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Paleobiogeography of Mesozoic brachiopod faunas from Andean–Patagonian areas in a global context

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Abstract

During the Mesozoic, the Andean region has played a hinging role between high- and low-latitude faunas, which are, respectively, characterized by stocks that display long-term fidelity. This paper is aimed at providing an updated review of Late Triassic to Late Cretaceous South American articulated brachiopods in the light of previous knowledge at worldwide scale. Late Triassic brachiopods from the Argentine–Chilean Andes show unmistakable Maorian (or Notal) faunal elements alongside some more cosmopolitan genera, with certain influence of Eastern Pacific taxa. By Early Jurassic times, differentiation of Tethyan and Boreal Realms became progressively evident in Europe. In South America, Hettangian–Sinemurian brachiopod faunules from the Argentinian Andes are somewhat impoverished, with mostly cosmopolitan genera showing certain affinities to Maorian species, and with the addition of some endemics later. Increasingly, diverse Pliensbachian Andean brachiopods denote close relationships to Celto-Swabian taxa, then by Domerian times, a certain degree of endemism was developed, though somewhat delayed Tethyan influences, and persistent links with New Zealand are subordinately recognizable, too; most Toarcian assemblages reveal basically Celto-Swabian and Iberian affinities as well. East-west austral links across the Pacific may have been favored by migratory routes fringing the Gondwana margin, whereas faunal exchange with the western end of the Tethys appears to reflect an intermittent shallow-marine connection through the Hispanic Corridor. During the Middle Jurassic, distinction of Tethyan and Boreal Realms was maintained in the northern Hemisphere, and the differentiation of an Ethiopian or Southern Tethyan fauna became better characterized. Aalenian and Bajocian brachiopods of the Andes display generic affinities mainly with those from western Europe, with some minor endemic developments; brachiopods recorded from the Bathonian–Callovian of Argentina (and Chile) also occur along the northern Tethyan margin, yet with some genera extending into Indo-Ethiopian areas. During the Late Jurassic, Boreal faunas from high-latitudes became even more strongly differentiated from low-latitude, Tethyan ones. Oxfordian and Tithonian brachiopods from the Andes apparently belong to genera of cosmopolitan or northern Tethyan affiliation, yet there are few elements in common with other eastern Pacific areas, such as Mexico. Early Cretaceous brachiopods, in addition to Andean basins of Chile and western Argentina, are known also from Patagonia and Tierra del Fuego. They belong mostly to widely distributed, mainly Tethyan genera, with some quasi-cosmopolitan and circum-Pacific components (some shared with Antarctica become noticeable). Late Cretaceous brachiopods from northern Patagonia show significant affinities to Maastrichtian ones of northwest Europe and central Asia, which calls for further assessing the potential role that may have played the trans-Saharan passageway in such dispersal. Broad aspects of Mesozoic brachiopod paleobiogeography are fairly well understood, yet details of ranking and naming of certain units are still in need of more agreement.

Keywords: Mesozoic; Brachiopod; Paleobiogeography; Andes; Patagonia

1. Introduction

Brachiopods, being marine benthonic organisms with brief planktonic larval stage, are sensitive to environmental distributional factors and hence suitable for biogeographical analyses. The fundamentals of paleobiogeographic patterns displayed by Mesozoic rhynchonelliform brachiopods in connection with the distribution of former paleocontinental masses and oceans were laid down and summarized in a series of bench-mark papers by Ager (1960, 1967, 1971, 1973), Ager and Walley (1977) and Ager and Sun (1989). Knowledge about South American representatives of the

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phylum from a variety of marine Mesozoic deposits has been substantially improved over the last three decades, and important advances have been similarly produced for other regions, too.

In the present contribution, the biogeographic affinities of such brachiopod faunas are reviewed on the basis of direct study of specimens housed in various museums as well as own paleontological collections, supplemented by perusal of reliable published information. Selectivity of the literature cited is unavoidable in a succinct overview like this; thus preference has been naturally given to those papers which explicitly address paleobiogeographical aspects, whilst citations strictly containing raw data have been kept to a minimum, unless they deal with Andean/Patagonian faunas. This state-of-the-art synopsis is meant to be a complement to (rather than a substitute of) Ager and Sun (1989) in which further earlier references can be found.

Repositories for illustrated material (and their respective acronyms) are as follows: Department of Invertebrate Paleontology, Natural Sciences Museum of La Plata (MLP), Paleontology Collection, Faculty of Exact and Natural Sciences, Buenos Aires University (CPBA) and Paleontology Collection, Sernageomin, Santiago de Chile (SNGM).

2. Discussion

For convenience, six successive time intervals have been considered, namely: Late Triassic, Early, Middle and Late Jurassic, and Early and Late Cretaceous, which are respectively displayed on a series of successive paleocontinental maps (Figs. 1–5). The term “biochorema” is herein used in the sense of “biochore” in Makridin (1973) and Westermann (2000a, b).

2.1. Late Triassic

This is the most favorable epoch for elucidating major patterns of Triassic brachiopod paleobiogeography, due to increased taxonomic diversity coupled with intensified geographical differentiation along the whole period, according to Dagys (1993). He (Dagis, 1974, Figs. 168–172; 1993, Fig. 1) recognized five biochoremas of first rank (i.e. realms, though it may be argued in favor of regarding them as subrealms, rather): (a) Boreal Realm/Subrealm (comprising Siberia, Primorye, Svalbard, Arctic Canada) characterized by *Canadospira*, *Viligella*, *Omolonella*, *Pseudohalorella*, *Aulacothyroides*, *Laevithyris*, *Anadyrella*. (b) Northern Tethyan Realm/Subrealm (extending from the

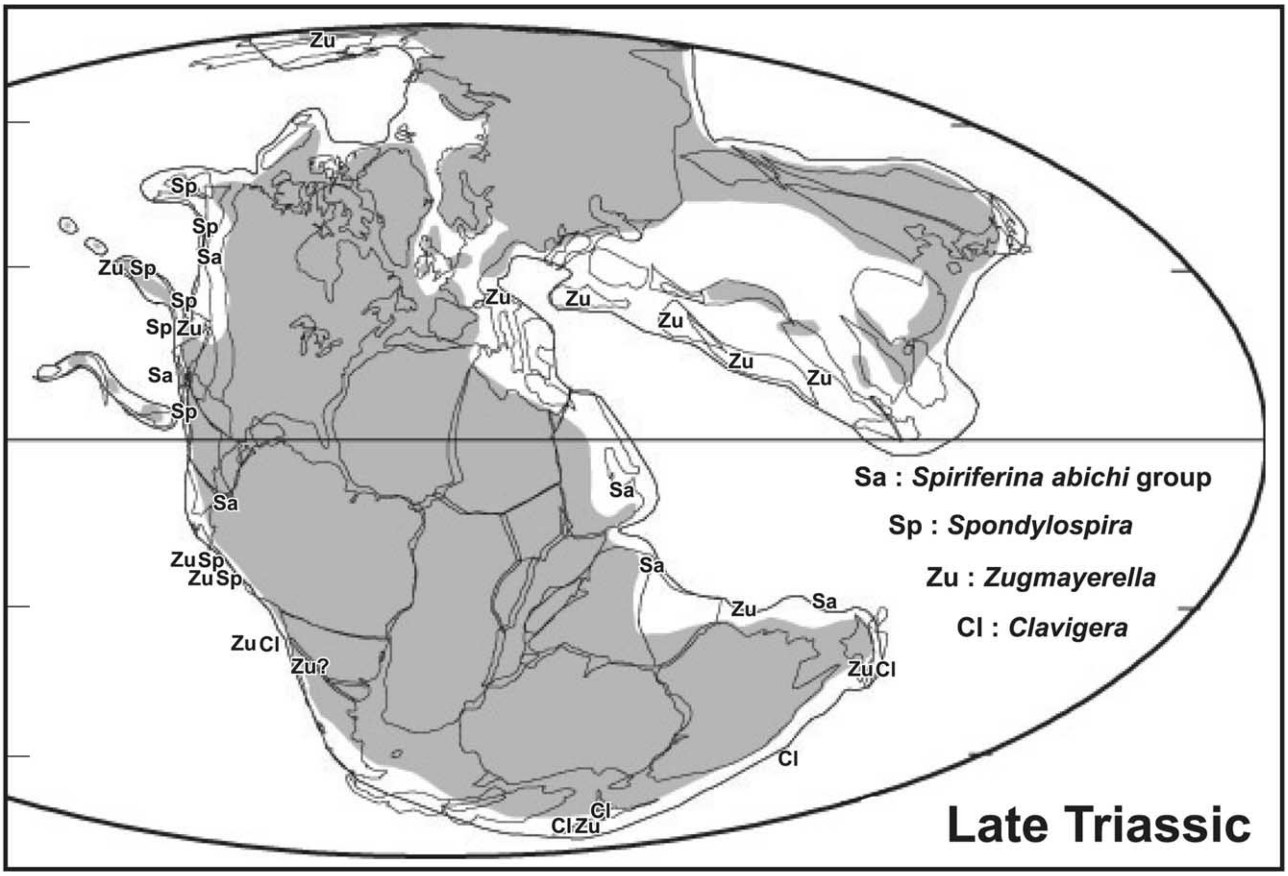


Fig. 1. Distribution of selected brachiopod genera for Late Triassic (mainly Norian–Rhaetian) times (base map after Scotese (1997), a single symbol may correspond to more than one locality).

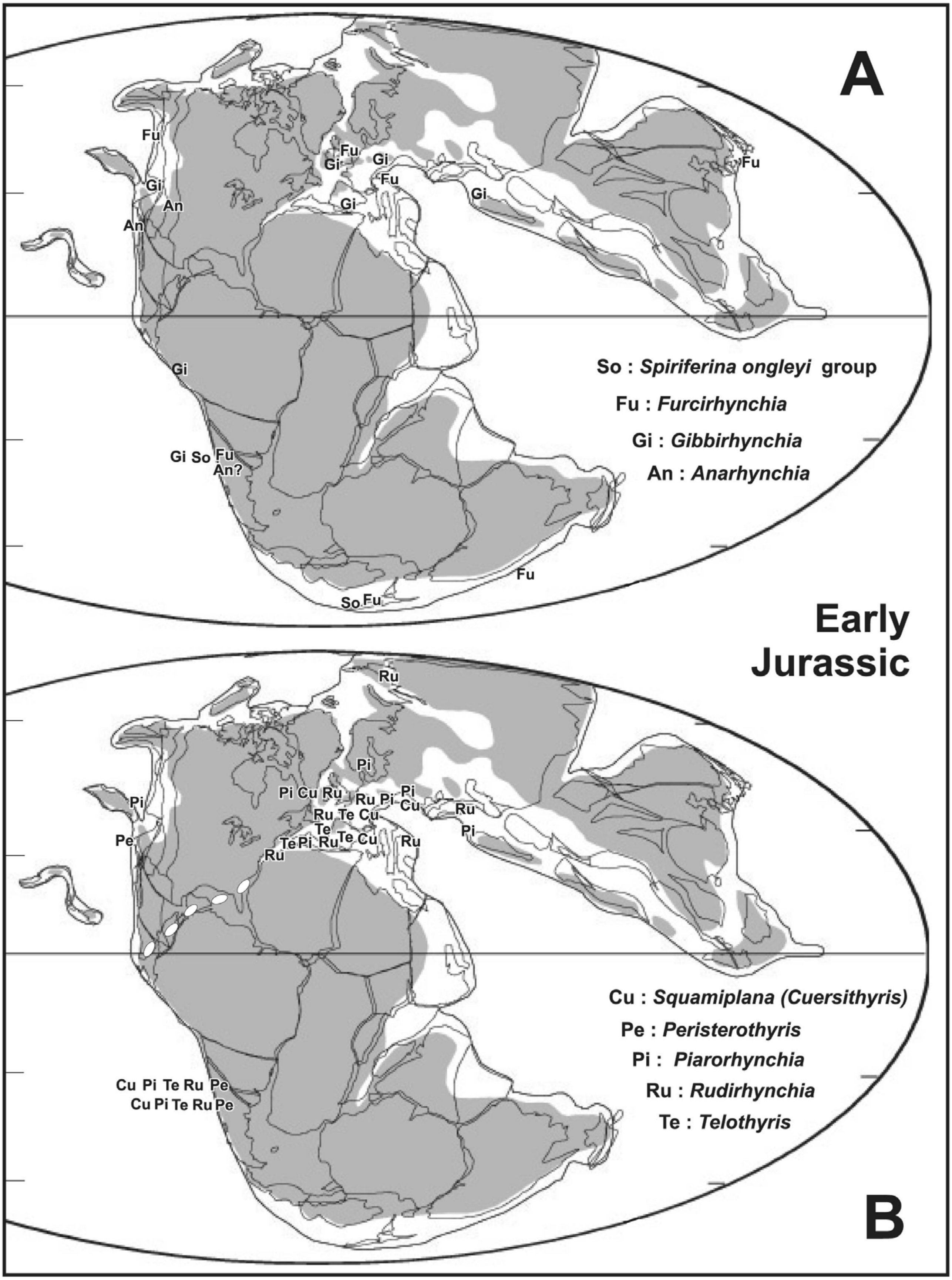


Fig. 2. Distribution of selected brachiopod genera for Early Jurassic times. (A) Hettangian–Sinemurian; (B) Pliensbachian–Toarcian (base map after Scotese (1997), a single symbol may correspond to more than one locality).

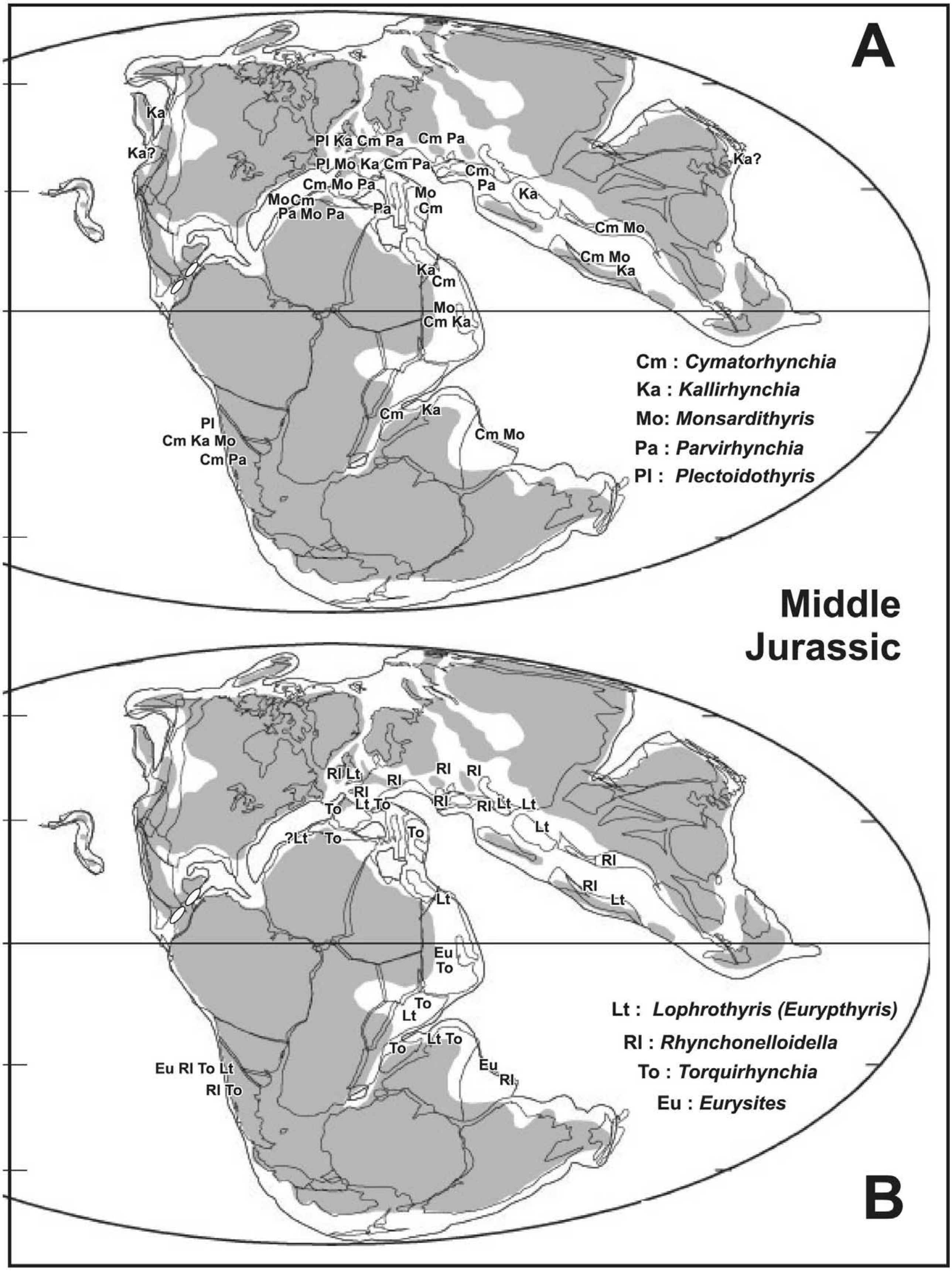


Fig. 3. Distribution of selected brachiopod genera for Middle Jurassic times. (A) Aalenian–Bajocian; (B) Bathonian–Callovian (base map after Scotese (1997), a single symbol may correspond to more than one locality).

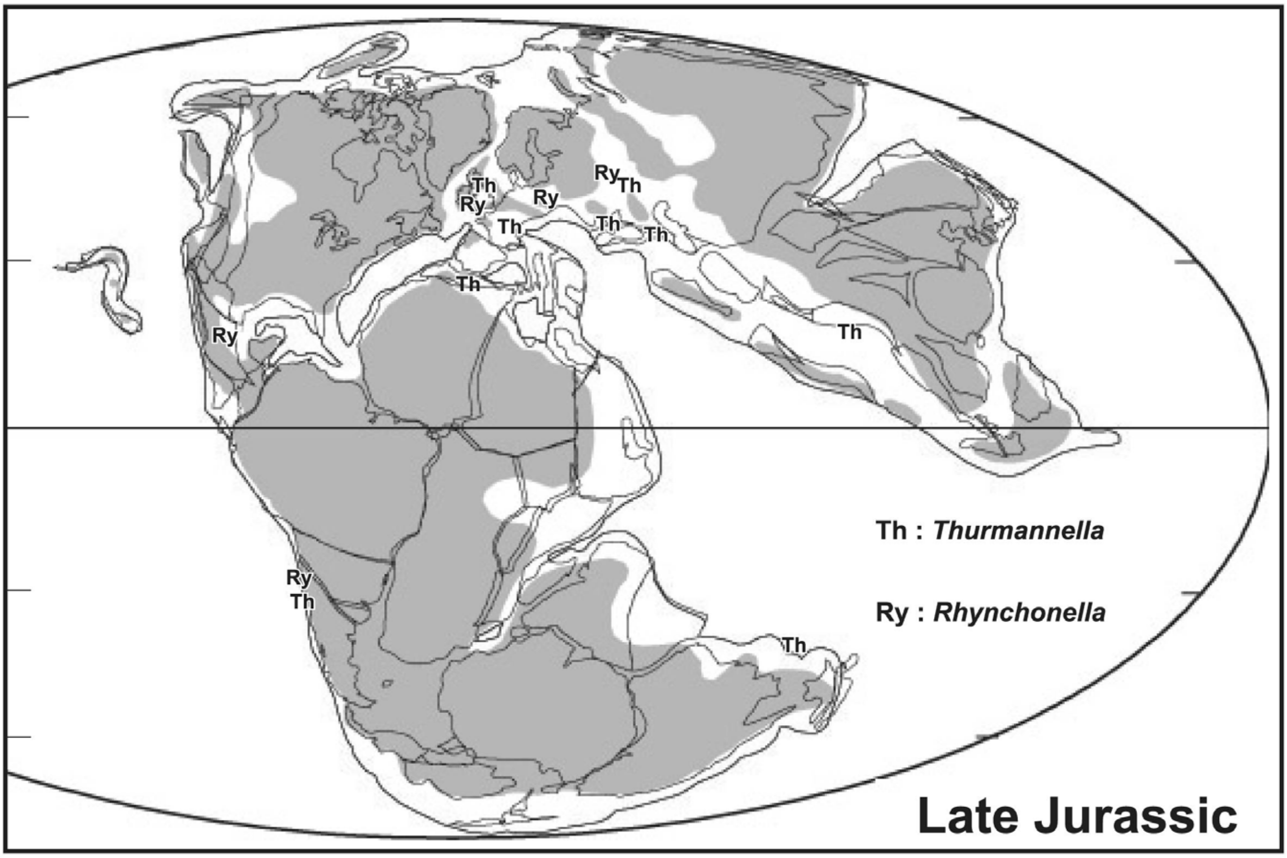


Fig. 4. Distribution of selected brachiopod genera for Late Jurassic (Oxfordian–Tithonian) times (base map after Scotese (1997), a single symbol may correspond to more than one locality).

Alps, along the Carpathians, Balkans, Anatolia, Crimea, the Caucasus, Karakorum, China, up to Viet Nam) characterized by koninckinoids, thecospiroids, retzioids; this was further subdivided into four provinces: (b1) Alpine–Carpathian, with *Bactrynium*, *Zugmayeria*, plus *Austrirhynchia*, *Zugmayerella*; (b2) Crimean–Caucasian, with *Majkopella*, *Triadispira*, plus *Euxinella*, *Oxycolpella*, *Rhaetina*; (b3) Pamirian, with *Pamirotheca*, *Pamirothyris*, plus endemic species of *Euxinella*, *Aulacothyropsis*, *Zeilleria*; and (b4) Indosinian (Indochina), with species level endemisms. (c) Perigondwanian (or Southern) Tethyan Realm/Subrealm (comprising eastern Arabian peninsula, the Himalayas, Indonesia) characterized by *Misolia*, *Hagabirhynchia*, *Timorhynchia* and the *Spiriferina abichi* group. (d) Notal or Maorian Realm/Subrealm characterized by *Clavigera*, *Rastelligera*, plus other genera, such as *Maorirhynchia*, *Murihikurhynchia* added by MacFarlan (1992) which are endemic to New Zealand–New Caledonia. (e) Eastern Pacific Realm/Subrealm (well represented in Nevada, Mexico, Peru) characterized by *Spondylospira*, *Eodallina*, *Pseudorhaetina*, etc. Dagys (1993) further pointed out that some genera (such as *Kolymithyris*, *Pseudolaballa*, *Viligella*) seem to be bipolar (didemic), and he also cautioned about interpretation of allochtonous faunas from suspect terranes.

The Late Triassic (Norian–Rhaetian) faunas from northern Chile (Cordillera de Domeyko–Sierra de Varas, Upper Unit; see Chong and Hillebrandt, 1985; Kristan–Tollmann, 1987) and western Argentina (Arroyo Malo Fm.; see Riccardi et al., 1997; Damborenea and Manceñido, 1998), include *Clavigera* (Fig. 6(2)), *Zugmayerella* (Fig. 6(1)), *Sakawairhynchia*? *Oxycolpella*? thus unmistakably revealing that they are Maorian (or Notal) in nature, though showing certain (East-) Pacific affinities, too (Fig. 1). The Late Triassic (Norian–Rhaetian) faunas from the Pucará Group (Chambará Fm.) of central (and northern) Peru (Körner, 1937; Vokes and Haas, 1944; Stehli, 1956; Rangel, 1978; Sandy, 1994), consists of *Spondylospira*, *Zugmayerella*, *Eodallina*, *Fissirhynchia*? *Laevithyris*? *Pamirothyris*? and *Lobothyris*? It thus represents a good example of the Eastern Pacific (sub)realm, although some Tethyan and even Boreal (didemic?) influences cannot be dismissed. The Late Triassic (Norian) fauna from the Payandé Formation in west central Colombia (Geyer, 1973) contains *Coenothyris*, *Wittenburgella*? and *Spiriferina abichi* OPPEL, which suggest

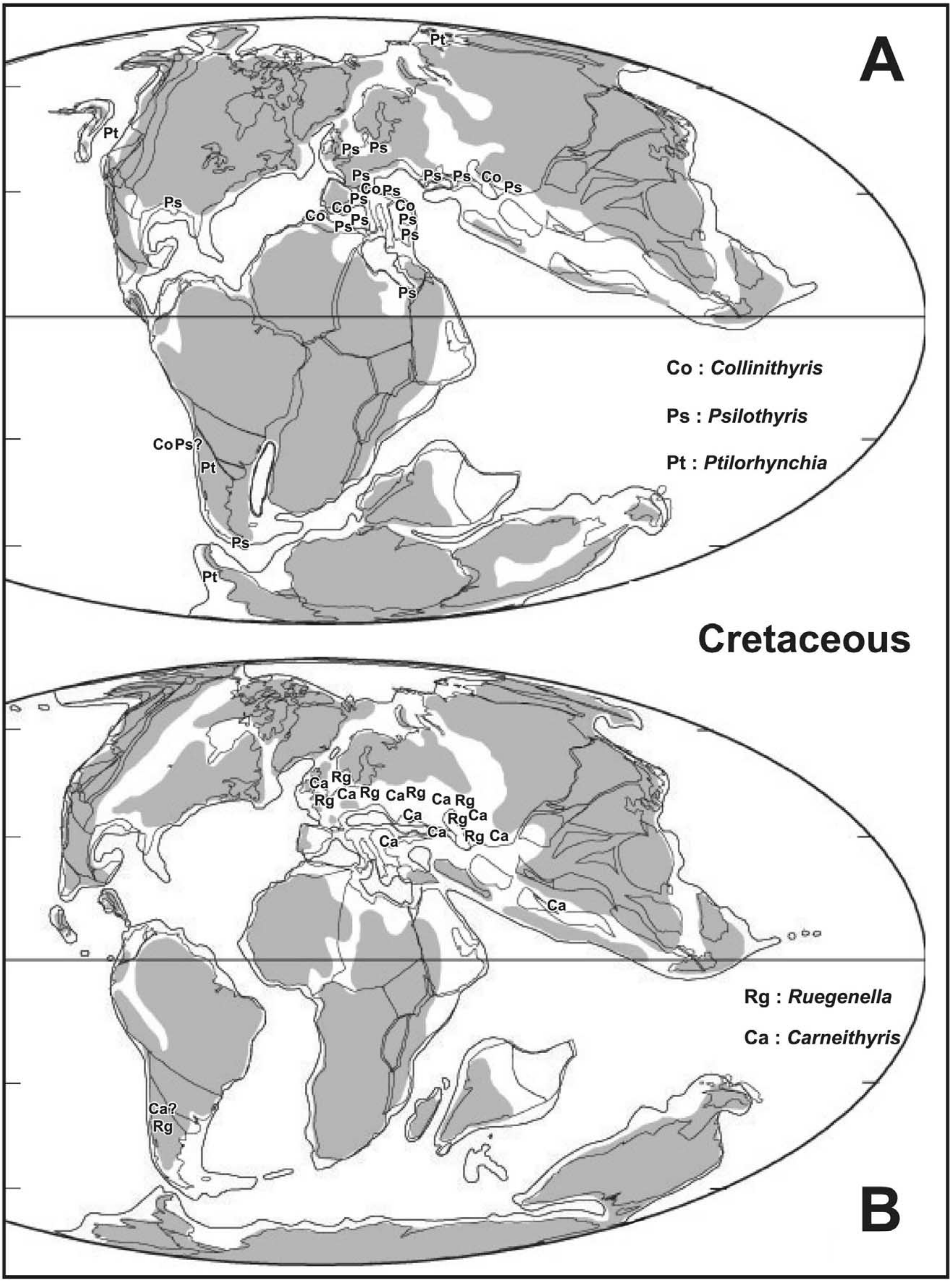


Fig. 5. Distribution of selected brachiopod genera for Early and Late Cretaceous times. (A) Valanginian–Albian; (B) Campanian–Maastrichtian (base map after Scotese (1997), a single symbol may correspond to more than one locality).

links with low-latitude Tethyan faunas (cf. also Sandy and Aly, 2000; Sandy, 2001).

2.2. Early Jurassic

In his sound foundational work on paleogeographical distribution of Early Jurassic brachiopods from Europe, Ager (1960, 1967, 1971, 1973) distinguished an “Alpine” core, successively surrounded by a “Tethyan” and a “Marginal” girdle beyond. Subsequent analysis by Vörös (1977, 1984, Figs. 2, 4 and 12, 1987, 1993a, Figs. 2 and 3, 1994, Fig. 3) and Prosorovskaya and Vörös (1988, Fig. 3) has focused on two clearly defined biochoremas of prime importance: (a) the European Province (or Subrealm?) spread from England, through south Germany, Rhone Basin, Serbian–Romanian southern Carpathians, up to Anatolia, is characterized by species of *Tetrarhynchia*, *Gibbirhynchia*, *Lobothyris*, *Zeilleria*, *Aulacothyris*. Delance (1972, Fig. 1, 1974, Fig. 4–1)—inspired in earlier work by Rollier (1916), Choffat (1880) and Dubar (1931)–distinguished a **Celto-Swabian** and a “Spanish” subunit. The latter was also called **Iberian** (Ager, 1986; Ager and Sun, 1989), as it extended from Portugal, across Iberides, Catalonia, Pyrenées, Balearics, to Provence and even Morocco–Tunisia, and is recognizable in Pliensbachian and Toarcian times by the occurrence of *Telothyris*, *Nannirhynchia*, *Soaresirhynchia*, *Plesiothyris*, *Sphaeroidothyris* (cf. also Alméras and Moulan, 1982; Fauré, 1985; Alméras and Fauré, 1990; Elmi et al., 1991; Alméras et al., 1996). (b) The Mediterranean (or Alpine) Province (or Subrealm?) ranging over the Alps, the Apennines, Transdanubian Hungary, the Betic Cordilleras, Sicily, Greece, is typified by species of *Pisirhynchia*, *Apringia*, *Linguithyris*, *Phymatothyris*, *Securithyris*. This unit was further subdivided into a **Carpatho-Sicilian** subprovince marked by predominance of *Cirpa*, *Tetrarhynchia* and ribbed spiriferinids, and an **Appennino-Transdanubian** subprovince with *Apringia*, *Securithyris* and smooth spiriferinids (Vörös, 1987, 1994).

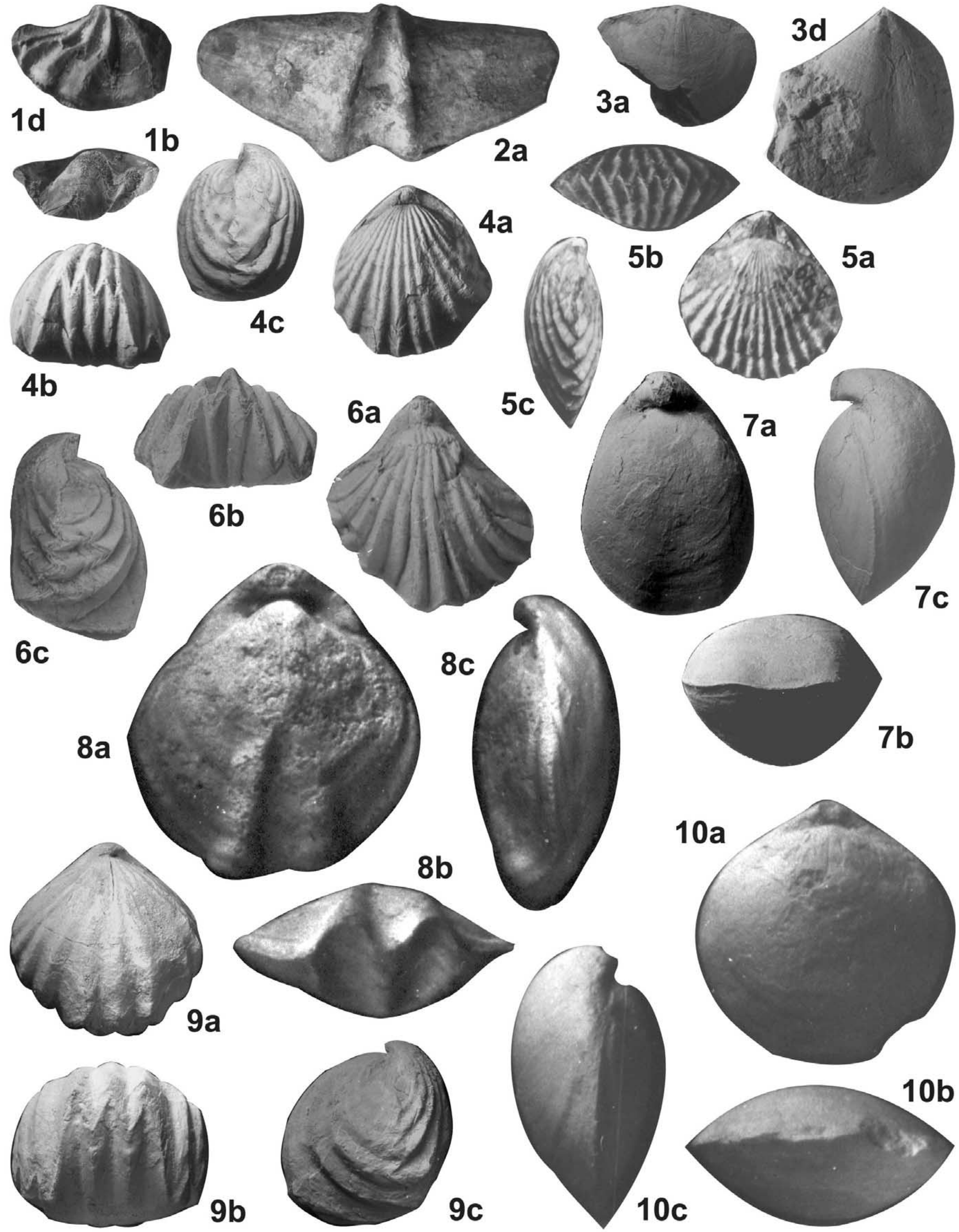
Progressive differentiation of Tethyan and Boreal Realms was attained by Pliensbachian times, especially by ammonites and belemnites, yet for other groups, that distinction was not free from controversial subtleties. Thus, although nobody would question that (b) belongs doubtless to the Tethyan (being currently interpreted as developed on a relatively isolated Mediterranean microcontinent), instead (a) has been regarded as extra-Tethyan by Ager, as Boreal by Hallam (1975), and even as marginally Tethyan (s.l.) by authors like Hölder (1979) or Prosorovskaya and Vörös (1988). Strictly Boreal Early Jurassic genera (i.e. those present in Scotland, eastern Greenland, across Siberia, up to the Okhotsk sea coast) include *Orlovirhynchia*, *Grandirhynchia*, *Ochotorhynchia*, *Viligothyris*, *Omolonothyris* (Ager, 1973; Manceñido and Dagys, 1992).

At an early stage and more local scale, Ager (1956, Fig. 1) proposed four provinces (and five subprovinces) for the Pliensbachian of Britain: **South-western** province (connecting Dorset to Normandy, western France, Spain and beyond) with *Prionorhynchia*, *Cirpa*, *Quadratirhynchia*, *Aulacothyris*, *Homoeorhynchia*, etc.; **Midlands** province (from Cotswolds, through Oxfordshire, Leicestershire, to Lincolnshire), an impoverished version of the previous; **Yorkshire** province (connecting to northern France, southern Germany, Austria) with *Tetrarhynchia*, *Rhynchonelloidea*, *Rudirhynchia*, etc.; and **Hebridean** province (linked to east Greenland, and Scania) with *Grandirhynchia*, *Rimirhynchia*; though some of these biochoremas avowedly deserve lower rank (subprovinces? and districts?), or to be merged with those of continental Europe (according to Ager himself, 1971).

In Toarcian times, the southern shore of (Neo)Tethys was the craddle to *Prototegulithyris* (according to Alméras et al., 1988), and as the East African seaway began to open towards Madagascar (Ager, 1986; Ager and Sun, 1989), an **Ethiopian** province (?) was incipiently differentiated over Arabia–East Africa, with *Calyptoria* and early *Apothyris* as strict endemics (cf. Cooper, 1989).

In the southern Pacific, as pointed by MacFarlan (1992) (also in Grant-Mackie et al., 2000), after the end-Triassic extinctions, most distinctive Maorian elements were wiped out, and Early Jurassic brachiopod faunas from the Murihiku Terrane of New Zealand—New Caledonia show few endemic genera, like *Herangirhynchia*, *Aucklandirhynchia* or *Caledorhynchia*.

During the Jurassic, the Andean region has played a pivotal role between high-latitude faunas and those from Europe, where Tethyan and Boreal Realms were already evident by Early Jurassic times. Hettangian brachiopod faunas were somewhat impoverished in general, and then reached a high-diversity peak in the Pliensbachian (detected in different areas of the world; Manceñido, 1990, p. 397; MacFarlan, 1992, p. 50; Vörös, 1993b, pp. 183–184), to decline afterwards by Toarcian times. Similarly, scarce Hettangian brachiopod faunules from the Argentinian Andes belong to almost pandemic genera. The incoming of *Furcirhynchia* is typical in such distant areas as the Austrian Alps, New Zealand and Western Argentina, the latter showing certain affinities to Maorian stocks at specific level (Riccardi et al., 2000). A similar pattern is repeated among Sinemurian faunas, with the occurrence in the El Cholo Fm. (see Manceñido, 1990; Riccardi et al., 1991) of western Argentina of *Gibbirhynchia* (also present in central Peru, Fig. 6(4)), a *Zeilleria* of the *Z. perforata* group, a faintly ribbed *Spiriferina* (closely akin to *S. ongleyi* Marwick from New Zealand, Fig. 6(3)), plus the addition of an endemic terebratulide like *Peristerothyris* (a genus that would later become more widespread along the Pacific). East-west austral links across the Pacific may have been favored by available migratory routes fringing the Gondwana margin (Damborenea and Manceñido, 1992; Manceñido and Dagys, 1992), whilst a translatitudinal eastern Pacific spread is suggested (Manceñido and Dagys, 1992; Sandy, 2001) by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the dominantly Sinemurian occurrences of *Anarhynchia* (Figs. 2(A) and 6(5)).

By the Early Pliensbachian, increasingly diverse Andean brachiopods denote close relationships to Celto-Swabian taxa, especially from Gresten-like facies, at the generic (and even specific) level, such as the rhynchonellides *Rhynchonelloidea*, *Tetrarhynchia*, *Rudirhynchia* (Fig. 6(6); Manceñido, 1990; Manceñido and Dagys, 1992), some spiriferinoids including both ribbed and almost smooth species of *Spiriferina* (Manceñido, 1981; Manceñido, 1990), three zeillerioid subgenera *Zeilleria* (*Z.*), *Z.* (*Cincta*), *Z.* (*Pirotella*) (Manceñido, 1990; Manceñido and Dagys, 1992; cf. Delance, 1974; Sucic-Protic, 1985). Also, most conspicuously, representatives of the peculiar terebratulide *Squamiplana* (*Cuersithyris*) which are known to have spread from the Iberian peninsula, through Provence, to the Carpato-Balkanids in Carixian times (Manceñido, 1990; Manceñido and Dagys, 1992, Fig. 6(7) herein; cf. Sucic-Protic, 1971; Alméras and Moulan, 1982; Fauré, 1985; Alméras and Fauré, 1990). This faunal exchange appears to reflect establishment of an intermittent shallow-marine connection through the Hispanic Corridor (Smith and Tipper, 1986; Damborenea, 2000; Aberhan, 2001, and references therein). Although some elements with broad European affinities persisted into the Late Pliensbachian of the Andes (*Lobothyris*, *Quadratirhynchia*, *Tetrarhynchia*), certain degree of endemism also developed as attested by the terebratulide *Peristerothyris* (an East Pacific genus described from Argentina and probably shared with California; see Fig. 6(8) and Manceñido, 1983), and the thecideide *Ancorellina* (a local development from ancestors with broad thecospirellid affinities; see Baker and Manceñido, 1997). This was combined with somewhat delayed Tethyan arrivals, such as *Cirpa* and *Fissirhynchia* which are first recorded much earlier in Alpine settings elsewhere (Manceñido, 1990; Manceñido and Dagys, 1992; cf. also Siblík, 1993), whereas affinities with New Zealand were still recognizable among certain spiriferinoids (Damborenea and Manceñido, 1992; cf. MacFarlan in Grant-Mackie et al., 2000).

Toarcian assemblages show that *Homoeorhynchia* reached Peru (unpublished record) and those from Argentina bear *Telothyris* (Fig. 6(10)), *Rhynchonelloidea*, *Piarorhynchia* (Fig. 6(9)), *Quadratirhynchia*, *Pseudogibbirhynchia*, *Lobothyris*, among others (Manceñido, 1990; Manceñido and Dagys, 1992). They, too, reveal basically Celto-Swabian and Iberian affinities, once again probably due to the effects of an open Hispanic Corridor (Manceñido, 1990; Manceñido and Dagys, 1992) (Fig. 2(B)).

2.3. Middle Jurassic

Khudolej and Prozorovskaya (1985, Figs. 2 and 3) offered a rather elaborate, multitiered, paleobiogeographical scheme, starting with two high-rank biochoremas (called Boreal and Tethyan “belts”, apparently meaning realms), with their boundary located at about 40° (N latitude): (a) The Boreal Realm/belt, seemingly coextensive with a *Borea*/Region/Subrealm, includes: a **North Pacific** Province (since the Aalenian) with *Inversithyris* (confined to the Far-East subprovince in Bathonian–Callovian), a **North Siberian** Province (since the Bajocian) with *Ptilorhynchia* (shared with western North America) plus *Rugithyris* (shared with England), a **Greenlandian** Province (added in the Callovian) bears *Laevigaterhynchia* (shared with central to eastern Europe), and a **European** province (becoming differentiared into eastern and western, by Callovian times) with *Acanthothiris*, *Loboidothyris*, *Septaliphoria*, etc. (b) The Tethyan Realm/belt comprises a *Mediterranean* Region/Subrealm, stretching from Spain to India, with *Stolmorhynchia*, *Sphenorhynchia*, *Gnathorhynchia*, *Ptyctothyris*, *Plectothyris*, *Goniothyris*, *Sphaeroidothyris*, *Linguithyris*, *Striirhynchia*. Lower-rank units named include: a **Caucasian** Province, with *Cubanirhynchia*, *Neocirpa*, *Paraacanthothyris*, *Bilaminella* as strict endemics and *Pseudogibbirhynchia*, *Striirhynchia*, *Linguithyris*, *Gusarella* also present, an **Ethiopian** Province with *Daghanirhynchia*, *Burmirhynchia*, *Septirhynchia*, *Bihenithyris* (also known as Abyssinian, in Ager (1967, 1971), further a Madagascan Province allegedly became differentiated southward in Callovian times, but without endemic genera), a **Himalayan** Province with *Burmirhynchia*, *Nyalamurhynchia*, *Pararhactorhynchia*, *Tanggularella*, *Moquellina*, and an **East Asian** Province, with endemic *Naradanithyris*.

It should be recalled that opinions about ranking of biochoremas may vary among different authors. So, for Makridin and Kats (1965, Fig. 6), the unified (central) **European** subunit is ranked as a subregion, belonging to (a) the Boreal Region (rather than realm) and, likewise, (b) corresponds to the Mediterranean Region, in turn divided into an **Alpine** Subregion and an **Ethiopian** Subregion. On the other hand, the meticulous analysis by Vörös (1984,

Fig. 6. Selected Andean brachiopods (Upper Triassic to Lower Jurassic). In all cases, a = dorsal, b = anterior, c = lateral, d = ventral, and e = posterior, views. (1) *Zugmayerella*? cf. *koerneri* SANDY; Norian–Rhaetian; Atuel River area, Argentina (MLP 27763, 1×). (2) *Clavigera* sp. B; Norian–Rhaetian; Doña Inés area, Atacama, Chile (Col. Muñoz SNGM, 1.5×). (3) “*Spiriferina*” cf. *ongleyi* MARWICK; Upper Sinemurian; Atuel River area, Argentina ((a) MLP 24482, 1×; (b) MLP 24482, 1.5×). (4) *Gibbirhynchia dereki* MANCEÑIDO; Upper Sinemurian; Atuel River area, Argentina (MLP 24413, 1×). (5) *Anarhynchia*? sp.; Lower Jurassic (Sinemurian?); Atuel River area, Argentina (MLP 24426, 2×). (6) *Rudirhynchia rothi* MANCEÑIDO; Pliensbachian; Piedra Pintada area, Argentina (MLP 24488, 2×). (7) *Squamiplana* (*Cuersithyris*) *davidsoni* (HAIME); Lower Pliensbachian; Atuel River area, Argentina (MLP 24414, 1.5×). (8) *Peristerothyris columbiniformis* MANCEÑIDO; Upper Pliensbachian; Piedra Pintada area, Argentina (MLP 17726, 1.5×). (9) *Piarorhynchia keideli* MANCEÑIDO; Lower Toarcian; Cerro Lotena area, Argentina (MLP 24429, 1.5×). (10) *Telothyris* ex gr. *jauberti* (DESLONGCHAMPS); Lower Toarcian; Cerro Lotena area, Argentina (MLP 24427, 1.5×).

Figs. 6, 8, 10 and 13, 1993a, Figs. 4 and 5) Prosorovskaya and Vörös (1988, Figs. 4 and 5) emphasized the distinction between those (same) three biochoremas, yet considering them as provinces of equal rank regarded as north-Tethyan, intra-Tethyan and south-Tethyan, respectively: Northwestern European Province, characterized by *Lobothyris*, *Cymatorhynchia*, *Acanthothiris*, *Rhactorhynchia*, *Parvirhynchia*, *Epithyris*, *Monsardithyris*, *Ferrythyris*, *Rhynchonelloidella*, *Ivanoviella*, *Ptyctothyris*, *Aulacothyris*, *Ornitella*, *Goniorhynchia*, *Morrisithyris*, *Dorsoplicathyris*, etc.; Mediterranean Province, characterized by *Apringia*, *Karadagella*, *Karadagithyris*, *Linguithyris*, *Calvirhynchia*, *Septocrurella*, *Caucasella*, *Striirhynchia*, etc.; and Ethiopian Province, characterized by *Burmirhynchia*, *Daghanirhynchia*, *Bihenithyris*, *Septirhynchia*, plus *Flabellothyris*, *Pycnoria*, *Striithyris*, *Sphriganaria*, *Apothyris*, *Arapsothyris*, *Thadiqithyris* (including *Pleuraloma*), *Magharithyris*, etc. (cf. also, Alméras, 1987; Cooper, 1989).

At a local scale and based on rhynchonellides only, Prosser (1993, Fig. 1) proposed a number of provinces for the Aalenian–Bajocian of England: **South West** province (extending to Normandy) with *Ptyctorhynchia*, *Trichorhynchia*, *Gnathorhynchia*, *Striirhynchia*, *Sphenorhynchia*, *Parvirhynchia*, etc.; **Cotswolds** province with *Globirhynchia*, *Granulirhynchia*, *Curtirhynchia*, *Capillirhynchia*, *Kallirhynchia*, etc.; and **Lincolnshire** province with *Microrhynchia*, *Parvirhynchia*; though these biochoremas probably deserve lower rank (subprovinces? districts?) bearing in mind that certain genera, such as *Homoeorhynchia*, *Rhynchonelloidea*, *Rhactorhynchia*, or *Flabellirhynchia*, are widespread, and *Acanthothiris* is present throughout.

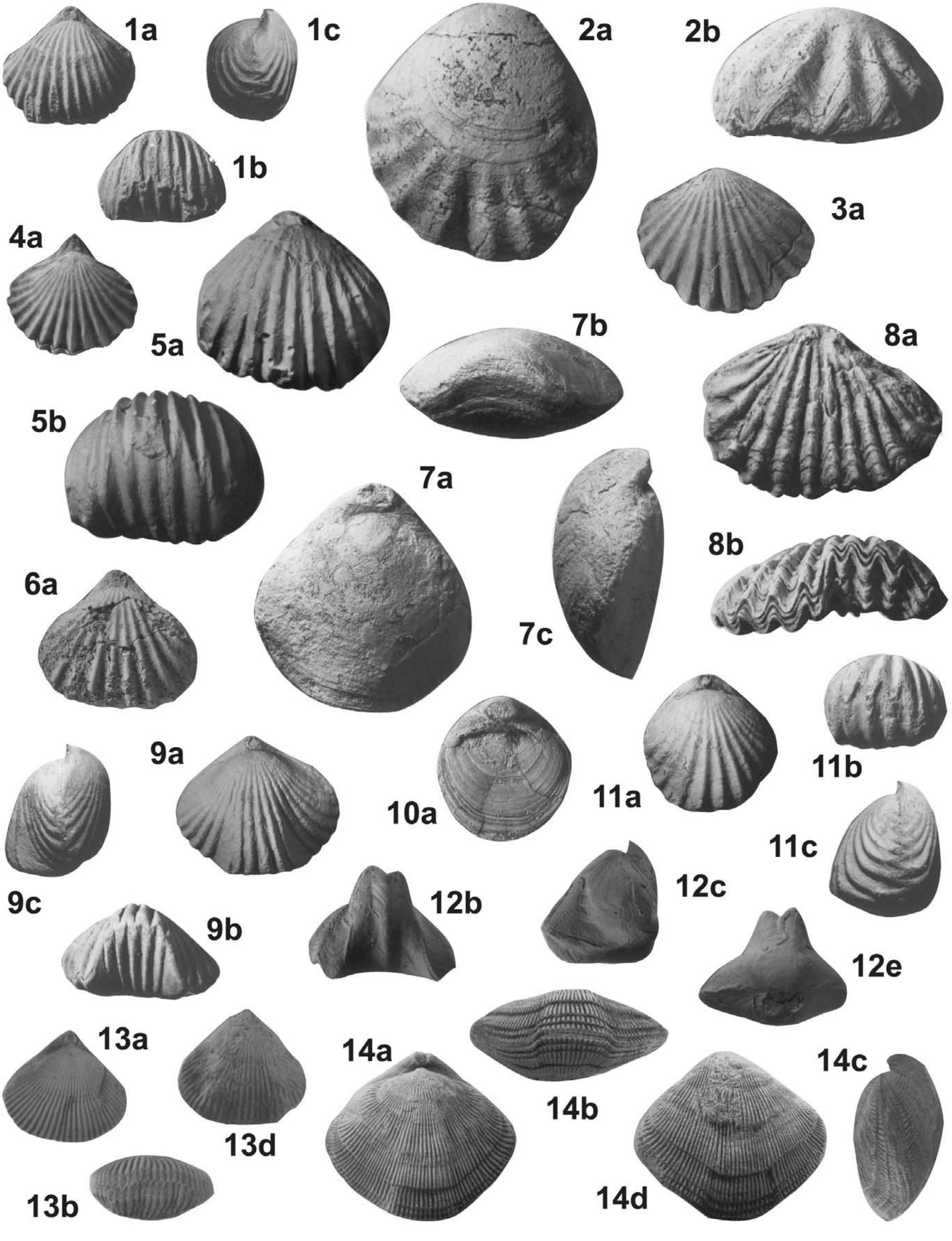
In the southern Pacific, according to MacFarlan (1992) (also in Grant-Mackie et al., 2000), in New Zealand (and New Caledonia), from the Middle Jurassic onwards, Maorian brachiopod faunas become impoverished, only endemic genera include surviving *Aucklandirhynchia* and *Caledorhynchia*, plus *Tainuirhynchia* and *Kawhiarhynchia*.

It is thus clear that, during the Middle Jurassic, distinction of Tethyan and Boreal faunas was maintained in the northern Hemisphere, and the differentiation of an Ethiopian, i.e. Southern Tethyan biochorema became better characterized (spreading over most of north and east Africa, the Middle East and the Arabian peninsula). The role played by Portugal basins for the faunal exchange between the S Tethyan and NW European provinces with an opening North Atlantic scenario at the western corner of Tethys has been stressed by Ager and Walley (1977) and Alméras et al. (1991). The bulk of Aalenian and Bajocian faunas of the Andes display generic affinities mainly with Celto-Swabian ones from western Europe (or, broadly, Northern Tethys), as attested by the frequent occurrence of *Kallirhynchia* (Fig. 7(1)), *Cymatorhynchia* (Fig. 7(3)), *Flabellirhynchia* (Fig. 7(4)), *Parvirhynchia*, *Zeilleria*, *Aulacothyris*, *Monsardithyris*, *Rhactorhynchia* (Fig. 7(5)) (see also Manceñido and Dagys, 1992; Riccardi et al., 1994); whereas the occasional presence of *Plectoidothyris*? sp., as in the Sierra Fraga Formation of Atacama, Chile (Fig. 7(2); Manceñido and Dagys, 1992), obviously reflects the southward incursion of distinctive Tethyan elements (Ager and Walley, 1977, Fig. 1), and even some minor endemic developments may be revealed, such as rhynchonellides of the "*R.*" *moerickeimanflasensis* group (Manceñido and Dagys, 1992) (Fig. 3(A)). Noteworthy, the *Cymatorhynchia*–*Monsardithyris* couplet, recorded in the Lajas and correlatable formations of Argentina, is recurrent in Bajocian deposits from Europe, northern Africa to Asia (Alméras and Moulan, 1988; Sadki and Alméras, 1992; Riccardi et al., 1994; Alméras and Elmi, 1998). On the other hand, most brachiopod genera recorded from the Callovian and Bathonian of Argentina (and Chile), like *Loboidothyris*, *Rhynchonelloidella* (Fig. 7(9)), *Zeillerina* (Fig. 7(10)), are widespread across Europe to the Crimea and the Caucasus, and thus likewise represent the northern Tethyan margin; nevertheless, some other genera, like *Eurysites* (Fig. 7(6)), *Torquirhynchia* (Fig. 7(8)), *Lophrothyris* (*Eurypthyris*) (Fig. 7(7)), are known to extend further into Indo-Ethiopian areas (Kutch, Somalia, Madagascar, Arabia, Tibet–Himalayas south of the Indus-Yarlung suture) which belong to the southern (Neo)Tethys shores (Manceñido and Dagys, 1992; cf. also Ager and Sun, 1989; Shi and Zhang, 1990; Sun and Zhang, 1998) (Fig. 3(B)).

2.4. Late Jurassic

A similar paleobiogeographical scheme by Khudolej and Prozorovskaya (1985, Figs. 3 and 4) is available for Late Jurassic faunas, with two high-rank biochoremas (called "planetary belts", apparently meaning realms), with their boundary located at about 40° (N latitude): (a) The Boreal Realm/belt (covering epicontinetal seas of north Eurasia) comprises, in the north: (a1) a **Greenlandian** Province

Fig. 7. Selected Andean brachiopods (Middle Jurassic to Upper Cretaceous). In all cases, a = dorsal, b = anterior, c = lateral, d = ventral, and e = posterior, views. (1) *Kallirhynchia transatlantica* (TORNQUIST); Lower Bajocian; Espinacito Range area, Argentina (MLP 24432, 2×). (2) *Plectoidothyris*? sp. Bajocian; Copiapó area, Chile (Col. Covacevich SGNM, 1.5×). (3) *Cymatorhynchia* sp.; Lower Bajocian, Sierra Chacaico area, Argentina (author's col. MLP, 1.5×). (4) *Flabellirhynchia* cf. *davidsoni* (CHAPUIS and DEWALQUE); upper Lower Bajocian, Sierra de Reyes area, Argentina (author's col. MLP, 1.5×). (5) *Rhactorhynchia*? *caracolensis* (GOTTSCHE); upper Lower Bajocian, Caracoles area, Chile (MLP 24436, 1×). (6) *Eurysites* sp.; Upper Bathonian, Sierra de Reyes area, Argentina (Gulisano's col. MLP, 1.5×). (7) *Lophrothyris* (*Eurypthyris*) cf. *euryptycha* (KITCHIN); Lower Callovian, Mount Puchenque area, Argentina (MLP 22041a, 1.5×). (8) *Torquirhynchia* sp. Lower Callovian, Vega de la Veranada area, Argentina (MLP 24437, 1.5×). (9) *Rhynchonelloidella* sp. Middle Callovian, Picún Leufú area, Argentina (MLP 244439, 2×). (10) *Zeillerina*? sp.; Middle Callovian, Picún Leufú area, Argentina (author's col. MLP, 1.5×). (11) *Thurmannella* sp.; Middle Oxfordian, Sierra de Reyes area, Argentina (MLP 24440, 2×). (12) *Rhynchonella* sp.; Upper Tithonian; Zapala area, Argentina (col. Leanza MLP, 1.5×). (13) *Cyclothyris transatlantica* (LEANZA and CASTELLARO); Barremian–Aptian? El Way area, Chile (CPBA 5562, 2×). (14) *Ruegenella* sp., Maastrichtian, Colorado River area, Argentina (col. Caba MLP, 2×).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(over East Greenland–Barents); (a2) **North Siberian** Province (between rivers Yenisey and Lena); (a3) a **North Pacific** Province (over northeastern Siberia, Beringia); (a4) a **Far-East** Province (over Far East Russia, Japan); immediately south and progressively eastwards; (a5) a **Central European** Province (roughly equivalent to the Portlandian Subregion of Makridin and Kats (1965); (a6) an **Eastern European** Province (over the Russian Platform, thus equivalent to the Volgian Subregion of Makridin and Kats, 1965), itself embracing a Central Russian subprovince plus a Petchorian subprovince; (a7) a **West Siberian** Province (between the Urals and the Yenisey); and (a8) for the Tithonian, a **Subboreal** Province (over southwest Europe) was added. European (s.l.) brachiopod faunas (a5–a8) are characterized by *Rhynchonella*, *Thurmannella*, *Rouillieria*, *Russirhynchia*, *Mosquella*, *Russiella*, *Juralina*, *Zeilleria*, *Aulacothyris*, whereas typical Siberian (s.l.) genera include *Boreiothyris*, *Pinaxiothyris*, *Lenothyris*, *Taimyrothyris*, *Uralella*, *Uralorhynchia*, plus *Ptilorhynchia* (shared with western Canada). (b) The Tethyan Realm/belt (stretching from Gibraltar to Indonesia) contains as subordinate units: (b1) a **Mediterranean** Province (occupying west and central parts of Tethys) bearing *Somalirhynchia*, *Nucleata*, *Septocrurella*, *Triangope*, *Pygope*, *Monticlarella*, *Lacunosella*, *Turkmenithyris*, *Gusarella*, etc.; (b2) an **Ethiopian** Province (over Ethiopia, Somalia, Arabia, Middle East, Kutch) with *Somalirhynchia*, *Ptyctothyris*, *Bejrutella*, *Somalithyris*, *Habrobrochus*, *Mycerosia*, etc.; (b3) a **Himalayan** Province (from Himalayas to Kun-Lun ranges) with endemic *Rutorhynchia*, *Paraulacothyris*, yet showing close links to both previous (*Lacunosella*, *Torquirhynchia*, *Gusarella*, *Pentithyris*); (b4) an **East Asian** Province (spread from Japan, across Indonesia to Australia) with endemic *Neumayrithyris*, plus *Burmirhynchia*, *Parvirhynchia*, *Disculina*? and (b5) for the Tithonian, a **Submediterranean** Province (over Caucasus, Crimea, west of Central Asia) with *Tropeothyris*, *Cheirothyris*, *Ismenia*, *Zeillerina*, *Terebrataliopsis* was added.

In addition, as reported by MacFarlan (1992) (also in Grant-Mackie et al., 2000), the Late Jurassic Maorian brachiopod faunas (mostly from New Zealand, rarer from New Caledonia) remain impoverished, scarce endemic genera *Tainuirhynchia* and *Kawhiarhynchia* are joined by *Waikatorhynchia*.

In general, during the Late Jurassic, Boreal faunas from high-latitudes became even more strongly differentiated from low-latitude, Tethyan ones. Oxfordian and Tithonian brachiopods from the Andes apparently belong to genera of pandemic or northern Tethyan affiliation, yet with few elements in common with other eastern Pacific areas, such as Mexico (cf. Manceñido and Dagys, 1992; Sandy, 1998, 2001). The occurrence of *Thurmannella* in the Oxfordian La Manga Formation of west-central Argentina is a salient feature (Fig. 7(11); Manceñido and Dagys, 1992; Riccardi et al., 2000), the genus being widespread from England, across France, Switzerland, the Russian Platform, Crimea, Caucasus, to southern China, and Indonesia (Islands of Timor and Roti). Likewise, *Rhynchonella* s.s., found in the Tithonian Vaca Muerta Formation of Mendoza and Neuquén (Fig. 7(12)), is also known from Britain, France, Germany, Poland, Russia, Slovakia, Bulgaria, and Mexico, and was regarded as a Boreal genus by Owen (1973), though not restricted to that realm (Sandy, 1991b). Both genera are specifically listed among those characterizing the northern shore of Tethys (Ager and Sun, 1989) (Fig. 4). On the other hand, a record of *Lacunosella* from Tithonian deposits of west-central Argentina (cf. Manceñido and Dagys, 1992, and references therein) requires confirmation.

2.5. *Early Cretaceous*

On the basis of brachiopod data from western Europe, Middlemiss (1973, 1984) discriminated three main biochoremas, controlled mainly by tectonic setting, sedimentary facies, and, partly, paleoclimatic factors (especially temperature and salinity): (i) Boreal Fauna (over England, northern Germany) characterized by species of *Rhombothyris*, *Aniabrochus* (= *Platythyris*), *Rouillieria*, etc. (ii) Jura Fauna (over intra-cratonic fold areas in southern France, eastern Spain, northeast Bulgaria) characterized by species of *Loriolithyris*, *Musculina*, etc. (iii) Tethyan Fauna (along the Alpine fold belts in southern Spain, the Balearic Islands, the Alps, the Carpathians, central Crimea, the northern Caucasus and Turkmenistan) characterized by pygopids, nucleatids, species of *Weberithyris*, *Dictyothyris*, etc. Some taxa were qualified as ubiquitous (i.e. pandemic).

In addition, Smirnova (1984, Figs. 65–76, 1990) expanded the paleobiogeographical scheme based on brachiopods to eastern Europe–Asia (and North America), recognizing the following biochoremas (originally ranked as regions, which exhibit dynamic boundaries and high degree of endemism): (a) Arctic Region/Subrealm (over western and northern Siberia, persisting Berriasian through Hauterivian) with *Uralorhynchia*, *Fusirhynchia*, *Taimyrothyris*, *Lenothyris*, *Siberiothyris*. (b) European Region/Subrealm (over England, northern Germany, Scandinavia, Russian Platform, Berriasian through Albian) with *Rhynchonella*, *Russiella*, *Rouillieria*, *Spasskothyris*, *Kabanoviella*, etc. (c) Mediterranean Region/Subrealm (over southern France, Spain, Italy, southern Germany, Dinarids, Carpathians, Crimea, Caucasus, Mangyshlak, Turkmenistan, Afghanistan, Berriasian through Albian; in late times expanding across southeast Asia to Japan, around Africa, from Morocco, Algeria, Zululand, to Madagascar, further to Angola, and even Mexico and central USA) with *Nucleata*, *Pygope*, *Lacunosella*, *Dictyothyris*, *Psilothyris*, *Cruralina*, *Monticlarella*, *Peregrinella*, *Tropeothyris*, *Weberithyris*, *Dzirulina*, *Thecidiopsis*, etc. (d) (North) Pacific Region/Subrealm (over Far East, Kamchatka, Primorye, during Berriasian through Albian, sometimes reaching western USA as well, as in Valanginian? Hauterivian–Barremian) with *Clathrithyris*, *Ptilorhynchia*, *Korjakirhynchia*, *Oriensellina*, *Penzhinothyris*, *Mametothyris*, etc. (e) Further, an Australian Region/Subrealm, characterized by *Australiarcula*, was added for Albian times. Sandy (1991a) suggested that from Aptian times onwards an "Austral fauna" may be distinguished for Antarctica and Australia, although evidence was admittedly scant (*Prochlidonophora*, and a few Late Cretaceous genera like *Inopinatarcula*, *Rossithyris*), whereas taxa like *Kingena* or *Rectithyris* were regarded as pandemic by him.

The occurrence of *Ptilorhynchia* in the Hauterivian (basal Agrio Fm.) of Mendoza (Riccardi et al., 2000) points to conspicuous circum-Pacific (if not bipolar) affinities: closely related species are known from the Early Aptian of Antarctica, as well as from Early Cretaceous deposits of Siberia.

The Hauterivan–Aptian faunule from central Chile (referable to the Totoralillo and Pabellón Formations) contains *Collinithyris* and *Psilothyris* (cf. Paulcke, 1903) of broadly Tethyan affiliation. Representatives of *Collinithyris* are known from the Valanginian–Aptian interval in SW France, Germany, Switzerland, Dinarids, Mangyshlak, and northern Africa. Whereas *Psilothyris*, which has been also reported from the Aptian (Hito XIX Fm.) of Tierra del Fuego (Manceñido, 1989), is widely recorded from the Valanginian–Albian interval in Spain, France, England, Germany, Switzerland, Sardinia, Dinarids, Carpathians, Bulgaria, Crimea, Caucasus, Mangyshlak, northern Africa, and Arizona, USA (Fig. 5(A)).

On the other hand, the report of "*Cretirhynchia transatlantica*" from El Way Fm. (Barremian–Aptian?) in northern Chile (Leanza and Castellaro, 1955) is more likely to represent the almost pandemic genus *Cyclothyris* (Fig. 7(13)). Besides, the presence of the widespread genus *Sellithyris* in Late Valanginian deposits of Zapatoca (Santander Department), Colombia, as well as a Hauterivian *Musculina* from northern? South America, may suggest direct transatlantic connections with western Europe (Sandy, 1990, 1991b).

Undescribed material from the southern Patagonian Andes of Argentina (currently under study) may reveal links to the incipiently differentiated Austral fauna, if inopinatarculid affinities are confirmed. Conversely, broad uncertain determinations involving other genera, such as *Kingena* and/or *Argyrotheca*, are inadequately substantiated thus far and should be better disregarded for the present purposes (cf. Richter, 1925; Feruglio, 1936–1939; Leanza, 1967).

2.6. Late Cretaceous

According to Makridin and Kats (1965, Figs. 9–11, 1966, Figs. 5–12), on the basis of brachiopod faunas, the following biochoremas can be recognized: (a) Boreal Region/Subrealm (confined to northernmost areas). (b) Central European Region/Subrealm subdivided into two: (b1) the *Germano-Caucasian* Subregion, comprising successively from west to east, a **West European** Province, a **Pericarpathian** Province (only for Maastrichtian times), a **Crimean** Province, a **Caucasian** Province, a **Donetzian** Province, a **Transcaspian** Province and a **Transuralian** Province; and (b2) the *Central Russian* Subregion (somewhat impoverished, located inland and northward of the former) comprising form east to west, an Uralian Province, a Volgian Province and (prior to the Late Maastrichtian) a Peridnieperian Province as well. (c) Mediterranean Region/Subrealm, likewise split into: (c1) the *Mediterranean* Subregion (not subdivided further); and c2) the *Central Asian* Subregion, comprising an **East Turkmenian** Province plus a **Tadzhikian** Province. (d) Indo-Pacific Region/Subrealm (stretching eastwards from east Africa up to Sakhalin and Kamchatka). Notice that Chiplonkar et al. (1977) concluded that the fauna of the Bagh Beds unmistakably belongs to an **Indo-Mediterranean** Province of the Tethyan Realm (its low endemism granting subprovince status at most). Besides, Ager (1973) (Ager and Sun, 1989) was rather sceptical about the whole scheme, with facies-linked oversplitting yielding endemisms at species/subspecies level only, but lacking genera with mutually exclusive ranges. Nevertheless, in broad terms, genera, such as *Rhynchorina*, *Magas*, *Grasirhynchia*, *Cretirhynchia*, *Rugia*, *Trigonosemus*, *Gemmarcula* may be conspicuous for (b), *Erymnaria*, *Parthirhynchia*, *Begiarslania*, *Bolgarithyris*, *Basiliola*, for (c), and *Rochatorhynchia*, *Malwirhynchia*, *Praeneothyris*, *Moraviaturia* for (d), whereas *Carneithyris*, *Orbirhynchia*, *Nucleatina*, *Septatoechia* may have wider Tethyan connotations. (e) To this overall picture, Makridin and Kats (1966, Fig. 15) added an ill-defined "Austral region", based on alleged bipolarity of Magasinae. Instead, Craig (1999) prefers to name a circum-Indo-Atlantic southern Province (characterized by species of *Zenobiathyris*, *Protegulorhynchia*, *Tegulorhynchia*, *Bouchardiella*) which occurs from western Australia to Antarctica, and persisted into Paleogene times.

The illustrated record, from Cenomanian? deposits at Santa Fé de Bogotá (Cundinamarca Department, Colombia), of *Gemmarcula* and *Arenaciarcula* which are conspecific (or nearly so) with well-known species from Europe, has been taken as evidence for a free, low-latitude, faunal exchange through a widening Central Atlantic seaway (Sandy, 1990, 1991b, cf. Fig. 5, route 1).

The recently discovered Maastrichtian faunule in southwestern La Pampa, Argentina (Caba et al., 1998), together with earlier findings in southern Mendoza (Camacho, 1971; Riccardi et al., 2000), reveals that the Malargüe Group locally bears representatives of *Ruegenella* (Fig. 7(14)), *Carneithyris*? and an indeterminate juvenile rhynchonellide. The first two show clear affinities with the Central European, and via the Transcaspian, to the Central Asian faunas. It is currently agreed that the Jagüel and Roca formations were deposited by a trangression of Atlantic provenance (instead of Pacific, like all the previous ones, cf. Riccardi, 1987). As an alternative to the South African and South Atlantic seaways to explain such distribution pattern (cf.

Sandy, 1991b, Fig. 5, routes 2 and 3), one should explore, in this connection, the dispersal role that may have played the trans-Saharan seaway, which is known to have enhanced the influx of Tethyan faunal elements into a widening South Atlantic (cf. Reyment and Dingle, 1987; Riccardi, 1991; Williams et al., 2000) (Fig. 5(B)). Furthermore, distinctive elements indicative of high-latitude austral faunas (as reported from Australia and Antarctica) are apparently lacking in northern Patagonia, though it remains to be checked whether they might have reached southernmost Patagonia. It is worth noting that by Early Paleocene times *Bouchardiella* is already widespread in Salamaquean deposits (Salamanca and Río Bueno Fms.) of Chubut, Santa Cruz and Tierra del Fuego (Doello-Jurado, 1922; Feruglio, 1936–1939; Furque and Camacho, 1949; Levy, 1964), whereas its forerunners inhabited in Western Australia during Late Cretaceous times (Levy, 1964; Craig, 1999).

3. Concluding remarks

During the Mesozoic, the Andean region has played a hinging role between higher- and lower-latitude marine benthonic faunas as attested by the paleobiogeographical analysis of the brachiopod fossil record. Brachiopod migration and faunal exchange may have been favored by phenomena, such as availability of shelf areas fringing the margins of major land-masses, or development of suitable seaways (like the Hispanic Corridor in the Jurassic, or the trans-Saharian in the Late Cretaceous), or eustatic rise of global sea-levels. Conversely, brachiopod migration and faunal exchange may have been hindered by isolation due to development of effective land or deep-ocean barriers, or eustatic drop of global sea-levels.

A long-term fidelity of certain high-rank taxonomic stocks to particular major biochoremas has been noticed: for instance, Nucleatidae, Peregrinellidae, Basiliolidae, Erymnariidae, Norellidae, Halorellidae, Koninckinoidea or Thecideoidea, for Tethyan; Boreiothyrididae, Uralorhynchiinae, for Boreal; Septirhynchiidae for Ethiopian; Clathrithyrididae or Ancorellininae, for Pacific.

In addition, there was a long-term fidelity of certain unusual morphotypes (independent of systematic position) to particular major biochoremas. This may be best exemplified by the occurrence of securiform, sulcate and perforate brachiopods in core Mediterranean areas (Ager, 1960, 1967, 1973, 1993). Observed departures from that pattern require an explanation, presumably, they might be linked to peculiar off-shore facies and/or chemosynthetic communities of the past.

Finally, there is a growing consensus about broad aspects of the paleobiogeography of Mesozoic brachiopods, which are fairly well understood. Nevertheless, certain details of ranking and naming of some individual units have not yet been fully agreed, in order to harmonize them with Westermann's (2000a, b) proposals (but it lies beyond the scope of this overview).

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