

# Comparison between western Tethys and eastern Pacific ammonites: further evidence for a possible late Sinemurian–early Pliensbachian trans-Pangaean marine connection

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**Abstract** – Comparing the Early Jurassic ammonoids found in three Italian Apennine sections (Bosso, Pallareto and Furlo) with those reported in the literature for some South American sections (Argentina and Chile), we noted that these two areas share the same late Sinemurian–early Pliensbachian faunal succession: *Paltechioceras* in the late Sinemurian (Raricostatum Zone), *Catriceras* in the earliest Pliensbachian (Jamesoni Zone, Taylori Subzone), *Miltoceras* in the middle part of the early Pliensbachian (Jamesoni Zone, Polymorphus Subzone). An overall similarity to Apennine and South American ammonite faunas of the same age can be found for some sections of Morocco and partially also for southern Spain. One of the Italian taxa (an unpublished early Pliensbachian Apennine genus, ascribable to the family Polymorphitidae) is reported in the South American Pacific coast by the middle to late part of the early Pliensbachian (Ibex Zone). Evolving towards more and more discoidal morphologies, it might have given rise to an endemic American ammonite group, which is represented by the genera *Eoamaltheus* Hillebrandt and *Fanninoceras* McLearn. This phylogenetic reconstruction is based on several lines of evidence (shell morphology, ontogenetic development, aspect of the suture lines, biostratigraphy), and can be safely traced back to the basal Pliensbachian strata of the Tethyan Palaeoprovince. As far as we know, the examined ammonoid taxa are exclusively found in the western Tethys (e.g. Italian Apennines) and American Pacific coast (e.g. Argentina), but they have never been recorded elsewhere, and they show no evidence of pantropical distribution. Our biostratigraphic and phylogenetic data suggest the existence of a late Sinemurian–early Pliensbachian marine connection between the western Tethys (Italian Apennines) and the South American Pacific coast (Argentina). This is the so-called Hispanic Corridor, the existence of which has already been supported by many authors using several geological and palaeontological pieces of evidence. According to our interpretation, as well as the conclusions of other workers, it was a temporary and intermittent seaway, which allowed a partial faunal exchange for some taxa (including certain shallow-water ammonoids) during Sinemurian and Pliensbachian times. This palaeobiogeographic model consistently relates the biostratigraphy and evolution of some western Tethys and South American ammonoids to the major palaeogeographic changes affecting this vast area. In any case, our working hypothesis does not have any claim of universal applicability; we deem the proto-Atlantic seaway model to be the most suitable (until proof of the contrary) for the ammonites we examined, but it may not be necessarily valid for all the currently known taxa.

Keywords: palaeogeography, Tethys, Early Jurassic, ammonoids, Mollusca, biostratigraphy.

## 1. Introduction

Jurassic ammonoids are normally considered biostratigraphically useful fossils, but they also have a remarkable palaeobiogeographic value, especially when the relative ages of the examined faunas can be adequately evaluated. The study of their distribution can help to check palaeogeographic reconstructions, for instance with regard to the existence and utility of seaways.

However, comparison between faunas from different geographic areas is often complicated by facies differences (both section lithology and thickness), as well as by the ecological and palaeoenvironmental factors which influenced the distribution and life

strategies of the various taxa. Therefore, to relate biostratigraphy and palaeobiogeography in the most correct way, specific and accurate data are needed.

Moreover, in the study of a highly diversified group such as the ammonoids, we believe that making too many generalizations can be risky. It is reasonable to think that taxa with marked morphological differences lived in different ways (including their reproductive strategies and dispersal mechanisms). Consequently, the response to variations in palaeogeographic conditions might be dissimilar from one species to another.

## 2. Palaeontological documentation

One of the best examples which can be used to illustrate the relations between ammonoids and palaeogeography

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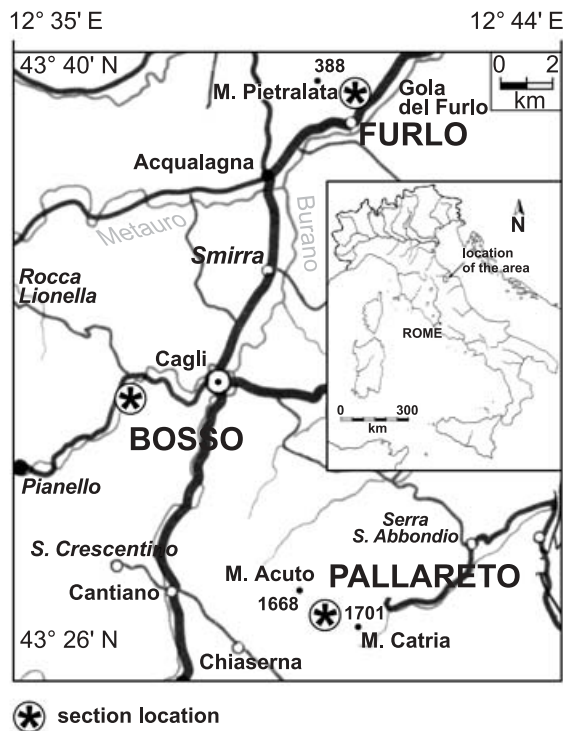


Figure 1. Site map, with asterisks marking locations of Pallareto, Bosso and Furlo sections. Their geographic position within the Italian Apennines is shown in the small box on the right.

comes from our studies of the biostratigraphy and the phylogeny of Early Jurassic ammonites of the Italian Apennine sections (Bosso, Pallareto and Furlo).

### 2.a. Biostratigraphy

The three studied sections occur within the Tuscany–Umbria–Marche Basin, which was established following the drowning of the Calcare Massiccio Early Jurassic carbonate platform (Colacicchi, Passeri & Pialli, 1970; Centamore *et al.* 1971; Ciarapica & Passeri, 1998, 2002; Colacicchi & Parisi, 1999). All the measured sections belong to the same lithostratigraphic unit (Corniola, which represents the first transgressive facies after the Calcare Massiccio), but they show significant depositional differences. The Furlo section is highly condensed (structural high), the Pallareto section is transitional, and the Bosso section is thicker and more complete, corresponding to a basinal environment. (Fig. 1; see also Fig. 3).

The abundant fossils from these sections allow detailed biostratigraphic studies across the Sinemurian–Pliensbachian transition in the studied area (Faraoni *et al.* 1996; Venturi, Nannarone & Bilotta, 2004). The Sinemurian–Pliensbachian transition is marked by a global change in ammonite faunas, with the disappearance of the Echioceratidae and subsequent diversification of the Eoderoceratoidea (Meister *et al.* 2003). This is well documented in the Apennine sections, where the Pliensbachian ammonite radiation

is represented by forms such as *Galaticeras* Spath, *Radstockiceras* Buckman and *Furlites* Venturi & Ferri. However, *Catriceras* Venturi is probably the most significant genus to mark the Pliensbachian faunal change in the Apennines. Until recently, this ancient member of the Tropidoceratinae with advanced morphological features (such as ventral keel and flexuous ribs, which we interpret as hydrodynamic adaptations) was known only from the calcareous rocks referable to the earliest Pliensbachian of the Umbria–Marche Apennines (Venturi, 1978; Venturi, Nannarone & Bilotta, 2004), but it has also now been recognized in two South American areas, namely northwestern Argentina (Arroyo Las Chilcas section; Hillebrandt, 2002) and Chile (A. Hillebrandt, pers. comm.). Other possible American representatives of *Catriceras* are the lower Pliensbachian specimens from British Columbia (western Canada) figured by Smith & Tipper (1996, pl. 11, figs 1–3) as *Tropidoceras* species 1. The characteristic, strongly projected ribs of the Canadian specimens seem to us more compatible with *Catriceras* than with *Tropidoceras*, however, this material is too poorly preserved to make detailed comparisons, so the existence of North American *Catriceras* cannot yet be confirmed.

In any case, the presence on the South American Pacific coast of a form which previously was deemed exclusive to the Mediterranean Tethys prompted us to compare the Apennine ammonite faunas with those reported in the literature for the American sections. According to our studies (as preliminarily reported in Venturi & Rossi, 2003), we noticed that, besides the presence of *Catriceras*, the Apennines and Argentina share the same Sinemurian–Pliensbachian ammonite faunal succession: a *Paltechioceras* assemblage in the late Sinemurian (referable to the standard *Raricostatum* Zone), a *Catriceras* assemblage in the earliest Pliensbachian (referable to the standard Jamesoni Zone, Taylori Subzone) and a *Miltoceras* assemblage in the middle part of early Pliensbachian (referable to the standard Jamesoni Zone, Polymorphus Subzone). As well as being similar to each other, the Apennine and South American ammonite faunas of this time interval share some genera with those reported for Morocco (e.g. Lachkar *et al.* 1998) and, in part, southern Spain (Braga *et al.* 1982, 1984) (Figs 2, 3).

On the other hand, we do not know of similar assemblages in sections of the Boreal Palaeoprovince (northwestern Europe), or in other geographic areas (such as equatorial and southern Africa, Arabia, Russia, Asia, etc.), although in these latter cases the available data for the late Sinemurian–early Pliensbachian are still very scarce.

### 2.b. Phylogenetic reconstruction

Comparing the Apennine Early Jurassic ammonoids with those of some South American sections of

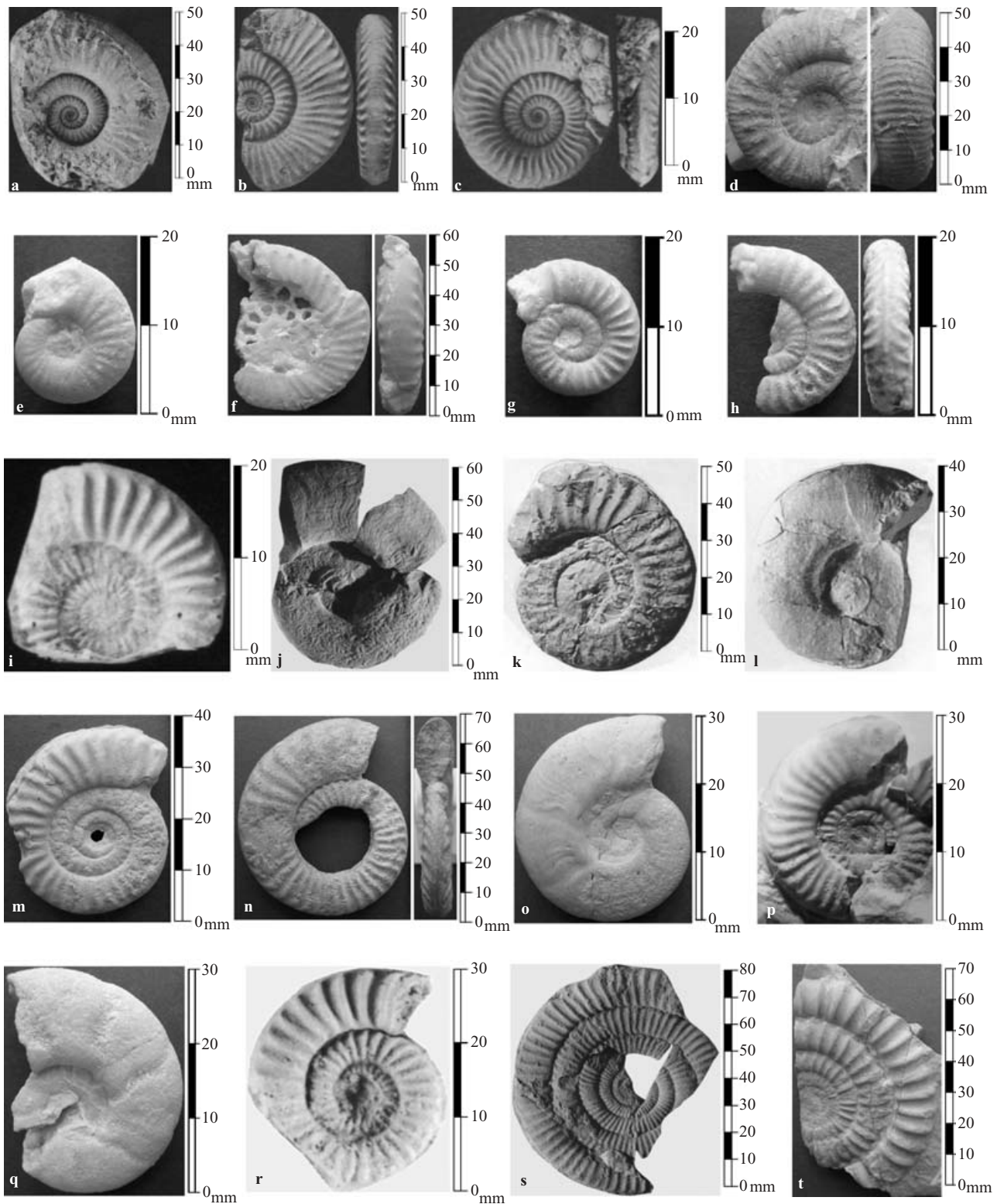


Figure 2. Ammonites indicating the same Sinemurian–Pliensbachian faunal succession in different sections. (a) Lateral view of *Miltoceras* cf. *sellae* (Gemmellaro); Arroyo Las Chilcas Section (Mendoza Province, Argentina); earliest Pliensbachian (from Hillebrandt, 1987, pl. 1, fig. 13). (b) Lateral and ventral view of *Dubariceras silviesi* (Hertlein); Arroyo Las Chilcas Section (Mendoza Province, Argentina); middle part of the early Pliensbachian (from Hillebrandt, 1987, pl. 2, fig. 5a, b). (c) Lateral and ventral view of the new polymorphitid; Arroyo Las Chilcas Section (Mendoza Province, Argentina); middle part of the early Pliensbachian (from Hillebrandt, 1987, pl. 2, fig. 10a, b). (d) Lateral and ventral view of *Miltoceras sellae* (Gemmellaro); Pallareto Quarry Section (Mount Catia; Apennines, Italy); middle part of the early Pliensbachian. (e) Lateral view of *Miltoceras* cf. *sellae* (Gemmellaro); Grilli Quarry Section (Furlo Pass; Apennines, Italy); middle part of the early Pliensbachian. (f) Lateral and ventral view of a form very similar to *Dubariceras silviesi* (Hertlein); Grilli Quarry Section (Furlo Pass; Apennines, Italy); middle part of the early Pliensbachian.



comparable age revealed an interesting evolutionary phenomenon concerning an unpublished early Pliensbachian Apennine genus from the *Miltoceras* fauna (Polymorphus Subzone, Jamesoni Zone), ascribable to the family Polymorphitidae, which we will formally describe in a forthcoming paper. We currently believe that this new polymorphitid reached the South American Pacific coast by the middle to late part of the early Pliensbachian. It then evolved towards progressively lenticular morphologies, giving rise to an endemic American ammonite group, which is represented by the genera *Eoamaltheus* Hillebrandt and *Fanninoceras* McLearn (Fig. 4).

Our phylogenetic reconstruction, based on shell morphology, early ontogenetic development (essentially, aspect of inner whorls), suture lines and biostratigraphy, can be summarized in six phases, as follows (Fig. 5):

- (1) Loss of the umbilical row of spines in the bispinate eoderoceratids gives rise to monospinate forms (basal Pliensbachian, *Catriceras* fauna, referable to the standard Jamesoni Zone, Taylori Subzone; Tethyan Palaeoprovince; Fig. 5a, b).
- (2) Our new polymorphitid originates among the monospinate eoderoceratoids; it is characterized by a subacute ventral area on the phragmocone and a false keel on the body chamber (earliest Pliensbachian, *Miltoceras* fauna, referable to the standard Jamesoni Zone, Polymorphus Subzone; Tethyan Palaeoprovince; Figs 2g, h, 5d).
- (3) Our new polymorphitid reaches South America, where it increases its shell involution and rib flexuosity, but maintains its subacute ventral area (middle to late part of the early Pliensbachian, referable to the standard Ibex Zone; Pacific Palaeoprovince; Figs 2c, 5e).
- (4) The same stock which gave rise to the South American variant of our new polymorphitid, also produces *Eoamaltheus*, with still more flexuous ribs and the typical crenulated keel on the body chamber (middle to late part of the early Pliensbachian, referable to the standard Ibex Zone; Pacific Palaeoprovince; Fig. 5f).
- (5) From a particularly streamlined form of the same parental stock of *Eoamaltheus*, *Fanninoceras* originates; the transition between the two genera (already supported by Dommergues & Meister, 1999, and references cited therein) can be clearly seen in the inner whorls of the specimens figured by Hillebrandt (1987), which show a roof-shaped or sub-keeled ventral area (late part of the early Pliensbachian, referable to the standard Davoei Zone; Pacific Palaeoprovince; Fig. 5g).
- (6) The latest representatives of *Fanninoceras* acquire an oxycone morphology, giving them a convergent aspect with *Radstockiceras* Buckman and related forms (which are absent in the eastern Pacific), and allowing them to fill the same ecological niche (late Pliensbachian, referable to the standard Spinatum Zone; Pacific Palaeoprovince; Fig. 5h).

These phylogenetic hypotheses are mainly based on the fact that the new polymorphitid, *Eoamaltheus* and *Fanninoceras* share a similarly structured suture line, with a large and broad E lobe, and a peculiarly shifted A lobe in the ES saddle, which is more or less advanced in regards to the LS1 saddle. On the other hand, the shell shape and ornamentation are different but, also judging from inner whorl similarities, it seems possible to recognize a clear transition from our new polymorphitid (earliest Pliensbachian) to its direct South American descendant (figured as *Polymorphites* (?) sp. by Hillebrandt (1987, pl. 2, figs 6–10); middle to late part of the early Pliensbachian), and from it to *Eoamaltheus* (middle to late part of the early Pliensbachian) and *Fanninoceras* (latest early Pliensbachian to late Pliensbachian). This phyletic lineage shows the tendency to increase shell involution and rib flexuosity, acquiring a more streamlined and hydrodynamically efficient shape. The structure of the suture line, as already noted, remains essentially constant during the

(g) Lateral view of the new polymorphitid; Grilli Quarry Section (Furlo Pass; Apennines, Italy); middle part of the early Pliensbachian. (h) Lateral and ventral view of the new polymorphitid; Grilli Quarry Section (Furlo Pass; Apennines, Italy); middle part of the early Pliensbachian. (i) Lateral view of *Catriceras* sp.; Arroyo Las Chilcas Section (Mendoza Province, Argentina); earliest Pliensbachian (from Hillebrandt, 1990, text-fig. 3, 6). (j) Lateral view of *Galaticeras* sp.; Guerss Section (Jebel Bou-Hamid; High Atlas, Morocco); earliest Pliensbachian (from Lachkar *et al.* 1998, fig. 5, 1). (k) Lateral view of '*Catriceras*' sp.; Bosso River Section (Apennines, Italy); earliest Pliensbachian (from Faraoni *et al.* 1996, pl. 4, fig. 7). (l) Lateral view of *Galaticeras* sp.; Bosso River Section (Apennines, Italy); earliest Pliensbachian (from Faraoni *et al.* 1996, pl. 4, fig. 6). (m) Lateral view of *Catriceras catriense* Venturi; Pallareto Quarry Section (Mount Catria; Apennines, Italy); beginning of the early Pliensbachian. (n) Lateral and ventral view of *Catriceras catriense* Venturi; Pallareto Quarry Section (Mount Catria; Apennines, Italy); beginning of the early Pliensbachian. (o) Lateral view of *Galaticeras catriense* (Venturi); Pallareto Quarry Section (Mount Catria; Apennines, Italy); beginning of the early Pliensbachian. (p) Lateral view of *Catriceras* cf. *campiliense* (Fucini); Grilli Quarry Section (Furlo Pass; Apennines, Italy); earliest Pliensbachian. (q) Lateral view of *Galaticeras canavarii* (Fucini); Grilli Quarry Section (Furlo Pass; Apennines, Italy); lower part of the early Pliensbachian. (r) Lateral view of *Paltechioceras* cf. *romanicum* (Uhlig); Arroyo Las Chilcas Section (Mendoza Province, Argentina); late Sinemurian (from Hillebrandt, 2002, pl. 11, fig. 22a). (s) Lateral view of *Paltechioceras* cf. *tardecrescens* (Hauer); Guerss Section (Jebel Bou-Hamid; High Atlas, Morocco); late Sinemurian (from Lachkar *et al.* 1998, fig. 8, 18). (t) Lateral view of *Paltechioceras romanicum* (Uhlig); Bosso River Section (Apennines, Italy); late Sinemurian.

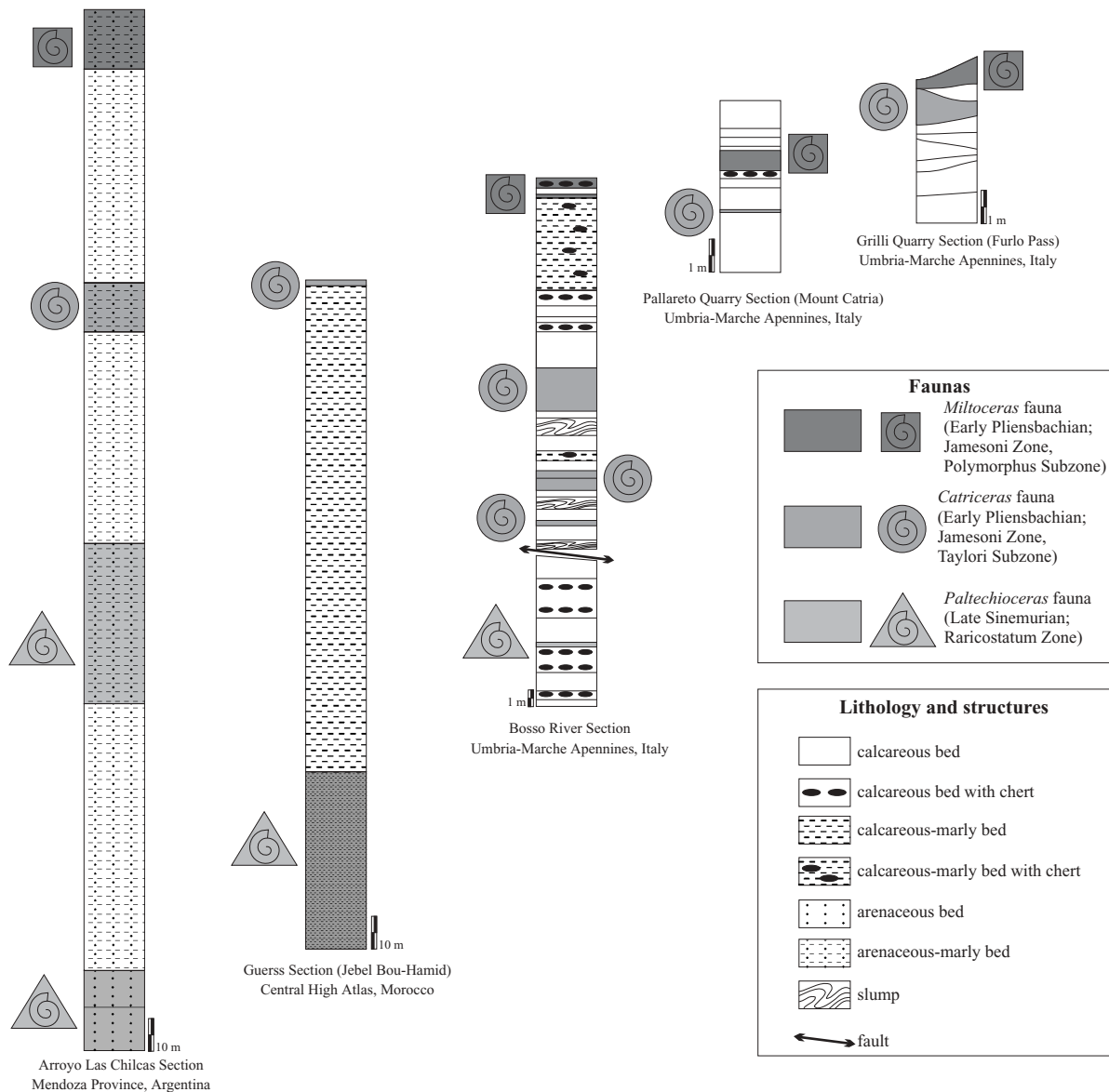


Figure 3. Schematic stratigraphy of the sections which show the same Sinemurian–Pliensbachian ammonite fauna succession. The shared faunas are indicated using different tones of grey: *Paltechioceras* in the late Sinemurian (referable to the standard Raricostatum Zone; triangular symbols), *Catriceras* in the earliest Pliensbachian (referable to the standard Jamesoni Zone, Taylori Subzone; round symbols), *Miltoceras* in the middle part of the early Pliensbachian (referable to the standard Jamesoni Zone, Polymorphus Subzone; square symbols). From left to right the sections are: Arroyo Las Chilcas (Mendoza Province, Argentina; from Hillebrandt, 2002), Guerss (Jebel Bou-Hamid; High Atlas, Morocco; from Lachkar *et al.* 1998), Bosso River (Apennines, Italy), Pallareto Quarry (Mount Catria; Apennines, Italy), Grilli Quarry (Furlo Pass; Apennines, Italy). Please note the great qualitative and quantitative differences in the facies existing among the various areas.

entire process, although an increase in complexity can be observed, especially in late representatives of *Fanninoceras* (Fig. 5h).

The transition from monospinate eoderoceratids (ancestral root stock) to polymorphitids (evolved branch) took place mainly with an outer whorl innovation, which was acquired several times over and at various degrees by different genera in subsequent times, starting early in the Pliensbachian. During this process, the monospinate ornamentation was preserved, but the secondary ribs crossing the venter were lost.

This fact is widely and clearly documented in the lower Pliensbachian Apennine sections (*Catriceras* and *Miltoceras* faunas), where we found many transitional forms between bispinate Eoderoceratidae, monospinate Eoderoceratidae and the very first Polymorphitidae (see Fig. 5).

The same ancestral eoderoceratid stock also gave rise to the early Pliensbachian monospinate group which includes *Miltoceras* Wiedenmayer (Figs 2a, d, e, 5c) and the form identified by Smith & Tipper (1996) as *Dubariceras silviesi* (Hertlein) (Fig. 2b, f); both

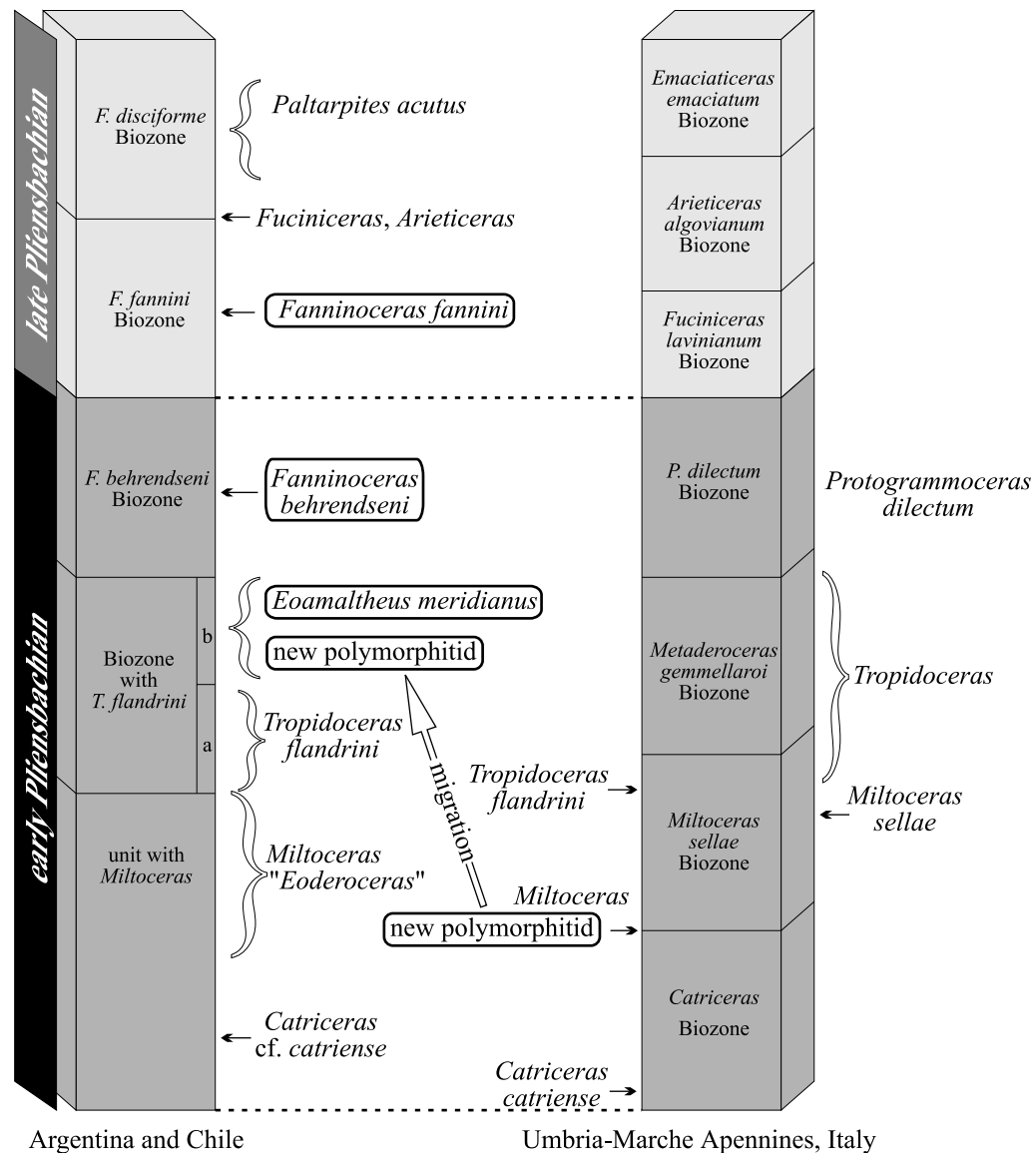


Figure 4. Schematic biostratigraphic framework for the early Pliensbachian (represented by dark grey blocks) and late Pliensbachian (represented by light grey blocks) of areas of Argentina and Chile, and Italian Apennines. For the Apennines (right column), according to the recently revised zonal scheme elaborated by Faraoni *et al.* (1996), the early Pliensbachian can be divided into four biozones. From the bottom to the top these are: the *Catriceras* biozone; the *Miltoceras sellae* biozone; the *Metaderoceras gemmellaroi* biozone; the *Protogrammoceras dilectum* biozone. For the same chronostratigraphic interval of the South American regions (left column), a re-interpretation of the zonal scheme proposed by Hillebrandt (1987) leads to recognition of only three biozones. From the bottom to the top these are: an unnamed biozone (roughly corresponding to the provisional 'Apoderoceras + Eoderoceras' biozone of Hillebrandt, 1987), characterized by a lower unit with *Catriceras* and an upper unit with *Miltoceras*; a biozone with *Tropidoceras*, characterized by a lower unit with *Tropidoceras* (provisional 'Tropidoceras' biozone of Hillebrandt, 1987) and an upper unit with *Eoamaltheus meridianus* (*E. meridianus* biozone of Hillebrandt, 1987; probably corresponding to the *Dubariceras* Andean Assemblage Zone of Iglesia Llanos & Riccardi, 2000); the *Fanninoceras behrendseni* biozone (*F. behrendseni* biozone of Hillebrandt, 1987). Quite detailed correlations are not possible yet, but one can clearly see a westward diachronism in the first occurrence of some ammonoid genera. In the Apennines, the new polymorphitid is found at the base of the *Miltoceras sellae* biozone (below the first occurrence of *Tropidoceras flandrini*); later on, migrating possibly through the proto-Atlantic seaway (white arrow), this ammonite reached the South American Pacific coast, where it is found, together with its relative *Eoamaltheus meridianus*, in the upper part of the biozone with *Tropidoceras* (above the first occurrence of *T. flandrini*). Please note that the lineage originated by the new polymorphitid (taxa enclosed in heavy-edged rectangles) initially appeared in the Apennines, and soon afterwards continued to evolve in the American regions, apparently disappearing in its native area.

taxa are found in Apennine and American areas, but for these ammonites we were not able to recognize evolutionary phenomena comparable to that involving our new polymorphitid.

### 3. Interpretation and discussion

The data presented in this paper seem to agree with the establishment of a trans-Pangaeian marine connection

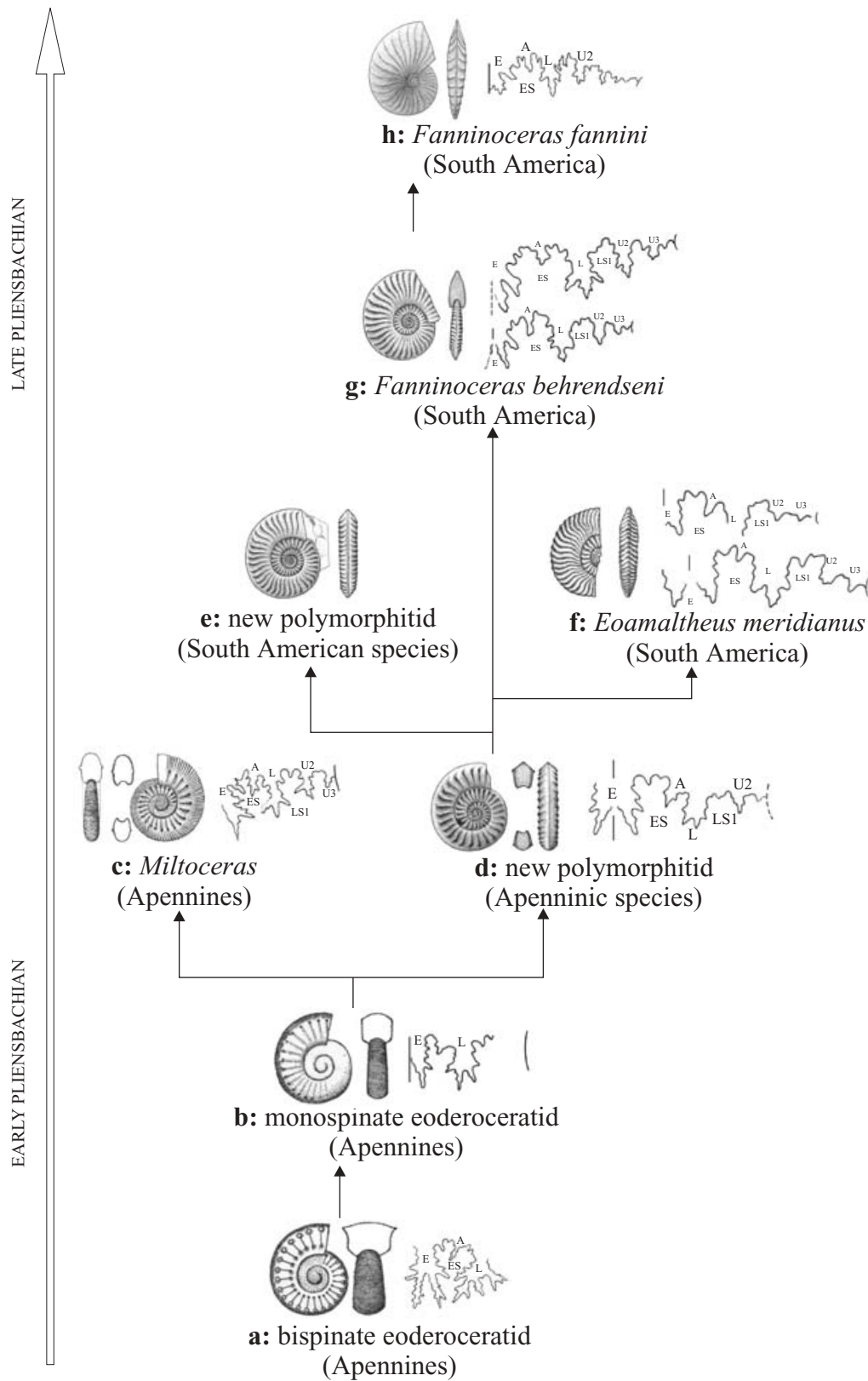


Figure 5. Phylogenetic reconstruction showing the probable ancestors of our new polymorphitid in the Apennines, as well as its successive descendants in South America. (a) Lateral view, ventral view and suture line of a bispinate eoderoceratid (nucleus); base of the early Pliensbachian, Apennines; about natural size. (b) Lateral view, ventral view and suture line of a monospinate eoderoceratid (nucleus); beginning of the early Pliensbachian, Apennines; about natural size. (c) Ventral view, whorl section, lateral view and suture line of *Miltoceras*; earliest Pliensbachian, Apennines; reduced about  $\times 0.5$ . (d) Lateral view, whorl section, ventral view and suture line of the new polymorphitid (Apennine species); earliest Pliensbachian, Apennines; reduced about  $\times 0.7$ . (e) Lateral and ventral view of the new polymorphitid (South American species); middle part of the early Pliensbachian, Argentina (redrawn from Hillebrandt, 1987;

between the western Tethys and the South American Pacific coast; in our opinion, they specifically support the idea that it allowed some faunal migrations at least by late Sinemurian–early Pliensbachian. Such a seaway is often accepted in the literature: this is the so-called proto-Atlantic seaway, better known as the Hispanic Corridor (Smith, 1983) (among the available names for this palaeogeographic element, we deem ‘proto-Atlantic seaway’ to be the simplest, although ‘Hispanic Corridor’ is more frequently used; in the following paragraphs we will refer to it with one of these two terms). Its existence has already been widely supported by many authors, with several geological and palaeontological pieces of evidence, and indeed there are a large number of papers concerning this issue (e.g. Broglio Loriga & Neri, 1976; Hallam, 1983; Smith & Tipper, 1986; Nauss & Smith, 1988; Smith *et al.* 1990; Westermann, 1993; Damborenea, 2000; Aberhan, 2001, 2002; Manceñido, 2002; Stampfli & Borel, 2002; Iturralde-Vinent, 2003*a, b* and references cited therein), although alternative hypotheses have been advanced (these imply a pantropical distribution of species in the entire proto-Pacific Ocean, with an eastward decrease of their diversity: Newton, 1988; Dommergues, 1994; Dommergues, Meister & Jaillard, 2004). (Fig. 6).

Even though a central trans-Pangaeic epicontinental marine connection might have been established earlier (Iturralde-Vinent, 2003*a*), the formation of the proto-Atlantic seaway was linked to the break-up of Pangaea, and in particular to the central Atlantic opening, which produced a complex of half-graben and graben. The consequent Mesozoic development of Mediterranean areas is linked to the evolution of two major basin systems: the Atlantic Ocean with its eastern branch (Ligure-Piemontese Ocean) and the Tethys sea, with its closing sectors to the north (Palaeotethys) and opening portions to the south (Neotethys). (Şengör, Yılmaz & Sungurlu, 1984; Kozur, 1991; Dercourt, Ricou & Vrielynck, 1993; Robertson *et al.* 1996; Ciarapica & Passeri, 1998, 2002; Stampfli & Borel, 2002).

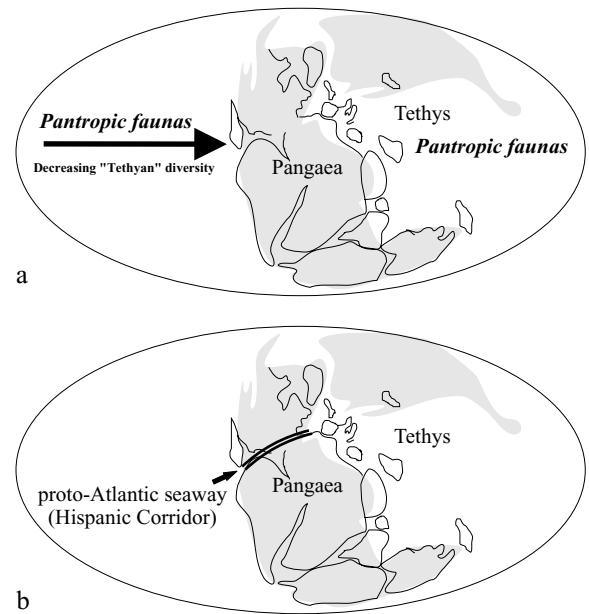


Figure 6. Simplified main palaeobiogeographic models adopted to explain Tethyan faunal occurrences in the American Pacific coast sections. (a) Pantropical distribution model: ‘Tethyan’ faunas are composed of pantropic species, extending through the entire proto-Pacific Ocean, with an eastward decrease of their diversity. (b) Seaway or marine-corridor hypothesis, showing the position of the Hispanic Corridor: this connection allowed the westward migration of some shallow-water taxa, promoting intermittent faunal exchange between western Tethys and the American Pacific coast (modified from Newton, 1988).

The progressive opening of the proto-Atlantic rift system influenced the basin development along its course (for instance, Jansa, 1991, noted a NE–SW trend in the diachronous initiation and termination of the evaporitic deposits and shallow-water carbonates) but also affected marine biotas, representing a new potential migration route (Figs 7, 8). At present, there is broad consensus about the important role of the proto-Atlantic seaway for the faunal exchange between the western Tethys and the South American Pacific coast in Early Jurassic times. Studies on the

reduced about  $\times 0.7$ ). (f) Lateral view, ventral view and suture lines of *Eoamalthus meridianus*; middle part of the early Pliensbachian, Argentina (redrawn from Hillebrandt, 1981; reduced about  $\times 0.7$ ). (g) Lateral view, ventral view and suture lines of *Fanninoceras behrendseni*; late part of the early Pliensbachian, Argentina (redrawn from Hillebrandt, 1987; reduced about  $\times 0.7$ ). (h) Lateral view, ventral view and suture line of *Fanninoceras fannini*; upper Pliensbachian, North America (redrawn from Smith & Tipper, 1996; reduced about  $\times 0.3$ ). The evolutionary process depicted here started in the Apennines, at the beginning of the early Pliensbachian, with the loss of a row of spines in the bispinate eoderoceratids, which gave rise to monospinate forms (lower part of the scheme). Among the monospinate eoderoceratoids, two main variants occur in the earliest Pliensbachian: taxa maintaining their secondary ribs on a raised ventral area (*Miltoceras*; middle part of the scheme, on the left); forms losing the secondary ribs, simplifying their suture line and further heightening the ventral area (new polymorphitid; middle part of the scheme, on the right). Representatives of this latter option reached South America by the middle to late part of the early Pliensbachian, starting to assume a more streamlined morphology, with an increase in shell involution and rib flexuosity; this lineage leads to *Fanninoceras*, giving rise also to *Eoamalthus* as a lateral branch (upper part of the scheme). As can be seen, all the members of the lineage that originated from the new polymorphitid share a similar structure in their suture line, characterized by a broad E lobe, larger than L, and a peculiarly shifted A lobe in the ES saddle, which is more or less advanced in regards to the LS1 saddle; an increase of complexity and indenting can be observed in *Fanninoceras*. An overall similarity in the basic aspect of the suture is found also in *Miltoceras*, being apparently inherited from the bispinate common ancestor (drawings by F. Venturi).



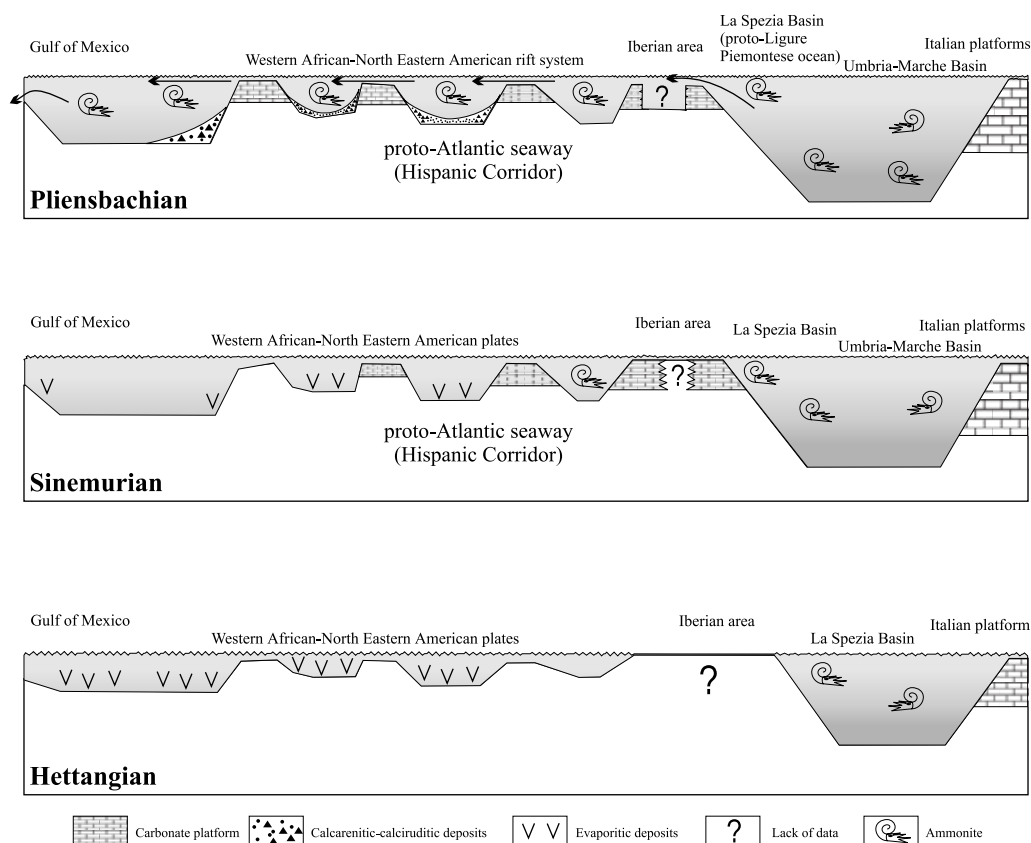


Figure 7. Hypothetical palaeogeographic evolution of the proto-Atlantic seaway. During the Hettangian (lower part of the scheme), the available data suggest that a marine connection between western Tethys and American areas was not already developed. In these early phases of proto-Atlantic opening, the transgressive Tethys sea was the site of a complex network of NE-trending sub-basins, characterized by an initial deposition of evaporitic facies. The NE–SW trend observed in the diachronous initiation and termination of evaporitic and shallow-water carbonate deposits supports a gradual opening of the proto-Atlantic from the Iberic areas (western Tethys) to the present-day Gulf of Mexico. The related progressive opening of the Hispanic Corridor allowed intermittent connections between these areas already by late Sinemurian times (middle part of the scheme). During eustatic cycles, sea level rise phases provided an occasional seaway for ammonite faunal exchanges. At the beginning of the Pliensbachian (upper part of the scheme), the proto-Atlantic seaway allowed a better (although incomplete) communication and faunal exchange between western Tethys and the South American Pacific coast. Evaporitic sedimentation stopped, carbonate platform systems grew and in the intra-platform basins, calcarenitic–calciruditic facies were resedimented.

palaeobiogeography of many marine animals (brachiopods, bivalves, reptiles), including ammonoids (e.g. Riccardi, 1991; Hillebrandt, 2002), suggest that this intermittent connection was already used by some shallow-water organisms at least by late Sinemurian–early Pliensbachian times (see also Westermann, 1993 and Iturralde-Vinent, 2003b and references cited therein). This means that the Hispanic Corridor functioned before the true separation of continental plates, and it is important to underline that the faunal exchange through a marine connection is independent of the presence of oceanic crust.

As noted by Iturralde-Vinent (2003b), the presence of marine environments (even of short duration) in the Lower Jurassic sections of the south-central Atlantic, Florida-Bahamas, Gulf of Mexico, northern South America, or the Caribbean area cannot be demonstrated conclusively. Therefore the current sedimentological, stratigraphic and tectonic evidence cannot document

convincingly the existence of a true Early Jurassic marine connection at tropical palaeolatitudes in the proto-Atlantic rift system. However, one can consider the possibility that some shallow-water marine animals might have crossed this area during even minor and local sea-level rises. Indeed, the available palaeontological evidence strongly supports such a connection, although intermittent and acting like a filter (see also Iturralde-Vinent, 2003b and references cited therein). The identical succession of faunas in areas situated along the hypothesized course of the Hispanic Corridor (from east to west: Apennines, Morocco, part of southern Spain, South America) suggests to us specifically that this marine connection was used by ammonoids at least immediately after the Sinemurian–Pliensbachian transition.

Our hypothesis is also supported by the data of Baldanza & Mattioli (1992); they indicated that the first occurrence of the calcareous nannofossil *Lotharingius*

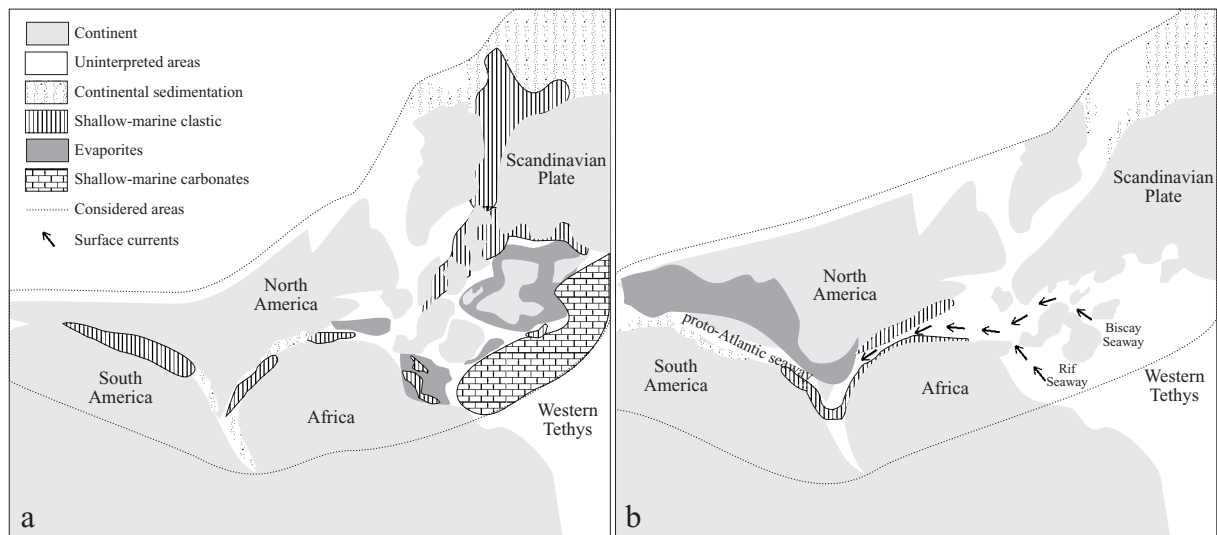


Figure 8. Evolution scheme showing the progressive opening of the proto-Atlantic rift system, with its complex of half-graben and graben. (a) In late Triassic times, the first deposits are mainly shallow-marine clastic sediments, roughly aligned in a NE–SW trend; evaporites are present only in the eastern areas (including the western Tethys region) (simplified from Jansa, 1991). (b) During Early Jurassic times, a progressively westward-shifting evaporitic deposition involved the proto-Atlantic rift, replacing the shallow-marine clastic sedimentation; our evidence suggests the existence of a still-precarious Atlantic seaway (mainly based on Iturralde-Vinent, 2003b and Jansa, 1991).

*hauffii* Grün & Zweili shows a clear rejuvenation E–W trend, ranging from early Pliensbachian (Jamesoni Zone) in Hungary to late Pliensbachian (Spinatum Zone) in Umbria–Marche and Portugal. A similar (although less evident) distribution pattern is reported for the first occurrences of *Biscutum finchii* (Crux) (Jamesoni Zone in Hungary and Portugal, Spinatum Zone in Umbria–Marche) and *Mitrolithus jansae* (Wiegand) (Jamesoni Zone in Hungary and Portugal, Davoei in Umbria–Marche). Baldanza & Mattioli (1992) relate these diachronous distributions mainly to the physiography of the southern border of the western Tethys and to the seawater circulation, suggesting an E–W Early Jurassic predominant current flow, from Hungarian areas through Greece and Italy towards Morocco and Portugal. It is reasonable to think that this kind of Tethyan circulation might have extended into the proto-Atlantic seaway, so that an E–W route could have been used by some ammonites to migrate from the western Tethys to the South American Pacific coast.

One can object that the model adopted in the present paper does not consider several factors, such as: (1) the presence of other currents; (2) a possible pantropical distribution for the examined taxa.

In reply to these objections, we can provide the following arguments:

(1) It is surely permissible to suppose, on an actualistic basis (considering both the presumed position of the major continental masses and Earth rotation), the existence of a Tethyan equivalent of the present-day eastward Cromwell

counter-current (Newton, 1988), but it is likewise sensible to admit at least one equatorial westward surface current, similar to its modern Pacific counterpart at comparable latitudes. Although present-day patterns of marine circulation cannot be completely extrapolated to evaluate all palaeobiogeographic scenarios (Iturralde-Vinent, 2003a), this kind of ocean current arrangement is consistent with atmospheric palaeocurrent reconstructions such as those by Parrish & Curtis (1982; for general comments on Early Jurassic oceanic circulation, see also Aberhan, 2001).

(2) As far as we know, there is no evidence of a pantropical distribution for the examined ammonoid taxa. By now, these forms are exclusively found in the western Tethys (e.g. Italian Apennines) and American Pacific coast (e.g. Argentina), but they have never been recorded in eastern areas (e.g. Asia), where late Sinemurian–early Pliensbachian ammonite faunas are very scarce or non-existent. Moreover, to follow a W–E route in the vast proto-Pacific Ocean, ammonoids like *Catriceras* and *Miltoceras* (which lived most likely in relatively shallow environments, at about 50–100 m depth) would have required a quasi-continuous chain of islands (or at least areas with not exceedingly deep water), whose existence is yet to be proven. Uncertainty about the exact longitudinal position of some tectonic terranes (such as Wrangellia) at this time means that the matter cannot yet be fully resolved. In any case, we feel that the kind of phylogenetic development recognizable for

our new polymorphitid is not consistent with a pantropical distribution of the involved taxa; the ancestral form occurs only in the Apennines, preceding the taxa interpreted as its descendants, which are found exclusively in the eastern Pacific. In our opinion, the chronological and geographic separation between the initial form of the lineage and its successors would never have been so sharp for pantropical animals. It is the migration through a seaway which allows previously restricted marine communities to extend their areal distribution and colonize new environments.

We believe that supposing the existence of a proto-Atlantic seaway (Hispanic Corridor) during the early–middle part of the Early Jurassic provides a sufficiently simple and reasonable explanation of various palaeontological data. In any case, this working hypothesis does not have any claim to be of universal applicability; we deem the proto-Atlantic seaway model to be the most suitable (until proof of the contrary) for the ammonites we examined, but it may not necessarily be valid for other taxa. As a general approach, we think it reasonable not to rule out a priori that different animals could have used different means and mechanisms of dispersal.

Indeed, it seems that not all ammonoids were able to pass through the Hispanic Corridor. This is the case with *Galaticeras* Spath, a genus which is quite abundant in early–middle Pliensbachian Tethyan sections (including Apennine and Morocco) but is not recorded in South America (Hillebrandt, 2002). This is also reported for the late Sinemurian *Bouh- amidoceras* Dubar and the Sinemurian–Pliensbachian *Partschiceras* Fucini. The absence of such forms in the American sections may show an incomplete faunal exchange between western Tethys and the South American Pacific coast. This can be linked to several factors, such as the initial precariousness and shallowness of the connecting channels (due, for example, to temporary sea-level falls) or other palaeoceanographic reasons, but also to the different life habits (including reproductive strategies) and ecological requirements of the various genera. It seems likely that trans-Pangaea current dispersal involved mainly ammonoids with a nekto-benthic adult phase (as was probably *Catriceras*) and planktonic embryos or early juvenile stages, according to the general models presented in Landman, Tanabe & Shigeta (1996) and in Westermann (1996).

The presence of planktonic embryos amongst ammonites cannot be safely proven, and in any case one can think that this phase is not indispensable for a planktonic or at least quasi-planktonic juvenile dispersion (J.-L. Dommergues, pers. comm.). Although it may sound too obvious, it is not necessarily true that all ammonoids possessed exactly the same kind

of ontogenetic development; based on the reasonable premise that taxa with different morphologies can follow different distribution and dispersal models (as a consequence of different adaptations and behaviours), we imagine that genera such as *Galaticeras*, *Bouh- amidoceras* and *Partschiceras* could have adopted a reproductive habit without embryonal and early juvenile planktonic stages.

#### 4. Conclusions

The palaeobiogeographic model which admits a more or less temporary proto-Atlantic trans-Pangaeian seaway starting from the late Sinemurian–early Pliensbachian seems better to explain the data presented here, as well as the other geopalaeontological evidence. Therefore, this is mainly the interpretation of our specific data set, and it is not a general statement with claims of universal applicability. Our hypothesis consistently relates the biostratigraphy and the evolution of some western Tethys and South American ammonoids with the major palaeogeographic changes involving this vast area.

A modification in the mutual arrangement of some continental masses during the Sinemurian–Pliensbachian transition is suggested by several lines of evidence. In the Apennines, the renewal of ammonite assemblages associated with this time interval corresponds to stable isotope variations (positive for  $\delta^{18}\text{O}$ , negative for  $\delta^{13}\text{C}$ ) and also to radiation or extinction episodes of calcareous nannoplankton (Mattioli *et al.* in press). Since the positive  $\delta^{18}\text{O}$  shift might imply a decrease in water temperatures, one can hypothesize a relationship with seaway openings (with consequent relatively cool water entry) and with a change in the palaeogeographic setting (Venturi, Nannarone & Bilotta, 2004). The opening phases of the proto-Atlantic rift system and subsequent seaway could have marked the beginning of the period of tectonic instability which characterized the Jurassic; this might help to explain the ‘noise’ (faults, slumps, hiatuses, intervals lacking fossils, etc.) observed in the deposits corresponding to the Sinemurian–Pliensbachian transition of the Apennine and other regions.

These palaeogeographic changes combined with palaeoecological factors could have led to the formation of an intermittent connection and selective dispersal between the western Tethys and the South American Pacific coast, as suggested by the incomplete exchange of ammonite faunas between the two areas.

The idea of a progressive NE–SW opening for the proto-Atlantic rift system is supported by a great deal of tectonic and sedimentological evidence (it is sufficient to consider the already-cited diachronism in the evaporitic and shallow-water carbonatic sediments; e.g. see Jansa, Bujak & Williams, 1980; Jansa, 1981; Hay *et al.* 1982; Jansa, 1991). However, the precise dating for some of the deposits (namely,

evaporites and carbonate platforms) in the 'key areas' of the Hispanic Corridor is still controversial, and the available tectonic, stratigraphic and sedimentological data cannot properly document that in Early Jurassic times some brief marine incursions occurred at tropical palaeolatitudes in the opening rift system. On an actualistic basis this is surely a reasonable idea, but further detailed research is needed to find possible solutions to such a complicated issue.

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## References

- ABERHAN, M. 2001. Bivalve palaeobiogeography and the Hispanic Corridor: time of opening and effectiveness of a proto-Atlantic seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology* **165**, 375–94.
- ABERHAN, M. 2002. Opening of the Hispanic Corridor and early Jurassic bivalve biodiversity. In *Palaeobiogeography and Biodiversity Change: the Ordovician and Mesozoic–Cenozoic Radiations* (eds J. A. Crame and A. W. Owen), pp. 127–39. Geological Society of London, Special Publication no. 194.
- BALDANZA, A. & MATTIOLI, E. 1992. Biostratigraphical synthesis of nanofossils in the early middle Jurassic of Southern Tethys. *Knihovnicka ZPN* **14a**(1), 111–41.
- BRAGA, J. C., COMAS-RENGIFO, M. J., GOY, A. & RIVAS, P. 1982. Comparaciones faunísticas y correlaciones en el Pliensbachiano de la Zona Subbética y Cordillera Ibérica. *Bolétin de la Real Sociedad Española de Historia Natural (Sección Geología)* **80**, 221–44.
- BRAGA, J. C., RIVAS, P., COMAS-RENGIFO, M. J. & GOY, A. 1984. The Pliensbachian of Spain: Ammonite successions, boundaries and correlations. In *International Symposium on Jurassic Stratigraphy – Erlangen, September 1–8, 1984: Symposium Volume I* (eds O. Michelson and A. Zeiss), pp. 159–76. Copenhagen.
- BROGLIO LORIGA, C. & NERI, C. 1976. Aspetti paleobiologici e paleogeografici della facies a «*Lithotis*» (Giurese inf.). *Rivista Italiana di Paleontologia* **82**(4), 651–706.
- CENTAMORE, E., CHIOCCHINI, M., DEIANA, G., MICARELLI, A. & PIERUCCINI, U. 1971. Contributo alla conoscenza del Giurassico dell'Appennino umbro-marchigiano. *Studi Geologici Camerti* **1**, 7–90.
- CIARAPICA, G. & PASSERI, L. 1998. Evoluzione Paleogeografica degli Appennini. *Atti Ticinensi di Scienze della Terra* **40**, 233–90.
- CIARAPICA, G. & PASSERI, L. 2002. The paleogeographic duplicity of the Apennines. *Bollettino della Società Geologica Italiana, Volume Speciale* **1**, 67–75.
- COLACICCHI, R., PASSERI, L. & PIALLI, G. 1970. Nuovi dati sul Giurese umbro-marchigiano ed ipotesi per un suo inquadramento regionale. *Memorie della Società Geologica Italiana* **1**(4), 839–74.
- COLACICCHI, R. & PARISI, G. (coordinators) 1999. A multidisciplinary approach to the geology of the Italian Jurassic: Twelve years of researches into the Umbria-Marche Basin (Central Italy). In *Bioevents and Integrated Stratigraphy of the Triassic and Jurassic in Italy* (eds R. Colacicchi, G. Parisi and V. Zamparelli), pp. 85–184. Paleopelagos Special Publication no. 3. Roma.
- DAMBORENEA, S. E. 2000. Hispanic Corridor: its evolution and the biogeography of bivalve mollusks. In *Advances in Jurassic Research* (eds R. L. Hall and P. L. Smith), pp. 369–80. GeoResearch Forum vol. 6.
- DERCOURT, J., RICOU, L. E. & VRIELYNCK, B. (eds) 1993. *Atlas Tethys Palaeoenvironmental Maps*. Paris: CCGM, BECIP-FRANLAB Gauthier-Villars, 307 pp.
- DOMMERGUES, J.-L. 1994. Les faunes d'ammonites pandémiques et téthysiennes du Lias confrontées à un modèle de distribution pantropicale. In *Proceedings of III Pergola International Symposium "Fossili, Evoluzione, Ambiente" Pergola, 25–30 October 1990* (ed. G. Pallini), pp. 93–107. Paleopelagos Special Publication no. 1. Roma: C. S. A. Università "La Sapienza".
- DOMMERGUES, J.-L. & MEISTER, C. 1999. Cladistic formalisation of relationships within a superfamily of Lower Jurassic Ammonitina: Eoderocerataceae Spath, 1929. *Revue de Paléobiologie* **18**(1), 273–86.
- DOMMERGUES, J.-L., MEISTER, C. & JAILLARD, E. 2004. Ammonites de la formation Santiago de la zone subandine du S-E de l'Équateur (Jurassique inférieur, Sinémurien). *Revue de Paléobiologie* **23**(1), 355–71.
- FARAONI, P., MARINI, A., PALLINI, G. & VENTURI, F. 1996. New Carixian ammonite assemblages of Central Apennines (Italy), and their impact on Mediterranean Jurassic biostratigraphy. *Paleopelagos* **6**, 75–122.
- HALLAM, A. 1983. Early and mid-Jurassic molluscan biogeography and the establishment of the central Atlantic seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology* **43**(3/4), 181–93.
- HAY, W. W., BEHENSKY, J. F. JR, BARREN, E. J. & SLOAN, J. L. II. 1982. Late Triassic–Liassic paleoclimatology of the proto-Central North Atlantic Rift System. *Palaeogeography, Palaeoclimatology, Palaeoecology* **40**, 13–30.
- HILLEBRANDT, A. VON. 1981. Faunas de ammonites del liásico inferior y medio (Hettangiano hasta Pliensbachiano) de América del Sur (excluyendo Argentina). In *Cuencas sedimentarias del Jurásico y Cretácico de América del Sur* (eds W. Volkheimer and E. A. Musacchio), pp. 499–538. Comité Sudamericano del Jurásico y Cretácico, 2. Buenos Aires.
- HILLEBRANDT, A. VON. 1987. Liassic ammonite zones of South America and correlations with other provinces. With description of new genera and species of ammonites. In *Bioestratigrafía de los Sistemas Regionales del Jurásico y Cretácico en América del Sur* (ed. W. Volkheimer), pp. 111–57. Contribution to I.G.C.P. no. 171, Circum-Pacific Jurassic, Mendoza, 1.



- HILLEBRANDT, A. VON. 1990. Der untere Jura im Gebiet des Rio Atuel (Provinz Mendoza, Argentinien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **181**, 143–57.
- HILLEBRANDT, A. VON. 2002. Ammoniten aus dem oberen Sinemurium von Südamerika. *Revue de Paléobiologie* **21**, 35–147.
- IGLESIA LLANOS, M. P. & RICCARDI, A. C. 2000. The Neuquén composite section: magnetostratigraphy and biostratigraphy of the marine lower Jurassic from the Neuquén basin (Argentina). *Earth and Planetary Science Letters* **181**, 443–57.
- ITURRALDE-VINENT, M. A. 2003a. The Evolution of the Caribbean Seaway: Jurassic to Present. In *From Greenhouse to Icehouse: The Marine Eocene–Oligocene Transition* (eds D. Prothero, L. Ivany and E. Nesbitt), pp. 386–96. New York: Columbia University Press.
- ITURRALDE-VINENT, M. A. 2003b. The Conflicting Paleontologic versus Stratigraphic Record of the Formation of the Caribbean Seaway. In *The Circum-Gulf of Mexico and the Caribbean: Hydrocarbon habitats, basin formation, and plate tectonics* (eds C. Bartolini, R. T. Buffler and J. Blickwede), pp. 75–88. AAPG Memoir no. 79.
- JANSA, L. F. 1981. Mesozoic Carbonate platforms and banks of the eastern North American margin. *Marine Geology* **44**, 97–117.
- JANSA, L. F. 1991. Processes affecting paleogeography, with examples from the Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* **87**, 345–71.
- JANSA, L. F., BUJAK, J. P. & WILLIAMS, G. L. 1980. Upper Triassic salt deposits of the western North Atlantic. *Canadian Journal of Earth Sciences* **17**, 547–59.
- KOZUR, H. 1991. The evolution of the Meliata-Hallstatt ocean and its significance for the early evolution of the Eastern Alps and Western Carpathians. *Palaeogeography, Palaeoclimatology, Palaeoecology* **87**, 109–35.
- LACHKAR, N., DOMMERGUES, J.-L., MEISTER, C., NEIGE, P., IZART, A. & LANG, J. 1998. Les ammonites du Sinémurien supérieur du Jebel-Bou-Hamid (Haut-Atlas central, Rich, Maroc). Approches paléontologique et biostratigraphique. *Geobios* **31**, 587–619.
- LANDMAN, N. H., TANABE, K. & SHIGETA, Y. 1996. Ammonite Embryonic Development. In *Ammonoid Paleobiology* (eds N. H. Landman, K. Tanabe and R. A. Davis), pp. 343–405. Topics in Geobiology, vol. 13. New York: Plenum Press.
- MANCENÍDO, M. O. 2002. Paleobiogeography of Mesozoic brachiopod faunas from Andean–Patagonian areas in a global context. *Geobios* **35**, *Mémoire spécial* **24**, 176–92.
- MATTIOLI, E., MORETTINI, E., PARISI, G. & VENTURI, F. In press. Nanofossil and ammonite assemblages, stable isotope stratigraphy and the paleoceanography of the Umbria-Marche basin during the Sinemurian–Pliensbachian (Lower Jurassic). *Eclogae geologicae Helveticae*.
- MEISTER, C., BLAU, J., DOMMERGUES, J.-L., FEIST-BURKHARDT, S., HART, M., HESSELBO, S. P., HYLTON, M., PAGE, K. & PRICE, G. 2003. A proposal for the Global Boundary Stratotype Section and Point (GSSP) for the base of the Pliensbachian Stage (Lower Jurassic). *Eclogae geologicae Helveticae* **96**, 275–97.
- NAUSS, A. L. & SMITH, P. L. 1988. *Lithiotis* (Bivalvia) bioherms in the Lower Jurassic of east-central Oregon, U. S. A. *Palaeogeography, Palaeoclimatology, Palaeoecology* **65**, 253–68.
- NEWTON, C. R. 1988. Significance of “Tethyan” Fossils in the American Cordillera. *Science* **242**, 385–91.
- PARRISH, J. T. & CURTIS, R. L. 1982. Atmospheric circulation, upwelling, and organich-rich rocks in the Mesozoic and Cenozoic eras. *Palaeogeography, Palaeoclimatology, Palaeoecology* **40**, 31–66.
- RICCARDI, A. C. 1991. Jurassic and Cretaceous marine connections between the Southeast Pacific and Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* **87**, 155–89.
- ROBERTSON, A. H. F., DIXON, J. E., BROWN, S., COLLINS, A., MORRIS, A., PICKETT, E., SHARP, I. & USTAÖMER, T. 1996. Alternative tectonic models for the Late Palaeozoic–Early Tertiary development of Tethys in the eastern Mediterranean region. In *Palaeomagnetism and Tectonics of the Mediterranean Region* (eds A. Morris and D. H. Tarling), pp. 239–63. Geological Society of London, Special Publication no. 105.
- ŞENGÖR, A. M. C., YILMAZ, Y. & SUNGURLU, O. 1984. Tectonics of the Mediterranean Cimmerides: nature and evolution of the western termination of Palaeo-Tethys. In *The Geological Evolution of the Eastern Mediterranean* (eds J. E. Dixon and A. H. F. Robertson), pp. 77–112. Geological Society of London, Special Publication no. 17.
- SMITH, P. L. 1983. The Pliensbachian ammonite *Dayiceras dayiceroides* and Early Jurassic paleogeography. *Canadian Journal of Earth Sciences* **20**, 86–91.
- SMITH, P. L. & TIPPER, H. W. 1986. Plate Tectonics and Paleobiogeography: Early Jurassic (Pliensbachian) Endemism and Diveristy. *Palaïos* **1**, 399–412.
- SMITH, P. L. & TIPPER, H. W. 1996. Pliensbachian (Lower Jurassic) Ammonites of the Queen Charlotte Islands, British Columbia. *Bulletins of American Paleontology* **108**, 1–122.
- SMITH, P. L., WESTERMANN, G. E. G., STANLEY, G. D. JR & YANCEY, T. E. 1990. Paleobiogeography of the ancient Pacific. *Science* **249**(4959), 680–83.
- STAMPFLI, G. M. & BOREL, G. D. 2002. A plate tectonic model for the Paleozoic and Mesozoic constrained by dynamic plate boundaries and restored synthetic oceanic isochrons. *Earth and Planetary Science Letters* **196**, 17–33.
- VENTURI, F. 1978. Ammoniti della “Corniola” del Monte Catria (Appennino Marchigiano). Un orizzonte fossilifero attribuibile all’intervallo Lotharingiano sup.-Carixiano inf. *Bollettino della Società Paleontologica Italiana* **17**, 99–117.
- VENTURI, F., NANNARONE, C. & BILOTTA, M. 2004. Eoderoceratidae (Mollusca, Ammonoidea) from the “Corniola” of the Central Apennines, related to the Sinemurian–Pliensbachian boundary in the Mediterranean area. *Bollettino della Società Paleontologica Italiana* **43**, 361–82.
- VENTURI, F. & ROSSI, S. 2003. *Subasio. Origine e vicende di un monte Appenninico*. Perugia: Porzi editoriali s. a. s., 112 pp.
- WESTERMANN, G. E. G. 1993. Global bio-events in mid-Jurassic ammonites controlled by seaways. In *The Ammonoidea: Environment, Ecology, and Evolutionary Change* (ed. M. R. House), pp. 187–226. The Systematics Association Special Volume no. 47. Oxford: Clarendon Press.
- WESTERMANN, G. E. G. 1996. Ammonoids Life and habitat. In *Ammonoid Paleobiology* (eds N. H. Landman, K. Tanabe and R. A. Davis), pp. 607–707. Topics in Geobiology Volume 13. New York: Plenum Press.