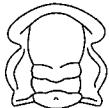


Shell microstructure of a Triassic patellogastropod limpet

CLAUS HEDEGAARD, DAVID R. LINDBERG AND KLAUS BANDEL

LETHAIA



Hedegaard, C., Lindberg, D.R. & Bandel, K. 1997 12 15: Shell microstructure of a Triassic patellogastropod limpet. *Lethaia*, Vol. 30, pp. 331–335. Oslo. ISSN 0024-1164.

The St. Cassian formation of northern Italy contains an unsurpassed diversity of Triassic organisms, often with original or only slightly recrystallized shells. The shell microstructure of *Patella costulata* Münster, 1869, is examined and compared with the shell microstructures of 14 extant gastropod limpet taxa. The distribution of shell structure characters supports the assignment of *P. costulata* to the patellogastropod taxon Patellidae. St. Cassian facies also include near-shore environments that are consistent with the habitat of extant *Patella* species. The corroboration of *Patella costulata* as a member of the Patellogastropoda reduces the hiatus between estimated origination and the previous unequivocal first occurrence by a minimum of 116 Ma. □*Patellogastropoda, shell structure, Triassic, ghost lineage*.

Claus Hedegaard [chedegaard@gia.org], Institute of Biology, University of Aarhus, Aarhus, Denmark; David R. Lindberg [davidl@ucmp1.berkeley.edu], Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California 94720-4780, USA; Klaus Bandel, Geologisch-Paläontologisches Institut der Universität, Bundesstraße 55, D-2000 Hamburg 13, Germany; 19th June, 1996; revised 31st October, 1997.

Limpet morphology in the Gastropoda is infamously homoplastic and has independently evolved among numerous gastropod taxa (e.g., Patellogastropoda, Coccinulidae, Phenacolepadidae, Hipponicacea, Siphonariidae) (Ponder & Lindberg 1997). Limpet morphologies are also widely distributed throughout the fossil record – the Monoplacophora of the earliest Cambrian (Yu 1979) to the giant *Anisomyon* limpets of the Cretaceous (Kanie 1975). While anatomy provides an independent means by which to allocate living limpets to respective taxa, allocating fossil limpets is problematic.

The Patellogastropoda are hypothesized to be the sister taxon of all other gastropods and one of the earliest branches of gastropod evolution (Golikov & Starobogatov 1975; Lindberg 1988; Haszprunar 1988; Ponder & Lindberg 1996, 1997). They are widely distributed in Phanerozoic sediments, but their limpet morphology imparts few clues and landmarks to distinguish them from limpet forms of crown groups. When available, muscle scars and associated impressions can be used to diagnose taxa (Lindberg & Squires 1990), but even these traces of soft anatomy become tentative in deeper time as comparisons with living taxa fail (e.g., Yochelson 1988). If the fossil limpet shells are not recrystallized, shell microstructures – the microscopic arrangement of calcium car-

bonate and organic material of the shell – are diagnostic in the Patellogastropoda and can be used to allocate individual fossils within this clade (MacClintock 1967; Lindberg 1988; Hedegaard 1990; Lindberg & Squires 1990; Kase 1994; Kase & Shigeta 1996).

The St. Cassian formation, which outcrops around Cortina d'Ampezzo in the Dolomites of northern Italy, contains an unsurpassed diversity of Triassic organisms. Zardini (1978) described over 300 species of molluscs as well as impressive numbers of echinoderms, bryozoa and other taxa. The fossils occur in clay and marl beds in a dolomitic limestone (Fürsich & Wendt 1976), which allows for the preservation of fossils with original or only slightly recrystallized aragonitic tests (Bandel 1988, 1991). The excellent preservation of skeletal material from this formation produces a more complete sample of this Triassic fauna and provides additional characters, such as shell structures, for the taxa present. Two putative patellogastropods have been reported from this fauna – *Patella costulata* Münster, 1844, and *Patella crateriformis* Broili, 1907. Here we report the results of a scanning electron microscopy study of the shell microstructures of *Patella costulata* to establish if this species is a patellogastropod limpet, and demonstrate it as the earliest member of this clade yet reported.

Material and methods

We examined the shell structures of 11 specimens of *Patella costulata* (Fig. 1A) from Campo, Cortina d'Ampezzo, Italy (Geol.-Paläont. Institut. Univ., Hamburg, Germany). The shell microstructures of 14 extant limpet taxa were also examined and tabulated for comparison with the St. Cassian specimens (Table 1). Fractured shells were examined using an Electroscan Environmental Scanning Electron Microscope (ESEM) at the University of California Museum of Paleontology, Berkeley (UCMP). We used fractured sections rather than cut and polished thin sections, because we believe that fractured sections produce more reproducible results. Patellogastropod shells tend to break along contours parallel to first-order elements of the shell microstructures, and we find this characteristic much easier to control than the angle at which a specimen is cut and polished. Moreover, if we were not successful in fracturing the specimen in the desired plane, or natural breaks were neither transverse or radial relative to the shell aperture, the orientation relative to growth lines (plane of deposition) is readily apparent and serves as an index from which to orient the microstructures. Fractured sections are also less prone to

artifacts associated with cutting, etching, and polishing, and leave more specimen unaltered and available for future research. This latter consideration is especially important when dealing with fossils. For descriptions of structures and orientation of fractures we follow the terminology of Carter & Clark (1985) with modifications and additions of Hedegaard (1990) and Lindberg & Hedegaard (1996).

Results

The specimens are relatively small, rarely exceeding 4 mm in length. The original outer shell structures, which are composed of calcite, are well preserved, but the inner aragonitic shell structures are largely recrystallized. The outermost layer has a calcitic com marginal crossed-lamellar structure (crossed-foliated of MacClintock 1967). This layer is followed by a thin layer of calcitic prisms, a thick recrystallized layer with possible remains of an aragonitic com marginal crossed-lamellar layer, a myostracal layer, and another recrystallized shell layer immediately below the myostracum (Figs. 1B, C).

Aragonitic and calcitic crossed-lamellar structures may be identified by their mode of deposition. Calcitic crossed-lamellar structures are deposited on a plane parallel to the first-order lamellae, i.e. the first-order lamellae are parallel to the inside of the shell (Fig. 1B). In contrast, aragonitic crossed-lamellar structures are deposited on a plane perpendicular to the first-order lamellae, i.e. the first-order lamellae are perpendicular to the inside of the shell (Fig. 1D). This difference provides criteria by which to distinguish between these two structures and reduces the problems associated with determining whether a calcitic crossed-lamellar layer is a diagenetic outcome of the alteration of aragonite to calcite. In the case of the St. Cassian specimens, the deposition is parallel to the first-order lamellae, and therefore we identify the structure as originally calcitic.

Table 1 summarizes the shell structures of *Patella costulata* and extant limpet-shaped gastropods, excluding some of the deep-sea and hot-vent forms (e.g., Hirtopeltidae). *Patella costulata* possesses a calcitic com marginal crossed-lamellar structure that is restricted in living gastropods to the Patellogastropoda clades. Within the Patellogastropoda this shell microstructure is found in the extant taxa *Scutellastra* and *Patella* (Patellidae), and *Celiana* (Nacellidae). There are no other structures diagnostic of any of the other limpet groups, such as the prismatic complex crossed-lamellar ones of Acmaeidae and Lottiidae, or the regularly foliated ones of some Nacellidae, Acmaeidae, Patellidae and Lepetidae, or the shell composed of purely aragonitic structures as it is in the Cocculinidae, Fissurellidae, Lepetellidae, Pseudococculinidae, and Siphonariidae.

Table 1. Shell microstructure sequence of *P. costulata* compared with summary data for extant limpets. Entries in parentheses indicate structures, which may be absent in some species; * = shell microstructure equivalents. Myostraca (Myo) are not necessarily homologous shell structures but serve as landmarks for alignment. Data from Boggild (1930), MacClintock (1967), Hedegaard (1990, unpublished).

Taxon	Exterior		Interior			
<i>P. costulata</i>	?	CComCL	ACL	Myo	ACL	
Acmaeidae	CHom	PrCCL	Fol	ACL	Myo	ACL
Cocculinidae		AHom		ACL	Myo	ACL
Emarginula				ACL	Myo	ACL
Lepetellidae				ACL	Myo	ACL
Lepetidae	(CHom)		Fol	ACL	Myo	ACL
Lottiidae	(CHom)	PrCCL		ACL	Myo	ACL
<i>Cellana</i> *	(CHom)		CComCL or Fol		Myo	ACL
<i>Helcion</i>	CHom		Fol	ACL	Myo	ACL
<i>Patella</i> *			CComCL or Fol	ACL	Myo	ACL
<i>Scutellastra</i> *	(CHom)		CComCL or Fol	ACL	Myo	ACL
Phenacolepadidae	CHom			ACL	Myo	ACL
Pseudococculinidae	AHom			ICP	Myo	ICP
Siphonariidae			ACL	ACL	Myo	ACL

AHom = aragonitic homogeneous

CHom = calcitic homogeneous

ACL = aragonitic crossed lamellar (com marginal or radial)

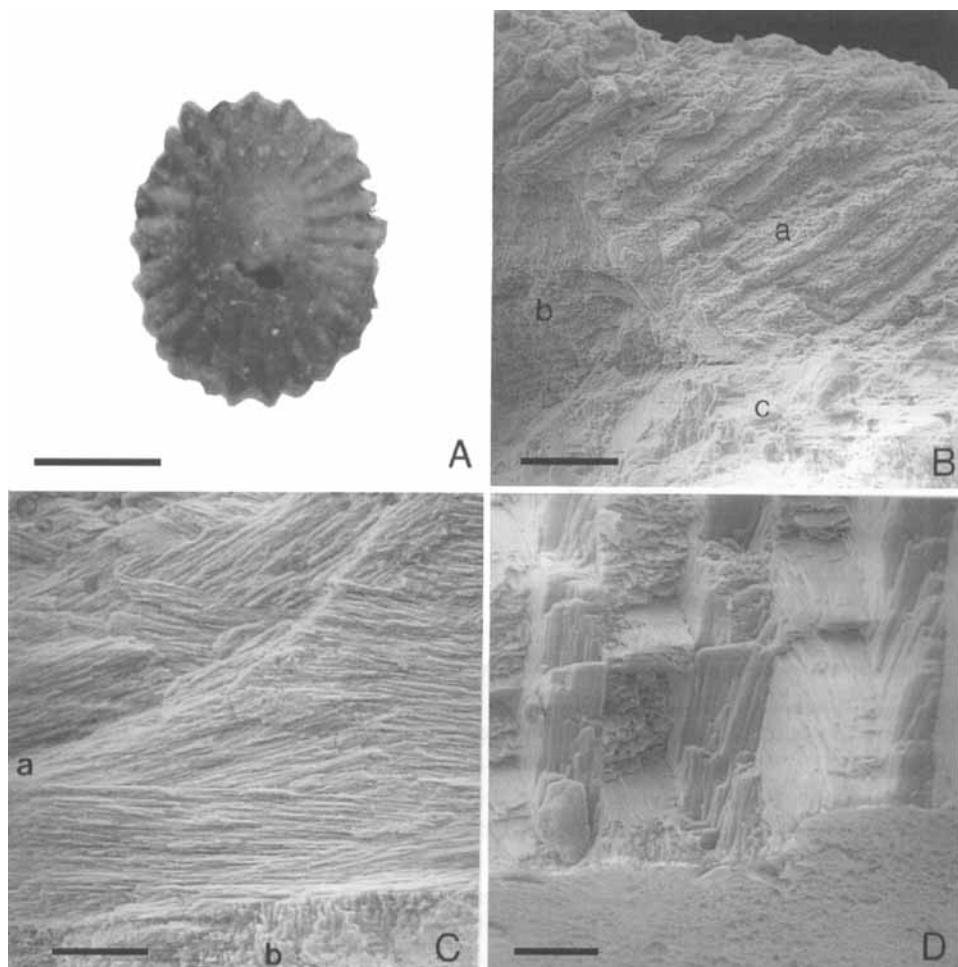
Fol = regularly foliated

CComCL = calcitic com marginal crossed lamellar

ICP = intersected crossed platy

PrCCL = prismatic complex crossed lamellar.

Fig. 1. □A. *Patella costulata* Münster, 1844, from Campo, Cortina d'Ampezzo, Italy (Paleo. Mus., Univ. of Hamburg, Germany). Scale bar 1.0 mm. □B. Radial section of *Patella costulata* taken close to the shell margin and showing outer com marginal calcitic crossed-lamellar layer (a), followed by the recrystallized remains of aragonitic layers (b). At the top of the recrystallized layer are possible remains of an aragonitic com marginal crossed-lamellar layer (c). Scale bar 40 µm. □C. Com marginal section of *Patella costulata* showing the outer com marginal calcitic crossed-lamellar layer (a), followed by the thin calcitic simple prismatic layer (b), and recrystallized remains of an aragonitic layer (c). Scale bar 20 µm. □D. Aragonitic com marginal crossed-lamellar structure of *Nerita polita* Linneaus, 1758, showing first-order lamellae oriented perpendicular to the interior surface. Scale bar 10 µm.



Scutellastra and *Patella* species are typically heavily sculptured, whereas *Cellana* are relatively smooth-shelled species. Given these character distributions, we consider *P. costulata* to be a member of the Patellidae. In addition, some of the St. Cassian facies represent a near-shore environment in the Triassic (Fürsich & Wendt 1976), a habitat consistent with the lifestyle of extant patellid species (intertidal to shallow subtidal on rocks).

Shell size of previously reported specimens of *P. costulata* has also been minute. Kittl (1891), in his treatment of the gastropods of St. Cassian, illustrated specimens approximately 5 mm long, and Zardini (1978) illustrated specimens of 7.5 mm and 4 mm in shell length. Zardini also suggested that these small limpets represented only the apices of much larger specimens and estimated the overall length of a complete specimen at about 5 cm. Most of the specimens examined by us are not partial specimens. In most cases, the ribs extend beyond the shell aperture, producing a crenulate shell margin (Fig. 1). When patellogastropod shells decollate, the apex separates from the lower portion of the shell at the myostracum, producing smooth margins regardless of the exte-

rior ribbing pattern (cf. Chapin 1968). In addition, muscle scars are visible on several of our specimens, indicating the entirety of the shell. Whether these specimens represent juveniles or full-sized specimens is not known. The smallest Recent patellid species – *Scutellastra chapmani* – reaches a maximum size of 30 mm in length (Powell 1973), while the median size of described living taxa is about 55 mm in length (24–225 mm; data from Powell 1973).

Discussion

Shell microstructure characters are the only unequivocal way to identify fossil patellogastropods, an approach greatly facilitated by patellogastropods having abundant calcitic shell structures that are more often preserved than aragonitic layers. Patellogastropoda also have more variable shell structures than any other similarly sized clade of gastropods, and their structures are distinct from all other extant limpets (MacClintock 1967; Lindberg 1988; Hedegaard 1990). Thus, these characters allow us to identify

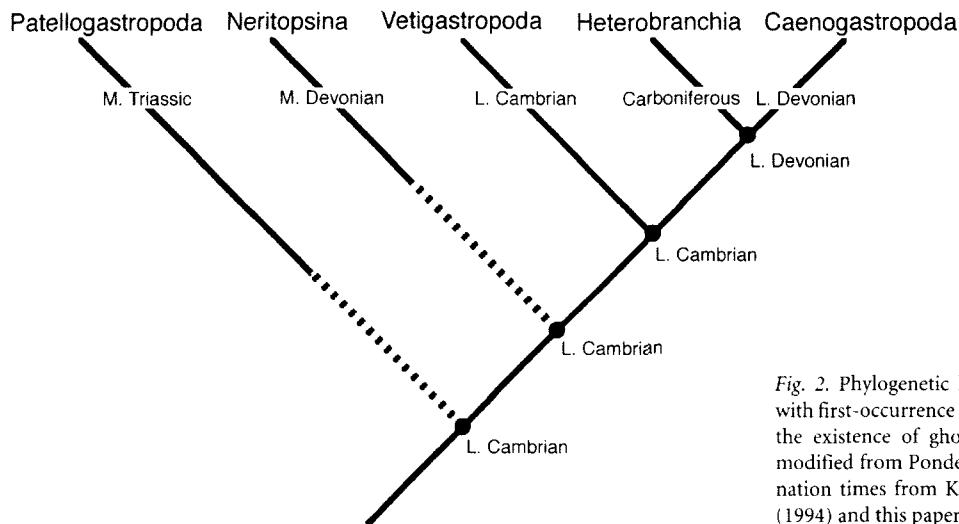


Fig. 2. Phylogenetic hypothesis of gastropod relationships with first-occurrence data overlain. The dashed lines indicate the existence of ghost lineages (Norell 1992). Phylogeny modified from Ponder & Lindberg (1997). Minimum origination times from Knight *et al.* (1960), Signor (1985), Yu (1994) and this paper.

fossil patellogastropods, not by taxonomic default because they are marine limpets, but as a taxon diagnosed by apomorphy. Moreover, these undisputed occurrences can be used to estimate fossil distributions, establish the minimum age of the clade, and ultimately, in conjunction with a phylogenetic hypothesis, estimate the minimum age of divergence of major subclades within the group.

MacClintock (1967) was the first to use shell microstructure to recognize patellogastropod limpets in the fossil record, identifying patellid and lottiid species from the Eocene of the Paris Basin. Lindberg & Hickman (1985) used shell microstructures to identify New World Eocene occurrences of *Cellana*, and, more recently, Kase (1994) and Kase & Shigeta (1996) used shell microstructures to recognize patellid limpets from the Miocene–Pliocene of Japan and the Cretaceous of Japan and Russia, a taxon absent from the Recent northwest Pacific Ocean. These and other studies depict a Tertiary distribution of patellogastropods that bears little resemblance to Recent distributions nor is indicated by present ranges (Lindberg & Hickman 1985; Lindberg 1988). However, comparable resolution and insights in the Paleozoic and Mesozoic have been few. With few exceptions (Lindberg 1988; Kase & Shigeta 1996), the remaining identifications of patellogastropod taxa in Paleozoic and Mesozoic rocks have been based on overt shell morphology and occasional muscle scars (e.g., McLean 1990; Yochelson 1988).

The Patellogastropoda are consistently the sister taxon of all other gastropods in phylogenies based both on morphology (Ponder & Lindberg 1996, 1997) and molecules (28s mRNA) (Tillier *et al.* 1992). And given minimum origination times for these sister taxa, the origin of the Patellogastropoda would be in the Cambrian (Fig. 2). The confirmation of *Patella costulata* as a member of the Patellogastropoda reduces the hiatus between estimated origination and the previous unequivocal first occurrence

(Albian, Cretaceous of England; Lindberg 1988) by a minimum of 116 Ma. We are confident that future investigations of shell microstructures will further reduce the hiatus. Moreover, these studies should not be limited just to fossil limpets, but should also include spirally coiled taxa in order to discover the sister taxon of the Patellogastropoda (Lindberg 1988; Ponder & Lindberg 1997).

Conclusions

Shell microstructure characters unequivocally identify *Patella costulata* as a member of the clade Patellogastropoda, and based on these characters we have assigned it to the taxon Patellidae. This assignment extends the record of the Patellogastropoda from the Cretaceous to the Triassic. However, a fossil record hiatus of over 300 Ma remains between this record and the estimated first occurrence of the common ancestor of the patellogastropods and all other gastropods. The postulated occurrence of this ghost lineage (Norell 1992) necessitates a re-examination of Paleozoic gastropods for patellogastropod taxa – both limpet-like and coiled.

Acknowledgements.—We thank J. Taylor and an anonymous reviewer for constructive criticism and comments and D. Reid for pointing out pertinent literature.

References

- Bandel, K. 1988: Schlitzbandschnecken mit perlmuttiger Schale in den triassischen St. Cassian-Schichten der Dolomiten. *Annalen des Naturhistorischen Museums in Wien, Serie A, Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie*, 92, 1–53.

Bandel, K. 1991: Trochomorpha (Archaeogastropoda) aus den St. Cassian-Schichten (Dolomiten, Mittlere Trias). *Annalen des Naturhistorischen Museums in Wien, Serie A, Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie*, 93, 1–10.

- ischen Museums in Wien, Serie A, Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie, 95, 1–99.
- Bøggild, O.B. 1930: The shell structure of the mollusks. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelige og Mathematische Afdeling*, 9. Række, II, 2, 231–325.
- Broili, F. 1907: Die Fauna der Pacycardientuffe der Seiser Alp. Scaphopoden und Gastropoden. *Palaeontographica* 54, 69–138.
- Carter, J.G. & Clark, G.R. II. 1985: Classification and phylogenetic significance of Molluscan shell Microstructure. In Broadhead, T.W. (ed.): *Mollusks, Notes for a Short Course*, 50–71. University of Tennessee, Department of Geological Sciences, Studies in Geology 13.
- Chapin, D. 1968: Some observations of predation on *Acmaea* species by the crab *Pachygrapsus crassipes*. *Veliger* 11 (Supplement), 67–68.
- Fürsich, F.T. & Wendt, J. 1976: Projektbereich B, Fossil-Lagerstätten, 4b, Faziesanalyse und paläogeographische Rekonstruktion des Ablagerungsräumes der Cassianer Schichten (Mittel- bis Obertrias, Langobard-Cordevol, Südalpen). *Zentralblatt für Geologie und Paläontologie, Teil II*, 196 (5–6), 233–238.
- Golikov, A.N. & Starobogatov, Y.I. 1975: Systematics of prosobranch gastropods. *Malacologia* 15, 185–232.
- Haszprunar, G. 1988: On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies* 54, 367–441.
- [Hedegaard, C. 1990: Shell structures of the recent Archaeogastropoda. Vol. 1, 154 pp. Vol. 2, 78 Pls. Unpublished Cand. Scient. Thesis, University of Aarhus.]
- Kanie, Y. 1975: Some Cretaceous patelliform gastropods from the North Pacific region. *Science Report of the Yokosuka City Museum* 21, 1–44.
- Kase, T. 1994: New species of *Patella* (Gastropoda: Mollusca) from the Miocene and Pliocene of Japan: A clade extinct from the Pacific. *Bulletin of the National Science Museum, Tokyo, series C*, 20:2, 53–65.
- Kase, T. & Shigeta, Y. 1996: New species of Patellogastropoda (Mollusca) from the Cretaceous of Hokkaido, Japan and Sakhalin, Russia. *Journal of Paleontology* 70, 762–771.
- Kittl, E. 1891: Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. *Annalen des K.K. Naturhistorischen Hofmuseums* 6, 166–262.
- Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. 1960: Systematic descriptions. In Moore, R.C. (ed.): *Treatise on Invertebrate Paleontology. Pt. I. Mollusca I*, I169–I331. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- Lindberg, D.R. 1988: The Patellogastropoda, *Malacological Review, Supplement* 4, 35–63.
- Lindberg, D.R. & Hedegaard, C. 1996: A deep water patellogastropod from Oligocene water-logged wood of Washington State, USA (Acmaeoidea: Pectinodonta). *Journal of Molluscan Studies* 62, 299–314.
- Lindberg, D.R. & Hickman, C.S. 1985: A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). *Journal of Paleontology* 60, 661–668.
- Lindberg, D.R. & Squires, R. 1990: Patellogastropods (Mollusca) from the Eocene Tejon Formation of southern California. *Journal of Paleontology* 64, 578–587.
- MacClintock, C. 1967: The shell structure of patelloid and bellerophontoid gastropods (Mollusca). *Peabody Museum of Natural History, Yale University, Bulletin* 22, 1–140.
- McLean, J.H. 1990: Neolepetopsidea, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. *Journal of Zoology, London* 222, 485–528.
- Münster, G.v. 1844: In Goldfuss, G.A.: *Petrefacta Germania tam ea, quae in Museo Universitatis regiae borussicæ Fridericiae Wilhelmae rhenaæ servantur quam alia quaecunque in Museis Hoenninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata. Abbildungen und Beschreibungen der petrefakten Deutschlands und der angränzenden Ländern, unter Mitwirkung des Herrn Grafen Georg zu Münster, herausgegeben von August Goldfuss. III:8*. Arnz, Dusseldorf.
- Norell, M.A. 1992: Taxic origin and temporal diversity: the effect of phylogeny. In Novacek, M.J. & Wheeler, Q.D. (eds.): *Phylogeny and Extinction*, 89–118. Columbia University Press, New York, N.Y.
- Ponder, W.F. & Lindberg, D.R. 1996: Gastropod phylogeny – Challenges for the 90s. In Taylor, J.D. (ed.): *Origin and Evolutionary Radiation of the Mollusca*, 135–154. Oxford University Press, Oxford.
- Ponder, W.F. & Lindberg, D.R. 1997: Towards a phylogeny of gastropod molluscs – a preliminary analysis using morphological characters. *Journal of the Linnean Society of London* 119, 83–265.
- Powell, A.W.B. 1973: The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca* 3, 75–206.
- Signor, P.W. 1985: Gastropod evolutionary history. In Broadhead, T.W. (ed.): *Mollusks, Notes for a Short Course*, 157–173. University of Tennessee Department of Geological Sciences Studies in Geology 13. 305 pp.
- Tillier, S., Massilot, M., Hervé, P. & Tillier, A. 1992: Phylogénie moléculaire des Gastropoda (Mollusca) fondée sur le séquencenge partiel de l'ARN ribosomique 28 S. *Comptes Rendus Académie des Sciences (Paris, Series 3)*, 314, 79–85.
- Yochelson, E.L. 1988: A new genus of Patellacea (Gastropoda) from the middle Ordovician of Utah: the oldest known example of the superfamily. *New Mexico Bureau of Mines and Mineral Resources, Memoir* 44, 195–200.
- Yu, E.W. 1994: Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. *Records of the Australian Museum* 46, 63–120.
- Yu, W. 1979: Earliest Cambrian monoplacophorans and gastropods from western Hubei with their biostratigraphic significance. *Acta Palaeontologica Sinica* 18, 233–270.
- Zardini, R. 1978: *Fossili Costulata (Trias Medio-Superiore)*. 58 pp. Edizioni Ghedina, Cortina d'Ampezzo.



New alliances for palaeontology

STEFAN BENGTSON

What do artificial life, computer art, and palaeontology have in common? Well, a meeting was recently (August 29th to September 1st, 1997) held at the Banff Centre for the Arts in the Canadian Rocky Mountains to find out. Entitled 'Digital Burgess', it was the brainchild of Bruce Damer of the Digitalspace Corporation, and the idea was to bring

together computer scientists, artists, palaeontologists and biologists around the theme of the Cambrian Explosion as a source of inspiration for interaction.

Why the Cambrian Explosion? This event has aroused great interest also outside palaeontological circles, largely thanks to Gould's (1989)