Athyridid diversity dynamics in the Prague Basin as shown by studies by Vladimír Havlíček

Dynamiky vývoje athyridních brachiopodů v pražské pánvi podle údajů z prací Vladimíra Havlíčka

(3 figs, 1 table)

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Athyridid diversity dynamics in the Prague Basin are studied based on the data in the articles and monographs devoted by Vladimír Havlíček to study of the biostratigraphy of the Barrandian area (Prague Basin, Czech Republic). General diversity, extinction, origination and turnover patterns were studied to assess general tendencies in athyridid evolution at species-level.

Key words: Havlíček, Prague Basin, Silurian, Devonian, Brachiopoda, Athyridida, endemism, diversity

Introduction

It is well known that one of Havlíček's main scientific interests was the study of the geology and biostratigraphy of the Prague Basin (Barrandian area). Since 1956, a great number of his articles were devoted to the study of Bohemian brachiopods (see Havlíček – Vaněk 1998 and references therein). Havlíček based his studies on both old collections and new specimens gathered during decades of field work. He described about 270 new brachiopod genera, becoming, together with G. A. Cooper, one of the great brachiopod taxonomists of the twentieth century. In the Pragian Stage of the Prague Basin, Havlíček recognized (see Havlíček – Štorch 1990, Havlíček – Vaněk 1998) 336 brachiopod species assigned to 167 genera, and in the Silurian more than 220 species of about 150 genera. As Havlíček himself wrote in Havlíček – Štorch (1990): "*The brachiopods are a significant component of the sessile benthos in the Prague Basin (Barrandian area). Most of them were figured (but not described) by Barrande in 1879 in the fifth volume of his famous monograph <Système silurien du Centre de la Bohême>. Our aim was to revise all Barrande's types that came from his <Étage E> (i.e. Silurian in the present-day concept). In this way, however, our attempt was not fully successful, because many specimens were so incomplete, deformed, or damaged that it was beyond our powers to assign them to relevant genera and families. Further, the locality and horizon are questionable in many specimens figured by Barrande; for this reason, a reliable comparison of these specimens with recently collected shells is not possible.*" Havlíček was a "*very good collector, careful and modern – always making notes about the locality, section, layer*" (see Kříž 2000). He gave special attention to the study of the brachiopods, their assemblages, ecology, and evolution in relation to the evolving deformation of the Prague Basin, and to describe and/or comment on those brachiopods that Barrande (1879) so nicely illustrated but never described (see, for example Havlíček – Kukal 1990, Havlíček – Vaněk 1998).

Of the brachiopods recognized by Havlíček in the Silurian and Devonian of the Prague Basin, about 60 are athyridid species or subspecies, 30 of which, and 7 genera and a subgenus were *new*. During his work of revision of athyridid species, Havlíček selected 12 lectotypes and refigured photographically several of Barrande's holotypes specifying, when possible, their occurrence. But, although very careful when describing new species and genera, and in spite of all his efforts, Havlíček himself recognized (Havlíček – Vaněk 1998:57) "*that the present state of brachiopod systematics is not fully satisfying... several problems still remain unsolved. For example, the limited and often recrystallized material does not allow an exact examination of the brachial apparatus in several genera and families*". So, and although the cardinalium and ventral interior was shown in more of the 60 % of the Barrandian athryridids, the jugal structure is only known from 3 %. Unfortunately this is the general situation in this order of spire-bearing brachiopods, the athyridid brachidium, and the jugal structure in particular, have been studied and clearly described or illustrated for only a few genera. Information about its growth, intraspecific variation and evolution is very scarce. The configuration of this important structure is known, often only superficially, in less than 50% of the genera commonly considered to be athyridides (see Alvarez 1999 and discussion therein).

Although aware of these and other problems – including different authors views on taxonomy and population dynamics and the dangers of using data bases for the study of extinction and survivals in the Brachiopoda (see discussion in Ager 1988), to investigate trends in athyridid diversity dynamics in the Prague Basin – I prepared cumulative distribution data for athyridids through the Silurian and Devonian based on the data of Havlíček and the Global Stratigraphic Chart of the IUGS compiled by Cowie – Bassett (1989). I assessed the total number of species, and those appearing (number of originations) and disappearing (number of extinctions), per stage, the shortest reliable correlatable interval of time (Figs 1, 2, Tab. 1). I treated all data with consistent methods for calculation of the average number of species, normalized origination, extinction and turnover rates per million years, and probabilities of extinction and origination (Tab. 1). The measures

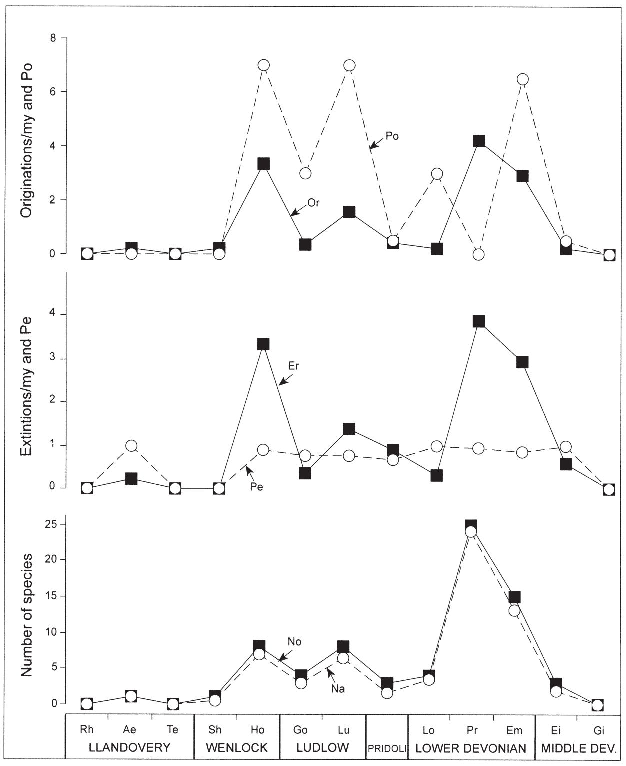

Fig. 1 Number of originations/million years *Or* (solid line) and probabilistic origination rate *Po* (number of originations/number of species entering an interval from the previous interval) (dashed line); number of extinctions/million years *Er* (solid line) and probabilistic extinction rate *Pe* (number of extinctions/total number of species) (dashed line); diversity *No* (solid line) and average *Na* (dashed line) numbers of athyridid species per unit (from late Early Silurian to Devonian) in the Prague Basin. Data derived from Tab. 1. Abbreviations: Rh – Rhuddanian; Ae – Aeronian; Te – Telychian; Sh – Sheinwoodian; Ho – Homerian; Go – Gorstian; Lu – Ludfordian; Lo – Lockhovian; Pr – Pragian; Em – Emsian; Ei – Eifelian; Gi – Givetian.

of diversity, extinctions, originations and turnover used here are those chosen and discussed by Olsen – Suess (1986) (see also Alvarez – Modzalevskaya 2000, and in press). Turnover rate was determined following McGhee (1989).

Trends in athyridid diversity dynamics on the Prague Basin

As shown by Havlíček's articles and monographs (see Havlíček – Vaněk 1998 and references therein), at the beginning of the Silurian (Llandovery–Wenlock) athyridid originations in the Prague Basin increase towards younger strata (see Figs 1, 2). For example, the endemic genus *Kozlenia* Havlíček, 1987 appeared during the Wenlock (Homerian). This diversification coincides with a general warming of climate and marine transgression. As Štorch (in Havlíček – Štorch 1990) wrote: "*the Silurian rocks as a whole were deposited in a shallower warm-water environment near the transition between subtropical and tropical climatic zones*". At the end of the Wenlock, the number of originations decreases towards younger strata (Fig. 1) this maybe connected with the volcanic activity increasing considerably in the basin (Havlíček – Štorch 1990), with a temporal recovery episode during the Ludfordian (e.g. *Jarovathyris* Havlíček, 1987 appeared in this stage). Extinctions show a similar trend but slightly below the rate of origination (Fig. 1). After this "crisis" at the end of the Silurian, a new athyridid fauna originated in the Early Devonian (see Havlíček 1999). During the Pragian a clear process of recovery started; the innovation and radiation rates as well as the degree of endemism seems to be at a maximum. Forty species were discriminated by Havlíček as well as the genera *Argorhynx* Havlíček, 1992, *Cammerista* Havlíček *in* Havlíček et Vaněk, 1998, *Ceresathyris* Havlíček *in* Havlíček et Vaněk, 1998, *Iuxtathyris* Havlíček *in* Havlíček et Vaněk, 1998, and *Ufonicoelia* Havlíček 1992 appeared. The small increase in endemic species during this interval coincides with sudden innovations. The Koněprusy area turned in the Early Devonian into a moderately rising zone "*with a gradual shallowing of the sea that induced an extreme diversification of benthic organisms*" (Havlíček – Vaněk 1998). "*The lower Pragian Vinařice Limestone presents the first step in occupying the vacant ecospace by new benthic organisms, the origin of which should be sought in the Lochkovian communities of the near-by areas within the Prague Basin … due to variations in depth-relation, consolidation of deposits, and food supply, in addition of local morphology of the sea floor, the Koněprusy area presented a set of 'microniches' which induced a much higher diversity of benthic organisms in the lower part of the Koněprusy Limestone than in the lower Pragian Vinařice Limestone … the features in common to almost all 'microniches' are a warm-water, well-aerated, nutrient-rich, shallow subtidal environment in a photic zone … the Koněprusy Limestone has yielded 150 species of brachiopods which are assigned to 117 genera. The coexistence of so many taxa in an area no longer than 3 km can be explained by a differentiation of life conditions in separate 'microniches'* (see Havlíček – Vaněk 1998). Later, at the end of the Pragian and through the Emsian (see Havlíček 1998) and the Eifelian, both originations and extinctions decrease quickly. Extinctions exceeded appearances, athyridids decline rapidly in the Middle Devonian. This coincided with a considerable increase in endemic athyridid genera globally (Fig. 3, see also Alvarez – Modzalevskaya 2000, and in press). Environmental factors seem to have played an important role in this crisis (e.g. Havlíček – Vaněk 1998). This general trend in athyridid diversity in the Prague Basin broadly resembles the patterns of global diversity and rates of endemism in cosmopolitan athyridid genera and subfamilies pointed out by Alvarez – Modzalevskaya (2000, and in press).

Patterns of diversity, origination and extinctions among Bohemian athyridid species

Viewed at the species level, athyridid diversity peaked between 426.1 and 424 Ma, 415.1 and 410.7 Ma, and between 396.3 and 390.4 Ma. These intervals correspond to the late Wenlock (Homerian), the late Ludlow (Ludfordian), and the Early Devonian (Pragian) respectively (Fig. 1, Tab. 1). The curve showing the average number of species displays a similar trend (Fig. 1). Athyridid species diversity declines at the end of both the Wenlock–Ludlow, and drops dramatically from the late Pragian to Givetian. The system was never very close to dynamic equilibrium (Fig. 1). Normalized extinction rates show a small peak in the Llandovery (Aeronian), a strong increase during the Wenlock, followed by a drastic decline at the end of this series (Fig. 1). There was a gradual increase in the normalized extinction rate from the early to late Ludlow, followed by a gradual decline to the Early Devonian (Lochkovian). The curve shows a clear peak in the Pragian, and continuous decrease through the late Early and Middle Devonian. The probability of extinction shows a higher peak in the Aeronian, but the other three peaks in the late Wenlock, late Ludow and Pragian are smoothed out (Fig. 1). The normalized extinction rate is highest in the late Wenlock and Pragian, but this is matched by the origination rates. Originations show three peaks: in the Wenlock (Homerian) between 426.1 and 424 Ma, in the Ludlow (Ludfordian) between 415.1 and 410.7 Ma, and the Early Devonian (Pragian) between 396.3 and 390.4 Ma (Fig. 1). The curve of normalized origination rates also shows three clear declines: in the late Wenlock, the late Ludlow, and from late Pragian to Givetian. The probability of origination curve shows the first two peaks clearly, a new peak in the Lochkovian, and the last one not in the Pragian but in the Emsian. The turnover rate curve (Fig. 2) shows that diversity at the species level decreases in the Přídolí and Eifelian.

Conclusions

With the genera and species data provided by Havlíček in his articles and monographs, and at the level here considered (stage), general diversity, extinction, origination and turnover patterns (Figs 1, 2, Tab. 1) show a considerable resemblance with the patterns of global diversity outlined by Alvarez – Modzalevskaya (2000, and in press) for the whole order. Especially noteworthy is the high diversity, extinction and origination rates, both normalized and probabilistic, in the Pragian, and at the end of both the Wenlock – Ludlow. The normalized turnover rates (*sensu* Olsen – Suess 1986), or the 'density' of total change show maxima in the Pragian, early Wenlock and late Ludlow (Fig. 2). Several recovery processes took place. For example, in the late Ludlow, with the appearance of several species of *Jarovathyris*; and in the Early Devonian (Pragian) with the appearance of the endemic genera *Argorhynx*, *Cammerista*, *Ceresathyris*, *Iuxtathyris* and *Ufonicoelia*. These recovery episodes were associated with a high degree of endemism in the faunas (Fig. 3). Considering the

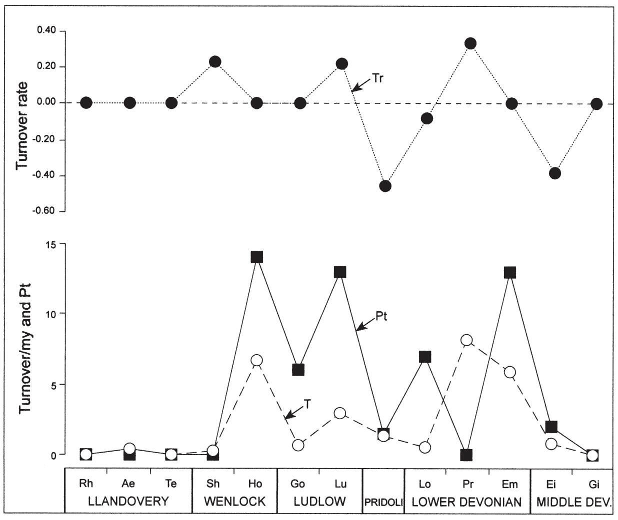

Fig. 2 Turnover/million years *T* (dashed line), turnover rate *Tr* (Or-Er) (line of points); and probabilistic turnover rate *Pt* [(number of originations + no. of originations)/number of species entering an interval from the previous interval] (solid line) of athyridid species in the Prague Basin. Abbreviations as in Fig. 1.

Table 1 Diversity, extinction, origination, and turnover data for athyridid species in the Prague Basin. Abbreviations: E – extinctions; O – originations; C – continuing; No – total number; En – entering; Na – average number of species; D – duration of stage; Er – extintion rate; Or – origination rate; T – turnover; Pe – probabilistic extinction rate; Po – probabilistic origination rate; Pt – probabilistic turnover rate; Tr – turnover rate. Abbreviations of unit names as in Fig. 1.

	E	O	C	No	En	Na	D	Er	Or	T	Pe	Po	Pt	Tr
Rh	0	0	0	0	0	0	2.10	0.00	0.00	0.00	–	–	–	0.00
Ae	1	1	0	1	0	1	4.30	0.23	0.23	0.47	1.00	–	–	0.00
Te	0	0	0	0	0	0	2.20	0.00	0.00	0.00	–	–	–	0.00
Sh	0	1	0	1	0	1	4.30	0.00	0.23	0.23	0.00	–	–	0.23
Ho	7	7	0	8	1	7	2.10	3.33	3.33	6.67	0.88	7.00	14.00	0.00
Go	3	3	0	4	1	3	8.90	0.34	0.34	0.67	0.75	3.00	6.00	0.00
Lu	6	7	0	8	1	7	4.40	1.36	1.59	2.95	0.75	7.00	13.00	0.23
(P)	2	1	0	3	2	2	2.20	0.91	0.45	1.36	0.67	0.50	1.50	–0.45
Lo	4	3	0	4	1	4	12.20	0.33	0.25	0.57	1.00	3.00	7.00	–0.08
Pr	23	25	0	25	0	24	5.90	3.90	4.24	8.14	0.92	–	–	0.34
Fm	13	13	0	15	2	13	4.40	2.95	2.95	5.91	0.87	6.50	13.00	0.00
Ei	3	1	0	3	2	2	5.20	0.58	0.19	0.77	1.00	0.50	2.00	–0.38
Gi	0	0	0	0	0	0	3.40	0.00	0.00	0.00	–	–	–	0.00

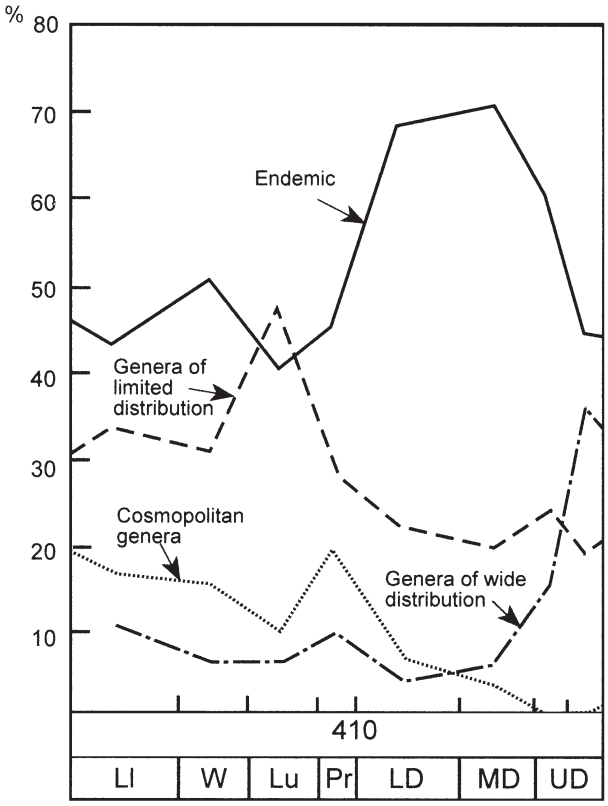

Fig. 3 Rate of endemism and cosmopolitanism among late Early Palaeozoic athyridid genera: endemics, distributed in one area; genera of limited distribution (in 2–3 listed areas); genera of wide distribution (in 4–9 listed areas); 'cosmopolitan' genera (present in more than 9 areas). Areas: 1 – North Europe (Britain, Baltic, Norway);2 – Central Europe (Bohemia, Germany, Poland); 3 – South Europe (France, Italy, Spain); 4 – North Africa (Morocco, Mauritania); 5 – Iran; 6 – Urals; 7 – Siberia; 8 – Kazakhstan; 9 – Central Asia; 10 – North China; 11 – South China; 12 – Greenland; 13 – North America; 14 – South America; 15 – Australia, New Zealand. Abbreviations: Ll – Llandovery; W – Wenlock; Lu – Ludlow; Pr – Přídolí; LD – Early Devonian; MD – Middle Devonian; UD – Late Devonian.

probabilistic turnover, there are peaks in the late Wenlock (Homerian), late Ludlow (Ludfordian), and two in the Early Devonian (Lochkovian and Emsian), with the lowest point on the turnover rate curve during the Přídolí (Fig. 2) coinciding with a strong decline in originations. Alvarez – Modzalevskaya (2000, and in press) suggested, the cessation of originations could have been more important in the crisis than an elevated extinction rate.

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Dynamiky vývoje athyridních brachiopodů v pražské pánvi podle údajů z prací Vladimíra Havlíčka

Na základě údajů z článků a monografií Vladimíra Havlíčka jsou sledovány dynamiky vývoje diverzity athyridních brachiopodů v barrandienu (pražská pánev, Česká republika). Pro zjištění obecných směrů vývoje athyridních brachiopodů na druhové úrovni byla studována celková diverzita, vymírání, vznik a změny této skupiny od llandoveru do středního devonu.