Early rissoid gastropods from the Jurassic of Italy: the meaning of first appearances

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Conti, M.A., S. Monari & M. Oliverio. Early rissoid gastropods from the Jurassic of Italy: the meaning of first appearances. — Scripta Geol., Spec. Issue 2: 67-74, Leiden, December 1993.

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Key words: palaeobiogeography, evolution, Jurassic, Tethys, Gastropoda.

Studies of Jurassic outcrops from Veneto, Central Italy and Sicily improved our knowledge on the gastropods of these areas, characterised by the presence, aside of archaic forms, of some modern ones. Noteworthy is the record from those outcrops of several species, which can be referred to the family Rissoidae (Rissooidea). Formerly, earliest rissoid records were only known from European outcrops of younger age. In the Italian records several species have been recognised belonging to at least two genera of Rissoidae, namely *Rissocerithium* and *Zebinostoma*.

The presence of such a relatively diversified number of species, bears witness of a well established group. They should have had a common ancestor with the *Rissoina*-like rissoids of the continental margins. Their diversification can be related to the peculiar characters of the Intra-Tethyan communities.

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Introduction

During the last ten years, several studies on Bajocian gastropods from Italian and Hungarian outcrops (Conti & Szabó, 1987, with references) improved the knowledge on some faunas, often neglected, from facies different from those of the carbonate platforms. These results can significantly contribute to the Jurassic palaeobiogeography, and bear important implications on the evolutionary history of the gastropods. These sites are situated within the Mediterranean Province (Neumayr, 1872).

Conti & Szabó (1988), introduced the Intra-Tethyan Unit (I.U.) to characterise a Bajocian faunistic unit, located in the infraoceanic area. Such a unit has characters distinct from coeval ones of the European and African continental margins. Data on the Eastern Tethys for this period are still wanting, thus it is not possible to define the longitudinal dimensions of the I.U.; even its connections to the northern and southern margins of the Tethys are still debatable.

As already highlighted by Conti & Szabó (1988), the presence of archaic forms (Szabó, 1984) and of some modern ones belonging to important caenogastropod groups is of particular interest. The relative isolation (both palaeoecological and palaeobiogeographical) of the Intra-Tethyan faunas, played an important role, especially in a scenario such as that depicted by Taylor et al. (1980): the E-W alignment of the Tethys determined a relative climatic homogeneity, and thus a lower number of Mesozoic provinces compared to the Recent ones.

In this respect, the record from those Toarcian to Lower Bajocian outcrops of several species, referable to the Rissoidae (Rissooidea), attracted our attention. This is a relatively homogeneous group of caenogastropods, recently revised (Ponder, 1985), and whose systematics, at a higher level, are reasonably well assessed. The rissoids' history can be traced back to the Jurassic, when, according to Ponder (1988), they probably originated. They are subdivided into two subfamilies (Rissoinae and Rissoininae), whose branching is supposed to have taken place very early in the family's history. More precisely the Rissoinae seem to be derived from an original stock of ancestral Rissoininae. This subfamily displays several primitive characteristics, and contains the oldest record of the family, thus allowing it to be considered the most primitive.

The fossil record

As summarised in Table 1, ten species belonging to 2 rissoid genera, namely *Rissocerithium* Conti & Fischer, 1981 and *Zebinostoma* Conti & Fischer, 1983 have been sorted out from four Bajocian outcrops in Italian sites. We have excluded from this survey *Trochoturbella*, since the attribution of some species usually included in this genus to the Rissoidae is questionable.

Some five still undescribed entities from Sicily (Rocca Busambra: Wendt, 1971; Szabó et al., 1993), would prove to be different species, but closely allied and belonging to either *Rissocerithium* or *Zebinostoma*. The oldest species from these latter outcrops, come from Toarcian levels.

Table 1. List of the species of Rissoidae from Italian Bajocian outcrops: BM = Bivio Macerino (Conti & Monari, 1986); CC = Case Canepine (Conti & Fischer, 1981, 1984); AF = Acque Fredde (Conti & Fischer, 1983); AFC = between Acque Fredde and Canevini (Conti, 1988).

	UMBRIA		VENETO	
	BM	CC	AF	AFC
Rissocerithium nicosiai Conti & Fischer, 1981	-	*	*	-
Zebinostoma eburnea (Parona, 1894)	-	-	*	*
Zebinostoma nicolisi (Parona, 1894)	*	*	*	*
Zebinostoma aff. *nicolisi* (Parona, 1894)	-	-	*	-
Zebinostoma tardeplicata (Parona, 1894)	-	-	*	*
Zebinostoma turrita (Parona, 1894)	-	*	*	-
Zebinostoma cf. *nicolisi* (Parona, 1894)	*	-	-	-
Zebinostoma sp. 1	*	-	-	-
Zebinostoma sp. 2	-	-	-	*

Both genera are related to the *Rissoina-Zebina* group, on ground of the general shape, the sculpture and the aperture of the shell. The main differences lie in the conspicuous 'beak-like' anterior channel, and in the relatively higher spire of some species (see also Conti & Fischer, 1984, p. 151). Thus they seem closely linked to the subfamily Rissoininae.

According to Ponder (1988) 'the main Rissoid stem may have been established in the warm Tethys Sea by the early Jurassic, rapidly spreading by utilising planktotrophic larvae' (p. 154) and 'the line that gave rise to the Rissoids presumably arose from a barleeid or prebarleeid ancestor in the Tethyan region, before the loss of planktotrophic larvae ..' (p. 152).

The scantiness of their Mesozoic fossil record is probably due in part to their minute size, that makes them either difficult to extract, or even neglected. Moreover, their habitats are certainly unsuitable for good fossil preservation. It can be assumed that, like most of the Recent Rissoininae (Ponder, 1985; Sleurs, pers. comm.; M.O., pers. obs.), these species lived in sheltered sites on firm or hard grounds, feeding on Foraminifera or more generally being deposit feeders.

The oldest records of this family in Europe, are that of *Rissoina parcicostata* Hudleston and *Rissoina obtusa* Lycett from the Inferior Oolite (Bajocian) of England (Hudleston, 1891, 1892). Cossmann (1921) included them in *Buvignieria,* but they seem to be better placed in *Rissoina* s.s. lacking prominent spiral ribs (Ponder, 1985). Numerous species are listed from classical Bathonian outcrops of France and England. In Table 2 the records from the main literature sources (Morris & Lycett, 1853; Lycett, 1863; Hudleston, 1891, 1892; Cossmann, 1921; Cox & Arkell, 1950; Fischer, 1969) and our own observations are summarised; *Thierachella, Calvadosiella* and *Hirsonella* are excluded from this list since their inclusion in the Rissoidae is uncertain (Ponder, 1985).

From the above data it can be concluded, that literature records of rissoids from European sites are all younger than our Toarcian ones: Bajocian records are scanty and isolated, and the flourishing of the group dates from the Bathonian, witnessing for a well-diversified group.

Conversely, in the I.U., the first appearance of the group is in the Toarcian, and the diversification dates from the Bajocian.

Table 2. Earliest rissoid records from European sites (E = England outcrops; F = France outcrops).

	BAJOCIAN	BATHONIAN
Rissoina obtusa Lycett, 1853	E	
Rissoina parcicostata Hudleston, 1891	E	
Rissoina ancliffensis Cox & Arkell, 1950		E F
Rissoina obliquata Sowerby, 1829		E
Rissoina subulata Lycett, 1863		E
? *Rissoina multistriata* Piette, 1855		F
Rissoina (Buvignieria) duplicata (J. de C. Sowerby, 1829)		E F
? *Zebina laevis* (J. de C. Sowerby, 1829)		E
? *Zebina pygmaea* (Morris & Lycett, 1850)		E

The palaeoenvironmental framework

We believe that to reconstruct palaeobiogeographic models it is necessary to understand the factors governing the evolutionary dynamics of faunas and single animal groups. To accomplish at least in part this aim we delineate the Jurassic history that led to the origin of our gastropod faunas.

The Middle Liassic gastropod faunas, particularly in the 'recifal' and 'subrecifal' assemblages (Dubar, 1948), already display a trend to a renewal. Furthermore, the relative modernity of the Liassic faunas of carbonate platforms, is already stressed in the 'Sicilian faunas' of Szabó (1991), compared to his 'Alpine faunas', characterised by a predominancy of archaic forms. Such a trend toward modernity of the carbonate shelf faunas seems to characterise them already in the Triassic, and can be due to their peculiar ecological characterization.

Recently, some Molluscan faunas from the Liassic Ammonitico Rosso facies of the Western Pontides have been studied (Conti & Monari, 1991), showing that in such environments of continental platforms (Altiner et al., 1991), a faunistic renewal can be traced, even at the Early/Middle Lias boundary. Such a renewal can be related to the arising of new environments.

In the region of the Mediterranean Tethys this renewal is closely related to geodynamic events. Particularly in the surveyed areas the Early Jurassic tectonics produced the advent of environments with new characteristics, that progressively evolved in conditions different from those of both the carbonate shelves and the continental platforms. The faunal assemblages were to a certain degree isolated in such areas, due mainly to sea-current patterns and to the environmental peculiarity of these areas (Conti, 1989). They will give origin to the characteristic fauna of the I.U.

The areas studied were mainly Veneto and the Umbro-Marchean Apennines, Italy. The former in the Middle Jurassic was a wide plateau characterised by a reduced sedimentation rate (Sturani, 1971). In these areas peculiar environments were present, with rich Bajocian gastropod faunas (Conti, 1988).

The Umbro-Marchean region was characterised by a number of structural heights separated by relatively deeper sea troughs (Farinacci et al., 1981), resulting in palaeoenvironments easily comparable to those of the Veneto area.

From the analysis of the faunal structures in the I.U. (see Conti & Szabó, 1987, with references), the peculiarity of these communities is evident. On the one side forms like *Trochotomaria* Conti & Fischer, 1981, *Naticopsis (Marmolatella)* Kittl, 1894, crossostomatids-ataphrids, and probably *Discohelix* Dunker, 1848 and *Pentagonodiscus* Wendt, 1968, are among the stocks inherited from the Triassic, and survived flourishing in the infraoceanic areas (Szabó, 1984, 1991; Conti & Szabó, 1988); these are what we regard as archaic forms. On the other hand several groups, allegedly of post-Bajocian origin, proved to be already present in the Middle Jurassic in this area. Among those there are the Rissoidae, and the groups related to genera such as *Maturifusus* and *Canepina*. These groups need a careful restudy in an attempt to define their position, but at first sight they seem to belong to an early neogastropod stock; in that case they would represent a crucial point to clarify the early history of this group. All the latter forms may be derived from Triassic ancestors (K. Bandel, pers. comm.). In any case they could testify to the first flourishing of groups whose main radiation occurred in post-Bajocian times.

Conclusions

The peculiarity of the Bajocian gastropod fauna in the I.U. arises from the contemporaneous presence of archaic forms and modern groups like the Rissoidae. The appearance of this family with at least two genera and several species, bears witness of an already well established group. These records leave two hypotheses to account for the early origin of the Rissoidae:

1) An in situ origin of this group, from older Alpine faunistic stocks: the latter were well-diversified faunas whose relationships with the succeeding ones are still not clearly defined. This hypothesis does not fit with the records from European Bajocian of *Rissoina* s.s. species.

2) A phylogenetic model for the Rissooidea proposed by Ponder (1988), includes a hypothesis of an early origin of the Rissooidea in the Tethys, with the main groups migrating from an eastern continental margin of the Tethys (Ponder, 1988, fig. 5). Some of the main colonization routes proposed by Ponder for the first stocks of rissoid-like gastropods, cross just the area studied herein. It can be postulated that first Rissoidae took their origin in some Eastern site of the Tethys, and later reached the I.U. area where radiation occurred. Alternatively, their very diversification was in the I.U. from a rissoid-like stem. These hypotheses can be tested and assessed only by a comparative analysis between I.U. faunas and nearly contemporaneous records from the eastern Tethys.

Anyway, after an analysis of the faunas of the continental margins, a particular situation of evolutionary dynamism seems to be evident: substitution of archaic faunas by modern forms is both gradual and continuous. This fact seems to be witnessed by the extensive bibliography on the European faunas, as well as by the recent data on the Lias of Turkey (Conti & Monari, 1991). From this material some unidentified barleeid-like gastropods have been isolated. This could be a very important record, but the poor preservation of the material does not allow a reliable identification.

After a more general analysis the faunistic diversity in the I.U. would as a result be lower than that on the continental platforms. This would render the intra-Tethyan ecosystems prone to environmental stresses: disappearance of few forms in a poorly diversified community often set wide ecological spaces free, allowing external colonization.

The I.U. can well have represented, at least for some groups and in some environments, an area with the characteristic suggested by Vermeij: '... Escalation becomes possible when ecological limitations are relaxed, especially in high-energy environments. Conditions favoring escalation include climatic warming (or the latitudinal spread of warm climates), increasing continental areas that are covered by .. productive shallow marine waters ...' (Vermeij, 1987, p. 387). In this area on the one side the archaic forms could survive, and new groups could find new open space.

The *Rissocerithium-Zebinostoma* group is present in its first appearance as well-diversified (at least five species in the Toarcian, and eight to ten species in the Bajocian); admitting an origin on the continental margin, colonization of our area would be dated to at least early Toarcian times, and it can be assumed that radiation occurred early in the I.U. In this respect *Rissocerithium* and *Zebinostoma* should share a common ancestor with the *Rissoina* of the European continental margins, and having diversified independently in this area, play the role of a sister group of the *Rissoina*-like rissoids.

In this framework it is difficult to evaluate the bearing of the generally recognised (Hallam, 1987; Jenkins, 1985) Toarcian crisis on the evolution of our faunas. In fact, in the Apennines the Toarcian is represented by the Rosso Ammonitico facies, a peculiar facies where the gastropods are rare. From the rest of the italian sites the few Toarcian gastropod faunas known are still not well studied. Anyway, Wendt (1971) recorded rich gastropod faunas from the Toarcian of Rocca Busambra: this material, currently still under study (Szabó et al., 1993), could gain particular attention in this respect. The Toarcian crisis could even have produced the conditions and the chances to explore new spaces. But, another, economical interpretation would consider the central Tethys as an area whose communities were vulnerable, and this simply taking into account their own biological characteristics, even without any claim for crisis.

The peculiarity of the intratethyan area is evident, and its importance for several aspects of the higher prosobranchs' evolution should be carefully considered. Some important groups of Caenogastropoda such as Rissoidae and perhaps Neogastropoda, took origin and/or radiated and diversified in this area. In the meantime archaic forms, already strongly declining at the continental margins, were important members of the intratethyan faunas. The reasons of such peculiarities will probably become clear from comparative studies of the intratethyan environments versus the continental margins' ones, giving important answers to some questions on both Jurassic palaeobiogeography and the early history of the higher prosobranchs.

Acknowledgements

We thank Klaus Bandel for the critical revision of the manuscript. We are indebted to the editorial committee of *Scripta Geologica* who greatly improved an earlier version of this paper. Financial support MURST 60% (Conti).

References

Altiner, D., A. Kocyigit, A. Farinacci, U. Nicosia & M.A Conti, 1991. Jurassic-Early Cretaceous stratigraphy and paleogeographic evolution of the southern part of North-Western Anatolia (Turkey). — Geol. Romana, 27: 13-80.

Conti, M.A., 1988. Some Middle Jurassic gastropods from Veneto area (Northern Italy). — Mem. Sc. Geol., 40: 185-193.

Conti, M.A., 1989. Le faune a gasteropodi della regione intratetisiana nel Giurassico medio (Bajociano): caratteristiche e ipotesi sulla loro differenziazione. — Atti Prima Giorn. St. Malac. CISMA, Roma, 1988 (I. Nofroni, ed.): 9-18.

Conti, M.A., & J.C. Fischer, 1981. Preliminary notes on the Aalenian gasteropods of Case Canepine (Umbria, Italy). — Proc. 'Rosso Ammonitico Symposium', Roma 16-21 June 1980 (A. Farinacci & S. Elmi, eds): 137-145.

Conti, M.A., & J.C. Fischer, 1983. Revisione della fauna mesogiurassica di Acque Fredde (Lago di Garda) descritta da Parona, 1894. — Boll. Mus. Civ. St. Nat. Verona, 9, 1982: 489-522.

Conti, M.A., & J.C. Fischer, 1984. La faune à gastropodes du Jurassiques moyen de Case Canepine (Umbria, Italie). Systématique, paléobiogéographie, paléoécologie. — Geol. Romana, 21, 1982: 125-183.

Conti, M.A., & S. Monari, 1986. A Middle Jurassic bivalve and gastropod fauna from Umbria (Central Italy). — Geol. Romana, 23, 1984; 175-209.

Conti, M.A., & S. Monari, 1991. Bivalve and gastropod fauna from the Liassic Ammonitico Rosso facies in the Bilecik Area (Western Pontides, Turkey). — Geol. Romana, 27: 245-301.

Conti, M.A., & J. Szabó, 1987. Comparison of Bajocian gastropod faunas from the Bakony Mts. (Hungary) and Umbria (Italy). — Annls. Hist.-Nat. Mus. Natn. Hung., 79: 43-59.

Conti, M.A., & J. Szabó, 1988. Bajocian gastropod fauna from Intratethian Region. — Proc. 2nd Intern. Symp. Jurassic Strat., Lisboa, 1987: 855-868.

Cossmann, M., 1921. Essais de paléoconchologie comparée, 12. — Cossmann, Paris: 1-349.

Cox, L.R., & W.J. Arkell, 1950. A survey of the mollusca of the British Great Oolite Series, 2. — Mon. Palaeontogr. Soc., 103: xiv-xxvi, 49-105.

Dubar, G., 1948. La faune domeriénne du Djebel Bou-Dahar (près de Beni-Tajjite). — Notes Mém. Serv. Géol. Maroc, 68: 1-248.

Farinacci, A., N. Mariotti, U. Nicosia, G. Pallini & F. Schiavinotto, 1981. Jurassic sediments in the Umbro-Marchean Apennines: an alternative model. — Proc. 'Rosso Ammonitico Symposium', Roma 16-21 June 1980 (A. Farinacci & S. Elmi, eds): 335-398.

Fischer, J.C., 1969. Géologie, paléontologie et paléoécologie du Bathonien au Sud-Ouest de Massif Ardennais. — Mém. Mus. Nat. Hist. Nat., N.S., C, 20: 1-319.

Hallam, A., 1987. Radiations and extinctions in relation to environmental change in the marine Lower Jurassic of northwest Europe. — Paleobiology, 13,2: 152-168.

Hudleston, W.H., 1891-1892. A monograph of the Inferior Oolite Gastropoda, 1(5, 6). — Mon. Palaeontogr. Soc., 45: 225-272 (1891); 46: 273-324 (1892).

Jenkins, H.C., 1985. The Early Toarcian and Cenomanian-Turonian anoxic events in Europe: comparisons and contrasts. — Geol. Rundschau, 74, 3: 505-518.

Lycett, J., 1863. Supplementary monograph on the Mollusca from the Stonesfield Slate, Great Oolite, Forest Marble, and Cornbrash. — Mon. Palaeontogr. Soc.: 1-129.

Morris, J., & J. Lycett, 1853. A monograph of the Mollusca from the Great Oolite, 2. Bivalves. — Mon. Paleontogr. Soc.: 1-80.

Neumayr, M., 1872. Ueber Jura-Provinzen. — Verh. k.k. Geol. Reichanst., 3: 54-57.

Ponder, W.F., 1985. A review of the genera of the Rissoidae (Mollusca, Mesogastropoda, Rissoacea). — Rec. Austr. Mus., Suppl. 4: 1-221.

Ponder, W.F., 1988. The Truncatelloidean (= Rissoacean) radiation - a preliminary phylogeny. In: W.F. Ponder (ed.). Prosobranch phylogeny. — Malac. Rev. Suppl. 4: 129-164.

Sturani, C., 1971. Ammonites and stratigraphy of the 'Posidonia alpina' beds of the Venetian Alps. — Mem. Ist. Geol. Min. Univ. Padova, 28: 1-190.

Szabó, J., 1984. Stratigraphical studies on Lower and Middle Jurassic gastropods from the Bakony Mountains, Hungary. In: O. Michelson & A. Zeiss (eds). International Symposium on Jurassic Stratigraphy, Erlangen, September 1-8, 1984. — Geol. Surv. Denm.: 848-862.

Szabó, J., 1991. Phylogeny of gastropods in the Jurassic Tethys. — Proc. Tenth Intern. Malacol. Congr., Tübingen, 1989: 511-514.

Szabó, J., M.A. Conti & S. Monari, 1993 (this volume). Jurassic gastropods from Sicily. New data to the classification of Ataphridae (Trochoidea). In: A.W. Janssen & R. Janssen (eds). Proceedings Symposium Molluscan Palaeontology, XI International Malacological Congress, Siena, 1992. — Scripta Geol., Spec. Issue 2: 407-416.

Taylor, J.D., N.J. Morris & C.N. Taylor, 1980. Food specialization and the evolution of predatory prosobranch gastropods. — Palaeontology, 23: 375-409.

Vermeij, G.J., 1987. Evolution and escalation. An ecological history of life. — Princeton Univ. Press, Princeton: 1-527 pp.

Wendt, J., 1971. Genese und Fauna submariner sedimentärer Spaltenfüllungen im Mediterranen Jura. — Palaeontographica, A, 136: 121-192.

Manuscript received 3 September 1992, revised version accepted 20 April 1993.