sont remplacés par les Zygopleuridae mésozoïques d'apparence proche. ***Pour citer cet article : A. Nützel, C. R. Palevol 4 (2005)***.

Keywords: Late Palaeozoic; Early Triassic; Gastropods; Mass extinction; Biotic recovery

Mots clés : Paléozoïque terminal ; Trias précoce ; Gastéropodes ; Extinction en masse ; Renaissance biotique

1. Introduction

Gastropods, as a major metazoan clade, play an important role for analyses of palaeodiversity at the Permian/Triassic boundary, because they were abundant in the Late Palaeozoic and Early Mesozoic, but nevertheless considerably affected by the end-Permian extinction, which eliminated as many as 20% of all families and correspondingly a much higher percentage of genera and species [3,10,11,15,17]. Recently discovered Latest Permian well-preserved gastropod faunas from southern China still contain typical Palaeozoic taxa, which suggests that the extinction was sudden [36,37]. Popular phrases like 'Lazarus-Taxon', 'Elvis Taxon', and 'Dead Clade Walking' were first coined for gastropods [3,16,18,23,24]. There is a consensus that gastropods and bivalves were less affected by the end-Permian mass extinction event than most other invertebrate clades and that this extinction resistance was a precondition for their high diversity in modern faunas (e.g., [10,11]). The Mesozoic radiation of the Gastropoda represents a continuation of a previous Palaeozoic expansion. Gastropods were not marginalized effectively by the extinction event, but recovered successfully; so it is obvious that extinction resistance must have formed the base for their post-Palaeozoic expansion. However, interesting shifts within the clade Gastropoda can be recognized during the aftermath of the extinction and during the recovery period.

Gastropods are one of the most diverse marine invertebrate groups of the Early Mesozoic: 2100 Triassic nominate gastropod species represent roughly 400 genera. These numbers are small when compared with the diversity of Recent gastropods, which is estimated between 40 000 to 150 000 species [6,40]. Despite the relatively high diversity of Triassic gastropods, analyses are hindered by several factors such as poor preservation or convergence of shell characters, which produce an unknown number of misleading taxonomic assignments. With the exception of the Moenkopi Formation [5,32], Early Triassic gastropod faunas (especially those from the Griesbachian) are generally poorly preserved. Therefore, most generic and family assignments of Early Triassic gastropods are questionable.

Triassic gastropod diversity is distributed unevenly among the Triassic stages. It is lowest in the Early Triassic, peeks in the Carnian and declines severely in the Norian and Rhaetian (Fig. 1). An ongoing diversity study on the species and genus level conducted by the author and D.H. Erwin (Smithsonian Institution, Washington D.C.) will tackle the question whether this pattern does reflect the evolution of biodiversity, and if so, to what degree. The Early Triassic is characterized by a historic low in the number of reported gastropod taxa. Only about 80 nominate gastropod species, representing roughly 40 genera (excluding Lazarus taxa), are known from the Scythian and by far most of these taxa

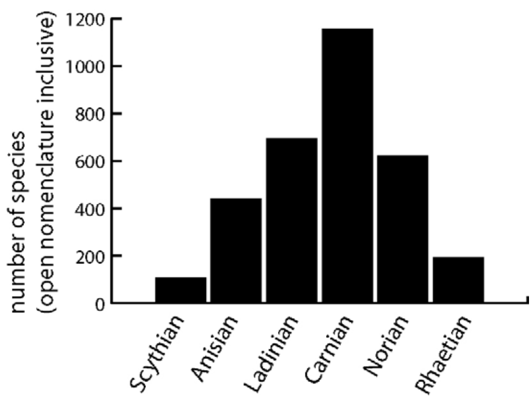

Fig. 1. Species diversity throughout the Triassic; after an Early Triassic low, the number of species increases rapidly, peeks in the Carnian and drops subsequently in the Norian and Rhaetian; includes species in open nomenclature; data from own species-level database.

Fig. 1. Diversité spécifique au cours du Trias ; après un creux au début du Trias, le nombre des espèces croît rapidement, culmine au Carnien et chute ensuite durant le Norien et le Rhétien ; les espèces en nomenclature ouverte ont été incluses. D'après une banque de données des espèces réalisée par l'auteur.

are from the Olenekian. Compared to the 150 000 Recent gastropod species, the number of Early Triassic gastropod taxa must be considered extremely low, even if a considerable incompleteness of the fossil record is assumed. The reported gastropod diversity seems to be even lower in the Induan, although abundance may be high. However, the stratigraphy of many Early Triassic gastropod occurrences is poorly resolved. Moreover, gastropod preservation is generally poor in the Induan, which represents a major handicap for any analysis. Most reports of Early Triassic gastropods come from North America, Europe and Asia (especially southern China). However, almost nothing is known from the Gondwana continents.

Induan gastropod faunas usually comprise only a few species, and reports of single species occurrences are common. The richest Griesbachian gastropod fauna was recently reported from Oman and contains just about ten taxa [49,53]. Early Triassic gastropod faunas with more than ten species and reasonable preservation have not been reported prior to the Olenekian. The Upper Werfen Formation (Alps) and the Sinbad Limestone (Moenkopi Formation, Utah) form the most diverse Olenekian gastropod Lagerstätten. However, these faunas are not highly diverse and still lack the complexity of Late Triassic or Late Permian gastropod faunas. They come both from shallow marine environments without true metazoan reefs. Together, the Werfen and the Moenkopi Formations contribute more than 50% to the global number of described nominate gastropod species from the Early Triassic. Early Triassic gastropod faunas, including those from the Werfen and Moenkopi Formations, have been interpreted as opportunistic faunas that were dominated by small, commonly abundant, *r*-selected species and are characterized by relatively low species richness [20,43]. The gastropod faunas of the Moenkopi and upper Werfen Formations differ strongly from each other on the species and even on the genus level, which suggests that cosmopolitism played no important role in Olenekian gastropods.

2. The gastropods of the Moenkopi Formation (Sinbad limestone)

The gastropod fauna from the Sinbad Limestone Member (Moenkopi Formation) from Utah is crucial for the understanding of recovery patterns, because it is virtually the only well-known and relatively diverse fauna from the Early Triassic. The Sinbad Limestone Member is a 15 m to 30 m thick carbonate unit within the predominantly siliceous clastic, terrestrial Moenkopi Formation [7]. Fossiliferous limestones, dolomite and calcareous siltstones are the major constituents of the Sinbad Limestone Member. These beds were deposited in a shallow, epicontinental sea. The best-preserved gastropod material comes from weathered mollusc coquinas (rudstones with grain- and packstones matrix) of the San Rafael Swell [5,7], which are interpreted as tempestites [7,43]. The coquinas are mainly composed of bivalves, gastropods, and annulated tubes (supposed scaphopods of the *Plagioglypta*-type) (Fig. 2). The presence of echinoderm ossicles indicates a normal salinity for these beds. There are also stromatolites and oolites in the marine limestones of the Moenkopi Formation, which indicates warm shallow marine conditions. The presence of stromatolites in normal subtidal marine environments was interpreted as a disaster phenomenon [42].

Twenty-six species representing 16 genera have been reported from the Moenkopi Formation [5], which forms about one third of the global Early Triassic gastropod diversity. Some of the species appear in 'astronomical' numbers [5]. Ongoing re-sampling and taxonomic re-evaluation of the Moenkopi gastropod fauna show that this species richness and diversity will not

Fig. 2. Thin section of Sinbad Limestone mollusc coquina (rudstone with grain-packstone matrix) with bivalves, supposed scaphopods (*Plagioglypta*), and gastropods as components; American Museum of Natural History (AMNH) locality 3026 [5]; oriented; 10 mm wide.

Fig. 2. Lame mince dans un calcaire coquillier du « Sinbad Limestone » (*rudstone* avec une matrice *grain-packstone*) comportant des lamellibranches, des scaphopodes probables (*Plagioglypta*) et des gastéropodes ; American Museum of Natural History (AMNH) localité 3026 (5) ; orienté ; largeur = 10 mm.

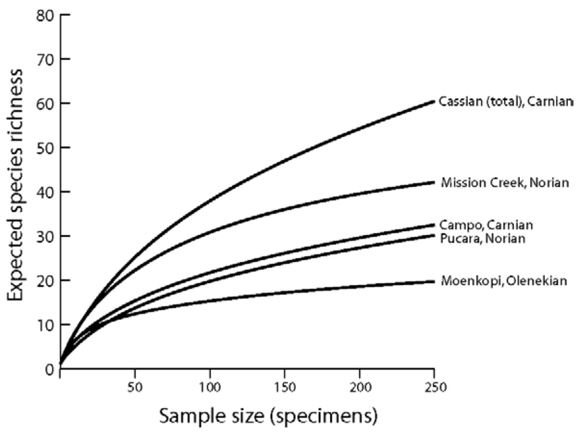

Fig. 3. Rarefaction analysis of the Moenkopi Formation and some Late Triassic gastropod faunas; the most diverse Early Triassic gastropod fauna is distinctly less diverse than the great Late Triassic faunas; from [33].

Fig. 3. Analyse de raréfaction de la formation de Moenkopi et de quelques faunes de gastéropodes du Trias supérieur ; la faune de gastéropodes la plus diversifiée du Trias inférieur est nettement moins diversifiée que les grandes faunes du Trias supérieur. D'après [33].

increase considerably, i.e. not many additional taxa can be found. The species richness and diversity of the Sinbad gastropod fauna can be considered as normal (or at least not extraordinarily low) for a non-reefal Mesozoic environment. However, rarefaction analyses of Late Triassic gastropod faunas have shown that the Sinbad fauna (i.e. the most diverse Early Triassic gastropod fauna) is clearly less diverse than the most diverse Late Triassic faunas [33] (Fig. 3).

Most of the Moenkopi snails have an adult size smaller than 10 mm [20]. The dominance of microgastropods and the lack or scarcity of large gastropod in the Early Triassic seem to be a global phenomenon. Open-shelf environments that were dominated by opportunistic microgastropods have been interpreted as a non-actualistic re-population phenomenon [20]. Reduced body size was also interpreted as a possible consequence of productivity decline [48]. However, even most Recent gastropods are small [9] and the abundant gastropods '*Turbo*' *rectecostatus* and *Natiria costata* from the Upper Werfen Formation are as large as 20–35 mm and therefore are not microgastropods.

The Moenkopi material yields the oldest Mesozoic gastropods with known protoconchs – it is in fact the only Triassic formation with well-preserved gastropod protoconchs (see below, Figs. 8–10) except of the Early Carnian Cassian Formation, in the Italian Alps. The protoconch morphology is crucial for phylogeny, systematics and recognition of larval strategies of gastropods. Batten and Stokes [5] reported the protoconch morphology of a few taxa from the Sinbad Limestone. Ongoing additional sampling produced many well-preserved specimens, so that the protoconch morphology of most species from the Moenkopi Formation can be reported in the near future. Meanwhile, even the protoconch morphology of the type species of several Late Triassic genera from the Cassian Formation has become known and can be compared with some of the gastropods from the Sinbad Limestone. This will change several generic assignments and improve substantially comparisons with Late Palaeozoic and other Early Mesozoic gastropods.

3. The gastropods of the Werfen Formation

The Lower Triassic Werfen Formation produced about 15 nominate gastropod species [27,56]. It crops out in a vast area of the Alps and overlies the Upper Permian (Wuchiapingian to Changhsingian) Bellerophon Formation, which yields a typical Late Palaeozoic marine fauna with abundant brachiopods and bellerophontids in its upper part. The Werfen Formation is up to several hundred metres thick and ranges from the earliest Early Triassic (Griesbachian, Induan) to the late Early Triassic (Olenekian). It yields an abundant marine fauna, which is dominated by bivalves and gastropods. The preservation of the gastropods is generally poor and the fauna consists commonly of steinkerns. The bellerophontid *Retispira*? *vacecki* seems to be restricted to the lower part of the Werfen Formation (Induan) – its taxonomy and stratigraphic occurrence was intensively discussed by Yochelson and Kollmann [60]. Abundant microgastropods occur in a facies that is called 'Gastropod Oolite'. This term is also used in a lithostratigraphic sense for a horizon between the Seis and Campil Members. This member consists of oolites in which gastropods may form the cores of the ooids, but more commonly they occur as iron oxide encrusted or impregnated components of wackestones and grainstones [8]. Some of these gastropod-dominated beds are tempestites. The occurrence of similar microgastropod coquinas seems to represent a global phenomenon [20] and is absent or rare in the Palaeozoic.

The microgastropods (gastropods smaller than 10 mm) of the Werfen Formation are poorly studied and generic assignments are usually doubtful, wrong or outdated. In part, this seems to be the result of the poor preservation of these gastropods. For example, *Polygyrina gracilior* is based on poorly preserved specimens (steinkerns) of Anisian age. This species name is frequently used as a dustbin for high-spired Early to Late Triassic gastropod specimens from the Alps and the German/Polish basin. Based on the study of the type specimens (housed in the 'Naturkundemuseum' of Coburg, Germany), it must be stated that these specimens are undeterminable and that the taxon is therefore a *nomen dubium*. Similarly, *Coelostylina werfenensis* is another taxon for high-spired small gastropods, which is based on poorly preserved, basically undeterminable material, as is indicated by an examination of the type material at the University of Tübingen. However, it is a fact that small high-spired gastropods are abundant in the Werfen Formation (Fig. 4), especially in the Gastropod Oolite. They represent probably caenogastropods (e.g., *Polygyrina*) or possibly heterobranchs (Allogastropoda). Their systematic and taxonomic placement is doubtful as long as no well-preserved material with protoconchs can be studied.

Werfenella rectecostata (the former '*Turbo*' *rectecostatus*) and *Natiria costata* represent the most abundant larger gastropods of the Werfen Formation. They occur in the upper part of the Werfen Formation (Olenekian) and form an important part of its fauna. As mentioned, both species are as large as two to four centimetres, and therefore they do not represent microgastropods. *Natiria costata* is commonly relatively well-preserved, because it probably has a thin calcitic outer shell layer, which is common among neritaemorph gastropods. This species closely resembles Late Palaeozoic species of the genus *Natiria* and species such as the Latest Permian *Naticopsis shizishanenensis* [37]. It is likely that *Natiria costata* belongs to an evolutionary line that crossed the P/T and was important in the Late Palaeozoic and Early Mesozoic. *Werfenella rectecostata* is normally preserved as steinkern, but is nevertheless characteristic and easy to recognize by its angular shape. *Werfenella rectecostata* does not belong to the modern genus *Turbo*, but represents the recently erected genus *Werfenella* [30], which is probably related to the Mesozoic family Purpurinidae and could represent the progenitor taxon of this family [30]. This genus originated in and is restricted to the Early Triassic. Therefore, it represents an example for an initially successful newcomer.

In conclusion, the fauna of the Werfen Formation shows that gastropods formed an abundant and considerable part of the marine benthic fauna in the Early Triassic of the western Tethys. A few gastropod taxa are sufficiently characteristic for an unproblematic species identification. However, most species are only known from poorly preserved specimens and provide limited phylogenetic and palaeobiogeographic information.

Fig. 4. Gastropod oolite facies; Valsugana (northern Italy, near Borgo) [56]; coll. Universität Tübingen (Germany); small high-spired gastropods are abundant and were commonly assigned to *Polygyrina gracilior*, which represents a *nomen dubium*, because it is based on poorly preserved material from the Recoaro area (northern Italy); width: 36 mm.

Fig. 4. Faciès oolitique à gastéropodes ; Valsugana (Nord de l'Italie, près de Borgo) [56] ; coll. université de Tübingen (Allemagne) ; de petits gastéropodes à spire étroite sont abondants et sont communément rapportés à *Polygyrina gracilior*, qui correspond à un *nomen dubium* parce que sa diagnose se réfère à un matériel mal conservé de la région de Recoaro (Nord de l'Italie) ; largeur : 36 mm.

4. Recovery in China

China, and particularly southern China, is one of the most important regions for the study of the end-Permian mass extinction event, because several continuous marine P/T-sections can be studied. Well-preserved Latest Permian (Wuchiapingian-Changhsingian) gastropod faunas from southern China are diverse and contain mostly typical Late Palaeozoic taxa [36,37]. Most of the Palaeozoic genera are not known after the Griesbachian [36]. Only a few Early Triassic taxa were described and most of them are based on poorly preserved material. Similar to the Werfen Formation, bellerophontids and several high-spired, smooth and poorly preserved caenogastropods (*Polygyrina*, *Omphaloptycha*, *Toxoconcha*) were reported from Lower Triassic Formations of China (e.g., the Zalishan and Maresongduo Formations) [47,51]. The number of reported genera in South China remains low during the Olenekian, e.g., five genera were reported from the Smithian [36], while the contemporaneous Moenkopi Formation alone produced as many as 16 genera. It is unclear whether this reflects preservation bias or represents a true regional signal.

5. Anisian recovery and the Muschelkalk of the German/Polish Basin

There are no marine P/T sections in Middle Europe; Late Permian marine deposits (Zechstein, Wuchiapingian–Changhsingian) are covered with the terrestrial red beds of the Buntsandstein (Early Triassic to Earliest Anisian). The Zechstein yields a typical Late Palaeozoic gastropod fauna. In the uppermost portions of the Buntsandstein (Röt), marine influence reappears, indicating a transgression. The Röt-facies contains several marine gastropod taxa. However, the stratigraphic position of this lithological unit is unclear but it probably encompasses Late Olenekian and Early Anisian. Since the transgression, the German/Polish Basin hosted a shallow epicontinental sea during the Anisian and part of the Ladinian, called the Muschelkalk Sea. The Muschelkalk Sea has produced about 250 described gastropod species (60 genera), most of them of Anisian age. This is about 50–60% of the described global Anisian gastropod diversity and although there are probably synonyms and questionable assignments, the Muschelkalk fauna is crucial for studies on gastropod recovery. Fig. 5 shows the number of gastropod species in the different lithostratigraphic units of the Muschelkalk according to a tabular compilation from Schmidt [41]. The lithostratigraphic subdivision in this work is outdated, but the data suggest that most units of the Anisian Muschelkalk produced as many as 50 to 90 species. This is much more than any Lower Triassic Formation and it suggests a certain stability without strong fluctuations of the diversity of the Muschelkalk populations. These data imply that recovery was completed or was progressing considerably during the Anisian.

Other diverse Anisian gastropod faunas were described from the Alps and especially from China (e.g.,

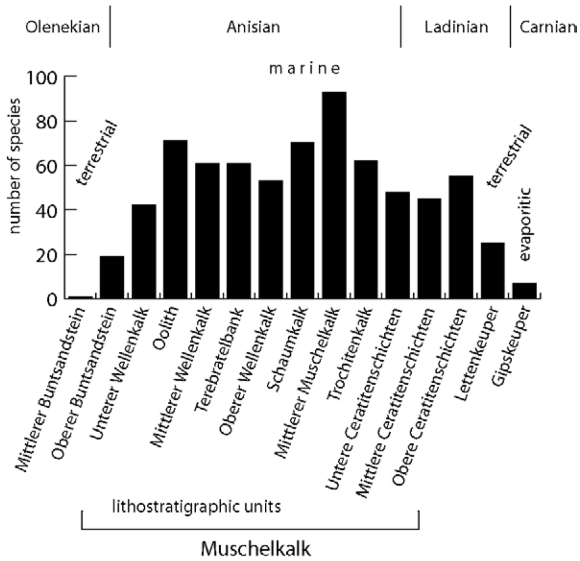

Fig. 5. Gastropod diversity in the Triassic German/Polish Basin (Anisian/Ladinian Muschelkalk), based on Schmidt's [41] compilation; the Muschelkalk is the greatest source of global Anisian gastropod diversity; the lithostratigraphic subdivision is partly outdated, but the data suggest that most units of the Anisian Muschelkalk produced as many as 50 to 90 species, which is much more than any Early Triassic Formation. This suggests that recovery was complete or progressing.

Fig. 5. Diversité des gastéropodes dans le Trias du bassin germano-polonais (Anisien/Ladinien, Muschelkalk), d'après une compilation des données de Schmidt (41) ; le Muschelkalk est la plus importante source pour la diversité des gastéropodes de l'Anisien ; les subdivisions lithostratigraphiques sont partiellement périmées mais les données suggèrent que la plupart des unités du Muschelkalk (Anisien) ont livré de 50 à 90 espèces, bien plus que n'importe quelle autre formation du Trias inférieur. Ceci semble indiquer que la reconquête était complète ou en cours.

[47,57–59]). A Late Anisian gastropod fauna from Qingyan (southwestern China) comprises about 120 species [46], which indicates that the recovery process was completed or still progressing at this time.

6. Diversity trends in specific gastropod groups

6.1. Bellerophontoideans

The bellerophontoideans crossed the P/T boundary with several genera in Europe, Asia, and North America. At least three genera (*Retispira*, *Bellerophon*, *Euphemites*) crossed the Permian/Triassic boundary, each represented by only one or two species [61]. However, most of the Triassic bellerophontoideans seem to be restricted to earliest Early Triassic, are absent or rare in the Olenekian and probably did not survive the Early Triassic. Thus, they represent a holdover taxon sensu Hallam and Wignall [22]. Because of their characteristic bilaterally-symmetrical shape, bellerophontoideans are relatively easy to recognize even if preservation is poor, although species identification and generic assignment are commonly problematic. There are no reports of Anisian bellerophontoids, except one from China [36], which should be confirmed. This enigmatic phenomenon of survival without recovery [18] has been christened 'Dead Clade Walking' [24]. Bellerophontoideans are not part of the gastropod recovery.

6.2. Limpets

Limpet-shaped gastropods are unknown from the Early Triassic. They are not even important parts of Late Palaeozoic gastropod faunas. Limpets which could belong to the patelloideans became more abundant and diverse during the Late Triassic. Limpets (of whatever systematic placement they were) do not play an important role in the recovery process. In part, this might be result of preservation bias because most patellids live on near-shore hardgrounds, an environment with a particularly bad preservation potential and fossil record. However, limpet-shaped gastropods may also occur in other more quiet environments.

6.3. Euomphalina

Planispiral euomphalid shells are abundant and widespread in the Late Palaeozoic. They are characterized by a vetigastropod-type protoconch [29], which is more or less openly coiled in some genera [2]. However, there seems to be no report of a planispiral or widely phaneromphalous gastropods from the Early Triassic. This suggests that the P/T selectively hits the euomphalines. Planispiral gastropods reappear in the Anisian but it is unknown whether these gastropods are descendants of the Palaeozoic euomphalines or whether the planispiral teleoconch shape is convergent as has been shown for various Late Triassic and younger taxa [1]. Generally, the family diversity of marine larger planispiral or widely phaneromphalous gastropods declined during the Phanerozoic [50]. This trend against planispiral morphology was not stopped by the emergence of Middle and Late Triassic euomphalid-like looking gastropods. True euomphalines either became extinct and were replaced by convergent forms or they survived but played no important role in gastropod recovery.

6.4. Vetigastropods

Slit-bearing vetigastropods (pleurotomarioideans) were highly diverse and abundant in the Late Palaeozoic and declined considerably at the P/T extinction event. They are unknown from the Werfen Formation and play a minor role in the Moenkopi Formation with only two species of the *Worthenia*-group, one of which is rare [5]. Subsequently, *Worthenia*-like gastropods and other slit-bearing vetigastropods recovered quickly and *Worthenia*-like gastropods (*Worthenia* or *Wortheniella*) are known from numerous Middle to Late Triassic species [57]. The slitless vetigastropods may represent an important component of Late Palaeozoic faunas, especially members of the Microdomatidae and Anomphalidae can contribute considerably to Late Palaeozoic gastropod faunas. Both families are absent in the Early Triassic. Similar forms reappear in the Middle Triassic and are among the most abundant gastropods in the Carnian Cassian Formation. The first occurrence of the Mesozoic trochomorph genus *Chartroniella* in the Early Triassic Moenkopi fauna is noteworthy [5].

The vetigastropods were severely hit by the end-Permian mass extinction and are generally rare in Early Triassic faunas. However, they rebound considerably and became a major component of Middle and Late Triassic gastropod faunas, e.g. of the fauna of the Carnian Cassian Formation.

6.5. Neritaemorpha

Neritaemorphs form an important part of Late Palaeozoic gastropod faunas and are well represented in Early Triassic gastropod faunas. They were reported from the Griesbachian and are abundant in the Olenekian. Small neritaemorphs are highly abundant and even dominant in the Sinbad limestone. The neritaemorph *Natiria costata* is one of the most abundant gastropods in the Upper Werfen Formation where it is even used as an index fossil (Fig. 6). Genera such as *Naticopsis* and *Natiria* seem to represent examples of survivors. However, the platyceratids, which are probably closely related to the neritaemorphs, became extinct. The taxonomy of neritaemorphs is particularly difficult and therefore conclu-

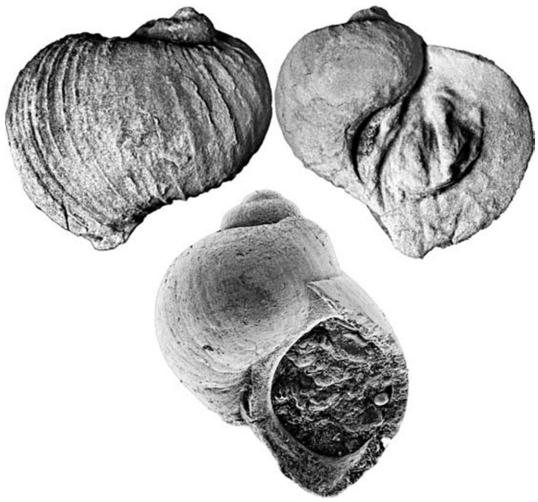

Fig. 6. Early Triassic neritaemorphs; upper figures: *Natiria costata*, common gastropod of the Upper Werfen Formation, Naturhistorisches Museum Wien (NHMW 1884 D 587), Grones, Gadertal, height 18 mm; Lower figure *Neritaria* sp. from the Sinbad Limestone (Utah) height 1.7 mm.

Fig. 6. Neritaemorphes du Trias inférieur ; figures du haut : *Natiria costata*, gastéropode commun dans la Formation supérieure de Werfen, Naturhistorisches Museum Wien (NHMW 1884 D 587), Grones, Gadertal, hauteur = 18mm ; figure du bas : *Neritaria* sp. du « Sinbad Limestone » (Utah, USA), hauteur = 1,7 mm.

sions about their diversity patterns are tentative. However, it seems obvious that several neritaemorph genera crossed the Palaeozoic/Mesozoic transition and that neritaemorphs contributed considerably to the recovery during the Olenekian and Anisian. They are diverse in the Anisian, e.g. in the European Muschelkalk and the Qinling Mountains in China [47].

6.6. Caenogastropoda

The caenogastropods are the most diverse Recent gastropod subclass. They represent an important group in the Late Palaeozoic but were seemingly not as diverse as the modern caenogastropods. However, their contribution to Late Palaeozoic faunas is generally underestimated. For instance, caenogastropods contribute about one third (32%) of the individuals and more than 50% of the species of the Middle Pennsylvanian gastropod fauna of the Flechado Formation (New Mexico, USA), which represents one of the most abundant and species-rich Late Palaeozoic gastropod collections [25]. Caenogastropods even form a considerable part of the Changsinghian gastropod fauna of South China [37]. There are 26 nominate Early Triassic caenogastropod species. All were assigned to Mesozoic to Modern genera and families [32]. Although many of these assignments are questionable, mainly due to poor preservation, this indicates a major faunal turnover within the Caenogastropoda on the genus and family levels. This turnover originated as early as the Early Triassic and was sudden, as is suggested by the fact that Changsinghian gastropod faunas from China still contain almost exclusively typical Late Palaeozoic caenogastropod taxa, such as the Meekospiridae, Soleniscidae, Pseudozygopleuridae, Orthonematidae, and Pithodeidae [35–37]. While the extinction on the genus and family level was rather profound, several higher rank clades passed the transition and must represent the ancestors of major Mesozoic to modern caenogastropod groups.

The Late Palaeozoic families Goniasmatidae and Pithodeidae are unusual for caenogastropods because they have a distinct selenizone and associated with this, a slit or pronounced sinus. In any other respect, they are typical caenogastropods (larval shell, shell structure). The families Goniasmatidae, Pithodeidae, and Orthonematidae are diverse and abundant from the Early Carboniferous to the Late Permian [31,35,62]. The evolutionary history of slit-bearing caenogastropods is largely restricted to the Palaeozoic. There are a few high-spired Triassic gastropod genera with a well-developed selenizone which could represent Mesozoic descendants of the Palaeozoic Goniasmatidae but their protoconch morphology is largely unknown so that their systematic placement is tentative. The genus *Pseudomurchisonia* was reported from the Werfen Formation [56] and could represent Early Triassic descendants of the Late Palaeozoic slit-bearing caenogastropods. However, wide-spread and long-ranging genera such as *Goniasma*, *Stegocoelia* and similar forms are restricted to the Middle and Late Palaeozoic. Therefore, most of these groups are victims of the end-Permian mass extinction event.

The subulitoid caenogastropod families Soleniscidae and Meekospiridae range from the Devonian to the Latest Permian (Changhsingian) (e.g., [34]) but also have some Early Triassic members, e.g., *Strobeus* and probably even *Soleniscus* are present in the Early Triassic of the Salt Range (Pakistan) and in the Moenkopi Formation (Fig. 7). Thus, subulitoids contain holdovers and are mentioned as an example for the Dead Clade Walking phenomenon [14]. However, similar and

Fig. 7. Early Triassic Soleniscidae as Palaeozoic holdovers; left *Strobeus* sp. "Upper Ceratite Beds, Bellerophon Bed, Mittialiwani near Chideru" (probably Mittiwali Member, Mianwali Formation [26]), Salt Range, Pakistan, height 20 mm, collection of the Universität Tübingen (Germany); middle and right, *Soleniscus* sp. or *Strobeus* sp., from the Sinbad Limestone, Moenkopi Formation, American Museum of Natural History (AMNH) locality 3026 [5]; middle 10.5 mm high; right 8.5 mm high.

Fig. 7. Les Soleniscidae du Trias inférieur, des survivants du Paléozoïque ; à gauche : *Strobeus* sp. « Couches supérieures à cératites, niveau à Bellerophon, Mittialiwani près Chideru » (probablement Membre Mittiwali, Formation Mianwali (26), Salt Range, Pakistan, hauteur = 20 mm, coll. université de Tübingen (Allemagne) ; au centre et à droite, *Soleniscus* sp. ou *Strobeus* sp., du « Sinbad Limestone », formation Moenkopi, American Museum of Natural History (AMNH) localité 3026 (5) ; hauteur : échantillon du centre = 10,5 mm, échantillon de droite = 8,5mm.

potentially related Mesozoic snails are found in the Coelostylinidae and Pseudomelaniidae. The Coelostylinidae have their first relatively well-documented appearance in the Permian (Wordian) [4] but radiated tremendously in the Triassic. Possible phylogenetic relationships of the largely smooth 'subulitoid' gastropods and similar Mesozoic forms are difficult to substantiate, because there are few discrete shell characters available and excellent preservation is needed for a meaningful taxonomy.

The Zygopleuroidea (formerly included in the catch-all Loxonematoidea) represent an important group of Late Palaeozoic to Early Mesozoic high-spired caenogastropods. On the generic and family levels, the Zygopleuroidea suffered heavy extinction at the P/T. The abundant caenogastropod family Pseudozygopleuridae became extinct at the P/T. They are well represented with several genera in the Changsinghian of South China [37]. However, there are no reports of Triassic pseudozygopleurids that have an extremely characteristic larval shell morphology, with strongly sinuous axial ribs forming a pseudospiral (Fig. 8). In

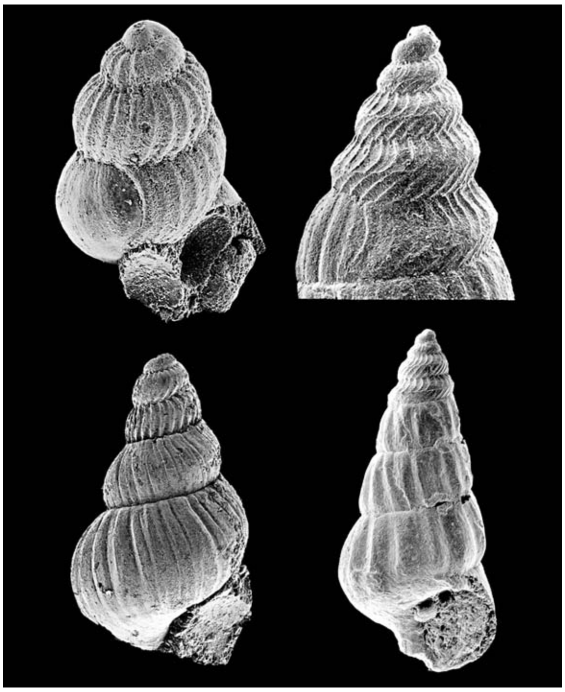

Fig. 8. The Pseudozygopleuridae (right) superficially resemble *Ampezzopleura* (Zygopleuridae) (left) but have a larval shell with strongly sinuous axial ribs forming a pseudospiral. These slight differences can only be observed in exceptionally well-preserved material and are highly diagnostic. They suggest that the very diverse Pseudozygopleuridae are restricted to the Palaeozoic and that the important Mesozoic Zygopleuridae originated in the Early Triassic as part of the caenogastropod turnover. Left: *Ampezzopleura rugosa* (Batten and Stokes) (new combination) from the Sinbad Limestone (Moenkopi Formation) represents the earliest certain member of the Zygopleuridae; it has a planktotrophic larval shell with simple axial ribs; upper left 0.6 mm high; lower left 1.3 mm high; right: *Pseudozygopleura* sp. from the Pennsylvanian of West Virginia (U.S.A.), Ames Shale; upper right 0.8 mm high; lower right 2.2 mm high.

Fig. 8. Les Pseudozygopleuridae (à droite) ressemblent superficiellement à Ampezzopleura (Zygopleuridae) (à gauche) mais possèdent une coquille larvaire avec des carènes spirales axiales très sinueuses formant une pseudospire. Ces légères différences peuvent uniquement être observées sur des échantillons exceptionnellement bien conservés et sont hautement significatives. Elles suggèrent que l'ensemble très diversifié des Pseudozygopleuridae est restreint au Paléozoïque et que l'important groupe des Zygopleuridae mésozoïques apparaît au Trias inférieur comme une composante du renouvellement des caenogastéropodes. À gauche : *Ampezzopleura rugosa* (Batten et Stokes) (nouvelle combinaison) du « Sinbad Limestone » (formation Moenkopi) représente le premier représentant avéré des Zygopleuridae ; il possède une coquille larvaire planctonique, avec des carènes axiales simples ; hauteur : en haut à gauche = 0,6 mm, en bas à gauche = 1,3 mm ; à droite : *Pseudozygopleura* sp. du Pennsylvanien de l'Ouest de la Virginie (USA), Ames Shale ; hauteur : en haut à droite = 0,8mm, en bas à droite = 2,2 mm.

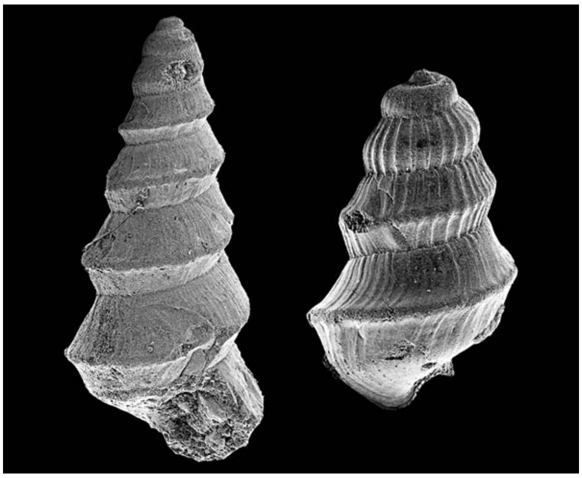

Fig. 9. The caenogastropod *Battenizyga eotriassica*, one of the more common, characteristic gastropods of the Sinbad Limestone (Moenkopi Formation); according to the current state of knowledge, *Battenizyga* originates and is restricted to the Early Triassic as part of the Early Mesozoic turnover within the Caenogastropoda; left 2.7 mm high; right 1.1 mm high.

Fig. 9. Le caenogastéropode *Battenizyga eotriassica*, un des gastéropodes les plus communs et les plus caractéristiques du « Sinbad Limestone » (formation Moenkopi) ; dans l'état actuel de nos connaissances, *Battenizyga* apparaît et reste limité au Trias inférieur, comme une composante du renouvellement des caenogastéropodes au début du Mésozoïque ; hauteur : à gauche = 2,7 mm, à droite = 1,1 mm.

contrast, the Mesozoic subfamily Ampezzopleurinae (family Zygopleuridae) has rather straight ribs on the larval shell. *Ampezzopleura rugosa* (Batten and Stokes) [5] (new combination, formerly in *Zygopleura*) from the Sinbad Limestone (Moenkopi Formation) represents the earliest certain member of the subfamily Ampezzopleurinae (family Zygopleuridae) (Fig. 8). The larval shell of this species is shown here for the first time. The comparison of the Palaeozoic *Pseudozygopleura* and the Triassic *Ampezzopleura* shows that the correct systematic placement relies on exceptionally well-preserved material with preserved protoconch. *Battenizyga* represents another caenogastropod genus with axial ribs on the early ontogenetic shell (Fig. 9). This genus is only known from the Moenkopi Formation [32] where it is relatively abundant. It was placed in the Triassic family Protorculidae which is closely related to the Zygopleuridae. The Ampezzopleurinae (Zygopleuridae) and Protorculidae are probably descendants of the Pseudozygopleuridae [28]. The highly diverse Pseudozygopleuridae are restricted to the Palaeozoic and the important Mesozoic Zygopleuridae occurs first in the Early Triassic and radiates subsequently as part of the caenogastropod turnover.

The caenogastropods are clearly a major contributor to the recovery process. Despite the poor preservation of many Early Triassic caenogastropod taxa, a profound faunal turnover on the genus and family levels can be recognized in the Olenekian.

6.7. Heterobranchia (Heterostropha)

The heterobranch order Allogastropoda was present with several geographically wide-spread genera in the Late Palaeozoic, most of which belong to the Streptacididae (e.g., the genera *Donaldina* and *Streptacis*). This family is well represented in the Changsinghian [37]. The Early Triassic record is relatively poor, probably because strepatcidids are small and knowledge of their protoconch is needed for recognition. However, protoconch preservation is generally rare and small gastropods are commonly not sufficiently well preserved. Nevertheless, the streptacidids *Donaldina*, *Streptacis*, and *Laxella* were reported from the Griesbachian of southwestern China and survived the P/T mass extinction [38]. The Griesbachian *Jiangxispira* from the same locality was interpreted as a strepatcidid that is transitional to the cylindrobullinids (opisthobranchs) [38]. This genus is very close to *Cylindrobullina*, a shelled opisthobranch that is abundant in the Mesozoic (see below). *Promathilda spirocostata* from the Moenkopi Formation is the only Early Triassic species which has been assigned to the mathildids [5]. However, its protoconch is unknown and the teleoconch morphology is not particularly typical for mathildids, so that family and generic assignment are not beyond doubt. The radiation of the mathildids started in the Anisian and continued into the Jurassic. Especially the genus *Promathilda* became highly diverse in the Late Triassic. The small architectonicoid planispiral allogastropod *Stuoraxis* was reported from the Changhsingian and reappears in the Carnian Cassian Formation [35]. In this case, the Lazarus phenomenon is probably preservation driven because the small planispiral shell with a heterostrophic larval shell needs exceptional preservation for recognition. Such delicate shells are only preserved under particular circumstances, i.e. the silicification of even the finest shell details as found in the Latest Permian gastropod from Yunnan [35,37] and the exquisite original shell preservation of the Late Trias-

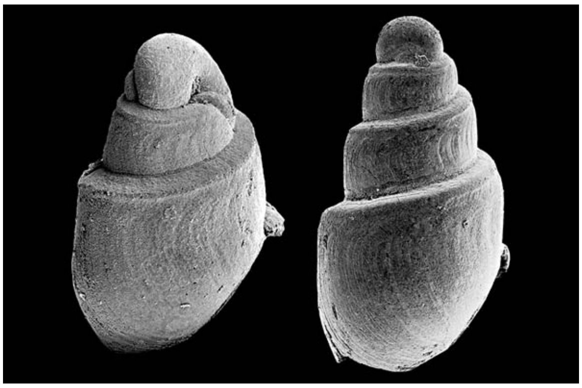

Fig. 10. *Cylindrobullina convexa*, the earliest certain opisthobranch as part of gastropod turnover in the aftermath of the end-Permian mass extinction event. Sinbad Limesteone (Moenkopi Formation); the excellently preserved material shows the sinistral, heterostrophic larval shell which was produced by a planktotrophic veliger larva; very similar species are known from the Carnian Cassian Formation and various Jurassic formations.

Fig. 10. *Cylindrobullina convexa*, le plus ancien opisthobranche avéré, une composante du renouvellement des gastéropodes au lendemain des extinctions en masse de la fin du Permien. « Sinbad Limestone » (formation Moenkopi) ; l'excellent état de conservation des échantillons montre la coquille larvaire hétérotrophique à enroulement sénestre, issue d'une larve véligère planctonique ; des espèces proches sont connues du Carnien de la formation Cassian et de diverses formations du Jurassique.

sic Cassian Formation. Such good preservation is largely unknown from the Early and Middle Triassic and thus it is unlikely that small genera like *Stuoraxis* are reported. Eventually, even reduced population sizes contributed to the discontinuous fossil record of *Stuoraxis*. Generally, small population sizes ('below detection limit') were hypothesized to contribute to the Lazarus phenomenon [54] (see below).

The genus *Cylindrobullina* as well as the family Cylindrobullinidae has its first certain occurrence in the Olenekian Moenkopi Formation, in which *Cylindrobullina convexa* is one of the most abundant gastropods (Fig. 10). This genus remains diverse and abundant during the Middle Triassic to Jurassic and produces very similar species throughout so that the group is almost morphostatic. *Cylindrobullina* is probably a member of the stem-line of the modern Opisthobranchia. However, the Palaeozoic precursors of *Cylindrobullina* still have to be identified. As mentioned, the Griesbachian genus *Jiangxispira* could link the cylindrobullinids to the Allogastropoda. The Palaeozoic genus *Acteonina* has a similar teleoconch morphology and was interpreted to represent Opisthobranchia. However, this genus is not heterostrophic and therefore not a shelled opisthobranch (e.g., [34]).

In conclusion, the Heterostropha cross the P/T-boundary with several genera. They contributed considerably to the recovery process through the origination and surprisingly early radiation of the opisthobranchs (cylindrobullinids) and even the later origination of the mathildids that radiate in the Middle and Late Triassic.

7. Discussion and conclusions

There is an active discussion about the term 'recovery' (see for a review: [13,14,45]). A sigmoidal increase of the number of taxa to a new equilibrium after the extinction has been suggested in various models. Accordingly, an exponential increase of taxa (rebound with high origination rates) characterizes the post-extinction interval and recovery is accomplished when origination rates drop. This view of recovery does not necessarily consider the absolute number of taxa before and after an extinction event, but refers to a stable equilibrium between originations and extinctions. The number of reported gastropod taxa is very low in the Early Triassic. There is no well-preserved Induan gastropod fauna, so that most taxonomic assignments of gastropods from this period are questionable or tentative, which is also reflected by an extensive use of open nomenclature for gastropods from this period. However, there is a considerable number of first occurrences in the Olenekian (notably several caenogastropod families and the opisthobranchs). Thus, the rebound of gastropods starts as early as Olenekian, as is indicated by the first occurrence of several taxa. Therefore, from a taxonomic or systematic point of view, the term 'recovery' is somewhat misleading, because it would suggest that Permian taxa regain their pre-extinction diversity. Below the family or superfamily level, this seems not to be the case and in these groups 'replacement' would be the more appropriate term. The main source of information about Olenekian gastropods is the Moenkopi Formation. The stable and relatively high number of marine gastropod taxa throughout lithostratigraphic units of the Anisian/Ladinian Muschelkalk Basin (Fig. 5) suggests that equilibrium was reached. Moreover, diverse Anisian faunas from China are much more diverse than any Early Triassic fauna. The number of reported species and genera continues to rise until the Carnian when Triassic diversity peeks (Fig. 1).

The Lazarus phenomenon is rather pronounced in Early Triassic gastropods and may exceed 30–50% of the genera [12,14]. It is unsure to what portion this phenomenon is caused by questionable or outdated generic assignments that are mainly due to the generally poor preservation. The contribution of preservation bias to the Lazarus phenomenon has been questioned because there is no correlation with the number of fossiliferous strata [54]. However, the number of such strata alone is not the only potential source of bias and preservation variations may also play a role [17]. The abundance of Lazarus taxa in the aftermath has also been interpreted as a reflection of the extreme rarity of organisms at this time [54]. Accordingly, such small populations were caused by a productivity decline [48]. Generally, there is still a need for a more sufficient quantification of the mentioned factors which potentially contribute to this phenomenon.

An important aspect of the Triassic recovery is the long lag phase in the aftermath of the extinction (e.g., [21]). Three possibilities were discussed to explain this phenomenon [17]: prevailing unfavourable conditions, preservation bias or the destruction of complex ecosystems was so complete that forming new ecosystems took a lot of time. There is no evidence that diverse and complex faunas as well as true metazoan reefs were present in Early Triassic [19,44]. Obviously, the main reef building organisms were hard hit by the extinction event. Reefs start to recover in the Anisian, but metazoan reefs are formed by other organisms than in the Palaeozoic and there are no undoubted Lazarus taxa among reef builders [44]. Therefore, it seems that the reefs did not recover but were reinvented and this probably took a considerable amount of time. An atmospheric oxygen drop was discussed as cause for the reef collapse [52]. It is possible that these or other unfavourable conditions were prolonged and suppressed metazoan reef formation for an extended time. However, the replacement of the main reef builders almost certainly delayed reef recovery. Today, the highest number of gastropod species are found in tropical shallow water and especially in or near reefs (e.g., [9]). Therefore, it is reasonable to assume that the worldwide species diversity of the gastropods is constrained to a high degree by the presence and frequency of reefs. This would explain the low diversity in the Early Triassic and the long duration of the recovery phase. The breakdown of the reef ecosystem results in a dramatic reduction of possible ecological niches, which causes or maintains a sharp decrease in the species richness of the gastropods. On the other hand, the diversity of the Anisian gastropod fauna from the German/Polish Muschelkalk Basin (which contains only a few, small reefs) exceeds that of the Werfen and Moenkopi Formation by far although the depositional environment and facies are similar to that of the Werfen and Moenkopi formations. This indicates that the absence of reefs was certainly not the only reason for the low diversity of Early Triassic gastropods. However, it would not be plausible to assume that the lack of reefs as speciation and diversity hotspots had no limiting impact on the global diversity. Another possible constraint for the duration of the recovery is the magnitude of the loss of species and thus genetic information during the mass extinction event. The lower the number of species was, the more speciation events and time were needed to accomplish recovery. A recent model suggests that there is a correlation between the magnitude of extinction and the pace of recovery, mainly if a certain percentage of primary producers is removed (become extinct) [45].

It is unknown how long unfavourable conditions prevailed after the extinction and what the nature of those conditions specifically was although oxygen minimum conditions are in discussion (e.g., [21,55]). Strong fluctuations of stable carbon isotopes during the Early Triassic indicate a profoundly disturbed carbon cycle during the aftermath of the end-Permian extinction which was related to the delayed recovery [39]. The richest Griesbachian gastropod fauna is from Oman (with just about ten taxa) and comes from a well oxygenated environment which is an exception for the Earliest Triassic [49,53]. The richest Olenekian gastropod faunas are from formations (Moenkopi and Upper Werfen) with environments which are devoid of black shales or other obvious signs of oxygen deficiency. These Early Triassic faunas are still by far less diverse than Late Permian or Late Triassic faunas but oxygen deficiency was seemingly not the limiting factor.

The impact of the Permian/Triassic mass extinction event on the evolution of the Gastropoda was considerable. If an Early Carboniferous gastropod fauna was found in the Late Permian, it probably would not stand out very much. There would be some bellerophontids, several pleurotomariids, euomphalids, pseudozygopleurids etc. However, if the Olenekian fauna from the Sinbad Limestone would be found in the Permian, it would appear very strange: the abundance of true heterostrophic opisthobranchs, the dominance of small neritaemorphs, presence of several Mesozoic caenogastropod genera as well as the absence of most of the mentioned Palaeozoic groups would make this fauna very unusual for the Permian, although some Palaeozoic holdovers are present too. This thought experiment shows that the end-Permian mass extinction and the subsequent recovery period caused major shifts within the Gastropoda.

Acknowledgements

I would like to thank Roger L. Batten (Phoenix, Arizona) for help during fieldwork (Sinbad Limestone, Moenkopi Formation), stimulating discussions and for reviewing the manuscript; an anonymous reviewer spend a lot of time and greatly improved the manuscript; Douglas H. Erwin (Washington, D.C.) for sharing data with me in a joint project; Chris Schulbert (Erlangen) for his great help during a collecting trip to the Sinbad Limestone; Margaret Fraiser (Los Angeles) for giving locality information to us; Barbara Seuß (Erlangen) for making the thin sections; Hartmut Schultz for his kind help in the palaeontological collection in Tübingen; the Deutsche Forschungsgemeinschaft is acknowledged for financial support (research grant NU 96/6–1).

References

[1] K. Bandel, Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden?, Mitt. Geol.- Pal. Inst. Univ. Hamburg 67 (1988) 1–33.

[2] K. Bandel, J. Frýda, The systematic position of the Euomphalidae, Senckenbergiana Lethaea 78 (1998) 103–131.

[3] R.L. Batten, The vicissitudes of the gastropods during the interval of the Guadalupian–Ladinian time, A. Logan, A. Hills (Eds.), The Permian and Triassic systems and their mutual boundaries, Calgary, Canada, Can. Soc. Pet. Geol. Mem. 2 (1973) 596–607.

[4] R.L. Batten, Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids, Am. Mus. Novitates 2829 (1985) 1–40.

[5] R.L. Batten, W.L. Stokes, Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah, Am. Mus. Novitates 2864 (1986) 1–33.

[6] R. Bieler, Gastropod phylogeny and systematics, Annu. Rev. Ecol. Syst. 23 (1992) 311–338.

[7] R.C. Blakey, Stratigraphic Depositional analysis of the Moenkopi Formation, Southeastern Utah, Utah Geol. Min. Surv. Bull. 104 (1974) 1–81.

[8] K. Boeckelmann, Die Werfener Schichten in den Karnischen Alpen und westlichen Karawanken (Österreich und Italien), PhD Thesis, Rheinisch-Westfälische Technische Hochschule Aachen, 1988, unpublished.

[9] P. Bouchet, P. Lozouet, P. Maestrati, V. Heros, Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site, Biol. J. Linn. Soc. 75 (2002) 421–436.

[10] D.H. Erwin, Carboniferous–Triassic gastropod diversity patterns and the Permo-Triassic mass extinction, Paleobiology 16 (1990) 187–203.

[11] D.H. Erwin, The great Paleozoic crisis: life and death in the Permian, Columbia University Press, New York, 1993.

[12] D.H. Erwin, Understanding biotic recoveries: extinction, survival, and preservation during the end-Permian mass extinction, in: D. Jablonski, D.H. Erwin, J.H. Lipps (Eds.), Evolutionary Paleobiology, University of Chicago Press, Chicago, 1996, pp. 398–416.

[13] D.H. Erwin, The end and the beginning: recoveries from mass extinctions, Trends Ecol. Evol. 13 (1998) 344–349.

[14] D.H. Erwin, Lessons from the past: Biotic recoveries from mass extinctions, Proc. Natl Acad. Sci. USA 98 (2001) 5399–5403.

[15] D.H. Erwin, S.A. Bowring, Jin Yugan, End-Permian mass extinctions: a review, Geol. Soc. Am. Spec. Pap. 365 (2002) 363–383.

[16] D.H. Erwin, M.L. Droser, Elvis Taxa, Palaios 8 (1993) 623–624.

[17] D.H. Erwin, Pan Hua-Zhang, Recoveries and radiations: gastropods after the Permo-Triassic mass extinction, M.B. Hart (Ed.), Biotic recovery from mass extinction events, Geol. Soc. Spec. Publ. 102 (1996) 223–229.

[18] D.H. Erwin, P.W. Signor, Extinction in an extinction-resistant clade: the evolutionary history of the Gastropoda, in: E.C. Dudley (Ed.), The Unity of Evolutionary Biology 1, Proc. 4th Int. Congr. System. Evol. Biol, Dioscorides Press, Portland, 1990, pp. 152–160.

[19] E. Flügel, Triassic Reef Patterns, W. Kiessling, E. Flügel, J. Golonka (Eds.), Phanerozoic Reef Patterns, SEPM Spec. Publ. 72 (2002) 391–463.

[20] M.L. Fraiser, D.J. Bottjer, The non-actualistic Early Triassic gastropod fauna: A case study of the Lower Triassic Sinbad Limestone Member, Palaios 19 (2004) 259–275.

[21] A. Hallam, Why was there a delayed radiation after the End-Palaeozoic extinction?, Hist. Biol. 5 (1991) 257–262.

[22] A. Hallam, P.B. Wignall, Mass extinctions and their aftermath, Oxford University Press, 1997 (320 p.).

[23] D. Jablonski, Background and mass extinctions: alternation of macroevolutionary regimes, Science 231 (1986) 129–133.

[24] D. Jablonski, Survival without recovery after mass extinctions, Proc. Natl Acad. Sci. USA 99 (2002) 8139–8144.

[25] B.S. Kues, R.L. Batten, Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico, J. Paleontol. 75 (Suppl. 1) (2001) 1–95.

[26] B. Kummel, C. Teichert, Stratigraphy and Paleontology of the Permian–Triassic boundary beds, Salt Range and Trans-Indus Ranges, West Pakistan, in B. Kummel, C. Teichert, Stratigraphic boundary problems: Permian and Triassic of West Pakistan, Univ. Kansas Dept. Geol. Spec. Publ. 4 (1970) 1–110.

[27] P. Leonardi, Il Trias inferiore delle Venezie, Mem. Istit. Geol. Min. Univ. Padova 11 (1935) 1–136.

[28] A. Nützel, Über die Stammesgeschichte der Ptenoglossa (Gastropoda), Berl. Geowiss. Abh, Reihe E 26 (1998) 1–229.

[29] A. Nützel, An evaluation of the recently proposed Palaeozoic gastropod subclass Euomphalomorpha, Palaeontology 45 (2002) 259–266.

[30] A. Nützel, A new gastropod genus from the Early Triassic Werfen Formation and the recovery of gastropods from the Permian/Triassic extinction, Acta Palaeontol Pol. 50 (2005) 19–24.

[31] A. Nützel, K. Bandel, Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda), N. Jahrb. Geol. Paläontol Abh. 9 (2000) 557–569.

[32] A. Nützel, D.H. Erwin, *Battenizyga*, a new Early Triassic gastropod genus with a discussion on the gastropod evolution at the Permian/Triassic boundary, Paläontol. Z. 76 (2002) 21–26.

[33] A. Nützel, D.H. Erwin, Late Triassic (Late Norian) gastropods from the Wallowa terrane (Idaho, USA), Paläontol. Z 78 (2004) 361–416.

[34] A. Nützel, D.H. Erwin, R.H. Mapes, Identity and phylogeny of the Late Paleozoic Subulitoidea (Gastropoda), J. Paleontol. 74 (2000) 575–598.

[35] A. Nützel, P. Hua-Zhang, D.H. Erwin, New taxa and some taxonomic changes of a Latest Permian gastropod fauna from South China, Documenta Naturae 145 (2002) 1–10.

[36] P. Hua-Zhang, D.H. Erwin, Gastropod diversity pattern in South China during the Chihsian–Ladinian and their mass extinction, Palaeoworld 4 (1994) 249–262.

[37] P. Hua-Zhang, D.H. Erwin, Gastropods from the Permian of Guanxi and Yunnan Provinces, South China, Paleontol. Soc. Mem. 56, J. Paleontol. 76 (Suppl. 1) (2002) 1–49.

[38] P. Hua-Zhang, D.H. Erwin, A. Nützel, Z. Xiang-Shui, *Jiangxispira*, a new Gastropod genus from the Early Triassic of China with Remarks on the phylogeny of the Heterostropha at the Permian/Triassic Boundary, J. Paleontol. 77 (2003) 44–49.

[39] J.L. Payne, D.J. Lehrmann, J. Wie, M.J. Orchard, D.P. Schrag, A.H. Knoll, Large perturbations of the carbon cycle during recovery from the end-Permian mass extinction, Science 305 (2004) 506–509.

[40] W.F. Ponder, D.R. Lindberg, Towards a phylogeny of gastropod molluscs: an analysis using morphological characters, Zool. J. Linn. Soc. 119 (1997) 83–265.

[41] M. Schmidt, Die Lebewelt unserer Trias, Nachtrag, Hohenlohe´sche Buchhandlung, Ferdinand Rau, 1938.

[42] J.K. Schubert, D.J. Bottjer, Early Triassic stromatolites as post-mass extinction disaster forms, Geology 20 (1992) 883–886.

[43] J.K. Schubert, D.J. Bottjer, Aftermath of the Permian–Triassic mass extinction event: Paleoecology of Lower Triassic carbonates in the western USA, Palaeogeogr. Palaeoclimatol. Palaeoecol. 116 (1995) 1–39.

[44] B. Senowbari-Daryan, R. Zühlke, T. Bechstädt, E. Flügel, Anisian (Middle Triassic) buildups of the northern Dolomites (Italy): the recovery of reef communities after the Permian/Triassic crisis, Facies 28 (1993) 181–256.

[45] R.V. Solé, J.M. Montoya, D.H. Erwin, Recovery after mass extinction: evolutionary assembly in large-scale biosphere dynamics, Phil. Trans. R. Soc. Lond. B Biol. Sci. 357 (2002) 697–707.

[46] F. Stiller, Fossilvergesellschaftungen, Paläoökologie und paläosynökologische Entwicklung im oberen Anisium (Mittlere Trias) von Qingyan, insbesondere Bangtoupo, Provinz Guizhou, Südwestchina, Münstersche Forsch. Geol Paläontol. 92 (2001) 1–523.

[47] J. Tong, D.H. Erwin, Triassic Gastropods of the Southern Quinling Mountains, China, Smithson. Contrib. Paleobiol. 92 (2001) 1–47.

[48] R.J. Twitchett, Incompleteness of the Permian–Triassic fossil record: a consequence of productivity decline?, Geol. J. 36 (2001) 341–353.

[49] R.J. Twitchett, L. Krystyn, A. Baud, J.R. Wheeley, S. Richoz, Rapid marine recovery after the end-Permian mass extinction event in the absence of marine anoxia, Geology 32 (2004) 805–808.

[50] G.J. Vermeij, The Mesozoic marine revolution: evidence from snails, predators and grazers, Paleobiology 3 (1977) 245–258.

[51] H.-J. Wang, Y.H. Xi, Fossil gastropods from the Late Permian to Early Triassic in West Guizhou Province, in: Nanjing Inst. Geol. Palaeontol, in: Academia Sinica (Ed.), Late Permian coal-bearing strata, fauna and flora of West Guizhan Province and East Yunnan Province, Science Press, Beijing, 1980, pp. 195–232.

[52] O. Weidlich, W. Kiessling, E. Flügel, Permian–Triassic boundary interval as a model for forcing marine ecosystem collapse by long-term atmosheric oxygen drop, Geology 31 (2003) 961–964.

[53] J. Wheeley, R.J. Twitchett, Palaeoecological significance of a new Early Triassic gastropod assemblage from Oman, Lethaia (accepted).

[54] P.B. Wignall, J.M. Benton, Lazarus taxa and fossil abundance at times of biotic crisis, J. Geol. Soc. Lond. 156 (1999) 453–456.

[55] P.B. Wignall, R.J. Twitchett, in: Lazarus Extent, duration and nature of the Permian-Triassic superanoxic event. Geol. Soc. Amer. Spec. Pap., 2002, pp. 395–423.

[56] P.V. Wittenburg, Beiträge zur Kenntnis der Werfener Schichten Südtirols, Geol. Palaeontol. Abh. 8 (1908) 251–289.

[57] Y. Hong-Fu, E.L. Yochelson, Middle Triassic Gastropoda from Qingyan, Guizhou Province, China: 1 – Pleurotomariacea and Murchisoniacea, J. Paleontol. 57 (1983) 162–187.

[58] Y. Hong-Fu, E.L. Yochelson, Middle Triassic Gastropoda from Qingyan, Guizhou Province, China: 2 – Trochacea and Neritacea, J. Paleontol. 57 (1983) 515–538.

[59] Y. Hong-Fu, E.L. Yochelson, Middle Triassic Gastropoda from Qingyan, Guizhou Province, China: 3 – Euomphalacea and Loxonematacea, J. Paleontol. 57 (1983) 1098–1127.

[60] E.L. Yochelson, H.A. Kollmann, Are there any Triassic Bellerophontacea in Central Europe?, Verh. Geol. B.-A. 2 (1978) 117–128.

[61] E.L. Yochelson, Y. Hong-Fu, Redescription of *Bellerophon asiaticus* Wirth (Early Triassic: Gastropoda) from China, and a survey of Triassic Bellerophontacea, J. Paleontol. 59 (1985) 1305–1319.

[62] E.K. Yoo, Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia, Rec. Austr. Mus. 46 (1994) 63–110.