Victims of the Early Toarcian anoxic event: the radiation and extinction of Jurassic Koninckinidae (Brachiopoda)

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The significant mass extinction attributed to the Early Toarcian anoxic event had a severe impact on the phylum Brachiopoda. Beyond a serious decrease of species diversity, the extinction of the orders Spiriferidina and Athyridida is connected with this episode. The order Athyridida was represented by the family Koninckinidae in the Early Jurassic. The stratigraphical and geographical distribution of the three Early Jurassic koninckinid genera (*Koninckella, Koninckodonta, Amphiclinodonta*) shows a definite radiative pattern. The number of their nominal species increased from 2 to 17 from the Sinemurian to Early Toarcian; in the same time interval, their area increased from the Alpine region to the whole Mediterranean and the NW-European domains. This radiative evolution can be explained as the result of different factors: (1) morphological adaptation to muddy bottoms, (2) fundamental changes in the current pattern in the Tethys/Laurasian Seaway, and, possibly, (3) utilization of methane-based chemosynthesis as alternative food source. The radiation of koninckinids, leading from the cryptic habitats of the Tethyan rocky floors to the extensive muddy bottoms of the open European shelves, was abruptly terminated by the anoxic event in the Early Toarcian Falciferum Zone. The main causes of the extinction might be: (1) the excessive warming of Tethyan deep waters by thermohaline circulation, (2) the anoxic event, which was not survived by the spire-bearers, handicapped by their stiff, calcareous spiralia. □ *Brachiopoda, Early Jurassic, Europe, extinction, Koninckinidae, radiation, Tethys.*

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The Early Toarcian times, a little more than 180 million years ago, saw a significant, global mass extinction event (see Little & Benton 1995), especially well-documented in the fossil record of the north-west European epicontinental seas (Hallam 1986, 1996). The synchrony between this extinction and the celebrated Early Toarcian oceanic anoxic event (Jenkyns 1988) offered a clear, and now widely accepted, extinction mechanism in that the oxygen-depleted waters caused a crisis in the marine biota.

Brachiopods, as members of the benthic communities, were extremely strongly affected by this extinction event. The change is dramatic on the species level: a very conspicuous Toarcian 'bottleneck' appears on the brachiopod species diversity curve constructed by Vörös (1993, fig. 2) on the basis of stratigraphical ranges of Alméras (1964). In some European shelf areas (e.g. Iberia) the Early Toarcian event is reflected by a complete turnover of species (García Joral & Goy 2000), whereas in other, intra-Tethyan, Mediterranean regions the crisis lasted longer and led to an apparent absence of brachiopods (Vörös 1993).

However, the most remarkable effect of the Early Toarcian event on brachiopod history was the extinction of two orders, the Spiriferinida and Athyridida. The true decline of the phylum Brachiopoda is connected with the end-Permian global extinction event, very pronounced in the subphylum Rhynchonelliformea (more or less equivalent to the Articulata *auctt.*): only four orders survived this crisis. The Early Toarcian loss of two orders from the four means a substantial change: this was the last major extinction of brachiopods at the level of orders.

The order Athyridida was represented by the family Koninckinidae in the Early Jurassic. These small, smooth, concavo-convex brachiopods are sporadic in the fossil record and are usually not much studied by palaeontologists. However, recent investigations on Hungarian and Italian koninckinids (Vörös 2002) have resulted in some new aspects of their adaptive radiation and extinction. It is believed that a study of stratigraphical and geographical distribution of the Early Jurassic koninckinids may help to reveal the history of the group and may contribute to a better
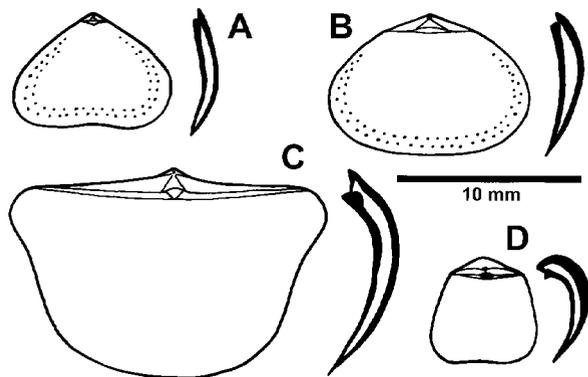
Fig. 1. Selected taxa representing the basic morphotypes of Early Jurassic Koninckinidae. □A. *Amphiclinodonta*. □B. *Koninckodonta eberhardi* (Bittner, 1888). □C. *Koninckodonta davidsoni* (Deslongchamps). □D. *Koninckella*.

understanding of the complex scenario of the Early Toarcian anoxic event and biotic crisis.

Koninckinidae: the distant homoeomorphs of Paleozoic *Leptaena*

The koninckinids, with their unusual, concavo-convex morphology, form a peculiar group of Mesozoic brachiopod communities. The three genera erected by classic authors were included in the 'Treatise' (Boucot *et al.* 1965: p. H666) and are still used in the 'new Treatise' (Williams *et al.* 2000) to embrace the different Early Jurassic morphotypes and nominal species (Fig. 1). *Amphiclinodonta* (Bittner, 1888) possesses relatively small, smooth, gently concavo-convex shells, with subtriangular outline, pointed beak and very narrow hinge line. The valve interiors are ornamented with marginal rows of tubercles. *Koninckella* (Munier-Chalmas, 1880) is also very small, but strongly concavo-convex, and possesses a strongly incurved beak; its valve interiors are weakly tuberculate. *Koninckodonta* (Bittner, 1894) is moderately concavo-convex, and has subquadrate, in some cases alate shells with a hinge line generally longer than half maximum width; the valve interiors are strongly tuberculate along the margins. As all koninckinids, they have very tiny, double spiral calcareous brachidia.

At the time of the discovery of their mass occurrences in Southern England (Davidson & Morris 1847) and in Normandy (Eudes-Deslongchamps 1853), the Lower Jurassic koninckinids have been regarded as late representatives or at least distant progeny of the Early Paleozoic *Leptaena*. As Davidson & Morris (1847, p. 251) expressed: The existence of *Leptæna* in the early part of the secondary period teaches us how cautious we should be in assigning to

any genus a limited duration in time. ... This view was held for decades, despite the comments by d'Orbigny (1850, p. 220) and the finding of spiralia in the closely related Triassic *Koninckina* (Suess *in* Davidson 1853, p. 92). Munier-Chalmas (1880) was the first to find spiral brachidia in some of the Liassic forms ascribed to his new genus *Koninckella*. But, even after these discoveries, some leading palaeontologists (e.g. Gemmellaro 1886) still used, intentionally, the generic name *Leptaena* instead of the new generic names. Rothpletz (1886, p. 166) doubted the presence of spiralia in the 'Liasleptaenen', but Bittner (1888, 1894) gave excellent proof of the double spiralia by serial sections in his two, newly erected koninckinid genera *Amphiclinodonta* and *Koninckodonta*.

Later on, owing to their spiral brachidia, the koninckinids were placed within the Spiriferida by many authors and this opinion was applied in the 'Treatise' (Boucot *et al.* 1965, p. H666) as well. Then it became evident that the koninckinids represent only the distant, heterochronous homeomorphs of the true *Leptaena*.

It must be remarked that the close similarity of the Early Jurassic koninckinids to the Paleozoic *Leptaeana* fits well only in the case of *Koninckodonta davidsoni* (Eudes-Deslongchamps, 1853), the abundant form of the Normandian and British 'Leptaena Beds'. This species possesses large, alate shells apparently suggesting a reclining habit, possibly shared with the alleged Paleozoic ancestors. The species *davidsoni* was, in fact, long assigned to the order Strophomenida. The discovery of spiral brachidia in '*Cadomella*' *davidsoni* by Cowen & Rudwick (1966), and recent studies by D. MacKinnon (Christchurch, New Zealand, 2000: pers. comm.) lead to the assignment of '*C.*' *davidsoni* to the Koninckinidae. In the new, revised 'Treatise' (Williams *et al.* 2000), the Early Jurassic koninckinids are ranged within the order Athyridida in the following way (D. MacKinnon 2000, pers. comm.):

Order Athyridida
Suborder Koninckinidina Davidson, 1853
Superfamily Koninckinoidea Davidson, 1853
Family Koninckinidae Davidson, 1853

Genus *Koninckella* Munier-Chalmas, 1880
        Amphiclinodonta Bittner, 1888
        Koninckodonta Bittner, 1894

Stratigraphical distribution of the Early Jurassic koninckinids (Table 1)

The Late Triassic bloom of Koninckinidae (Bittner 1890; Dagis 1974) was followed by an apparent

Table 1. Stratigraphical distribution of Early Jurassic Koninckinidae species.

Species	Hett	E.Sin	L.Sin	E.Pli	L.Pli	E.To
Amphiclinodonta adnethica Bittner, 1894		++++				
Amphiclinodonta liasina Bittner, 1888					++++	
Amphiclinodonta bittneri Böse, 1898					++++	
Koninckodonta pichleri (Bittner, 1894)		++++	++++			
Koninckodonta eberhardi (Bittner, 1888)			++++	++++	++++	?+
Koninckodonta styriaca (Bittner, 1888)			?+?	++++	++++	++
Koninckodonta geyeri Bittner, 1894			?+?	++++	++++	++
Koninckodonta aquoniae (Parona, 1883)				++++	++++	
Koninckodonta canavarii (Caterini, 1919)				++++	++++	
Koninckodonta convexa (Caterini, 1919)				++++	++++	
Koninckodonta intermedia (Caterini, 1919)				++++	++++	
Koninckodonta fornicata (Canavari, 1883)				++++	++++	++
Koninckodonta sicula (Gemmellaro, 1886)				++++	++++	++
Koninckodonta alfurica ionica (Renz, 1932)				++++	++++	++
Koninckodonta davidsoni (Deslongchamps, 1853)				?+?	++++	++
Koninckodonta waehneri (Bittner, 1894)					++++	++
Koninckodonta fuggeri Bittner, 1894					++++	
Koninckodonta variolata (Deslongchamps, 1853)						++
Koninckodonta auriculata Vörös, 2001						++
Koninckella gibbosula (Gemmellaro, 1874)				++++	++++	++
Koninckella choffati (Gemmellaro, 1886)				?+?	++++	++
Koninckella rostrata (Deslongchamps, 1853)					?+	++
Koninckella liasiana (Bouchard in Davidson, 1847)					+	++
Koninckella bouchardii (Davidson & Morris, 1847)						++
Koninckella meneghinii (Gemmellaro, 1886)						++
Koninckella tiburtina Vörös, 2001						++

Hett = Hettangian, E. = Early, L. = Late, Sin = Sinemurian, Pli = Pliensbachian, To = Toarcian.
Sources are cited in the text + Alméras (1964).

extinction near the Triassic/Jurassic boundary. The earliest Jurassic representatives of *Koninckodonta* and *Amphiclinodonta* are known to occur in the Sinemurian of the Northern Calcareous Alps (Geyer 1889) and in the Transdanubian Central Range, Hungary (Dulai 1998). [Another record of '*Koninckina* sp.' by Dulai (1992, pl. 6, fig. 6) should be rejected because the figured specimen belongs definitely to the genus *Rhynchonellina*.]

In the Pliensbachian, the koninckinids became very common in the Alpine region (Northern Calcareous Alps: Bittner 1888, 1894; Böse 1898; Southern Alps: Parona 1893; De Toni 1911; Transdanubian Central Range: Vörös 1983, 1986, 1993) but also in the Appennines (Canavari 1883; Caterini 1919; Ramaccioni 1936) and in the Ionian Zone of Greece (Steinmann 1894; Renz 1932; Mancenido 1993). The stratigraphically oldest representative of the genus *Koninckella* (*K. gibbosula*) is also recorded from the Pliensbachian of Western Sicily by Gemmellaro (1874).

At the very end of the Pliensbachian, and/or in the earliest Toarcian, koninckinids did not occur any more in the Alpine region. The genus *Amphiclinodonta* apparently became extinct, or at least never appeared again. On the other hand, in the Appennines, Western Greece and in Sicily (mainly in the Taormina Zone), the genera *Koninckodonta* and *Koninckella* showed a

secondary burst in diversity, as illustrated by Gemmellaro (1886), Renz (1932), Mancenido (1993) and Vörös (2002).

Most Sinemurian and Pliensbachian stratigraphical records of the Alpine-Mediterranean region mentioned above lack the proper ammonoid biochronological assessment. This is obvious with the old descriptions, but even in the case of the recent records there are uncertainties (see Vörös 2002). Perhaps the only exception is the fauna of the Bakony (Hungary) (Vörös 1983, 1986, 1993), where the detailed ammonoid biostratigraphy (Géczy 1971, improved by Géczy & Meister 1998) offered stratigraphical control of zonal subdivision. Here, most of the Late Pliensbachian records fall within the Margaritatus Zone. The single west-European Pliensbachian occurrence of *Koninckella liasiana* in Southern Germany (Rau 1905) is restricted to the *Leptaena* Bed just below the 'Costatenkalke of Lias δ' (Engel 1908), which corresponds to the '*Spinatumkalk*' in modern usage, and is interpreted as representing the lower, Apyrenum Subzone of the Spinatum Zone (Urlichs 1977; Schlatter 1985).

The Early Toarcian stratigraphical record is better. It is still true that some diverse Mediterranean occurrences (e.g. in Taormina, Eastern Sicily: Gemmellaro 1886; Western Greece: Renz 1932) are only traditionally held to be Toarcian and the lowermost
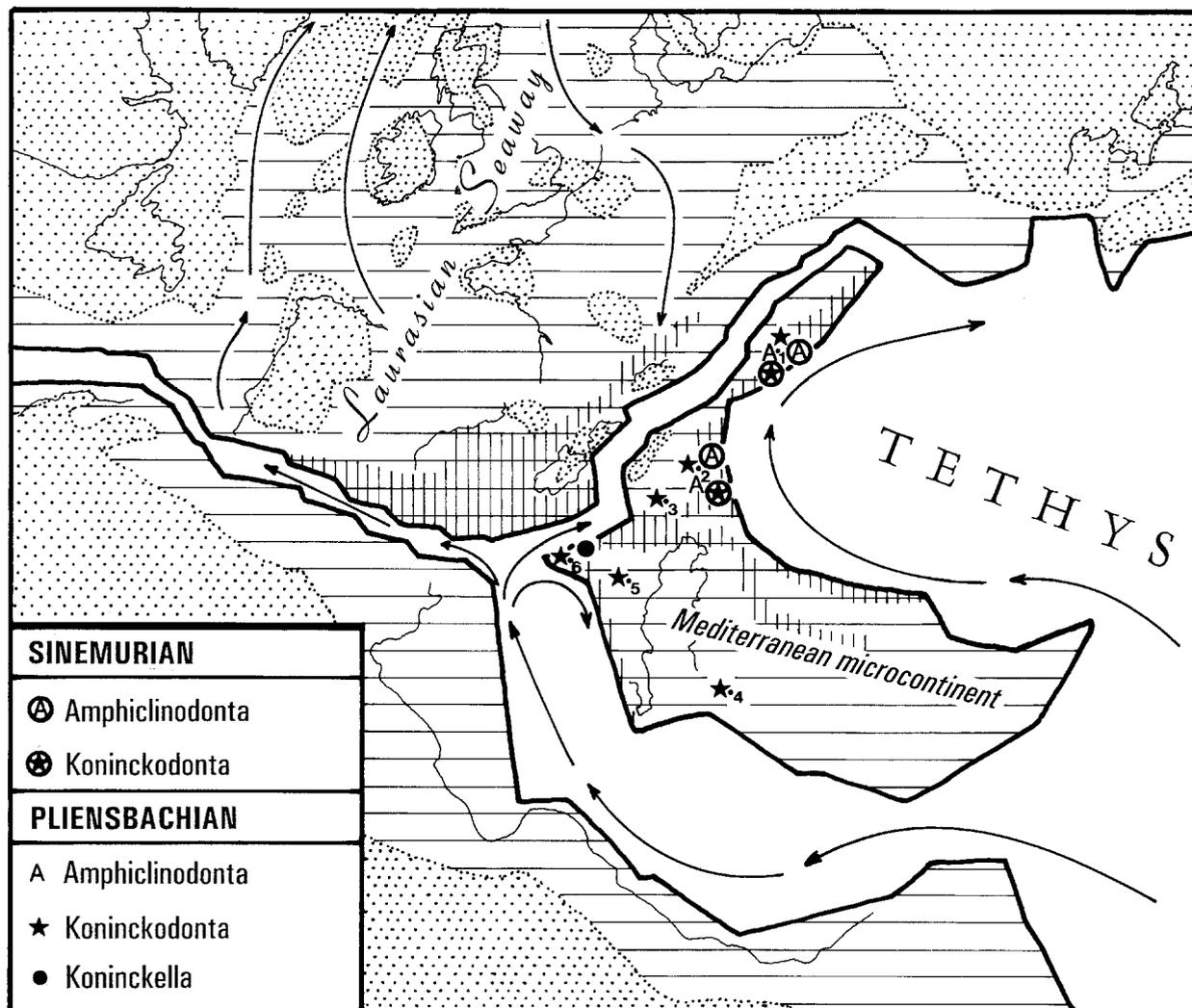
Fig. 2. Palaeogeographic sketch map of the western Tethyan region showing the distribution of Sinemurian and Pliensbachian koninckinid genera and the inferred surface current directions (arrows). Base map after Meister & Stampfli (2000); slightly modified. *Stippled*: land; *horizontally ruled*: shallow sea; *vertically ruled*: deeper sea; *blank*: oceans and deep basins with oceanic crust. 1: Northern Calcareous Alps; 2: Bakony Mts., Hungary; 3: Southern Alps, 4: Western Greece; 5: Central Appennines, 6: Western Sicily.

Toarcian age was only inferred for the Tivoli fauna (Appennines) described by Vörös (2002).

There is a very good stratigraphical dating of koninckinid localities in Western Europe. The widespread occurrences in France, Portugal, Morocco (and some others along the Atlas range) were definitely classed into the upper, Semicelatum Subzone of the Lowermost Toarcian Tenuicostatum Zone by Alméras et al. (1988, 1997). Alméras et al. (1988) and Alméras & Faure (1990) defined a special 'Koninckella fauna' (with *K. liasiana* and *K. bouchardii* as fundamental elements, accompanied by *Nannirhynchia pygmaea* (Morris), *Sphaeroidothyris* (?) *globulina* (Davidson), *Cadomella moorei* (Davidson), *Suessia* sp. and *Pseudokingena* sp.). A particular environmental control was attributed to this fauna (restricted to 'ombilics' ~ local

basins with marly sedimentation) and its distribution was found to be connected with the onset of the 'black shale' ('schistes cartons') formation. The narrow stratigraphical interval of this event was dated to the late Tenuicostatum Zone (Semicelatum Subzone) in Portugal (Alméras et al. 1995), Morocco (Alméras et al. 1988) and in Normandy (Rioult 1980) (see a summary in Alméras et al. 1997).

An analogous fauna of minute brachiopods is known from the *Leptaena* Bed of Southern England (Dorset, Somerset, especially in Ilminster; Arkell 1933), including the classical fauna of Davidson & Morris (1847) and Davidson (1876). Besides the koninckinids (*Koninckella bouchardii, Koninckodonta davidsoni*), other characteristic elements of the fauna are *Nannirhynchia pygmaea, Cadomella moorei* and
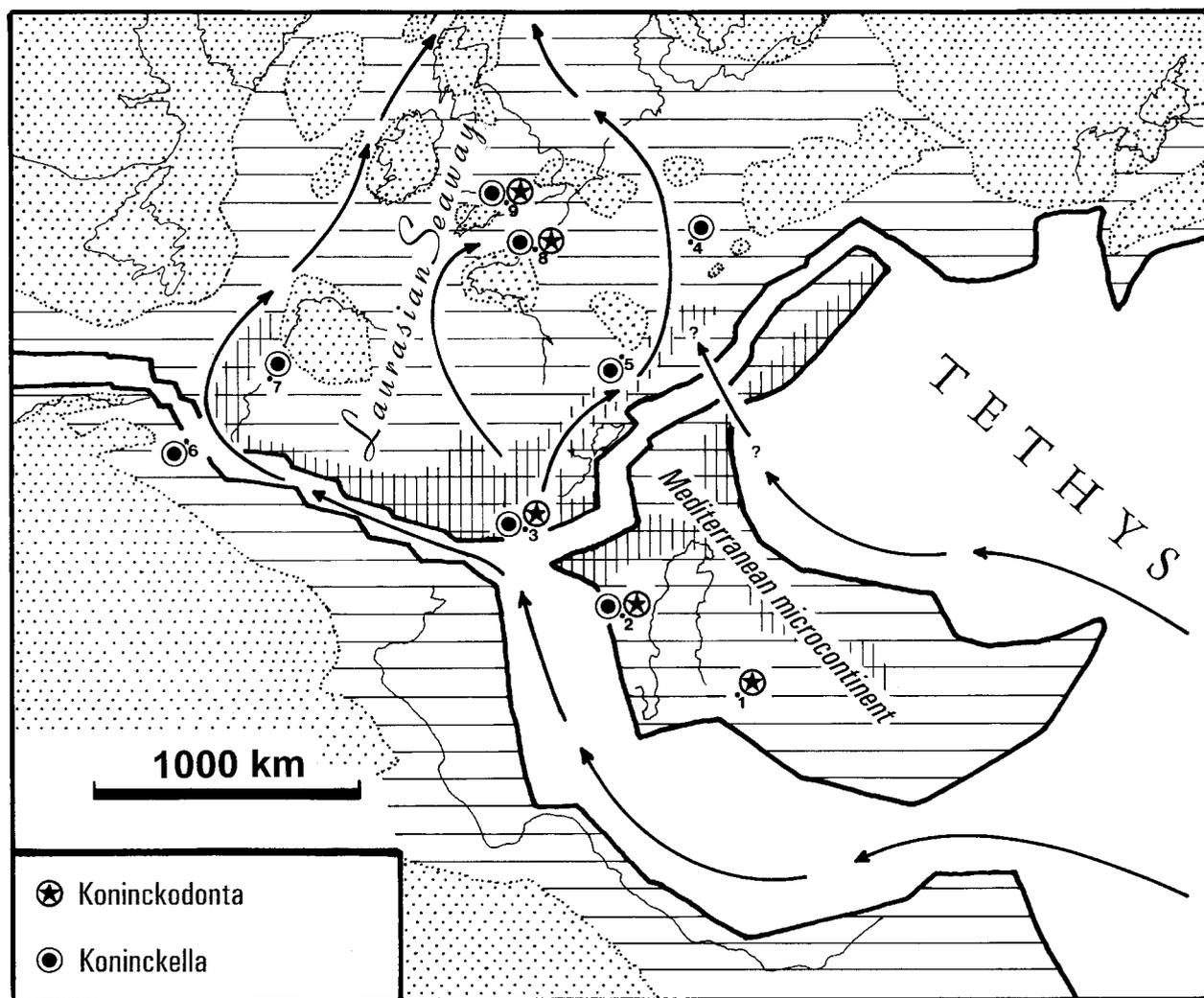
Fig. 3. Palaeogeographic sketch map of the western Tethyan region showing the distribution of latest Pliensbachian and Early Toarcian koninckinid genera and the inferred surface current directions (arrows). Base map after Meister & Stampfli (2000); slightly modified. *Stippled*: land; *horizontally ruled*: shallow sea; *vertically ruled*: deeper sea; *blank*: oceans and deep basins with oceanic crust. 1: Western Greece, 2: Central Appennines, 3: Eastern Sicily, 4: SW-Germany, 5: Montpellier, France; 6: Beni Snassen, Morocco, 7: Peniche, Portugal, 8: Normandy, France, 9: Ilminster, UK.

Orthotoma globulina (Davidson) (Ager 1956–67, p. 139 and Ager 1990, p. 39). Ager (l.c.) suggested an environmental control as the explanation of this micromorphic association, but instead of stunting he invoked a selection of small taxa. This *Leptaena* Bed lies just above the top of the Marlstone Rock Bed ranging into the Tenuicostatum Zone (Arkell 1933, p. 170). Recent studies by Howarth (1992, pp. 20–23) based on bed-by-bed ammonid collections at Barrington (Ilminster) proved that the *Leptaena* clay belongs to the lowermost part of the Falciferum Zone (to the base of the Exaratum Subzone).

The Exaratum Subzone of Howarth (1992) is considered as equivalent to the Strangewaysi horizon of

the Elegantulum Subzone of the French authors (Elmi *et al.* 1997) which is the lower part of the Serpentinum (=Falciferum) Zone. This means that both the British and the French '*Leptaena* Beds' lie very closely at the Tenuicostatum/Falciferum zonal boundary and may be taken as the results of a single event.

Brachiopods [e.g. *Soaresirhynchia bouchardi* (Davidson)] occur higher up in the Falciferum Zone in Britain (Ager 1956–67), France (Alméras *et al.* 1997) and Portugal (Alméras *et al.* 1995), but koninckinids do not appear again at all. The Early Toarcian Falciferum Zone may be taken as the time of final extinction of the family Koninckinidæ (Alméras & Faure 1990) and, by this, the order Athyridida.

Geographical distribution of the Early Jurassic koninckinids

The geographical distribution of koninckinid genera in different intervals of the Early Jurassic seems to be restricted to the western Tethyan region: therefore their occurrences are presented on palaeogeographical sketch-maps of this area (Figs 2, 3). The base map was drawn after the Sinemurian/Pliensbachian map of Meister & Stampfli (2000) with slight modifications. The western end of the Tethys is envisaged here as a bifurcate ocean, penetrating westward into Pangaea, with the Adriatic block (*sensu lato*) between the two oceanic arms. The Central Atlantic rifting caused a limited separation between the Laurasian and the African plates. The continuation of this rift zone (the Ligurian–Penninic belt) detached the Adriatic block from the European craton and resulted in the individualization of the intra-Tethyan Mediterranean microcontinent (see Vörös 1993, and further palaeogeographic references and discussion therein). A remarkable feature of this palaeogeographical picture is the 'Laurasian Seaway'. This N–S oriented shallow seaway formed a connection between the equatorial Tethys Ocean and the boreal Arctic Basin and its climatically induced current system substantially controlled the character of sedimentation and the distribution of marine biota (Bjerrum *et al.* 2001).

After the end-Triassic 'pseudo-extinction', the first, rare, Sinemurian occurrences of *Koninckodonta* and *Amphiclinodonta* were restricted to the Alpine segment around the northern arm of the western Tethys (Fig. 2).

In the Pliensbachian, koninckinids became more abundant in the Alpine segment but they spread also to the Apennines, Western Sicily and Greece, i.e. to the margin of the southern arm of the western Tethys (Fig. 2). The stratigraphically oldest representative of the genus *Koninckella* (*K. gibbosula*) is also recorded from the Pliensbachian of Western Sicily.

In the latest Pliensbachian, and/or the earliest Toarcian, the Alpine segment, became barren of koninckinids and the genus *Amphiclinodonta* disappeared. On the other hand, the bloom of *Koninckodonta* and *Koninckella* continued in the southern arm of the western Tethys, in the Apennines and Eastern Sicily. During the Spinatum Zone a short episode of invasion of *Koninckella* to the Laurasian Seaway, i.e. to the European epicontinental seas (SW Germany) was recorded (Fig. 3).

In the time of the Tenuicostatum (and the earliest Falciferum) Zone, two species (*Koninckodonta davidsoni* and *Koninckella liasiana*) abruptly extended their areas to the northwest and invaded distant areas in the Maghrebian seas and in the Laurasian Seaway. They were recorded at many places, mainly along the outer shelves open to the Early Jurassic arms of the western Tethys ocean (Fig. 3).

Radiation and extinction of the koninckinids in the Early Jurassic

In the time of their Late Triassic bloom, koninckinids were confined to the Tethyan margins (Alps, Caucasus, Southern China). They might have survived the end-Triassic crisis probably in deep-sea refugia.

The stratigraphical and geographical distribution of Early Jurassic Koninckinidae shows a clear radiative pattern. After the end-Triassic apparent extinction, they slowly started to colonize the subsided Alpine carbonate platforms around the northern arm of the western Tethys. During the Pliensbachian diversification they occupied the other side of the Mediterranean microcontinent. From this southern branch of the western Tethys they started to invade the European epicontinental seas at the Pliensbachian/Toarcian boundary.

From the Early Sinemurian to the Late Pliensbachian, the number of nominal species increased from 2 to 18, and, even after a limited extinction and turnover at the end of the Pliensbachian, 17 species were recorded in the Early Toarcian (see Table 1). This radiative evolution can be interpreted and explained in terms of different, partly independent factors and mechanisms.

Adaptive radiation

The most remarkable change in the pattern of the distribution of Early Jurassic koninckinids is the sudden invasion from the Tethys to the epicontinental seas, involving an adaptation to relatively shallow, muddy bottoms.

In Sinemurian and Pliensbachian times, the western Tethyan margins – the homeland of koninckinids at those times – were dominated by disintegrated and subsided former carbonate platforms (Bernoulli & Jenkyns 1974). These current-swept, rocky submarine highs were dissected by faults and fissures and were the sites of peculiar, mainly biocalcarenitic sedimentation, e.g. crinoidal limestones, 'Hierlatz' limestones (Jenkyns 1971; Vörös 1991). The extremely diverse brachiopod faunas of the Mediterranean faunal province lived on these submarine highs and the intervening basins (Vörös 1986, 1994). The usual, conservative forms of koninckinids (subpentagonal or
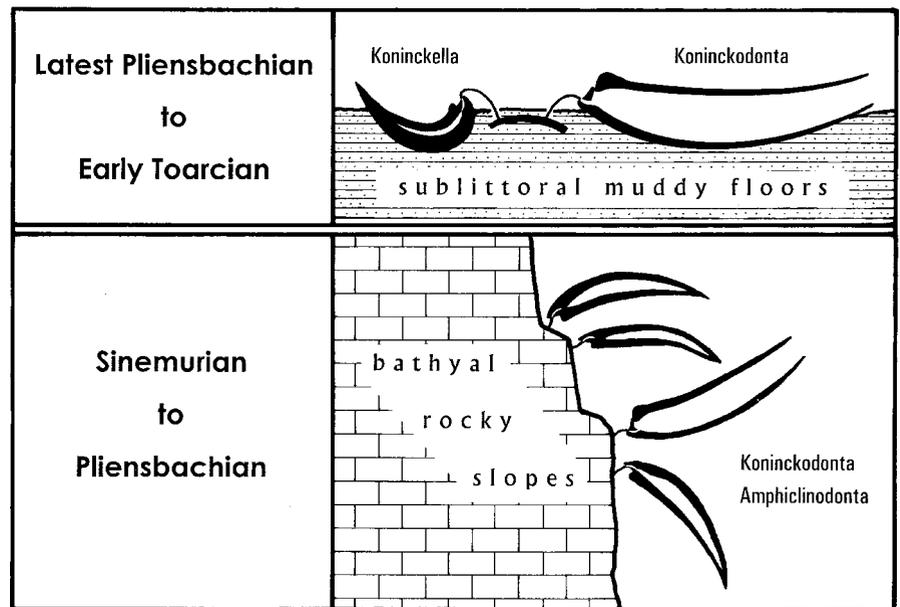
Fig. 4. Temporal change in the adaptation of Early Jurassic koninckinids to different substrata.

elliptical outline, less convexity, hinge of medium length, type A and B in Fig. 1; i.e. *Amphiclinodonta* and the most of *Koninckodonta*), used a normal pedicle attachment to rocky bottoms (Fig. 4). In fact, these morphotypes preferred the crevices, fissures and steep rocky surfaces of the submarine horsts, as was shown by Vörös (1986) for the example of the Bakony (Hungary).

The end-Pliensbachian to Early Toarcian occupation of the European epicontinental seas required a special adaptation of some koninckinids to soft muddy substratum. The 'conservative' stock failed to pass through this filter; only the genus *Koninckella* and the alate species of *Koninckodonta (K. davidsoni)* were successful in the invasion. The preparation for the invasion, i.e. the adaptation to soft bottoms was managed in the Tethyan margins, as exemplified by the composition of the faunas described from eastern Sicily by Gemmellaro (1886) and from the Apennines by Vörös (2002). Here, the koninckinid faunas of latest Pliensbachian and/or Early Toarcian age occur in marly sediments and are dominated by two peculiar morphotypes (Fig. 4).

(1) *Gryphaeoid morphotype.* This is characterized by a strongly convex pedicle valve, with incurved beak, small pedicle foramen and in some cases by secondary thickening in the pedicle valve (*Koninckella*). This morphotype can be interpreted as an adaptation to a soft muddy bottom, lying with the convex pedicle valve downward, partly sunken into the soft sediment. This model has strong analogy with the functional morphology of some Palaeozoic productids and the bivalve *Gryphaea*. (It is worth mentioning that even Bouchard (in Davidson & Morris 1847, p. 251)

stressed the resemblance of his '*Leptaena*' (=*Koninckella*) *liasiana* to *Productus*).

(2) *Flat-lying morphotype.* This comprises the large, flat, alate species with a long hinge margin (e.g. *Koninckodonta davidsoni*). With their flat, thin shell with extended wings or auricles, these forms were capable of lying on the surface of a soft bottom, with their pedicle valve down. These thin shells were supported by a large and extended surface, which might stabilize them on the bottom. An obvious morpho-functional analogy appears with some Palaeozoic strophomenids, e.g. the true *Leptaena* itself.

Both morphotypes suggest (especially if we consider the Palaeozoic analogues) a free-lying mode of life. It must be remarked, however, that all these forms possess small but clearly visible pedicle foramen; therefore, they were probably tethered by a tiny pedicle during life.

Ways and aids of dispersal

The above two morphotypes were able to invade the deeper sublittoral muddy environments of the European epicontinental seas in latest Pliensbachian to Early Toarcian times, but their sudden dispersal to distant areas needs further explanation.

Floating algae(?)

The '*Koninckella*-faunas' of the W. European and Maghrebian localities show a peculiar composition (Alméras *et al.* 1988) characterized by notoriously

small-sized brachiopod taxa (Ager 1967, 1990). We may follow Ager (1965) in assuming that the peculiar, small-sized brachiopod associations, widely dispersed in muddy sediments, might be epiplanktonic, and may represent the habitat of 'attached to floating weed' (habitat no. 7, in Ager 1965). In our case, this would imply that *Koninckella* and *Koninckodonta davidsoni* (and the whole association of the *Koninckella* fauna) would have been adapted to be attached to macro-algae which, swept by northward currents, carried the brachiopods from the Tethys and released them at random in the European epicontinental seas. This hypothesis, however tempting, is contradicted by the nature of the occurrences of the koninckinids in the '*Leptaena* beds', where they usually form closely packed 'pavements'. This hints more at a local taphocoenose than at an accumulation of randomly dispersed shells.

Changing current pattern

Another, more usual and regular, way of dispersal for brachiopods is by means of planktonic larvae. The efficiency of this mechanism may also be promoted by currents. It is widely accepted that the Jurassic Tethys ocean was dominated by westerly directed equatorial surface currents that turned back at the closed western end of the ocean (Ager 1975, Berggren & Hollister 1977; Röhl *et al.* 2001). The Mediterranean micro-continent is assumed to have been swept around by currents which might influence the dispersal of brachiopods (Vörös 1993).

The current system of the Laurasian Seaway, crucial for the present discussion, was studied recently by numerical modelling (Bjerrum & Surlyk 1998; Bjer-rum *et al.* 2001). It was pointed out that the main flow directions in this N–S oriented seaway, which con-nected the Arctic basin with the equatorial Tethys Ocean, were governed by the density-difference of the global ocean waters. In most of the Early Jurassic, Arctic waters flowed southwards in the eastern side of the Laurasian Seaway, and warmer, Tethyan, water flowed northwards in the western part; the dominant flow was northwards and deep water formation occurred in high latitudes. In times of warmer climate (as at the end-Pliensbachian to Early Toarcian 'green-house' period; see Pálfy & Smith 2000; Hesselbo *et al.* 2000) the oceanic thermohaline circulation led to deep water formation in the Tethys, and the Laurasian Seaway was dominated by southward flowing currents (Bjerrum & Surlyk 1998; Bjerrum *et al.* 2001).

The above principles were followed in Figs 2 and 3 in the tentative presentation of the dominant current pattern in the Laurasian Seaway. The end-Pliens-bachian–Early Toarcian map (Fig. 3) needs further

discussion. According to Bjerrum *et al.* (2001, p. 403) 'southward currents dominated in the Toarcian'. The northward spread of koninckinids in the latest Pliensbachian and Early Toarcian seems to contradict this. For an explanation, we have to count with short periods of reversal in the dominant current directions, as suggested by Bjerrum *et al.* (2001).

Another remarkable feature seen in Fig. 3 is that the distribution of koninckinids seems to be controlled partly by the sea-floor morphology: most of the occurrences are connected with the margins of deeper troughs. The Moroccan locality lies near the Central Atlantic rift zone. A deep basin of oceanic basement (Tagus Abyssal Plain) existed in the Early Jurassic to the west of the Lusitanian shelf (Ziegler 1988, pl. 11). It is noteworthy that in Portugal the *Koninckella* fauna occurs only in the western sections of more pelagic facies (e.g. Peniche: Mouterde 1955) but it is missing at the eastern localities, closer to the Iberian continent (e.g. in Tomar; Mouterde 1967). The rifting, or at least downfaulting of the Western Approaches Trough (between Britain and Brittany) started in the Early Jurassic (Ziegler 1988, p. 54). The two important and well-known koninckinid localities lie at both sides of this trough: no occurrences were reported further north than Somerset, and the famous Normandian *Koninckella* fauna disappears southwards in the Paris Basin (Rioult 1980). Alméras *et al.* (1988) also recognized that the distribution of the *Koninckella* fauna is related to deeper environments. A possible interpretation is that the pathways of the currents of Tethyan waters were driven, or partly controlled, by these elongated, rifted basins.

The incipient opening of the North Atlantic played an important role in the migration of Jurassic brachiopods, as recognized and illustrated by Ager & Walley (1977). Multicostate and sulcate terebratulids of Tethyan origin arrived in Southern England via the Maghrebian and western Portuguese zones in the Early and Middle Jurassic; the famous, perforate pygopides reached as far north as East Greenland (Ager 1967) along the Late Jurassic northern seaway. An interest-ing, common feature of these distributions is that the migration pathways, leading from the Tethys to the northern part of the Laurasian Seaway, made a turn around the Iberian continent. The dispersal pattern of the latest Pliensbachian to Early Toarcian koninck-inids (Fig. 2) fits well with this migration route, with the notable exception of the occurrence in South Germany.

Methane metabolism(?)

This part of the present paper is admittedly highly speculative, because the supporting stable isotope
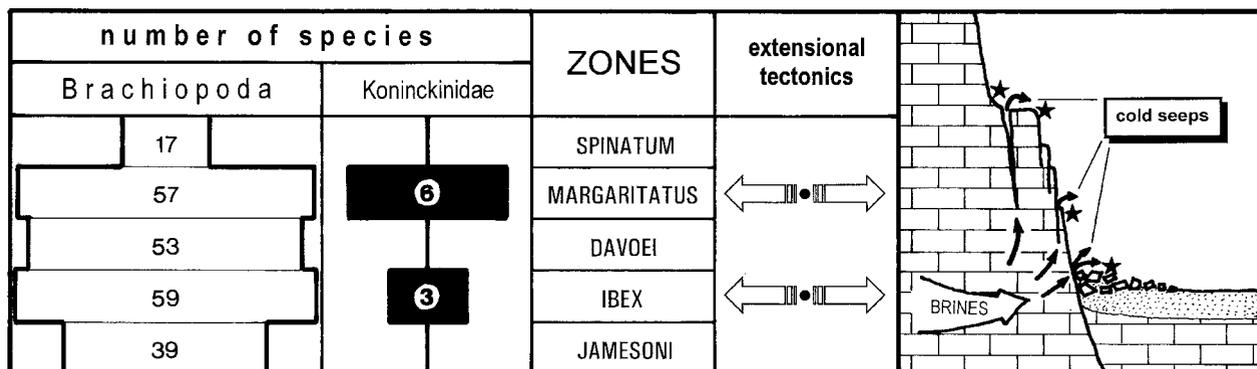
Fig. 5. Relationship between the extensional tectonic phases and the species diversity of brachiopods and koninckinids in the Pliensbachian of the Bakony Mts. (Hungary). The tectonic phases are thought to increase the activity of submarine cold seeps with possible methane exhalation. The insert figure (on the right) is modified after Vörös (1995).

evidence is missing or the investigations have just started. Nevertheless, the following ideas are put forward as a tentative, partial explanation of the phenomena recorded.

Chemosynthesis, as a possible base of higher life, is a recent discovery in marine research. Peculiar fossil brachiopod associations, members of chemosynthetic communities supported by deep-water cold seeps, were described (e.g. Von Bitter *et al.* 1992; Sandy & Campbell 1994). Especially methane, seeping from buried carbonate bodies, was metabolized by bacteria, and this carbon source was used by the fossil communities of Mesozoic brachiopods, e.g. the Jurassic Rhynchonellininae (Sandy 1995). The 'cold seep hypothesis' was used by Vörös (1995) for explaining anomalous Lower Jurassic brachiopod accumulations in the Bakony (Hungary), and some mass occurrences of *Rhynchonellina* in the Apennines were also interpreted in this way (Taddei Ruggiero 1997), although definitive evidence of the methane metabolism by studies on stable isotopes of O and C is still lacking.

Up to now, Koninckinidae were not suspected as belonging to methane-based chemosynthetic communities, but their pattern of distribution in the Alpine localities, especially in the Pliensbachian of the Bakony (Hungary) seems to support that idea. In the Northern Calcareous Alps, koninckinids are frequently found in neptunian dykes. A detailed study of palaeoenvironmental distribution of Pliensbachian brachiopods in the Bakony (Vörös 1986) revealed that the koninckinids preferred the, mainly bathyal, submarine rocky escarpments. Repeated tectonic movements along these fault-scarps produced empty rocky surfaces for settlement of brachiopods. The close relationship between the tectonic episodes and the diversity of brachiopod fauna was described by Vörös (1993, 1995) and is also shown here in Fig. 5. If cold seeps,

carrying methane, worked along the fault zones bordering the submarine horsts, their activity was probably increased in episodes of tectonic rejuvenation because the fault planes, and the resulted fissures and fractures might serve as conduits for the fluids. In fact, the stratigraphical distribution of Koninckinidae in the Pliensbachian of the Bakony shows two peaks, coinciding with the tectonic pulses (in the Ibex and Margaritatus Zones) (Fig. 5). This may indicate that the koninckinids were more stongly dependent on the cold seep activity, and hence the possible methane discharge, than other members of the brachiopod community.

Release of enormous amounts of methane from gas hydrate contained in continental margin and slope sediments has occurred several times in the history of the Earth owing to a raised temperature at the ocean floor, for example at the Late Paleocene thermal maximum (Dickens *et al.* 1995). The Early Toarcian times saw one of the largest known methane hydrate dissociation events, probably triggered by the thermohaline circulation and warming of the Tethyan deep bottom waters by up to 5 °C and extensional tectonics (Hesselbo *et al.* 2000). Methane passes ultimately to the atmosphere and increases the greenhouse effect of the gases emitted by the simultaneous volcanism (Pálfy & Smith 2000), but the influence of the excess methane to the marine biota should also be considered.

Fig. 6 shows the Late Pliensbachian to Early Toarcian $\delta^{13}C$ curve, redrawn from Hesselbo *et al.* (2000), where the sharp negative excursion at the base of the Falciferum Zone marks the great Early Toarcian methane dissociation. (An even stronger negative anomaly was found at the same horizon in the Posidonia Shale of SW Germany by Röhl *et al.* 2001.) The positive excursion in the higher part of the Falciferum Zone corresponds to the maximum of
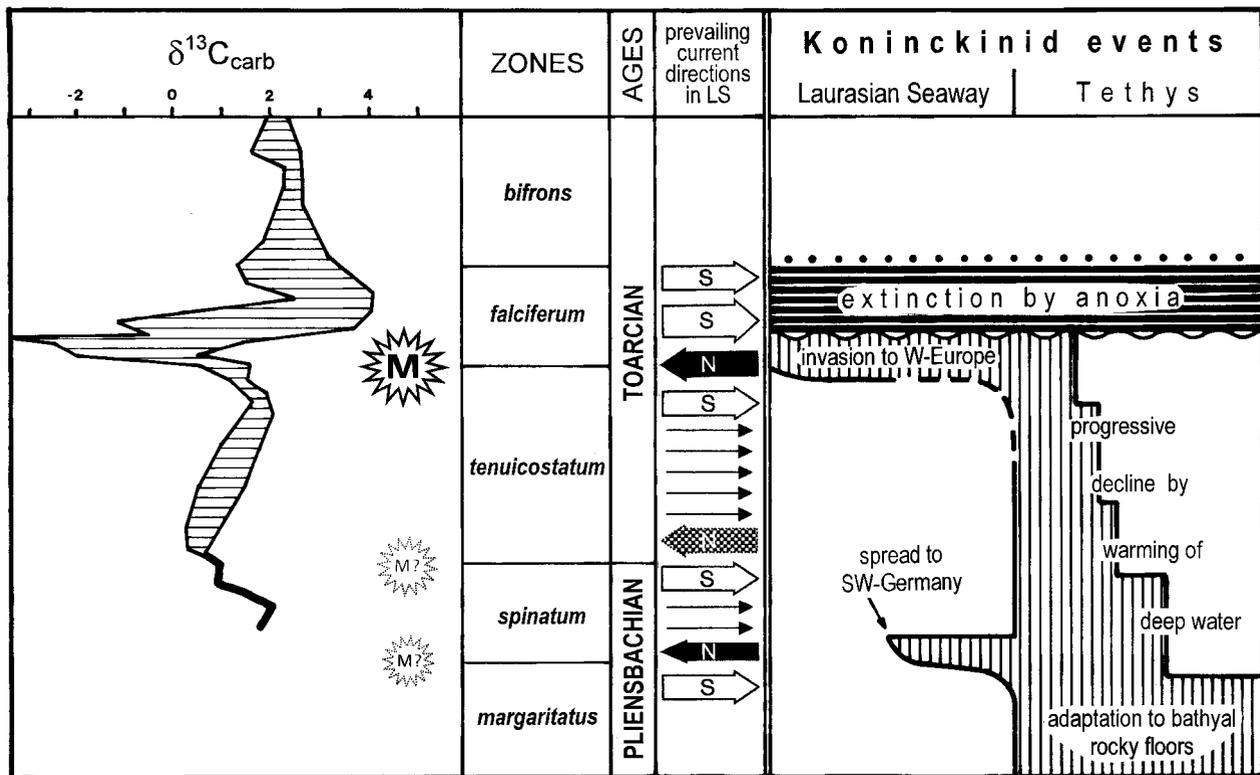
Fig. 6. Radiation, decline and extinction of Koninckinidae as related to some important Late Pliensbachian to Early Toarcian environmental changes in the western Tethyan region. The $\delta^{13}C$ envelope curve is redrawn after fig. 2 of Hesselbo *et al.* (2000), who suggested also the large-scale methane dissociation event. The two earlier hypothetical methane events are hypothesized by the present author. The dominant southward flow and intermittent northward-flowing episodes in the Laurasian Seaway are predicted by Bjerrum *et al.* (2001), but the timing of the northward-flowing episodes is deduced by the author from the koninckinid distributions.

the 'anoxic event'. Looking at the events in the history of the koninckinids (Fig. 6) the invasion to European epicontinental region closely coincides with the great methane release. There may, or may not be a causal relationship, but at least it is worth taking into account as an indication of methane-dependence of the koninckinids.

Two other, supposed, queried methane events are indicated in Fig. 6. One corresponds to a second-order negative excursion on the $\delta^{13}C$ curve of Hesselbo *et al.* (2000) near the base of the Tenuicostatum Zone; no brachiopod migration event seems to be connected with this. The other, at the base of the Spinatum Zone, is even more circumstantially evidenced by the wide-spread occurrence of the *Koninckella* fauna in SW Germany, but lacks the isotope proof.

It is a remarkable fact that the European Early Toarcian koninckinids are members of a peculiar brachiopod association called 'Koninckella fauna' by Alméras & Faure (1990). As mentioned above, according to Alméras & Faure (1990) and Ager (1956–67, 1990) this association is characterized by minute brachiopods belonging to the genera *Koninckella, Koninckodonta, Cadomella, Nannirhynchia, Ortho-*

toma, Suessia and *Pseudokingena*. A similar composition characterizes the fauna of the latest Pliensbachian 'Leptaena beds' of SW Germany (Rau 1905).

It is also remarkable that, besides the koninckinids, the representatives of *Nannirhynchia* [*N. reynesi* (Gemmellaro), *N. gemmellaroi* (Parona)] and *Orthotoma* [*O. apenninica* (Canavari)] were recorded also in the Pliensbachian of the Bakony Mountains (Hungary) and that their stratigraphical distribution shows the same two peaks in the Ibex and the Margaritatus Zones:

Zones	Specimens	
	Orthotoma	*Nannirhynchia*
Spinatum	–	1
Margaritatus	32	51
Davoei	–	11
Ibex	3	16
Jamesoni	–	–

Thus, the koninckinids of the Bakony, accompanied by relatives of two important members of the 'Koninckella fauna', together show maximum abun-

dances in the times of tectonic episodes (suspected as triggering methane discharge). This may also be accidental, but the coincidence is at least worth considering.

Late success and extinction of the Koninckinidae

The Late Pliensbachian to Early Toarcian history of the koninckinids can be interpreted as governed by the interplay between the prevailing currents in the Laurasian Seaway and the Tethys and methane dissociation event(s).

In the background, there is a complex scenario of global environmental changes, including extensional tectonics, volcanism, acid rains, extreme greenhouse conditions, transgression and global oceanic anoxia (Pálfy & Smith 2000; Hesselbo *et al.* 2000). The triggering factor was most probably the enormous Karroo-Ferrar flood basalt volcanism (starting as early as the Pliensbachian Margaritatus Zone), which produced voluminous CO_2 emissions to the atmosphere increasing greenhouse conditions (Pálfy & Smith 2000). The resulting global warming might have caused changes in the thermohaline circulation and a deep-water formation might have occurred in the Tethys (Bjerrum *et al.* 2001). Finally, the increased bottom-water temperature in the Tethys and extensional tectonics triggered the methane release from buried gas hydrate, which amplified the greenhouse effect. Southward currents in the Laurasian Seaway introduced nutrient-rich bottom waters from the north and resulted in anoxic conditions (Hesselbo *et al.* 2000).

The Late Pliensbachian warming of the deep Tethyan bottom waters badly affected the brachiopod communities of the bathyal rocky floors: a serious decline of the very rich Pliensbachian brachiopod fauna of the Bakony took place in the Spinatum Zone (Vörös 1995). Koninckinids were gradually expelled from this habitat and, within the Tethys, survived only in the marly basins of the Apenninic-Sicilian shelf (Fig. 6).

The deterioration of the bathyal environment was the consequence of the deep-water formation in the Tethys and the dominantly southward current directions in the Laurasian Seaway, as predicted for this time interval by Bjerrum *et al.* (2001). However, changes in north–south density differences and hence in the direction of seaway currents might have been relatively fast, within the magnitude of 10^6 year, comparable to the duration of an ammonoid zone (Bjerrum & Surlyk 1998; Bjerrum *et al.* 2001). This relationship is indicated here in Fig. 6. According to Bjerrum *et al.* (2001), 'southward currents dominated

in the Toarcian' in the Laurasian Seaway. Obviously, the southward-flowing Arctic waters exerted an effective cooling on the Tethyan water mass: thus the thermohaline deep-water formation might have stopped and the northward current system re-established from time to time. At least two short, northward flowing episodes of this kind can be suggested on the basis of koninckinid distribution: one for the time of the early Spinatum Zone (the *Leptaena* Bed in SW-Germany) and another for the late Tenuicostatum and/or the early Falciferum Zone (the widespread Maghrebian and European occurrences of the *Koninckella* fauna) (Fig. 6).

Thus, the following, repeated sequence of events is envisaged here: southward-flowing currents and warming of Tethys culminated in methane release; this was abruptly followed by a short northward flowing episode. In this hypothetical system, the base of each ammonoid zone (Spinatum, Tenuicostatum, Falciferum) was marked by a methane release and a short northward-flowing episode.

The northward-flowing currents, carrying brachiopod larvae (or floating weed), are necessary conditions of the invasion of koninckinids to the European epicontinental areas. The establishment of the brachiopod communities might have been promoted by the increased supply of methane. After the evacuation from the Tethyan areas, the koninckinids had no chance of returning to the hostile, overwarmed bathyal rocky floors.

None of the koninckinids survived the Early Toarcian Falciferum Zone. This final extinction can readily be explained by the synchronous, great 'anoxic event'. Ager (1987) offered an elegant explanation of the selective extinction of 'spire-bearers' (including koninckinids) in contrast to other brachiopods. According to this author, the spire-bearers were restrained by their calcareous spiralia, whereas the others were more flexible and able to extend their lophophores from the shells; this advantage was decisive in the oxygen-depleted waters. However, if the koninckinid-dominated communities were really methane-dependent, the termination of the great methane-release event might have been a sufficient cause of their extinction.

Conclusions

The stratigraphical and geographical distribution of Early Jurassic Koninckinidae shows a definitely radiative pattern. The number of their nominal species increased from 2 to 17 from the Sinemurian to Early Toarcian; in the same time interval, their area increased from the Alpine region to the whole

Mediterranean and the NW European domains. This radiative evolution can be explained as the result of different, partly independent factors: (1) morphological adaptation to muddy bottoms, (2) fundamental changes in the current pattern in the Tethys/Laurasian Seaway, and, speculatively, (3) utilization of methane-based chemosynthesis as alternative food source.

The adaptive radiation of koninckinids, leading from the cryptic habitats of the Mediterranean rocky floors to the extensive muddy bottoms of the open European shelves, was abruptly terminated by the 'anoxic event' in the Early Toarcian Falciferum Zone. The main causes of the extinction: (1) in the Mediterranean areas, the excessive warming of Tethyan deep waters by thermohaline circulation, (2) in the European epicontinental seas, the anoxic event, which was not survived by the spire-bearers, handicapped by their stiff, calcareous spiralia.

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