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Early Jurassic (Pliensbachian) brachiopod biogeography in the western Tethys: the Euro-Boreal and Mediterranean faunal provinces revised.

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Abstract

The Pliensbachian brachiopod biogeography of the western Tethyan region and the Euro-Boreal vs. Mediterranean faunal provinciality is evaluated. The data base was developed from improved and mostly revised taxonomical data of 25 Pliensbachian brachiopod occurrences selected from Europe and North Africa. The revised list and presence-absence data of 405 Pliensbachian brachiopod species formed the taxonomic units of the numerical analysis based on similarity coefficients. Cluster analysis (hCA) carried out from the Jaccard and Raup-Crick coefficient data showed clear dichotomy between the Euro-Boreal and Mediterranean brachiopod biochores. Principal coordinates (PCO) technique and non-metric multi-dimensional scaling (NMDS), complemented with the minimal spanning trees, resulted in similar grouping of the Pliensbachian brachiopod faunas. In de-trended correspondence analysis (DCA), besides the clearly separated Euro-Boreal and Intra-Mediterranean units, the Peri-Mediterranean assemblage formed a discrete scatter between the two major biochores. The three Algerian faunas (Ouar, Trar, Ksou) appear in a somewhat marginal position within the Euro-Boreal province. The above Pliensbachian brachiopod biochores reveal very high degree of endemicity, probably related to the limited dispersal potential of brachiopods. From the complete data set distinctive Euro-Boreal and Mediterranean species, ten from both provinces, were selected. Distinctive Euro-Boreal morphological groups are the ribbed spiriferinids, whereas some rhynchonellid and terebratulid morphotypes with expanded anterior margins characterize the Mediterranean Province. In the Early Jurassic Tethyan palaeogeography, the marked dichotomy between the Euro-Boreal and Mediterranean provinces is interpreted in terms of deep-sea/oceanic barriers, which isolated the intra-Tethyan microcontinent from the European and African shelf regions. Geographical position and local environmental factors caused the differentiation of the Peri-Mediterranean subprovince along the north-western margin of the microcontinent. This palaeobiogeographical unit formed an interface between the Intra-Mediterranean and the Euro-Boreal biochores.

Keywords: Early Jurassic; Tethys; Brachiopoda; biochores; palaeogeography.

1. Introduction

The principles of the Jurassic palaeobiogeography of the Tethyan region have been set a century ago when the two major units have been defined by Neumayr (1883: “Boreal” versus “Equatorial” Zones) and by Uhlig (1911: “Boreal Reich” versus “Mediterranean Reich”). The subject, as part of a complex attempt at biochore classification, was recently summarized and evaluated by Westermann (2000a; 2000b). The definition of Jurassic palaeobiogeographical units were based chiefly on the distribution of ammonoid faunas and the ammonoid matters were exhaustively documented and discussed in the last decades (Donovan, 1967; Géczy, 1973, 1984; Dommergues, 1983; Cariou et al., 1985). Recently, comprehensive, numerical studies on the Euro-Boreal and Mediterranean ammonoid palaeobiogeography were also presented (Dommergues et al., 2009; Dera et al., 2011). The middle Early Jurassic (Pliensbachian) appeared as suitable to demonstrate the provinciality of the Tethyan marine fossil groups because then, at first time in the Mesozoic, the “Boreal” vs. Tethyan” differentiation reached the realm level (Westermann, 2000b).

The remarkable patterns of brachiopod distribution in the western part of the Early Jurassic Tethys and their implications to the palaeogeography were recognized long ago by Ager (1967, 1971, 1973, 1986); and the subject was analyzed and discussed in details by the present author in a series of former papers (Vörös, 1977, 1980, 1984, 1987, 1988, 1993). These works used mostly the simple occurrence data of characteristic brachiopod taxa; numerical methods were only partially applied. In their conclusions, the above authors separated the Mediterranean Province from the contemporaneous Euro-Boreal Province (called NW-European in those publications) and outlined their area of distribution in Europe and partly in North Africa. As for the Jurassic palaeogeography, Ager (1980, 1986) placed the Mediterranean fauna to and around the “Adriatic microplate”, and, as a somewhat similar solution; Vörös (1980, 1987, 1993) introduced the concept of the “Mediterranean microcontinent” as the homeland of the brachiopods of Mediterranean faunal character. In both interpretations the NW European brachiopod province was confined to the European shelf and epicontinental areas, plus some regions in the Balkans and/or in North Africa in the Early Jurassic.

Although many of the above conclusions are still regarded as valid, the more than two decades progress in science gives reason to re-evaluate the subject of the Early Jurassic brachiopod biogeography in the western Tethys. A revision of this kind seems to be justified particularly by the following reasons. (1) New attempts at classification in paleobiogeography, with special attention to the formal nomenclature of Mesozoic marine faunal realms/biochores were published (Westermann, 2000a, 2000b; Manceñido, 2002; Cecca and Westermann, 2003). (2) Comprehensive softwares of palaeontological statistics (PAST) became widespread, facilitating the use of numerical methods in comparative palaeobiogeograhy (Hammer et al., 2001). (3) Recently, several new, well illustrated publications and monographic descriptions appeared, greatly improving the knowledge of the Early Jurassic brachiopod faunas both in the Euro-Boreal (France: Alméras et al., 2010; Alméras and Fauré, 2000, 2013; Germany: Höflinger, 2012; Northern Spain: Comas-Rengifo et al., 2006; Serbia: Ruban et al., 2015), and in the Mediterranean provinces (Subbetic zone: Baeza-Carratalá, 2008, 2013; Northern Calcareous Alps: Siblík, 2003, 2008; Bakony Mts.: Vörös, 2009).

It is worth mentioning also that, after more than two decades pause, the subject of the palaeobiogeography of Tethyan Jurassic brachiopods emerged again, although in a somewhat specified approach or in limited framework, e.g. in context of the similarity of the NW-Caucasian fauna (Ruban and Vörös, 2015) and of the palaeobiogeographical changes in the Serbian terranes (Ruban et al., in press) and around the Iberian region (Andrade et al., 2016; Baeza-Carratalá et al., in press). These studies evaluate mainly the faunas of transitional zones between the Euro-Boreal and Mediterranean provinces. For comparative studies of this kind (which are anticipated in the near future) it is crucial to have a firm knowledge on the faunal (taxonomical) content of the two major west-Tethyan palaeogeographical units and to formulate their updated definition. Therefore, a re-evaluation of the Early Jurassic Euro-Boreal and Mediterranean brachiopod provinces and the numerical assessment of their similarity versus difference seem to be reasonable and well-timed.

2. Data and methods

For the purpose of the numerical comparison, 25 occurrences of Pliensbachian brachiopod faunas were selected from the area of Europe and North Africa (Algeria) (Fig. 1). The major criteria of the selection were: (1) an approximately complete coverage of the investigated areas with Pliensbachian sedimentary outcrops; (2) nearly equal representation of the occurrences with Euro-Boreal versus Mediterranean faunal character; (3) large size of the faunas (more than 20 species each), for the sake of the statistical confidence; and (4) proper documentation of the respective faunas with current taxonomical revision. The two latter criteria need some further explication.

Large sized faunas were preferred because the numerical methods of faunal similarity use presence-absence data; therefore a comparison of small faunas to much larger ones may produce rather misleading results. The palaeontological literature on Pliensbachian brachiopods comprises hundreds of items with a wide spectrum of species numbers from one to nearly one hundred. In the data base of the present study the lower limit was drawn at faunas containing at least 20 species.

Proper documentation of a brachiopod fauna means photographical illustration of the brachiopod species in the taxonomical paper or monograph. In the case of recent publications by well-trained brachiopod specialists this circumstance guarantees the correct taxonomy. The data of many older monographs were revised by the present author by studying the original specimens in the respective collections (museums). In a few publications by authentic authors, the lists of brachiopod species were not fully illustrated; in these cases the authenticity of the data source was relied upon the respective author.

The above limitations somewhat restricted the scope of the study. Some important Pliensbachian faunas of low number of species, e.g. in Gibraltar (Owen and Rose, 1997); Tunisia (Fauré et al., 2007); Calabria (Taddei Ruggiero and Vörös, 1987) or Portugal (Comas-Rengifo et al., 2015), and some old monographic materials with no up-to-date revision, e.g. in northwestern France (Deslongchamps, 1862, 1862-1885), Alsace-Lorraine (Haas and Petri, 1882), or eastern Algeria (Dareste de la Chavanne, 1920), regrettably were not involved to the present study.

The 25 selected Pliensbachian brachiopod occurrences are listed below, in a kind of geographical order, with their acronyms (used in Figs. 1-5), short remarks on the locality, number of brachiopod species and the literature sources.

England (**Engl**). Including all four faunal regions studied by Ager (1956) from South-western England to the Hebrides (United Kingdom). 66 species. Davidson (1851-1852, 1876-1878); Ager (1956a, 1956-67b).

Southern Germany (**SGer**). Numerous localities in the Swabian and Franconian Albs, Alpine localities excluded. 73 species. Höflinger (2012).

Jura Mts. (**Jura**). Diverse localities in the Swiss and partly in the French Jura. 24 species. Sulser (1999).

Massif Armoricain (**MArm**). Several localities along the southern margin of the Armorican Massif (France). 24 species. Alméras et al. (2010).

Southern France (**SFra**). Numerous localities along the southern margin of the Massif Central, including Quercy and Ardèche. 30 species. Alméras & Elmi (1987); Alméras & Fauré (2013).

Pyrenees (**Pyre**). Numerous localities along the Pyrenean Chain, both in the French and in the Spanish sides. 51 species. Alméras and Fauré (2000).

Northern Spain (**NSpa**).Many localities along the Iberian Range, mostly in Lleida (Lérida) and Guadalajara provinces. 36 species. Delance (1969); Comas-Rengifo and Goy (1975); Calzada (1981); Comas-Rengifo et al. (2006).

Subbetic Zone (**Subb**). Several localities in the eastern part of the Betic Range (Spain). 66 species. Baeza-Carratalá (2008, 2013).

Western Sicily (**WSic**). The localities Erice, S. Anna and Chiusa Sclafani (Palermo province, Italy). 53 species. Gemmellaro (1874); Di Stefano (1891); revised by the author.

Central Appennines (**CApp**). Several localities in the Umbrian Ranges (Umbria and Marche provinces, Italy). 71 species. Zittel (1869); Canavari (1880, 1881, 1883-1884); Principi (1910); Revised by Vörös (1994).

Toscana (**Tosc**). Monte Pisano and Monte Calvi (Toscana province, Italy). 34 species. (Fucini 1895, 1897); revised by the author.

Gozzano (**Gozz**). Single locality in the Lombardian Alps (Piemonte province, Italy). 31 species. Parona (1880, 1893); Sacchi Vialli and Cantaluppi (1967); revised by the author.

Arzo (**Arzo**). Single locality in the Lombardian Alps (Ticino province, Switzerland). 21 species. Parona (1885) (revised by the author); Sulser and Furrer (2005).

Trento Zone (**Tren**). Several localities from the Garda Lake to Cortina d'Ampezzo (Trento, Vicenza and Belluno provinces, Italy). 45 species. Schauroth (1865);, Böse and Schlosser (1900); Haas (1912); Benigni (1978); partly revised by the author.

Salzkammergut (**Salz**). Localities Schafberg, Sommeraukogel and Mitterwand (Oberösterreich, Austria). 48 species. Böse (1898); Siblík (2003, 2008); partly revised by the author.

Kostelec (**Kost**). Single locality in the Western Carpathians (Pieniny Klippen Belt, Slovakia). 24 species. Siblík (1965, 1966, 1967a, 1967b, 1968); partly revised by the author.

Inner West Carpathians (**WCar**). Several localities in the Tatric and Fatric units of the West Carpathians, Slovakia). 22 species. Pevný (1964); Siblík (1964, 1967a, 1967b, 1968); partly revised by the author.

Bakony (**Bako**). Several localities in the Bakony Mountains (Transdanubian Range, Hungary). 86 species. Vörös (2009).

Mecsek and Villány (**MeVi**). Localities in the Mecsek and Villány Hills in southern Transdanubia, Hungary. 27 species. Vörös (1997).

Apuseni (**Apus**). Localities in Pădurea Craiului and Someşul Cald regions in the Apuseni Mountains (Transylvania, Romania). 25 species. Preda (1967); Mantea et al. (1981); partly revised by the author.

Eastern Serbia (**Serb**). Localities in the Getic and Danubian units in eastern Serbia. 50 species. Ruban et al. (2015).

Western Greece (**WGre**). Several localities along the Ionian islands and Epirus (Greece). 31 species. Manceñido (1993).

Ouarsenis (**Ouar**). Single locality in the Tell Atlas (northern Algeria). 34 species. Tchoumatchenco (1994); Alméras et al. (2007).

Traras (**Trar**). Localities in the Traras and Rhar Roubaine Mountains, Tell Atlas (northwestern Algeria). 24 species. Alméras et al. (2007).

Ksour (**Ksou**). Localities in the western and eastern Ksour Mountains, Saharian Atlas (Algeria). 22 species. Alméras et al. (2007).

The above localities provided 424 Pliensbachian brachiopod species representing 78 genera. The names of the uncertainly identified species (with cf.) were taken into account. On the other hand, the names published with open nomenclature, i.e. aff. (*affinis*) or ex gr. (*ex* *gruppo*), were omitted from the revised data base because they refer obviously to different species, with ambiguous attribution.

The revised list of the 405 Pliensbachian brachiopod species forming the taxonomic units of the analysis is given in Table 1. together with their distribution in the Euro-Boreal and Mediterranean biochores. The complete data set with presence-absence data is shown in the supplementary electronic file. This data base is significantly more reliable and accurate than those used previously for numerical comparison of the major brachiopod provinces (Vörös, 1977, 1980, 1984). Recently, many of the most important Euro-Boreal faunas were revised and published by the same authors (Alméras and Elmi, 1987; Alméras and Fauré, 2000; Alméras et al., 2007, 2010; Alméras and Fauré, 2013). Similarly, the majority of the Mediterranean faunas were revised and/or recently published by the present author (Vörös, 1994, 2009). Thus the degree of subjectivity of many different authors is reduced and the data base of the present work is expected to be more or less consistent, and as homogeneous as possible.

The palaeobiogeographic patterns were surveyed for the entire Pliensbachian Stage because the overwhelming majority of the brachiopod species are long-ranging, many of them running from the Sinemurian to the Pliensbachian (Alméras, 1964; Vörös, 1983; Vörös and Dulai, 2007). Significant turnover appears only at the end of the Pliensbachian (Garcia Joral et al. 2011, Baeza-Carratalá, 2013). Therefore further stratigraphical division of the Pliensbachian brachiopod fauna was not reasonable.

The faunal distinctions were investigated using Q-mode cluster (hCA) and various ordination analyses. These techniques are recommended by the PAST software package (Hammer et al., 2001) and most of them were successfully used by palaeobiogeographical studies on Triassic (Brayard et al., 2007, 2009) and Jurassic ammonoids (Dommergues et al., 2009; Dera et al., 2011). All computations were performed with PAST 2.17c (Hammer et al., 2001).

From the incidence matrix of the Pliensbachian brachiopod species the similarity coefficients Jaccard, Kulczynski, Simpson and Raup-Crick were computed. Clustering was done by unweighted pair-group average (UPGMA) algorithm from each coefficient. This method generated dendrograms with groups of localities according to their faunal similarity and outlined the main faunal provinces. In addition, the ordination techniques PCO (Principal coordinates) and NMDS (Non-metric multidimensional scaling) were applied to all four similarity coefficients. In all scatters the minimal spanning trees (MST) were superposed as visual aids in grouping close points. Both in clustering and in ordination techniques, the use of the Jaccard and Raup-Crick coefficients appeared the most helpful, partly in accordance with the recommendation by Hammer et al. (2001). Finally, correspondence analysis (CA) and detrended correspondence analysis (DCA) were performed on the entire presence-absence matrix of the Pliensbachian brachiopod species.

3. Results

The Jaccard, Kulczynski, Simpson and Raup-Crick similarity coefficient values computed from the incidence matrix of the Pliensbachian brachiopod species at 25 localities show regular difference between the Euro-Boreal and Mediterranean units (see in supplementary electronic file).

Cluster analysis (hCA) carried out from the Jaccard and Raup-Crick coefficient data resulted in dendrograms showing clear dichotomy between the Euro-Boreal and Mediterranean brachiopod biochores (Fig. 2A-B). Further provincialism within the

Mediterranean unit is shown primarily by the Raup-Crick dendrogram (Fig. 2B) where three assemblages (CApp, Bako and Salz) form a cluster clearly split from the rest. The Greek fauna (WGre), on a separate branch of the larger cluster, seems to be in transitional position. The other, larger Mediterranean cluster comprises the Alpine and Sicilian faunas and also the south Iberian assemblage (Subb), in both dendrograms. The Euro-Boreal cluster is rather homogeneous, exceeding the 0.75 threshold in the Raup-Crick similarity coefficient value. Only two of the Algerian faunas (Ouar, Ksou) are somewhat separated in both dendrograms (Fig. 2A-B), whereas the third Algerian fauna (Trar) is integrated to the major part of the Euro-Boreal group.

Fig. 2C-D show the results of the principal coordinates (PCO) technique, based on the Jaccard and Raup-Crick coefficients. Arbitrarily drawn ellipses emphasize that the Euro-Boreal cluster is well separated from the Mediterranean in both plots. The Mediterranean assemblage is portrayed here by two, somewhat overlapping ellipses: one Mediterranean (s.s.), with the faunas Salz, Bako, CApp, Tren and possibly WGre and another, comprising the Carpathian, Lombardian, Sicilian faunas plus Tosc and Subb. The minimal spanning trees (MST) offered by PAST (Hammer et al. 2001) are also shown and help to envisage the closest faunistical relationships within and between the provinces and subprovinces. In the Jaccard plot (Fig. 2C), the interprovincial connection is between SFra (southern France) and Gozz (Piemonte), whereas in the Raup-Crick plot (Fig. 2D) it appears between Gozz (Piemonte) and Trar (Algeria).

Non-metric multidimensional scaling (NMDS) resulted in also distinct clusters (Fig. 2E-F). The grouping of Pliensbachian brachiopod faunas (indicated by ellipses) is very similar to that shown by the PCO method: a discrete and consistent Euro-Boreal province and two, partly overlapping ellipses representing the two subprovinces within the Mediterranean province are visible. The minimal spanning trees (MST) display rather similar networks as in the case of the PCO plots; the scatter of the individual faunas within the provinces seem to be expanded and the distances between them are more discernible. The possible relays between the two main provinces are also visible.

Fig. 3. shows the results of the de-trended correspondence analysis (DCA) performed on the data base of the Pliensbachian brachiopod species. The Euro-Boreal and the Mediterranean assemblages are differentiated along the axis 1. The polygon embracing the Euro-Boreal assemblages stretches near axis 2, only the three Algerian faunas (Ouar, Trar, Ksou) are in somewhat remote position (encircled in Fig. 3). The Mediterranean (s. s.) faunas lie the farthest from axis 2 (between 4.34 and 5.26), while the other Mediterranean faunas appear as a separate scatter in the middle of the plot, a discrete unit forming a kind of interface or transition between the major provinces.

4. Discussion

4.1. Western Tethyan brachiopod biochores

The scatter and grouping of faunas by de-trended correspondence analysis (DCA) in itself would suggest a triple provincialism among the Pliensbachian brachiopod faunas of the western Tethys. However, considering the results of the other ordination techniques (PCO, NMDS) and clustering (hCA) one can conclude that two main biochores existed: one rather coherent Euro-Boreal and another, Mediterranean province. The latter can be further divided into the Intra-Mediterranean (Mediterranean s.s.) and the Peri-Mediterranean subprovinces. (In a previous paper (Vörös, 1987) the subprovincial names “Appennino-Transdanubian” and “Carpatho-Sicilian” were applied to more or less the same partial biochores.) Following the above categorization, the provincial characters of the individual faunas are indicated by consistent symbols: open lozenges for Euro-Boreal and black dots and lozenges for Intra-Mediterranean and Peri-Mediterranean faunas, respectively (Figs. 2-4).

The clear dichotomy seen in the cluster analysis (Fig. 2A, B) delineates the Euro-Boreal and the Mediterranean provinces and roughly corresponds to a reasonable pattern of distribution on a present-day geographical map (Fig. 4). However, a few, apparently anomalous occurrences appear in both provinces. The present geographical position of the Subbetic fauna (Subb) of Mediterranean character is very far from the rest of the Mediterranean province. Even more contrasting is the case of the Serbian and two intra-Carpathian faunas (Serb, Apus, MeVi); these localities lie adjacent to the Mediterranean province, but their faunas are definitely Euro-Boreal. These substantial contradictions reappear in all other similarity analyses (Figs. 2C, D, E, F and 3).

The situation of the north Algerian faunas (Trar, Ouar, Ksou) is also unusual. Considering the regular latitudinal partitioning of Jurassic faunas (e.g. Dera et al., 2011), according to their southern position they may be expected to belong to the Mediterranean province. On the contrary, the similarity analyses (clustering, PCO, NMDS) render them to the Euro-Boreal province. In de-trended correspondence analysis (Fig. 3) they appear in marginal position within the Euro-Boreal scatter, but the present data base does not seem enough to formulate a discrete subprovince.

The minimal spanning trees generated by PCO and NMDS analyses reveal also some intriguing relationships. The Euro-Boreal plots form rather close networks in both similarity coefficients and in both analyses, except the two Algerian faunas (Ouar, Ksou) which stand a little far from the rest in the MNDS spanning trees. Within the Mediterranean assemblage, the situation of the western Greek fauna (WGre) seems ambiguous in the PCO plots (Fig. 2C-D) because it falls to the ellipse of the Peri-Mediterranean group and the minimal spanning line connects it to the Gozzano (Gozz) fauna. On the other hand, in the NMDS plots (Fig. 3E-F) appears as a integral part of the Intra-Mediterranean subprovince directly linked to the Appenninic (CApp) fauna.

In the Jaccard PCO plot (Fig. 2C), the Euro-Boreal and Mediterranean (Peri-Mediterranean) networks are linked between SFra (southern France) and Gozz (Piemonte), whereas in the Raup-Crick PCO plot (Fig. 2D) the interprovincial connection appears between Gozz (Piemonte) and Trar (Algeria). The possible relays between the two main provinces seems to be the same in the NMDS plots. Considering their present-day (and possible Jurassic) geographical situation, the interprovincial connection of Gozzano to Southern France is much more likely than to Traras (Algeria).

The most useful method to delineate the Pliensbachian brachiopod biochores in the western Tethys is offered by the de-trended correspondence analysis (DCA) (Fig. 3). In this approach the distinction between the Euro-Boreal and the Mediterranean assemblages is very clear. The Euro-Boreal province is rather coherent, except three Algerian faunas (Ouar, Trar, Ksou) which are in a somewhat marginal position towards the Mediterranean assemblages. The Intra-Mediterranean faunas form a distinct group (Bako, CApp, Salz, Tren), definitely including the western Greek fauna (WGre) as well. The Peri-Mediterranean faunas appear as a separate scatter in the middle of the plot, in a transitional, but isolated position between the major provinces.

4.2. Endemicity

On the basis of the comprehensive data set in Table 1, the Pliensbachian brachiopod species number data and the number of endemic species in the above defined west-Tethyan palaeobiogeographical units are summarized in Table 2. Following the widespread practice in biogeography, recapitulated by Westermann (2000a, p. 6), the degree of endemicity is expressed in percentage of endemic species in the respective biochore. The scale of rank quantification suggested by Westermann (2000a) is the following: Realm >75% of species are endemic; Subrealm 50–75%; Province 25–50%; Subprovince 10–25%. If we apply this scale to our data (Table 2), the Mediterranean (s.l.) unit (77%) would be rated as Realm, the Euro-Boreal (70%) and Intra-Mediterranean (58%) units would be at the rank of Subrealm and even the Peri-Mediterranean unit (27%) would reach the level of the Province. This would severely confront the widespread, traditional practice, where all above biochores (mostly at province or subprovince rank) are subordinate units of the Tethyan Realm.

The anomalously high degree of endemicity revealed by the Pliensbachian brachiopod faunas may be the result of their rather limited dispersal potential. Brachiopods, being sessile organisms, can migrate only by means of their planktonic larvae; the free-swimming period of life of articulate (Rhynchonelliform) brachiopod larvae is usually only a few hours, and this short time allows a very limited dispersal (Ager, 1986; Vörös, 1987, 1988, 1993). Apparently, brachiopods are more prone to be endemic than many other groups of marine organisms. Therefore, in spite of the high values of endemicity in Table 2, it is advisable to keep the ranks of the western Tethyan brachiopod biochores at the widely used scheme, i.e. keep the names Euro-Boreal Province and Mediterranean Province.

4.3. Distinctive and cosmopolitan species

The complete data set with presence-absence data of 405 Pliensbachian brachiopod species at 25 localities allows to select a series of species whose record is restricted to one of the main provinces. These may be called distinctive Euro-Boreal and Mediterranean species, respectively. (The Mediterranean Province was not subdivided into subprovinces in this part of the analysis.) The distinctive species are defined as present in at least five localities in the respective province and absent in the other province. On the other hand, many species were recorded frequently in both provinces; these may be regarded as cosmopolitan in distribution.

Table 3. shows the list of ten distinctive species by each province; the cosmopolitan species are listed as well.

The selection of the distinctive species listed in Table 3. was based on objective criteria, yet, the high number of records may be subjectively biased in a few cases, especially among the cosmopolitan taxa. Some species of smooth brachiopod genera, as of *Lobothyris* or *Liospiriferina*, but even of the ribbed *Gibbirhynchia*, are very widely interpreted by many palaeontologists and are willingly identified, even if some degree of uncertainty arises. Nevertheless the record of a few distinctive species can be very useful in finding out the palaeobiogeographical affinity of small faunas, i.e. in the cases of localities with limited number of species, where a detailed analysis is not possible (Vörös, 1984, 1988, 1993).

The lists of distinctive species comprise some remarkable taxa with special, partly adaptive morphology. Distinctive Euro-Boreal morphological types are the ribbed spiriferinids, notably *Dispiriferina oxyptera* (Buvignier) and *Callospiriferina verrucosa* (Buch). They are frequent in the Euro-Boreal but missing from the Mediterranean faunas. On the other hand, some of the smooth spiriferinids: *Liospiriferina obtusa* (Oppel) and *L. gryphoidea* (Uhlig) are abundant in the Mediterranean province but were not recorded in the Euro-Boreal assemblages. It was previously recognized that some peculiar Pliensbachian brachiopods, e.g. the “axiniform” (=axe-shaped) morphotypes with expanded anterior margin are markedly frequent in the Mediterranean Province (Ager, 1965, 1967; Vörös, 1987, 1993, 2005). In the present study this morphological group is represented by *Prionorhynchia flabellum* (Gemmellaro), *Securina partschi* (Oppel) and *Securithyris adnethensis* (Suess); these distinctive Mediterranean taxa seem to be absent from the Euro-Boreal Province.

4.4. Palaeogeographical interpretation

The faunistical data of the present study were tentatively plotted onto a few, widely known Early Jurassic palaeogeographical maps or plate tectonic reconstructions (e.g. Stampfli and Borel, 2002; Golonka, 2004; Stampfli and Kozur, 2006). The resulted distributions appeared at least as conflicting as they were seen in the case of the present-day geographical map (see Fig. 4). The contradictions were the most obvious for the Subbetic (Subb) and the Serbian and two intra-Carpathian faunas (Serb, Apus, MeVi).

In the second step, a different, newly constructed Early Jurassic palaeogeographical sketch was used as base map, and the results of the present study, i.e. the provincial characters of the 25 selected Pliensbachian brachiopod occurrences and their minimal spanning network were plotted on it (Fig. 5).

This base map is a strongly modified version of the Toarcian map by Dercourt et al. (2000), or, rather it is an amalgamation of this map with the Early Jurassic Tethys sketch maps by Vörös (1993, 2002, 2005). The central element of this palaeogeographical scheme is a complex microcontinent in the internal part of the western Tethys Ocean, isolated from the European and African shelves. This picture corresponds to the concept of the “Mediterranean microcontinent” as outlined by the present author (Vörös, 1980, 1984, 1988, 1993, 2005). In these papers the problems of barriers, filters and stepping stones governing the distribution of Tethyan Jurassic brachiopods were also discussed in length. The microcontinent is the homeland of the Mediterranean Province whereas the Euro-Boreal Province is confined to the European and north African epicontinental and shelf seas. The isolation between the main provinces is established by narrow belts of deep sea which serve as barriers or partly filters in the dispersal of brachiopods.

The area of the Mediterranean microcontinent was dominated by shallow subtidal carbonate platforms and surrounding deep subtidal carbonate ramps and slopes; intervening deeper marine basins and submarine horsts were also frequent. Fine-grained siliciclastic sedimentation occurred only subordinately along the north-western rim (Channell et al., 1979; D'Argenio et al., 1980; Vörös, 1987; Dercourt et al., 2000). On the other hand, the European and African shelf seas were characterized by siliciclastic sediments in the Early Jurassic (Dercourt et al., 2000). Moreover, the typical Mediterranean brachiopod morphotypes were claimed to be specially adapted to deeper environments with reduced food supply (Ager, 1965, 1967; Vörös, 1986, 2005). The above circumstances may suggest that the provincial separation of the Mediterranean biochore might partly be due to palaeoenvironmental factors.

No matter which factor was decisive in separation of the two main biochores, the symbols of Euro-Boreal versus Mediterranean faunas in Fig. 5 clearly outline the provinces. The open lozenges of the Euro-Boreal faunas spread over the European epicontinental and shelf regions, whereas the black symbols of the Mediterranean faunas are confined to the intra-Tethyan microcontinent. The minimal spanning network, drawn after the non-metric multidimensional scaling results, based on the Jaccard index data (Fig. 2E), gives a quite reasonable system of connecting links between the faunas of the respective provinces.

The territory of the intra-Tethyan Mediterranean microcontinent palaeogeographically was further divided by deeper, narrow belts or basins. These might facilitate further differentiation between the Intra-Mediterranean and Peri-Mediterranean subprovinces. In the palaeogeographical map (Fig. 5) the Peri-Mediterranean faunas are distributed along the north-western margin of the intra-Tethyan microcontinent. This belt was somewhat isolated by a narrow deep sea basin from the rest of the microcontinent and, due to its transitional geographical position, as a row of stepping stones, it helped the dispersal of brachiopod larvae. From palaeobiogeographical point of view it formed an interface between the Intra-Mediterranean and the Euro-Boreal biochores. This idea is apparently supported by the minimal spanning network, based on the Jaccard index data (Fig. 5), where the connecting link between the two main provinces is seen between Southern France (SFra) and the western part of the Southern Alps (Gozz). It has to be mentioned that the minimal spanning network executed from the Raup-Crick coefficient data resulted in another connecting link, between Gozz and Trar (Algeria). In both cases, the intermediate role of the Peri-Mediterranean subprovince is obvious.

In this palaeogeographical reconstruction the localities/faunas, which were seen in odd positions in the present-day geographical map (Fig. 4), attain their more realistic place. In this way the Mediterranean-type Subbetic fauna (Subb), as part of the Alboran unit, joins the Mediterranean microcontinent. Two intra-Carpathian (MeVi, Apus) and the Serbian (Serb) faunas of Euro-Boreal character, are in a proper position along the European shelf, closely connected to the south-French (SFra) fauna. The substantially Euro-Boreal character of the three, rather southerly lying, Algerian faunas (Trar, Ouar, Ksou) is reasonable, considering that the African and European shelf environment was continuous at this time and facilitated the free migration of brachiopods.

5. Conclusions

The present study confirms with quantitative methods the existence of the markedly different Pliensbachian brachiopod biochores in the western Tethyan region. The numerical analyses, i.e. the ordination techniques (PCO, NMDS) and clustering (hCA) endorsed that two main biochores existed: one rather coherent Euro-Boreal and another, Mediterranean province. The latter can be further divided into the Intra-Mediterranean (Mediterranean s.s.) and the Peri-Mediterranean subprovinces, as proved by the de-trended correspondence analysis (DCA). The minimal spanning trees/networks and the de-trended correspondence analysis shows that three Algerian faunas (Ouar, Trar, Ksou) are in a somewhat marginal position within the Euro-Boreal province.

The Pliensbachian brachiopod biochores reveal very high degree of endemicity (Euro-Boreal = 70%, Mediterranean (s.l.) = 77%, Intra-Mediterranean = 58%, Peri-Mediterranean = 27%). This anomalously high endemicity is obviously related to the very limited dispersal potential of brachiopods.

From the complete data set (presence-absence data of 405 Pliensbachian brachiopod species at 25 localities) a series of species were selected whose record is restricted to one of the main provinces. These, ten species from both provinces, were called distinctive Euro-Boreal and Mediterranean species, respectively. Further five species, recorded frequently in both provinces, were termed as cosmopolitan in distribution. Distinctive Euro-Boreal morphological types are the ribbed spiriferinids, whereas some rhynchonellid and terebratulid morphotypes with expanded anterior margins are particularly frequent in the Mediterranean Province.

In the present interpretation, the marked palaeobiogeographical differentiation of the Euro-Boreal and Mediterranean provinces was caused by deep-sea/oceanic barriers, which isolated an intra-Tethyan microcontinent from the European and African shelf regions. In this palaeogeographical picture the distribution of the Euro-Boreal vs. Mediterranean faunas brachiopod faunas forms a reasonable pattern and clearly outlines the provinces. The Euro-Boreal faunas spread over the European and north African epicontinental and shelf seas, whereas the Mediterranean brachiopod assemblages are confined to the Mediterranean microcontinent. The large carbonate platforms of the Mediterranean microcontinent were subdivided by intervening deeper marine basins and submarine horsts; this facilitated the differentiation of the Peri-Mediterranean subprovince along the north-western margin of the microcontinent. This margin, facing the European shelf, might form an interface between the Intra-Mediterranean and the Euro-Boreal biochores.

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Figure captions

Fig. 1. Locality map of the 25 Pliensbachian brachiopod occurrences considered in the present work. Acronyms: **Engl:** England, **SGer:** Southern Germany, **Jura:** Jura Mts., **MArm:** Massif Armoricain, **SFra:** Southern France, **Pyre:** Pyrenees, **NSpa:** Northern Spain, **Subb:** Subbetic Zone, **WSic:** Western Sicily, **CApp:** Central Appennines, **Tosc:** Toscana, **Gozz:** Gozzano, **Arzo:** Arzo, **Tren:** Trento Zone, **Salz:** Salzkammergut, **Kost:** Kostelec, **WCar:** Inner West Carpathians, **Bako:** Bakony Mts., **MeVi:** Mecsek and Villány Mts., **Apus:** Apuseni Mts., **Serb:** Eastern Serbia, **WGre:** Western Greece, **Ouar:** Ouarsenis, **Trar:** Traras Mts., **Ksou:** Ksour Mts. Further explanation in the text

Fig. 2. Dendrograms and plots portraying the similarity relationships between the 25 Pliensbachian brachiopod faunas. **A, B.** Dendrograms resulting from hierarchical cluster analyses (hCA) computed from Jaccard (**A**) and Raup-Crick (**B**) coefficients; **C, D**. Plots of the principal coordinates (PCO) analysis from Jaccard (**A**) and Raup-Crick (**B**) coefficients, with faunal networks computed using minimal spanning trees; **E, F.** Plots of the non-metric multidimensional scaling (NMDS) analysis from Jaccard (**A**) and Raup-Crick (**B**) coefficients, with faunal networks computed using minimal spanning trees. Acronyms as in Fig. 1

Fig. 3. Plot of the de-trended correspondence analysis (DCA) applied to the Pliensbachian brachiopod data matrix. Eigenvalue/gradient length are: Axis 1: 0.78/5.26, Axis 2: 0.45/3.24. Legend: same as in Fig. 2. Note the clear distinction between the Euro-Boreal and Intra-Mediterranean assemblages, as well as the intermediate position of the Peri-Mediterranean faunas. The Algerian faunas (marginal within the Euro-Boreal assemblage) are circled. Legend as in Figs. 1 and 2

Fig. 4. Map showing the palaeobiogeographical characters of the 25 Pliensbachian brachiopod faunas considered in the present work. Legend as in Figs. 1 and 2

Fig. 5. Early Jurassic palaeogeographical map of the western Tethyan region showing the distribution and provincial character of the 25 Pliensbachian brachiopod faunas and their possible connections by minimal spanning network. Base map combined from Dercourt et al. (2000) and Vörös (1993; 2002)

Cover Letter, for Editor only

The Editor
Palaeogeography, Palaeoclimatology, Palaeoecology
Elsevier

January, 25, 2016

Dear Editor,

Attached please find the electronic files of a digitally submitted manuscript titled ”*Early Jurassic (Pliensbachian) brachiopod biogeography in the western Tethys: the Euro-Boreal and Mediterranean faunal provinces revised*”, by Attila Vörös, to be considered for publication in *Palaeogeography, Palaeoclimatology, Palaeoecology*

Therein I analyze the palaeobiogeography of Pliensbachian brachiopods from the western Tethys by advanced numerical comparative methods. Previous authors, including myself, dealt with this subject decades ago. A re-evaluation seems to be justified particularly by the following reasons. (1) New attempts at classification in paleobiogeography, with special attention to the formal nomenclature of Mesozoic marine faunal realms/biochores were published. (2) Comprehensive softwares of palaeontological statistics became widespread, facilitating the use of numerical methods in comparative palaeobiogeograhy. (3) Recently, several new, well illustrated publications and monographic descriptions appeared, greatly improving the knowledge of the Early Jurassic brachiopod faunas both in the Euro-Boreal, and in the Mediterranean provinces. The data base includes revised taxonomical data of 25 Pliensbachian brachiopod occurrences from Europe and North Africa. The presence-absence data of 405 Pliensbachian brachiopod species are the basis of the numerical analysis. Cluster analysis, principal coordinates technique and non-metric multi-dimensional scaling, complemented with the minimal spanning trees carried out from the Jaccard and Raup-Crick coefficient data showed clear dichotomy between the Euro-Boreal and Mediterranean brachiopod biochores. In de-trended correspondence analysis the Peri-Mediterranean assemblage formed a discrete scatter between the two major biochores. The above Pliensbachian brachiopod biochores reveal very high degree of endemicity, due to the limited dispersal potential of brachiopods. Distinctive Euro-Boreal morphological groups are the ribbed spiriferinids, whereas some rhynchonellid and terebratulid morphotypes with expanded anterior margins characterize the Mediterranean Province. The marked dichotomy between the Euro-Boreal and Mediterranean provinces is interpreted in terms of deep-sea/oceanic barriers, which isolated the intra-Tethyan microcontinent from the European and African shelf regions in Early Jurassic. The Peri-Mediterranean subprovince is defined as an interface between the Intra-Mediterranean and the Euro-Boreal biochores. I believe that my results will be of interest to the broad readership of Palaeogeography, Palaeoclimatology, Palaeoecology.

I have no other recently published or in press works on related topics.

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I hope that you will find my contribution worthy of consideration for publication in *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Yours sincerely,

Attila Vörös

Highlights

- Pliensbachian brachiopod biogeography analyzed by numerical methods.
- Three Pliensbachian brachiopod biochores outlined in the western Tethys.
- The endemicity of brachiopod biochores was extremely high.
- Deep-sea barriers caused the Euro-Boreal versus Mediterranean dichotomy.

Figure_1
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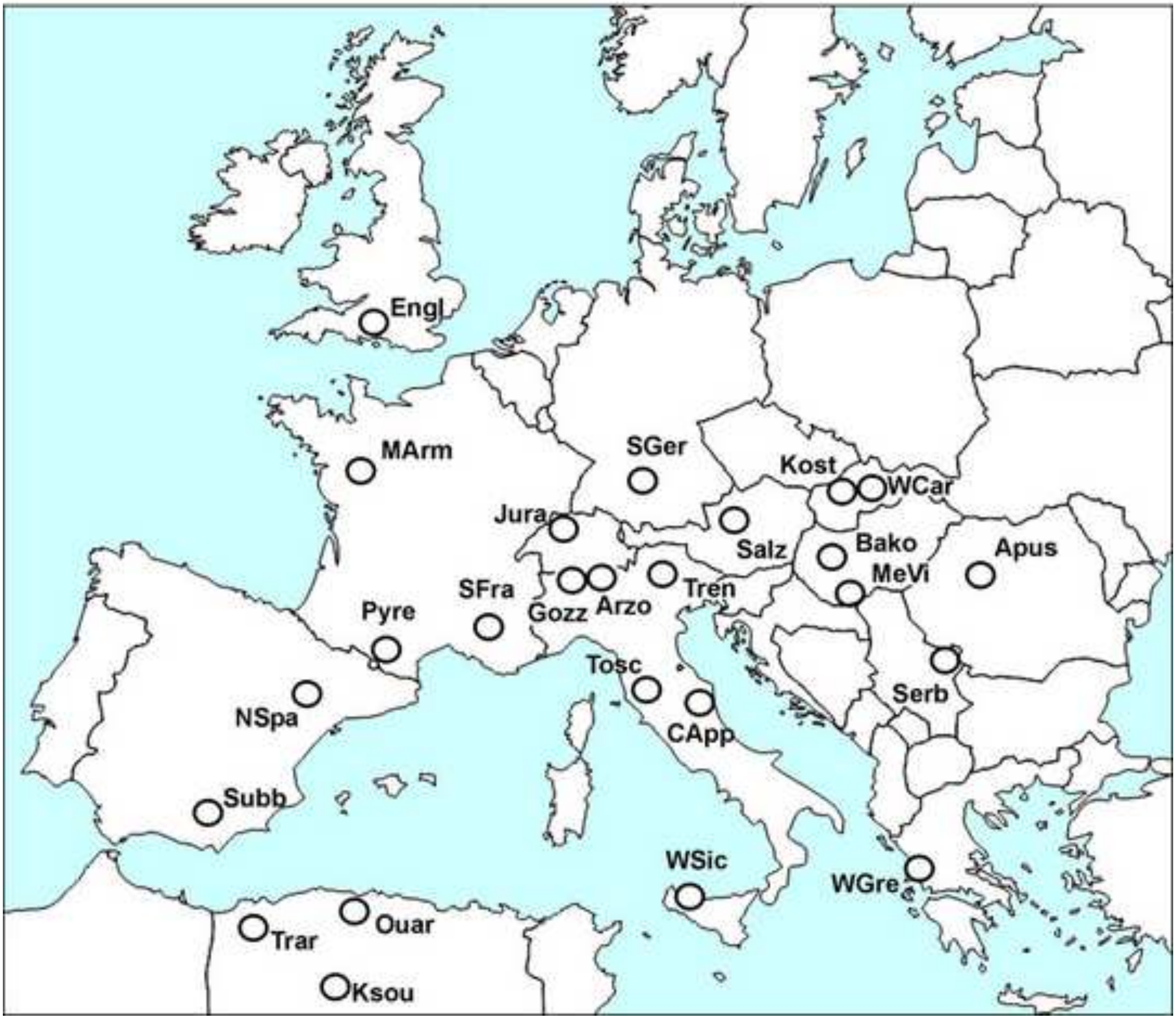
Fig. 1. (Voros) 1.5-column - color online only



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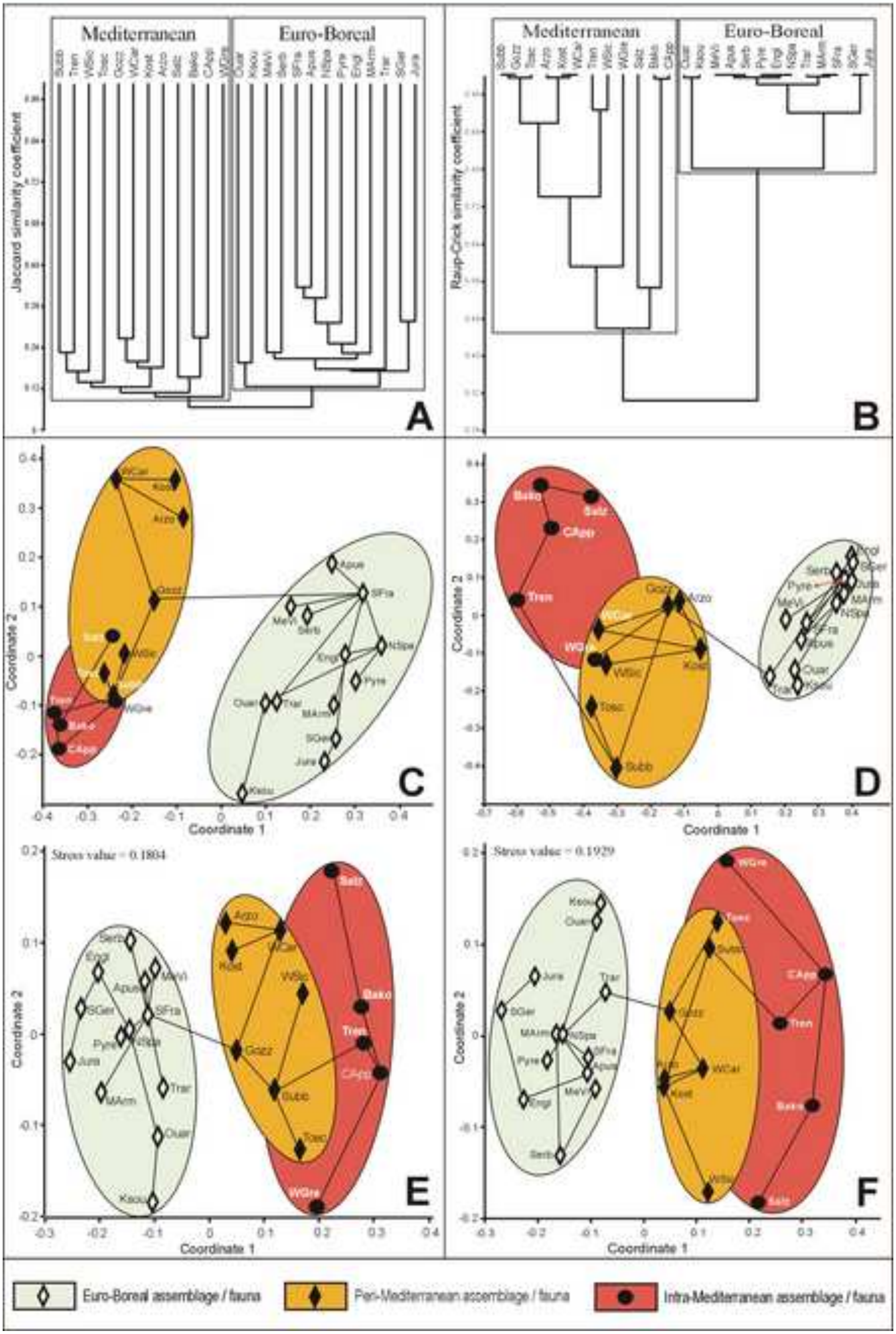

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Fig. 3. (Voros)

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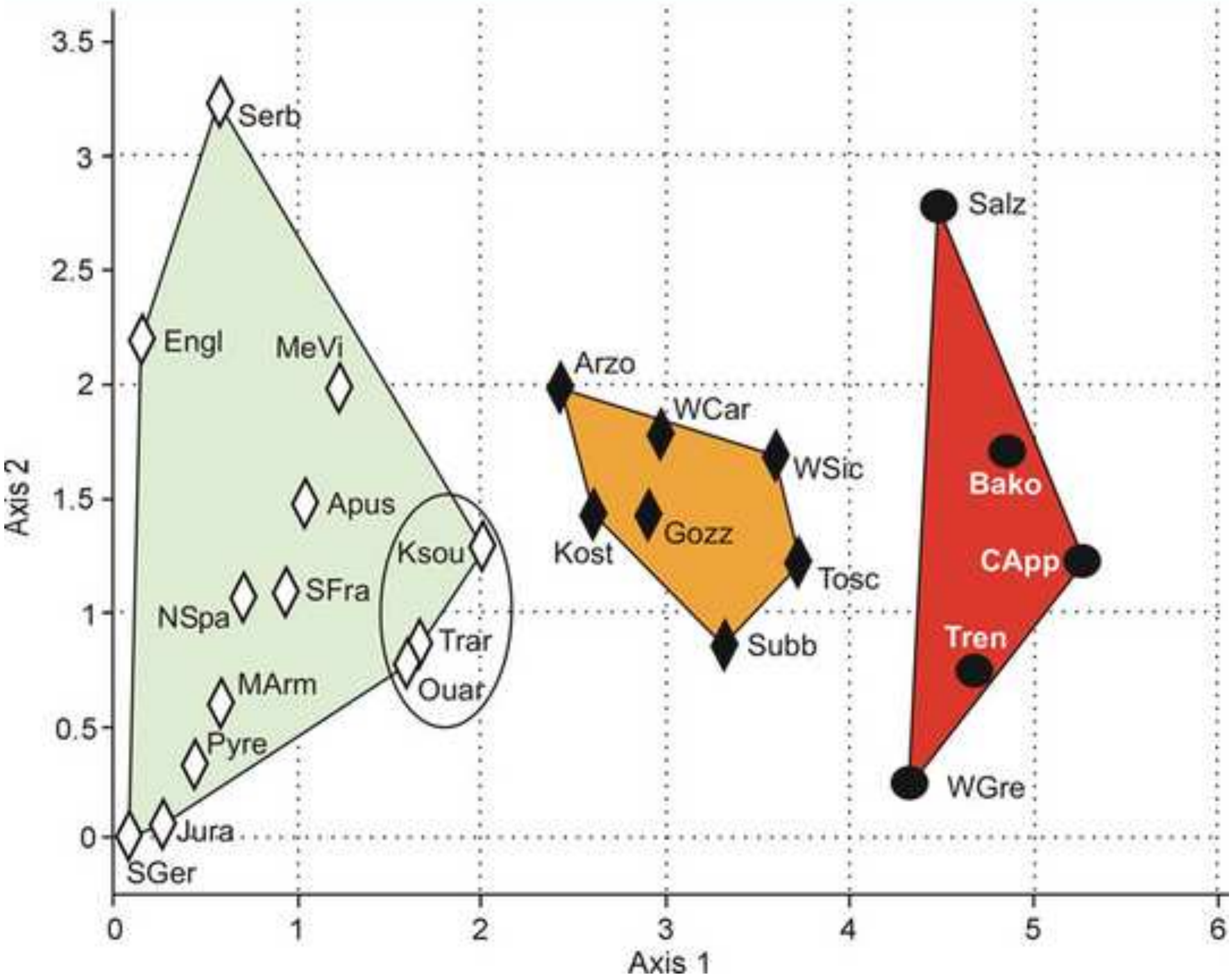

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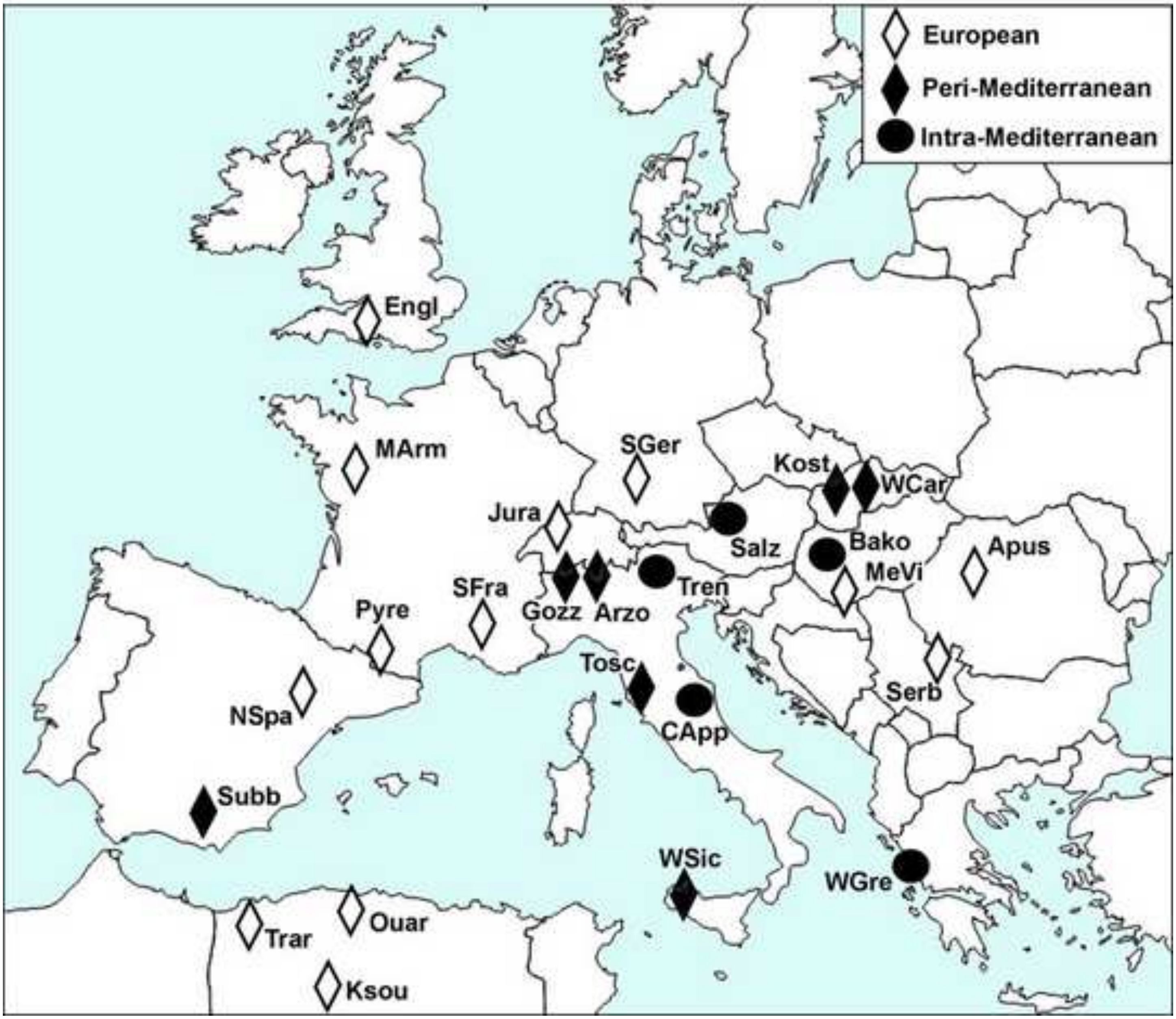
Fig. 4 (Voros) 1.5-column - color online only



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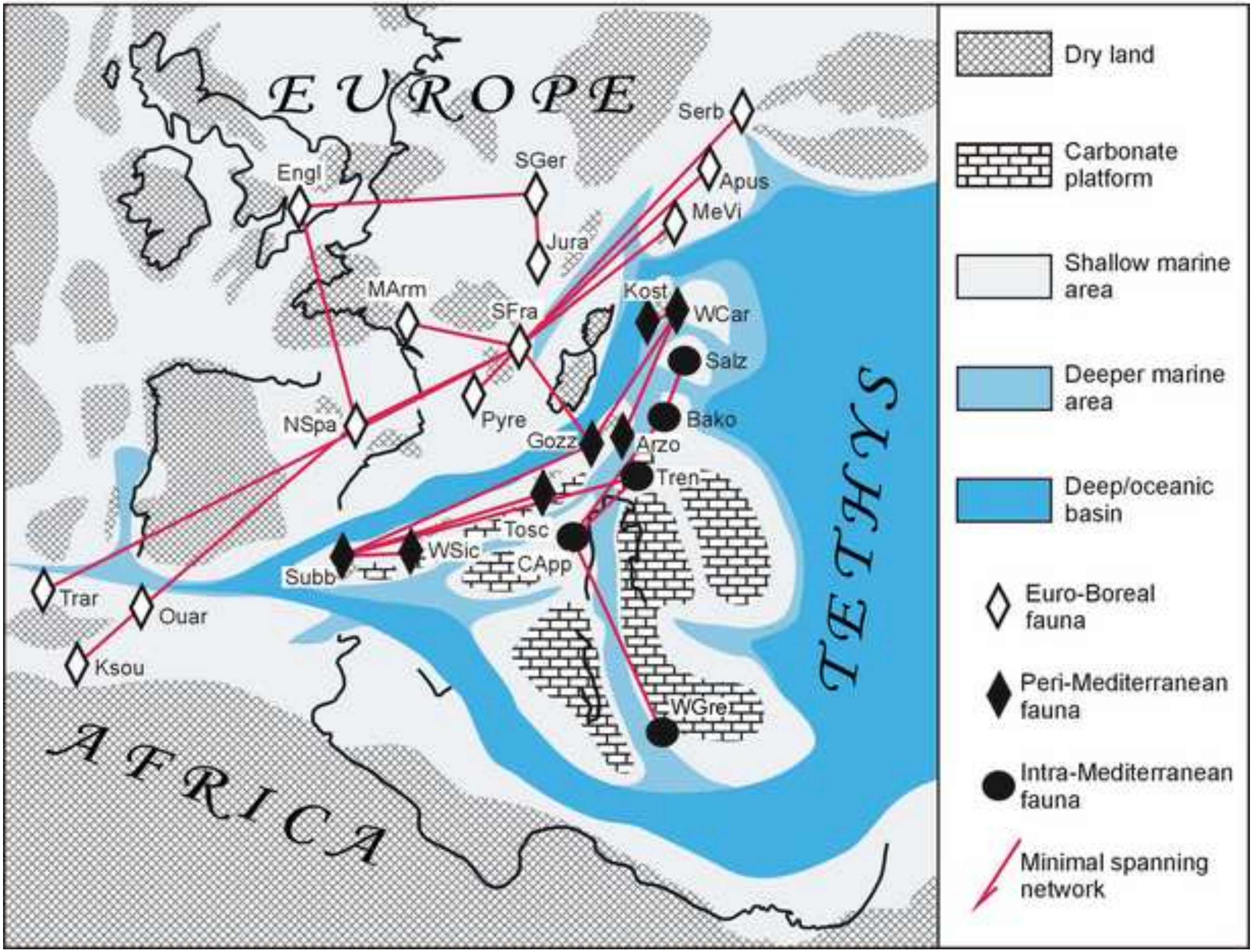

Table 1. List of Pliensbachian brachiopod species and their distribution in west-Tethyan palaeobiogeographical units

	Euro-Boreal	Mediterranean	Intra-Mediterranean	Peri-Mediterranean
Alebusirhynchia jorali Baeza-Carratalá		x		x
Amphiclinodonta bittneri Böse		x	x	
Amphiclinodonta liasina Bittner		x	x	
Antiptychina ? rothpletzi (Di Stefano)		x	x	x
Apringia barnabasi Vörös		x	x	
Apringia deltoidea (Canavari)		x	x	
Apringia diptycha (Böse)		x	x	x
Apringia margaritati (Böse)		x	x	
Apringia mariottii (Zittel)		x	x	
Apringia paolii (Canavari)		x	x	x
Apringia piccininii (Zittel)		x	x	x
Apringia stachei (Böse)		x	x	
Arzonella exotica (Sulser)		x		x
Aulacothyris ? amygdaloides (Canavari)		x	x	
Aulacothyris ? ballinensis (Haas)		x	x	
Aulacothyris florella (d'Orbigny)	x			
Aulacothyris fuggeri (Böse)		x	x	
Aulacothyris fusiformis Rollier	x			
Aulacothyris iberica Dubar	x			
Aulacothyris moorei (Davidson)	x			
Aulacothyris pyriformis (Tate)	x	x		x
Aulacothyris reclusa (Quenstedt)	x			
Aulacothyris resupinata (J. Sowerby)	x			
Austriellula ? renzi Mancenido		x	x	
Bakonyithyris apenninica (Zittel)	x	x	x	x
Bakonyithyris avicula (Uhlig)		x	x	
Bakonyithyris elegantula (Haas)		x	x	
Bakonyithyris gastaldii (Parona)		x		x
Bakonyithyris meneghinii (Parona)		x	x	x
Bakonyithyris ovimontana (Böse)		x	x	x
Bakonyithyris pedemontana (Parona)		x	x	x
Buckmanithyris cornicolana (Canavari)		x	x	
Buckmanithyris nimbata (Oppel)	x			
Cadomella moorei (Davidson)	x			
Cadomella quenstedti Rau	x			
Calcirhynchia ? cornicolana (Canavari)		x	x	
Calcirhynchia ? hungarica (Böckh)		x	x	x
Calcirhynchia ? zugmayeri (Gemmellaro)		x	x	x
Calcirhynchia latecostata (Rollier)	x			
Calcirhynchia ? mendax (Fucini)		x		x
Calcirhynchia plicatissima (Quenstedt)		x		x
Calcirhynchia rotunda Sučić-Protić	x			
Calcirhynchia sanctihilarii (Böse)	x	x	x	
Calcirhynchia subdiscoidalis (Böse)		x	x	
Calcirhynchia subpectiniformis (Böse)		x	x	
Calcirhynchia subserrata (Roemer)	x			
Callospiriferina bosniaskii (Canavari)		x	x	
Callospiriferina gillieroni (Haas)	x			
Callospiriferina haueri (Suess)	x	x		x
Callospiriferina laevigata (Quenstedt)	x			
Callospiriferina tumida (Buch)	x	x		x
Callospiriferina verrucosa (Buch)	x			
Callospiriferina villosa (Quenstedt)	x			
Carinatothyris canavarii (Parona)		x	x	
Carinatothyris carinata (Haas)		x	x	
Cincta conocollis (Rau)	x			
Cincta kerastis Delance	x			
Cincta numismalis (Lamarck)	x	x	x	x
Cincta peiroi Baeza-Carratalá		x		x
Cincta subquadrifida (Oppel)	x			
Cirpa planifrons (Ormős)		x		x
Cirpa ? subfurcillata (Böse)		x	x	
Cirpa ? variabilis (Schlotheim)	x	x	x	x
Cirpa ? latissima (Fucini)		x		x
Cirpa ? eleutheria (Di Stefano)		x		x
Cirpa briseis (Gemmellaro)	x	x	x	x
Cirpa fronto (Quenstedt)	x			
Cirpa iphimedia (Di Stefano)		x	x	x
Cirpa langi Ager	x			

Cirpa major (Rau)	x			
Cirpa minor (Rau)	x			
Cirpa slovenica Siblík		x		x
Cirpa subcostellata (Gemmellaro)	x	x	x	
Cisnerospira adscendens (Deslongchamps)		x		x
Cisnerospira angulata (Oppel)	x	x	x	x
Cisnerospira darwini (Gemmellaro)		x	x	x
Cisnerospira gibba (Seguenza)		x		x
Cisnerospira graeca (Renz)		x	x	
Cisnerospira meneghiniana (Canavari)		x	x	
Cisnerospira sylvia (Gemmellaro)		x		x
Cisnerospira zignoi (Di Stefano)		x		x
Cuersithyris davidsoni (Haime)	x			
Cuersithyris radstockiensis (Davidson)	x			
Cuneirhynchia ? palmata (Oppel)		x	x	
Cuneirhynchia cartieri (Oppel)	x	x		x
Cuneirhynchia dalmasi (Dumortier)	x	x	x	x
Cuneirhynchia lacuna (Quenstedt)	x			
Cuneirhynchia oxynoti (Quenstedt)	x			
Cuneirhynchia persinuata (Rau)	x			
Cuneirhynchia rastuensis Benigni		x	x	x
Cuneirhynchia retusifrons (Oppel)	x	x	x	x
Cuneirhynchia serbiensis Sučić-Protić	x			
Dispiriferina davidsoni (Deslongchamps)	x			
Dispiriferina oxygonia (Deslongchamps)	x	x		x
Dispiriferina oxyptera (Buvignier)	x			
Dispiriferina segregata (Di Stefano)		x	x	x
Eplenyithyris cerasulum (Zittel)		x	x	x
Eplenyithyris ? taramellii (Gemmellaro)		x	x	
Exceptothyris expressa Sučić-Protić	x			
Fimbriothyris guerangeri (Deslongchamps)	x			
Fimbriothyris ? tranzensis (Dal Piaz)		x	x	
Fenyveskutella pseudouhligi Vörös		x	x	
Fenyveskutella theresiae Vörös		x	x	
Fenyveskutella vighi Vörös		x	x	
Furcirhynchia cotteswoldiae (Upton)	x			
Furcirhynchia furcata Buckman	x			
Furcirhynchia furcillata (Theodori)	x	x		x
Furcirhynchia ilminsterensis Ager	x			
Furcirhynchia laevigata (Quenstedt)	x			
Furcirhynchia melvillei Ager	x			
Gibbirhynchia ? cf. urkutica (Böckh)		x	x	x
Gibbirhynchia ageri (Rousselle & Bisch))	x			
Gibbirhynchia amalthei (Quenstedt)	x			
Gibbirhynchia curviceps (Quenstedt)	x	x	x	x
Gibbirhynchia gibbosa Buckman	x			
Gibbirhynchia liasica (Reynes)	x			
Gibbirhynchia lua (Di Stefano)	x			
Gibbirhynchia micra Ager	x			
Gibbirhynchia muirwoodae Ager	x			
Gibbirhynchia nerina (D'Orbigny)	x			
Gibbirhynchia northamptonensis (Davidson)	x			
Gibbirhynchia orsinii (Gemmellaro)	x	x	x	x
Gibbirhynchia reyi Alméras & Fauré	x			
Gibbirhynchia sordellii (Parona)	x	x	x	x
Gibbirhynchia thorncombiensis (Buckman)	x			
Gibbirhynchia tiltonensis Ager	x			
Gibbirhynchia tounatensis (Rousselle & Bisch)	x			
Grandirhynchia grandis Buckman	x			
Grandirhynchia laevigata Buckman	x			
Hesperithyris ? cf. costata (Dubar)		x	x	
Hesperithyris atlantis (Dubar)				
Hesperithyris renierii (Catullo)		x	x	
Hesperithyris sinuosa (Dubar)				
Hesperithyris termieri (Dubar)				
Holcorhynchia meneghinii (Zittel)		x	x	
Holcorhynchia yakacikensis Ager	x			
Homoeorhynchia ? lubrica (Uhlig)		x	x	x
Homoeorhynchia ? ptinoides (Di Stefano)		x	x	x
Homoeorhynchia acuta (Sowerby)	x	x	x	x
Homoeorhynchia capitulata (Tate)	x			
Homoeorhynchia cynocephala (Richard)	x			
Homoeorhynchia maninensis (Siblík)	x	x		x
Inaequalis dubari Sučić-Protić	x			
Ismenia suessi (Deslongchamps)	x			
Jakubirhynchia ? cf. laevicosta (Geyer)		x	x	x

Jakubirhynchia ? fascicostata (Uhlig)		x	x	x
Jakubirhynchia latifrons (Geyer)		x		x
Karpatiella valeriae Sučić-Protić	x			
Kericserella inversaeformis (Schlosser)		x	x	
Koninckella bolivari (Cisneros)		x		x
Koninckella gibbosula (Gemmellaro)		x	x	x
Koninckella liasina (Bouchard)	x	x	x	
Koninckodonta davidsoni (Deslongchamps)	x	x		x
Koninckodonta eberhardi Bittner		x	x	
Koninckodonta fornicata (Canavari)		x	x	x
Koninckodonta fuggeri Bittner		x	x	
Koninckodonta geyeri (Bittner)		x	x	x
Konickodonta ionica (Renz)		x	x	
Koninckodonta sicula (Gemmellaro)		x	x	
Koninckodonta waehneri (Bittner)		x	x	x
Linguithyris aspasia (Zittel)	x	x	x	x
Linguithyris cf. linguata (Böckh)		x	x	
Linguithyris chrysilla (Uhlig)		x	x	
Linguithyris nimbata (Oppel)	x			
Liospiriferina alpina (Oppel)	x	x	x	x
Liospiriferina apenninica (Canavari)		x	x	
Liospiriferina brevirostris Oppel)	x	x	x	x
Liospiriferina cantianensis (Canavari)		x	x	
Liospiriferina cordiformis (Böse)		x	x	
Liospiriferina decipiens (Schlosser)		x	x	
Liospiriferina epirotica (Renz)		x	x	
Liospiriferina falloti (Corroy)	x			
Liospiriferina geyeri (Di Stefano)		x		x
Liospiriferina globosa (Böse)		x	x	
Liospiriferina gryphoidea (Uhlig)		x	x	x
Liospiriferina handeli (Di Stefano)	x			
Liospiriferina hartmanni (Zieten)	x			
Liospiriferina moriconii (Canavari)		x	x	
Liospiriferina nicklesi (Corroy)	x			
Liospiriferina obovata (Principi)		x	x	
Liospiriferina obtusa (Oppel)		x	x	x
Liospiriferina pichleri (Neumayr)		x	x	
Liospiriferina praerostrata (Flamand)	x			
Liospiriferina rostrata (Schlotheim)	x	x	x	x
Liospiriferina salomoni (Böse)		x	x	
Liospiriferina saximontana (Böse)		x	x	
Liospiriferina semicircularis (Böse)		x	x	
Liospiriferina sicula (Gemmellaro)		x	x	x
Liospiriferina statira (Gemmellaro)		x		x
Liospiriferina subquadrata (Seguenza)				
Liospiriferina undata (Canavari)		x	x	
Liospiriferina villosa (Quenstedt)	x			
Lobothyris ? andleri (Oppel)		x		x
Lobothyris ? ceres (Di Stefano)		x	x	
Lobothyris ? gracilicostata (Böse)		x	x	
Lobothyris ? schlosseri (Böse)		x	x	
Lobothyris ? swifti (Gemmellaro)		x	x	
Lobothyris ? uniplicata Tuluweit				
Lobothyris arcta (Dubar)				
Lobothyris clevelandensis Ager	x			
Lobothyris crassa (Dubar)	x			
Lobothyris edwardsi (Davidson)	x			
Lobothyris fusiformis (Dubar)	x			
Lobothyris lata (Dubar)	x			
Lobothyris medioliasica (Sučić-Protić)	x			
Lobothyris punctata (J. Sowerby)	x	x	x	x
Lobothyris subovoides (Deslongchamps)	x			
Lobothyris subpunctata (Davidson)	x			
Lokutella ? cuneiformis (Canavari)		x	x	
Lokutella deangelisi (Principi)		x	x	
Lokutella kondai Vörös		x	x	
Lokutella liasina (Principi)		x	x	
Lokutella palmaeformis (Haas)		x	x	x
Lychnothyris lancisi Baeza-Carratalá		x		x
Lychnothyris rotzoana (Schauroth)		x	x	x
Megapringia ? atlaeformis (Böse)		x	x	
Megapringia altesinuata (Böse)		x	x	
Megapringia stoppanii (Parona		x	x	x
Merophricus ? foetterlei (Böckh)		x	x	
Merophricus ? hypoptycha (Canavari)		x	x	
Merophricus cf. mediterraneus (Canavari)		x	x	x

Moorellina parca (Rau)	x			
Nannirhynchia ? zeina (Canavari)		x	x	
Nannirhynchia gemmellaroi (Parona)		x	x	
Nannirhynchia pillula (Schlosser)		x	x	x
Nannirhynchia pusilla (Gemmellaro)		x		x
Nannirhynchia pygmaea (Morris)	x	x		x
Nannirhynchia reynesi (Gemmellaro)		x	x	x
Nannirhynchia sinuata (Haas)		x	x	
Nannirhynchia ? cerasulum (Fucini)		x		x
Orthotoma ? heyseana (Dunker)	x	x		x
Orthotoma apenninica (Canavari)		x	x	
Orthotoma globulina (Davidson)				
Orthotoma quenstedti Buckman	x			
Orthotoma solidorostris Rau	x			
Orthotoma spinati Rau	x			
Papodina bimammata (Rothpletz)		x		x
Papodina bittneri (Geyer)		x	x	x
Paronarhynchia ? cf. verrii (Parona)		x	x	x
Paronarhynchia bulga (Parona)		x	x	x
Paronarhynchia estherae Vörös.		x	x	
Phymatothyris ? civica (Canavari)		x	x	
Phymatothyris ? consobrina (Canavari)		x	x	
Phymatothyris ? rheumatica (Canavari)		x	x	x
Phymatothyris ? rudis (Gemmellaro)		x		x
Phymatothyris ? taramellii (Gemmellaro)		x		x
Phymatothyris kerkyraea (Renz)	x	x	x	
Piarorhynchia buchi (Roemer)	x			
Piarorhynchia juvenis (Quenstedt)	x			
Piarorhynchia radstockiensis (Davidson)	x			
Piarorhynchia rostellata (Quenstedt)	x			
Piarorhynchia thalia (d'Orbigny)	x			
Piarorhynchia ? caroli (Gemmellaro)		x		x
Pirotella petkovici Sučić-Protić	x			
Pisirhynchia ? lottii (Principi)		x	x	
Pisirhynchia ? meneghinii (Zittel)		x	x	
Pisirhynchia inversa (Oppel)		x		x
Pisirhynchia pisoides (Zittel)		x	x	
Pisirhynchia retroplicata (Zittel)		x	x	
Planirhynchia parvirostris (Roemer)	x			
Planirhynchia tantilla Sučić-Protić	x			
Plesiothyris verneuili (Deslongchamps)	x	x		x
Praesphaeroidothyris cisnerosi Baeza-Carratalá		x		x
Prionorhynchia ? hagaviensis (Böse)		x	x	x
Prionorhynchia ? catharinae Vörös		x	x	
Prionorhynchia ? sejuncta (Böse)		x	x	
Prionorhynchia ? triquetra (Gemmellearo)		x	x	x
Prionorhynchia ? civininii (Fucini)		x		x
Prionorhynchia ? pavida (Fucini)		x		x
Prionorhynchia belemnitica (Quenstedt)	x			
Prionorhynchia calderinii (Parona)	x	x		x
Prionorhynchia canavarii (Fucini)	x			
Prionorhynchia cf. capellinii (Parona)		x	x	
Prionorhynchia cf. forticostata (Böckh)		x		x
Prionorhynchia flabellum (Gemmellaro)		x	x	x
Prionorhynchia greppini (Oppel)		x	x	x
Prionorhynchia guembeli (Oppel)	x	x		x
Prionorhynchia kiliani (Di Stefano)		x		x
Prionorhynchia polyptycha (Oppel)		x	x	x
Prionorhynchia pseudoscherina (Böse)		x	x	
Prionorhynchia quinqueplicata (Zieten)	x	x		x
Prionorhynchia regia (Rothpletz)	x	x		x
Prionorhynchia scherina (Gemmellaro)		x	x	x
Prionorhynchia serrata (J. de C. Sowerby)	x	x		x
Pseudogibbirhynchia ? fissicostata (Canavari)		x	x	
Pseudogibbirhynchia ? pectiniformis (Canavari)		x	x	
Pseudogibbirhynchia moorei (Davidson)	x			
Pseudokingena capellinii (Di Stefano)		x		x
Pseudokingena josephinia (Gemmellaro)		x		x
Pseudokingena deslongchampsi (Davidson)		x	x	
Quadratirhynchia attenuata (Dubar)	x			
Quadratirhynchia crassimedia Buckman	x	x		x
Quadratirhynchia quadrata Buckman	x	x		x
Rhapidothyris ? lokutica Vörös		x	x	
Rhapidothyris arciferens Tuluweit	x			
Rhapidothyris beyrichi (Oppel)		x	x	
Rhapidothyris delorenzoi (Böse)		x	x	x

Rhapidothyris ovimontana (Böse)		x	x	x
Rhapidothyris reversa (Ager)	x			
Rhynchonelloidea austriaca (Quenstedt)	x			
Rhynchonelloidea delmensis (Haas)	x			
Rhynchonelloidea lineata (Young & Bird)	x	x		x
Rimirhynchia anglica (Rollier)	x			
Rimirhynchia elevata Buckman	x			
Rimirhynchia rimosa (Buch)	x			
Rimirhynchia tardata Buckman	x			
Rudirhynchia calcicosta (Quenstedt)	x			
Rudirhynchia dubia (Sučić-Protić)	x			
Rudirhynchia fallax (Deslongchamps)	x			
Rudirhynchia huntcliffensis Ager	x			
Rudirhynchia mediterrana Sučić-Protić	x			
Rudirhynchia rudis Buckman	x			
Salgirella ? goicoecheai Baeza-Carratalá		x		x
Salgirella alberti (Oppel)	x	x		x
Scalpellirhynchia parvirostris (Roemer)	x			
Scalpellirhynchia scalpellum (Quenstedt)	x			
Securina hierlatzica (Oppel)	x	x	x	x
Securina oxygonia (Uhlig)		x	x	x
Securina partschi (Oppel)		x	x	x
Securina plicata (Geyer)		x		x
Securina pseudoxygonia (Haas)		x	x	
Securina securiformis (Gemmellaro)		x	x	x
Securithyris adnethensis (Suess)		x	x	x
Securithyris filosa (Canavari)		x	x	
Securithyris paronai (Canavari)		x	x	
Securithyris paronai (Canavari)		x	x	
Serratapringia ? cf. suetii (Haas)		x	x	
Serratapringia fraudatrix (Böse)		x	x	
Soaresirhynchia bouchardi (Davidson)	x			
Sphaeroidothyris ? naxensis (Gemmellaro)		x	x	
Spiriferina betacalcis (Quenstedt)	x			
Spiriferina muensteri (Davidson)	x	x		x
Spiriferina oppeli Rollier	x			
Spiriferina slovenica Siblík	x	x		x
Spiriferina tessoni Davidson	x			
Spiriferina tonii (Canavari)		x	x	
Spiriferina walcotti (J. de C. Sowerby)	x			
Spirifrina ? expansa (Stoppani)		x		x
Squamirhynchia squamiplex (Quenstedt)	x			
Squamirhynchia sublatifrons (Böse)	x	x	x	
Suessia liasiana (Deslongchamps)	x			
Sulcirostra alpina (Parona)		x		x
Tauromenia brevicostata (Dubar)	x			
Tauromenia itoensis (Dubar)	x			
Tauromenia polymorpha (Seguenza)	x	x		x
Tetrarhynchia ? fraasi (Oppel)		x	x	
Tetrarhynchia ? rusconii (Canavari)		x	x	
Tetrarhynchia ? zitteli (Gemmellaro)		x	x	x
Tetrarhynchia ? peristera (Uhlig)		x		x
Tetrarhynchia argotinensis (Radovanović)	x			
Tetrarhynchia dumbletonensis (Davidson)	x	x		x
Tetrarhynchia dunrobinensis (Rollier)	x			
Tetrarhynchia makridini (Sučić-Protić)	x			
Tetrarhynchia ranina (Suess)	x			
Tetrarhynchia rostrata (Sučić-Protić)	x			
Tetrarhynchia subconcinna (Davidson)	x	x		x
Tetrarhynchia tetrahedra (J. Sowerby)	x	x		x
Viallithyris ? eurydice (Fucini)		x	x	
Viallithyris ? furlana (Zittel)		x	x	x
Viallithyris ? neumayri (Haas)		x	x	
Viallithyris ? salisburgensis (Böse)		x	x	
Viallithyris ? sphenoidalis (Gemmellaro)	x	x		x
Viallithyris gozzanensis (Parona)		x	x	x
Zeilleria laboniae (Greco)				
Zeilleria livingstonei Gemmellaro		x		x
Zeilleria ? aquilina (Franceschi)		x	x	
Zeilleria ? grecoi (Fucini)		x		x
Zeilleria alpina (Geyer, x889)		x	x	
Zeilleria batilla (Geyer)	x	x		x
Zeilleria batillaeformis (Böse)		x	x	
Zeilleria bicolor (Böse)		x	x	
Zeilleria capitulata Höflinger	x			
Zeilleria catharinae Gemmellaro		x		x

Zeilleria cor (Lamarck)	x			
Zeilleria cornuta (J. de C. Sowerby)	x			
Zeilleria cossae Gemmellaro	x	x		x
Zeilleria culeiformis (Rollier)	x			
Zeilleria darwini (Deslongchamps)	x	x		x
Zeilleria elliotti Ager	x			
Zeilleria engelhardti (Oppel)		x		x
Zeilleria indentata (J. de C. Sowerby)	x	x		x
Zeilleria laboniae (Greco)	x			
Zeilleria livingstonei (Gemmellaro)		x		x
Zeilleria lycetti (Davidson)	x			
Zeilleria mariae (d'Orbigny)	x			
Zeilleria meridiana Delance	x			
Zeilleria moorei (Davidson)	x			
Zeilleria mutabilis (Oppel)	x	x	x	x
Zeilleria oenana (Böse)		x	x	
Zeilleria peybernesi Alméras & Fauré	x			
Zeilleria quadrifida (Lamarck)	x	x		x
Zeilleria quiaiosensis Choffat	x			
Zeilleria roemeri (Schloenbach)	x	x		x
Zeilleria ruthenensis (Reynes)	x			
Zeilleria sarthacensis (d'Orbigny)	x	x		x
Zeilleria sestii (Fucini)	x			
Zeilleria stapia (Oppel)	x	x		x
Zeilleria subdigona (Oppel)	x			
Zeilleria subnumismalis (Davidson)	x	x		x
Zeilleria subovalis (Roemer)	x			
Zeilleria thurwieseri (Böse)		x	x	
Zeilleria venusta (Uhlig)		x		x
Zeilleria vicinalis (Schlotheim)	x			
Zeilleria waterhousi (Davidson)	x	x		x
Zeilleria wurttembergica Rollier	x			

Table 2. Pliensbachian brachiopod species number data and endemicity of the west-Tethyan palaeobiogeographical units

	Euro-Boreal	Mediterranean	Intra-Mediterranean	Peri-Mediterranean
Number of species	199	259	178	151/
Number of endemic species	139	199	104	41
Endemicity	70%	77%	58%	27%

Table 3. Distinctive and cosmopolitan Pliensbachian brachiopod species

	Euro-Boreal occurrences	Mediterranean occurrences
Distinctive Euro-Boreal species (at least 5 occurrences)		
Lobothyris subpunctata (Davidson)	9	-
Aulacothyris resupinata (J. Sowerby)	8	-
Cirpa fronto (Quenstedt)	8	-
Gibbirhynchia amalthei (Quenstedt)	8	-
Zeilleria mariae (d'Orbigny)	8	-
Callospiriferina verrucosa (Buch)	7	-
Squamirhynchia squamiplex (Quenstedt)	6	-
Cuersithyris radstockiensis (Davidson)	5	-
Dispiriferina oxyptera (Buvignier)	5	-
Lobothyris edwardsi (Davidson)	5	-
Distinctive Mediterranean species (at least 5 occurrences)		
Prionorhynchia flabellum (Gemmellaro)	-	10
Liospiriferina obtusa (Oppel)	-	8
Viallithyris gozzanensis (Parona)	-	6
Apringia paolii (Canavari)	-	5
Eplenyithyris cerasulum (Zittel)	-	5
Liospiriferina gryphoidea (Uhlig)	-	5
Lychnothyris rotzoana (Schauroth)	-	5
Prionorhynchia scherina (Gemmellaro)	-	5
Securina partschi (Oppel)	-	5
Securithyris adnethensis (Suess)	-	5
Cosmopolitan species (at least 15 occurrences)		
Gibbirhynchia curviceps (Quenstedt)	13	5
Lobothyris punctata (J. Sowerby)	12	6
Liospiriferina alpina (Oppel)	7	10
Liospiriferina rostrata (Schlotheim)	10	7
Cirpa briseis (Gemmellaro)	5	10

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