A new Early Triassic gastropod genus and the recovery of gastropods from the Permian/Triassic extinction

ALEXANDER NÜTZEL

Nützel, A. 2005. A new Early Triassic gastropod genus and the recovery of gastropods from the Permian/Triassic extinction. *Acta Palaeontologica Polonica* 50 (1): 19–24.

The common Early Triassic (Olenekian) gastropod *Turbo rectecostatus* from the upper Werfen Formation of the Alps is placed in the new genus *Werfenella*. Elimination of the wrong or outdated generic assignments of Late Palaeozoic and Early Mesozoic gastropods to archetypical genera such as *Turbo*, *Trochus*, or *Natica* (all with Recent type species) represents an important step toward understanding the evolutionary history of the gastropods across the Permian/Triassic mass-extinction event. The first appearance of *Werfenella* in the Olenekian, as well as the origination of other groups of gastropods, suggests an early turnover in the aftermath of the end-Permian mass extinction event. The relatively large size of *Werfenella* (up to 35 mm) sheds doubt on assertions that all Early Triassic gastropods are microgastropods (Lilliput effect). The new genus is placed in the caenogastropod family Purpurinidae and represents its earliest occurrence. However, a placement of *Werfenella* in the Archaeogastropoda (Vetigastropoda) is also possible because it resembles the paraturbinid genus *Chartronella*. The characteristic *Werfenella rectecostata–Natiria costata* gastropod association from the Werfen Formation is not found in the approximately contemporaneous Sinbad Limestone of the Moenkopi Formation (Utah, USA) nor elsewhere outside Europe. This suggests that the similarities between Olenekian gastropod faunas from the Tethys and western North America are more limited than previously thought.

Key words: Gastropoda, Purpurinidae, Permian/Triassic mass extinction, Olenekian, Werfen Formation, Alps.

Alexander Nützel [nuetzel@pal.uni-erlangen.de], Universität Erlangen, Institut für Paläontologie, Loewenichstr. 28, D-91054 Erlangen, Germany.

Introduction

The widespread, abundant Early Triassic (Olenekian) gastropod "*Turbo" rectecostatus* from the Werfen Formation of the Alps is most probably not a representative of the genus *Turbo*. Its assignment to the modern genus *Turbo* has been questioned previously (Neri and Posenato 1985: 91). Wrong or outdated generic assignments hinder the interpretation of the evolutionary history of fossil groups, especially across mass extinction events. A considerable number of Triassic gastropod species have been placed in genera with modern (Cenozoic/Recent) type species (Table 1). Many of these species were proposed in the 19th century and their generic assignment has not changed since then. In the first half and in the middle of the 19th century, only a limited number of gastropod genera was available and most of these genera were based on modern forms. The most important of these so-called archetypical genera are *Patella*, *Trochus*, *Turbo*, *Neritopsis*, *Natica*, and *Turritella*. These genera represent basic shell shapes of the Gastropoda. Hundred twenty five Triassic gastropod species have been assigned to these genera (Table 1). There are approximately 380 genera which hold nominate Triassic species and about 30 of these genera have a modern type species. These 30 modern genera contain about 190 nominate Triassic species. This means that about 8% of Triassic gastropod species are attributed to modern genera. In most, if not in all, cases these generic assignments are incorrect and therefore do not reflect unusually long ranges. The reasons why questionable generic assignments have not been changed in more than one hundred years are basically threefold: (1) Lack of modern taxonomic work and a large number of fossil taxa relative to the number of professional taxonomists; (2) bad preservation or (3) too few primary shell characters. Generally, it is well known that the taxonomy of many Triassic gastropods is out of date as is reflected by the fact that such early occurrences of modern genera are not accepted in major compilations (e.g., Knight et al. 1960; Hickman and McLean 1990). Alleged Triassic members of modern genera are ignored in Sepkoski's (2002) database (with the exception of *Neritopsis*) as is indicated by the stratigraphic ranges of the genera given in that compilation (Table 1). While it is possible to exclude such problematic generic assignments in the compilation of genus ranges, the only adequate long-term solution is to find more appropriate generic assignments for such species. It is particularly important not to eliminate information in the study of diversity patterns through critical intervals of evolutionary history such as the Permian–Triassic transition. For instance, "*Turbo*" *rectecostatus* is one of the most abundant, most cited, and most characteristic gastropod species from the Early Triassic. Its exclusion from diversity studies eliminates crucial information about Early Triassic gastropod faunas and therefore the systematic placement of this species is evaluated and changed here.

Table 1. Modern archetypical genera, their stratigraphic ranges according to Sepkoski (2002) and the number of Triassic species that are still assigned to these genera; these assignments are outdated in most, if not in all, cases.

Archetypical genera	Nominate Triassic species	Range according Sepkoski (2002)	Age of type species
Neritopsis Grateloup, 1832	31	Ladinian–Recent	Miocene
Turritella Lamarck, 1799	23	Aptian–Recent	Recent
Patella Linnaeus, 1758	21	Albian–Recent	Recent
Turbo Linnaeus, 1758	19	Oligocene–Recent	Recent
Natica Scopoli, 1777	17	Thanetian–Recent	Recent
Trochus Linnaeus, 1758	14	Miocene–Recent	Recent

Institutional abbreviations.—Abbreviations of the collections in which the illustrated material is housed: NHMW, Naturhistorisches Museum, Wien; BMNH, Museum of Natural History, London; MHI, Muschelkalk Museum Hagdorn, Ingelfingen, Germany.

Systematic palaeontology

Subclass Caenogastropoda Cox, 1959

Family Purpurinidae Zittel, 1895

The new genus *Werfenella* is placed in the caenogastropod family Purpurinidae because it resembles typical purpurinid genera such as *Purpurina* and *Angularia*. However, *Werfenella* is also similar to members of the archaeogastropod (vetigastropod) family Paraturbinidae and a close phylogenetic relationship seems to be possible (although it is less likely) as will be discussed below. According to Tracey et al. (1993), the Purpurinidae range from the Ladinian to the Late Cretaceous with *Angularia* Koken, 1892 as its oldest genus. The placement of *Werfenella* in the Purpurinidae pushes the origination of this important Mesozoic family back to the Olenekian.

Genus *Werfenella* nov.

Type species: *Turbo rectecostatus* Hauer, 1851

Derivation of the name: After the Early Triassic Werfen Formation.

Diagnosis.—Turbiniform, relatively low-spired purpurinid gastropods with angular, step-like whorl profile, gently sloping subsutural ramp; ornament of axial ribs and nodes where ribs and angulations intersect; aperture wide, oblique subrectangular to oval.

Discussion.—*Werfenella* is a characteristic gastropod genus with an angulated whorl profile and a rather strong ornament of axial ribs and nodes where ribs and angulations intersect. Its type species *Turbo rectecostatus* was placed in the modern genus *Turbo* Linnaeus, 1758 by Hauer (1851) and the systematic position of this species has not been changed subsequently. However, according to Hickman and McLean (1990) and Knight et al. (1960), the genus *Turbo* appears first in the Late Cretaceous while Sepkoski (2002) noted an Early Tertiary origin. The modern type species of the genus *Turbo*, *Turbo petholatus* Montfort, 1810, is almost smooth to strongly ornamented but has no prominent angulations. The modern subgenus *Turbo* (*Callopoma*) has an angulation but is lacks the numerous pronounced axial ribs that are typical of *Werfenella*.

The Jurassic genus *Purpurina* d'Orbigny, 1850 and the Triassic purpurinid genus *Angularia* Koken, 1892 resemble *Werfenella* but are generally more high-spired and have only one angulation. In contrast to *Werfenella*, *Purpurina* has a cancellate ornament and *Angularia* lacks a nodular ornament. However, a close phylogenetic relationship between *Werfenella* and these purpurinids seems to be likely as is suggested by the shell shape and by the elongate aperture with an anterior outlet in *Werfenella*.

Even the vetigastropod genus *Chartronella* Cossmann, 1902 resembles *Werfenella* in shape and in the angular whorl profile but *Chartronella* lacks a prominent axial ornament and is generally more low-spired. Moreover, the aperture of *Chartronella* is almost circular (Fig. $1I_2$) while that of *Werfenella* is more elongate. The overall similarity of the type species of *Chartronella* (*Ch. diagonata* Cossmann, 1902 from Hettangian, France, reproduced herein after Gründel's 1997; Fig. 1I) suggests a possible phylogenetic relationship to *Werfenella* while the aperture does not suggest such a relationship. *Chartronella* was placed in the Family Paraturbinidae, which ranges form the Triassic to the Cretaceous (Knight et al. 1960). Two *Chartronella* species described by Batten and Stokes (1986) from the Olenekian Sinbad limestone (Moenkopi Formation, Utah) resemble *Werfenella rectecostata* in some respects: *Chartronella*? *pagina* (Fig. 1G) and *Chartronella unicostata* (Fig. 1H). *Chartronella*? *pagina* Batten and Stokes, 1986 resembles *Werfenella* in shell shape and in having carinations. Like *Werfenella*, *Chartronella*? *pagina* has axial ribs. However, the ribs are weaker, almost thread-like, and intersections with carinae are not nodular. *Chartronella*? *pagina* is known from a single specimen and was only tentatively assigned to *Chartronella* by Batten and Stokes (1986). The genus *Guidonia* Stefani, 1880 is similar to *Werfenella* but this genus lacks a prominent axial ornament.

In conclusion, *Werfenella* resembles genera of the caenogastropod family Purpurinidae and the archaeogastropod

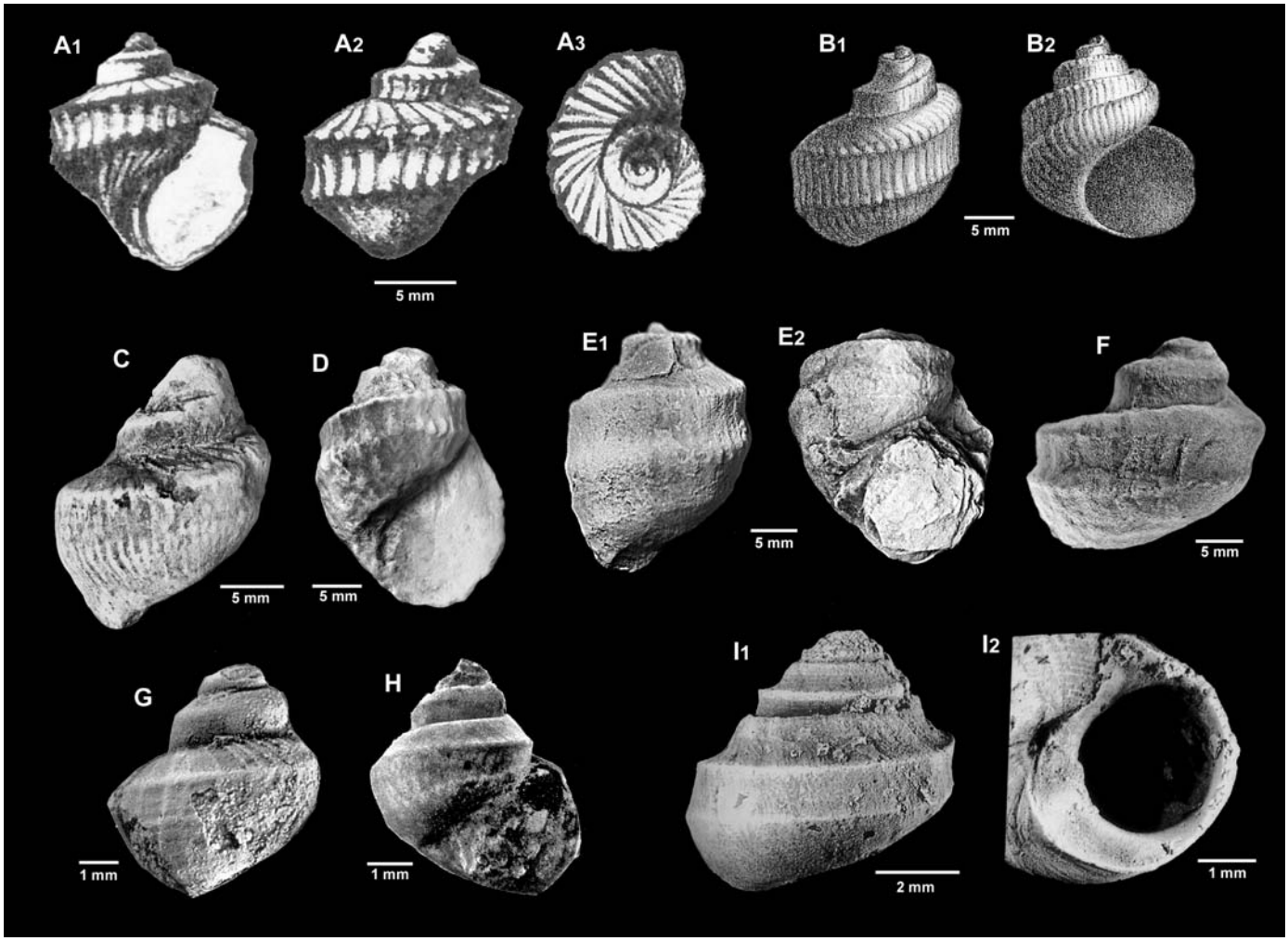

Fig. 1. **A–F**. *Werfenella rectecostata* from the Early Triassic (Olenekian) Werfen Formation. **A**. Reproduction of Frech's (1912: pl. 7: 7a–c) illustrations of exceptionally well-preserved specimens of *Werfenella rectecostata* from the *Tirolites*-Marls near Csopak (Iszkahegy, Hungary). **B**. Reproduction of Hauer's (1851: pl. 20: 10) original illustrations of "*Turbo" rectecostatus*. **C–F**. *Werfenella rectecostata* in typical preservation as more or less deformed steinkerns. Despite poor preservation species identity is strongly suggested by the characteristic shape and traces of the axial ornament. **C**. NHMW 1865 IX 22, Heilig Kreuz near St. Cassian, Südtirol. **D**. NHMW 1858 IX 3A, Heilig Kreuz near St. Cassian, Südtirol. **E**. NHMW 1884 D 475, Pitzberg, Südtirol. **F**. BMNH G 9059314A, Fachiade Monzoni. **G**. *Chartronella*? *pagina* Batten and Stokes, 1986, from Batten and Stokes (1986: fig. 10); this species from the Olenekian of Utah resembles *Werfenella rectecostata*. **H**. *Chartronella unicostata* Batten and Stokes, 1986, from Batten and Stokes (1986: fig. 8). **I**. *Chartronella diagonata* Cossmann, 1902, topotype material of the type species of *Chartronella* from the lowermost Jurassic (Hettangian) of France (from Gründel 1997: pl. 2: 1, 2).

family Paraturbinidae. Therefore, the subclass assignment of *Werfenella* is not beyond doubt and can only be resolved with certainty if the protoconch of *Werfenella* is reported. However, given the relatively bad preservation of gastropods in the Werfen Formation, I do not expect that this protoconch will be reported in the near future. The shell shape and the aperture make it more likely that *Werfenella* is a purpurinid caenogastropod.

Werfenella rectecostata (Hauer, 1851)

Figs. 1A–F, 2–4.

Turbo rectecostatus sp. nov; Hauer 1851: 117, pl. 20: 10.
Turbo rectecostatus Hauer; Wittenburg 1908: 284, pl. 5: 15.
Turbo gronensis sp. nov; Wittenburg 1908: 285, pl. 5: 17.
Turbo rectecostatus Hauer; Frech 1912: 42, pl. 7: 6, 7.
Turbo rectecostatus Hauer; Ogilvie-Gordon 1927: 31, pl. 3: 37a–c.
Turbo rectecostatus Hauer; Leonardi 1935: 84, pl. 5: 16.
Turbo rectecostatus Hauer; Haas 1953: 87.
Turbo rectecostatus Hauer; Zapfe 1958: 156, 159.
Turbo rectecostatus Hauer; Broglio Loriga, Masetti, D. and Neri 1983: 540, 545, pl. 49.
"*Turbo" rectecostatus* Hauer; Neri and Prosenato 1985: 91, table 1, pl. 3: 7, 8.
"*Turbo" rectecostatus* Hauer; Broglio Loriga, Neri and Posenato 1988: 127, 128, pl. 9: 19.
Turbo rectecostatus Hauer; Boeckelmann 1988: 80, table 8.
See Diener (1926) and Kutassy (1940) for more synonymy.

Description.—Shell turbiniform, middle sized, up to 35 mm high; slightly higher than wide (a specimen of 26 mm height is 20 mm wide); whorls rapidly increasing, with two pronounced carinations; whorls between upper and lower cari-

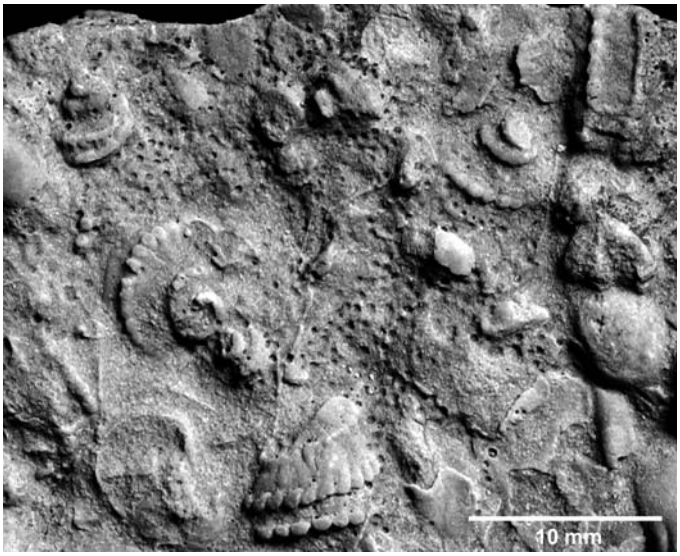

Fig. 2. Limestone slab with several specimens of *Werfenella rectecostata*; Werfen Formation, Cencenighe Member, Bad Radein/Redgano, Italian Dolomites, Weißhorn (MHI 1819). The specimens show unusually well-preserved shells with a pronounced nodular ornament at the carinations which cannot be seen in the steinkern-preservation which is usual for gastropods from the Werfen Formation.

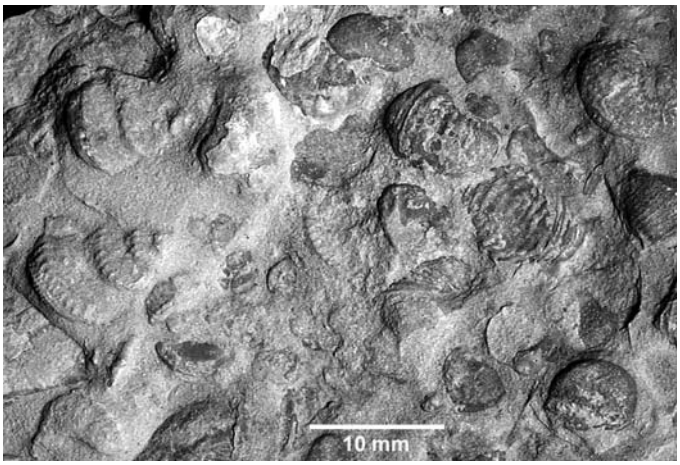

Fig. 3. Limestone slab with specimens of *Werfenella rectecostata* and *Natiria costata* forming a characteristic gastropod assemblage in the Werfen Formation; Werfen Formation, Cencenighe Member, Bad Radein/Redgano, Italian Dolomite, Weißhorn (MHI 1820).

nation concave to almost straight, parallel to whorl axis; whorls with broad subsutural slope ending at upper carination; third spiral rib on base in mature whorls; slope gentle to almost perpendicular to shell axis; whorls ornamented with numerous (up to 30 per whorl) straight axial ribs; nodules at intersection of ribs and carinae; inner lip concave, reflexed, forming moderate pseudoumbilicus; aperture wide, oblique subrectangular to oval, possibly with anterior outlet.

Discussion.—*Werfenella rectecostata* is one of the most abundant gastropods of the Early Triassic Werfen Formation (Alps) where it seems to be restricted to its upper members (Val Badia and Cenenighe Members). Its occurrence is almost identical with the outcrop area of the upper Werfen Formation (Zapfe 1958). It has been reported from the Bükk and Bakony Mountains (Hungary), East Alps (Austria), South Alps (Italy), North Alps (Austria, Germany), and Western Serbia (e.g., Diener 1926; Kutassy 1940). *Werfenella rectecostata* forms a characteristic gastropod assemblage with the neritaemorph *Natiria costata* (Münster, 1841). Both species are relatively large when compared to other Early Triassic gastropods (Nützel and Erwin 2002; Fraiser and Bottjer 2004). Generally, the gastropods from the Werfen Formation are badly preserved. *Werfenella rectecostata* is normally present as deformed steinkerns (Fig. 1C–F). Despite this poor preservation, *Werfenella rectecostata* is relatively easy to recognize because of its size, characteristic shape, and its angulate whorl profile. Commonly even steinkerns show remains of the costae. Frech (1912) illustrated unusually well-preserved specimens from the Werfen Formation of Hungary (here reproduced in Fig. 1A). This material is not or only slightly deformed and shows the axial and nodular ornament in detail. Here, we illustrate specimens on the bedding planes of two limestone slabs (MHI 1819, 1820) from the Werfen Formation (Cencenighe Member) from Bad Radein/Redagno (Dolomites, Weißhorn) (Figs. 2, 3). This material also shows details of the strong nodular ornamentation that is not visible or only indistinct in the normal steinkern-preservation of this species (Fig. 1C–F). Undeformed steinkerns not only show remains of the teleoconch costae and the elongated shape of the aperture but also the purpurinid shape as can be seen in the specimen illustrated by Neri and Posenato (1985) and Broglio-Loriga et al. (1988), which is also redrawn here (Fig. 4).

Implications for the recovery of gastropods from the end-Permian mass extinction event

Elimination of outdated assignments of late Palaeozoic and early Mesozoic gastropods to archetypical genera such as *Turbo*, *Trochus*, or *Natica* is not an end in itself but rather helps to correct databases for diversity studies. It also represents an important step toward understanding the evolutionary history of the Gastropoda across the Permian/Triassic mass extinction event. Taxonomic and systematic corrections are especially important if they concern dominant faunal elements such as *Werfenella rectecostata*. According to the current state of knowledge, the genus *Werfenella* appears first in (and is restricted to) the Olenekian. *Werfenella rectecostata* probably represents the earliest member of the important Mesozoic family Purpurinidae. The assignment of *Werfenella* to this family is rather likely, although an assignment to the vetigastropods seems to be possible and knowledge of the protoconch morphology is needed to cor-

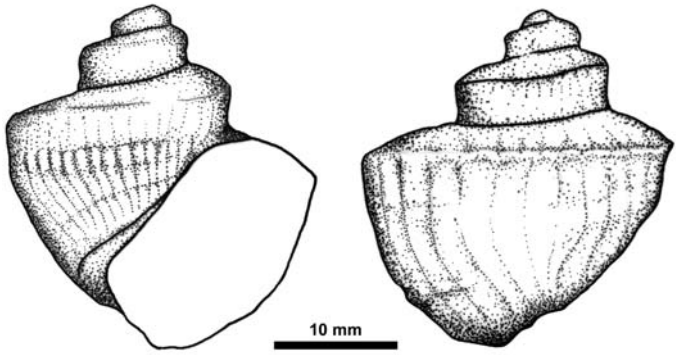

Fig. 4. *Werfenella rectecostata* redrawn from Neri and Posenato (1985: pl. 3: 7, 8). This relatively large and undeformed steinkern (composite mould from Val Sorda, western Dolomites, Italy) shows the purpurinid shape of *Werfenella* and its obliquely elongated, subrectangular aperture. The axial ornament is visible while the nodular ornament at the carinations is obscured.

roborate the placement within the Purpurinidae. Several other caenogastropod genera appear first in the Early Triassic (Nützel and Erwin 2002). The relatively high proportion of genera that first appear in the late Early Triassic (Olenekian) suggests an early and pronounced radiation within the Caenogastropoda in the aftermath of the end-Permian mass extinction event. Similarly, Erwin (1990: fig. 3) found that in the Olenekian, gastropod originations slightly exceeded extinctions, resulting in a relatively modest rise in diversity (see also Erwin and Pan 1996). However, within the caenogastropods, this radiation was more pronounced and origination rates were much higher. Even data from South China indicate that Mesozoic gastropod genera have outnumbered Palaeozoic holdovers since the Spathian (Pan and Erwin 1994). Therefore, the replacement of Palaeozoic genera in the Early Triassic was rather complete and probably more pronounced than in other gastropod clades.

Acknowledgements

I thank Hans Hagdorn (Muschelkalkmuseum Ingelfingen) for the loan of specimens, Roger L. Batten (Phoenix) and Joachim Gründel (Berlin) for letting me reproduce some illustrations, and Mrs Rachel Rau (Hamburg) for drawing the Fig. 4. I am grateful to Jonathan L. Payne (Cambridge, Massachusetts) and Robert B. Blodgett (Anchorage, Alaska) for their helpful reviews. I acknowledge research grants from the Deutsche Forschungsgemeinschaft, Grant NU 96/3-1, NU 96/6-1.

References

Batten, R.L. and Stokes, W.L. 1986. Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *American Museum Novitates* 2864: 1–33.

Boeckelmann, K. 1988. *Die Werfener Schichten in den Karnischen Alpen und westlichen Karawanken (Österreich und Italien)*. 213 pp. Unpublished Ph.D. thesis, Rheinisch-Westfälische Hochschule Aachen.

Broglio Loriga, C., Masetti, D., and Neri, C. 1983. La Formazione di Werfen (Scitico) delle Dolomiti occidentali: Sedimentologia e Biostragrafia. *Rivista Italiana di Paleontologia* 88: 501–598.

Broglio Loriga , C., Neri, C., and Posenato, R. 1988. The Werfen Formation (Lower Triassic) in the Costabella Mt., Uomo Section. *In*: Italian IGCP 203 group members (eds.), *Field Conference on Permian and Permian–Triassic Boundary in the South-Alpine Segment of the Western Tethys; Excursion Guidebook*, 116–133.

Cossmann, M. 1902. Rectification de nomenclature. *Revue critique de la nomenclature* 6: 223.

Cox, L.R. 1959. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33: 239–261.

Diener, C. 1926. *Fossilium Catalogus, I Animalia, 34, Glossophora triadica*. 242 pp. W. Junk, Berlin.

Erwin, D.H. 1990. Carboniferous–Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. *Palebiology* 16: 187–203.

Erwin, D.H. and Pan, H.-Z. 1996. Recoveries and radiations: gastropods after the Permo-Triassic mass extinction. *In*: M.B. Hart (ed.), Biotic recovery from Mass extinction events. *Geological Society of America Special Publication* 102: 223–229.

Fraiser, M. and Bottjer, D.J. 1999. Microgastropods as opportunists during the biotic recovery from the end-Permian mass extinction. *Geological Society of America Annual Meeting Abstract* 2989. Denver.

Frech, F. 1912. Die Leitfossilien der Werfener Schichten und Nachträge zur Fauna des Muschelkalkes der Cassianer und Raibler Schichten. *Resultate der wissenschaftlichen Erforschung des Balatonsees* 2 (Anhang): 1–96. Wien.

Grateloup, J.P.S. De 1832. Description d'un genre nouveau de coquilles appelé Néritopside. *Actes de la Société linnéene de Bordeaux* 5: 125–131.

Gründel, J. 1997. Zur Kenntnis einiger Gastropoden-Gattungen aus dem französischen Jura und allgemeine Bemerkungen zur Gastropodenfauna aus dem Dogger Mittel- und Westeuropas. *Berliner geowissenschaftliche Abhandlungen E* 25: 69–129.

Haas, O. 1953. Mesozoic invertebrate faunas of Peru. *Bulletin of the American Museum of Natural History* 101: 1–328.

Hauer, F. v. 1851. Ueber die vom Herrn Bergrath W. Fuchs in den Venetianer Alpen gesammelten Fossilien. *Denkschriften der Kaiserlichen Akademie der Wissenschaften; Mathematisch-Naturwissenschaftliche Classe* 2: 109–126.

Hickman, C. and McLean, J.S. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Science Series, Natural History Museum of Los Angeles County* 35: 1–169.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L., and Robertson, R. 1960. Systematic descriptions. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Part I, *Mollusca 1*, I169–I310. Geological Society of America and University of Kansas Press, Lawrence.

Koken, E. 1892. Ueber die Gastropoden der rothen Schlernschichten nebst Bemerkungen über Verbreitung und Herkunft einiger triassischer Gattungen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 2: 25–36.

Kutassy, A. 1940. *Fossilium Catalogus, I Animalia, 81, Glossophora triadica*, 243–477. W. Junk, Berlin.

Lamarck, J.B.P.E. de Monet de 1799. Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. *Mémoires de la Societé Histoire naturelle, Paris* 1: 63–91.

Leonardi, P. 1935. Il Trias inferiore delle Venezie. *Memoirie degli Istituti de Geologia e Mineralogia dell' Università di Padova* 11: 1–136.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.

Montfort, D. de 1810. *Conchyliologie Systématique. Vol. 2: Conchyliologie systématique, et classification méthodique de coquilles*. 676 pp. Paris, Schoell.

Münster, G. von 1841. Beschreibung und Abbildung der in den Kalk-

mergelschichten von St. Cassian gefundenen Versteinerungen. *In*: G. v. Münster (ed.), *Beiträge zur Geognosie und Petrefacten-Kunde des Südöstlichen Tirol's vorzüglich der Schichten von St. Cassian*, Heft 4, 1–152. Buchner, Bayreuth.

Neri, C. and Posenato, F. 1985. New biostratigraphical data on uppermost Werfen Formation of western Dolomites (Trento, Italy). *Geologisch-Paläontologische Mitteilungen Innsbruck* 14: 83–107.

Nützel, A. and Erwin, D.H. 2002. *Battenizyga*, a new Early Triassic gastropod genus with a discussion on the gastropod evolution at the Permian/Triassic boundary. *Paläontologische Zeitschrift* 76: 21–26.

Ogilvie-Gordon, M. 1927. Das Grödener-Fassa und Enneberggebiet in den Südtiroler Dolomiten. *Jahrbuch der Geologischen Bundesanstalt* 24: 1–379.

Orbigny, A. d' 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés, I et II*. 427 pp. Masson, Paris.

Pan H.-Z. and Erwin, D.H. 1994. Gastropod diversity patterns in South China during the Chihsia-Ladinian and their mass extinction. *In*: Jin Yugan, J. Utting, and B.R. Wardlaw (eds.), Permian stratigraphy, environments and resources, 1 Paleontology and stratigraphy. *Palaeoworld* 4: 249–262.

Scopoli, J.A. 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium, hactenus detecta, characteristibus essentialibus donate, in tribus divisa, subinde ad leges naturae, VIII*. 506 pp. W. Gerle, Prague.

Sepkoski, J.J., Jr. 2002. A compendium of fossil marine animal genera (posthumous, edited by D. Jablonski and M. Foote). *Bulletins of American Paleontology* 363: 1–563.

Stefani, C., de. 1880. I fossili triasici nelle Alpi Apuane. Rendic R. Ist. *Lombardo Science e Lettre, series 2*, 13: 493–497.

Tracey, S., Todd, J.A., and Erwin, D.H. 1993. Mollusca: Gastropoda. *In*: M.J. Benton (ed.), *The Fossil Record 2 (Chapter 8)*, 131–167, Chapman and Hall, London.

Wittenburg, P. v. 1908. Beiträge zur Kenntnis der Werfener Schichten Südtirols. *Geologische und Palaeontologische Abhandlungen* 8: 251–289.

Zapfe, H. 1958. Die Fauna der Werfener Schichten vom Ulrichsberg bei Klagenfurt in Kärnten. *Verhandlungen der Geologischen Bundesanstalt* 2: 155–164.

Zittel, K.A. 1895. *Grundzüge der Palaeozoologie*. 971 pp. Oldenbourg, München.