Palaeobiogeography and Evolutionary Trends in Lower Kimmeridgian Ataxioceratids from Spain

(Paläobiogeographie und Grundzüge der Evolution von Unterkimmeridge-Ataxioceraten aus Spanien)

FRANÇOIS ATROPS, Villeurbanne & GUILLERMO MELÉNDEZ, Zaragoza

With 1 Text Figure

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Abstract: Recent studies carried out on Lower Kimmeridgian ammonite fauna from the northeastern Iberian Chain, Spain (Calanda region and surrounding areas), has evidenced the close faunal affinities between recorded ataxioceratid successions and those studied in SE France, the observed differences normally falling within the range of intraspecific variability. The affinities appear closer to more northerly European regions, such as the Swabian and Franconian Albs, than to more southerly areas, such as the Betic region (S. Spain), but they reappear on the North African Shelf (Algeria). Representatives of Ataxioceratinae (= *Ataxioceras* and related forms) seem to become independent taxa along the shallow platform environments of the western and northern Tethys. During the Upper Oxfordian to Lower Kimmeridgian, their evolution generally seems to follow the classical adaption to shallow areas and restricted sea conditions; "primitive" and "simple" serpenticones existed in the Uppermost Oxfordian and evolved towards more platycone-oxycone forms in the Lower Kimmeridgian (Platynota-Hypselocyclum Zones). These are typically characterized by progressively elaborated ornamentation as well as by modification in ribbing and the style of coiling. Important time-size variations, already observed in some other perisphinctid groups, are detected here as well.

The recorded fauna suggests good communication between SE France (Ardèche) and the NE Iberian Chain, most probably along the northwestern margin of the Corso-Sardinian Massif. Connections with more southerly areas were probably along the southeastern margin of that massif, rather than across the central-southern Iberian Chain. This seems especially clear from the Upper Platynota Zone upwards, where the recorded ammonite fauna in this area markedly declines.

Resumen: Recientes estudios realizados sobre la fauna de Ammonites del Kimmeridgiense inferior de la región de Calanda y alrededores, en la parte nororiental de la Cordillera Ibérica (España), han permitido poner de manifiesto las estrechas afinidades faunísticas entre las sucesiones de Ataxiocerátidos registradas con las estudiadas en el SE de Francia, cayendo las diferencias observadas normalmente dentro del rango de la variabilidad intraespecífica. Estas afinidades aparecen igualmente más estrechas con los representantes procedentes de áreas más septentrionales de Europa, tales como las plataformas de Suevia y Franconia que con las de áreas más meridionales, tales como las Cordilleras Béticas (S. España), mientras que vuelven a ser notables con las de la plataforma Nor-Africana (Argelia). Los representantes de la Subfamilia Ataxioceratinae (= *Ataxioceras* y formas próximas) parecen individualizarse como un taxón independiente en los ambientes poco profundos de plataforma del Tethys

Occidental y Septentrional. Su evolución en conjunto, durante el Oxfordiense Superior y Kimmeridgiense inferior parece seguir un modelo adaptativo clásico a las condiciones ambientales de aguas someras y mares restringidos; serpenticonos "primitivos" y "simples" (en su desarrollo y ornamentación) del Oxfordiense Superior dan lugar a descendientes de tipo platycono-oxycono en el Kimmeridgiense inferior (zonas Platynota -Hypselocyclum). Estos últimos se caracterizan por su ornamentación, progresivamenta más elaborada, al igual que por la modificación de la costulación y del tipo de enrollamiento. Importantes variaciones temporales cíclicas de talla, ya observadas en otros grupos de Perisphinctidos, han sido detectadas aquí también.

Como consecuencia de estos análisis el registro faunístico parece indicar la existencia de buenas comunicaciones entre el SE Francia (Ardèche) y el NE de la Cordillera Ibérica, con más probabilidad a lo largo del margen noroccidental del Macizo Corso-Sardo. Las conexiones paleogeográficas con áreas más meridionales pudieron tener lugar, probablemente a lo largo del margen Suroriental de dicho macizo, mejor que a través de la parte central y meridional de la Cordillera Ibérica. Esto parece especialmente claro a partir de la parte superior de la Zona Platynota en adelante, en que el registro de Ammonites en esta región (= S. de la Provincia de Teruel, y provincias de Valencia y Cuenca), desciende bruscamente.

Authors' addresses: Dr. F. Atrops, Département des Sciences de la Terre, Université cl. Bernard, Lyon-1, 27-43 Bd. 11 Novembre, 69622 Villeurbanne, France. — Dr. G. Meléndez, Departamento de Paleontología, Facultad de Ciencias, Universidad, 50009-Zaragoza, Spain.

1. Introduction

"Ataxioceratids" are an important group of perisphinctaceans, extending widely throughout southern Europe and northern Africa and ranging from the Upper Oxfordian (Bimammatum Zone) to the upper Lower Kimmeridgian (Hypselocyclum Zone). They probably arise in the Lower or Middle Bimammatum Zone from a "primitive" serpenticone Oxfordian perisphinctid stem, i.e., Passendorferiinae Meléndez 1984. Their diversification during the uppermost Oxfordian and Lower Kimmeridgian is marked by: (1) a progressive geographic segregation from true Tethyan to southern European Platform and inland seas areas; (2) a gradual morphologic change in coiling and shape from a primitive serpenticone pattern (*Orthosphinctes*) to typically platycone (*Ardescia*) and even oxycone shells (*Ataxioceras* s. str.); and (3) a increasing complexity of ornamentation, from simple, biplicate, symmetrically divided ribs (Passendorferiinae) to polygyrate ribs (= *Orthosphinctes* s. str.) monoschizotome polyfurcation (= *Orth. (Ardescia)*), and double bifurcation at a different level (= *Ataxioceras* s. str.). This distinct change in ornamentation, not known in Oxfordian perisphinctids, has led Callomon (1979) (in Donovan et al. 1981) to classify the group as entirely independent family, Ataxioceratidae. This classification has been followed by one of the present authors in his recent revision of the subfamily Ataxioceratinae (Atrops 1982) and has been justified with evidence of progressive "specialisation" of the group.

Recent studies carried out by the present authors on ataxioceratids from the northeastern Iberian Chain (Atrops & Meléndez 1984, 1985) in the Calanda region have shown a close relationship with those from southeastern France and southern Germany. There are, however, some slightly distinct features individualising them from the "classical" French and German representatives and suggesting, to some extent, a geographic control on the Iberian population. The biogeographic pattern

resulting from paleontologic evidence supplies important data on the paleogeography and faunal migration paths in the western Tethys during the Lower Kimmeridgian.

2. Geographic distribution

Ataxioceratids appear widely distributed throughout several different areas of the southern European platform. They have been the subject of some important, classical monographs on assemblages in Ardèche in southeastern France (Dumortier & Fontannes 1876, Fontannes 1879), the Swabian and Franconian Alb in southern Germany (Quenstedt 1888, Von Ammon 1875) and Switzerland (Oppel 1863, De Loriol 1894). Monographs worth noting from this certainly include Wegele (1929) and Geyer (1961) for southern Germany, and Karvé-Korvinus (1966) and Atrops (1982) for southeastern France.

As far as the Iberian Chain is concerned, the first references to Kimmeridgian ammonites is by Dereims (1898: 147-48), who reports *Per. polyplocus* from the Sequanian in the Calanda region. More recently, Bulard (1971, 1972), Marin (1977), Geyer & Pelleduhn (1979), Moliner & Olóriz (1984), and Atrops & Meléndez (1984, 1985) have described the Lower Kimmeridgian ataxioceratids successions from the Calanda area. For the central and southern parts of the Iberian Chain, there are few references to ataxioceratids; these come mainly from O. Riba (1959), Bulard (1972), Viallard (1973), Gómez (1978), Fernández-López, Meléndez & Suárez-Vega (1978), Goy, Meléndez, Sequeiros & Villena (1979), and Meléndez, Olóriz & Sáez (1981). The marked scarcity of Kimmeridgian ammonite fauna in these areas should be noted.

In the Subbetic Zone i.e., (a more external shelf facies from the southernmost Jurassic outcrops) in the Betic Chain Kimmeridgian ammonites have been the subject of an extensive work by Olóriz (1978). It is important to note that ataxioceratids are apparently represented from the Upper Oxfordian and Lowermost Kimmeridgian (Platynota Zone) only by the genus *Orthosphinctes* and its allies whereas in the "Prebetic Zone" (i.e., a more internal shelf facies) the ataxioceratids successions during the Platynota and Hypselocyclum Zones appear more complete (García Hernandez et al. 1979: 531).

Further references to Ataxioceratinae come from the Algarve in southern Portugal (Marques 1983) and from the Tellian area in Algeria in northern Africa (Atrops & Benest 1981, 1984). Notable references to some striking "primitive" *Orthosphinctes* from the Divisum Zone are by Pavía (pers. comm.) and Cecca et al. (1985) from central Apennines, Italy (a typically "Tethyan sensu strictu" area). These Italian ammonites, with serpenticone, "primitive", *Orthosphinctes*-like, strongly "passendorferioid" elements, are tentatively interpreted as a persistent, conservative stock existing unmodified throughout the entire Lower Kimmeridgian (Pavía and the present authors, in prep.).

3. On the biogeographic status of Kimmeridgian ataxioceratids

This brief review of the main geographic distribution area of ataxioceratids throughout the southern European Shelf shows that representatives of this group extend along quite a restricted area which is typically "Submediterranean" in character; that is, they are recorded mainly in those areas where neither Subboreal nor Tethyan influences are significant. They are not commonly recorded in central and northern Europe or in typically Tethyan regions (at least not the genus *Ataxioceras*), such as in the Subbetics, Sicily, etc. This "restricted" distribution strongly suggests an environmental, geographic control, the bathymetry probably acting as a predominant factor in the distribution and evolution of the group as a whole. The role of bathymetry in the geographic distribution of ammonites has been stressed by many authors in recent years (Marchand 1980, 1982, Tintant et al. 1982) and by the present authors (Meléndez 1984, Atrops 1982) for perisphinctids and ataxioceratids, respectively. According to recent paleogeographic reconstructions of the Tethys by different authors, ataxioceratids spread in southern Europe throughout a progressively more restricted area along the shallow shelf corresponding to the northern slope of the Tethys, between the true Tethyan faunas along one side and the Boreal faunas on the other — (Thierry & Charpy 1982). This idea seems to receive further support from stratigraphic evidence:

(1) Several authors (i.e., Sequeiros 1974, Rozak & Brochwicz-Lewinski 1978, Meléndez 1984, Meléndez et al. 1984) have pointed out the mass occurrences of "mesogean" perisphinctids (i.e. *Passendorferia* and related forms) and some morphologically intermediate elements between these and the primitive *Orthosphinctes* (= *O. tiziani* group) at the boundary between the Bifurcatus and Bimammatum Zones.

(2) In the Bimammatum and Planula Zones, several successive species of *Orthosphinctes* (i.e., *tiziani-colubrinus-polygyratus*) and their corresponding macroconch (*O. (Pseudorthosphinctes)* and *O. (Lithacosphinctes)*) appear widespread throughout the whole southern European Shelf from Bulgaria to southern Spain (Betics) and even northern Africa. These species of *Orthosphinctes* are characterised by evolute, serpenticone coiling, becoming progressively modified towards a more platycone pattern in *Orth. polygyratus* (Rein.)[1)]

(3) However, from the Platynota Zone (Desmoides Subzone) onwards, representatives of the next ataxioceratids stage, *Orthosphinctes (Ardescia)* Atrops, appear markedly more geographically restricted to peripheral, presumably shallower areas (see above). This geographic restriction is followed by important changes in ornamentation (= monoschizotome polyfurcation) and in coiling (progressive shift towards typically involute, compressed platycones), which take them farther from their assumedly serpenticone Tethyan ancestors.

[1)]It should be kept in mind that there is a great intraspecific variability affecting this species, if the classification proposed by Schairer (1974) is correct.

(4) In the Hypselocyclum Zone, representatives of *Ataxioceras sensu strictu* and related forms display an even more restricted geographic distribution: they seem absent from the Subbetic Range and the eastern part of the European Shelf. They also display accentuate evolute features, showing a distinct trend to involute, compressed oxycone shells and ornamentation characterised by the first appearance of double, dischizotome bifurcation.

(5) On the other hand, homogeneous population formed by evolute serpenticone representatives of *Orthosphinctes* has been reported from the Verona region, i.e., a typically Tethyan area (see above), as remaining unchanged during the Lower Kimmeridgian up to the Divisum Zone.

It therefore appears reasonable to a certain extent to interpretate the evolutionary processes of perisphinctaceans during the Upper Jurassic in terms of iterative evolution, that is, the arrival of mesogean elements in various successive periods of good marine communication and the invasion of peripheral, epicontinental shallow seas, followed by a more or less intense period of allopatric speciation (which seems to fit a punctuated equilibrium pattern). This period is indeed characterised by high morphological diversification and formation of new evolutionary lines (Enay 1980, Atrops 1982, Meléndez 1983, 1984), this diversity is not merely an artifact of the "overweight of taxa" (Pozaryska & Brochwicz-Lewinski 1975). Extinctions in these new groups may occur due to further "invasions" or the arrival of new Mesogean elements. This would lead to the "recruitment of fauna" (Meléndez et al. 1984) at that point. The Bifurcatus-Bimammatum boundary may be interpretated in this way, explaining the extinction on the southern European Shelf of representatives of the subfamily Perisphinctinae, and the origin of mesogean substitutes, the first representatives of Ataxioceratinae. The boundary between the Hypselocyclum and Divisum Zones may be regarded in the same way, the representatives of the subfamily Ataxioceratinae being sharply replaced by the first, serpenticone representatives of *Crussoliceras,* which clearly show a Mesogean character. This adaptative pattern accords quite well with that recently proposed by Tintant et al. (1982) for the adaptative radiations of Liassic ammonites.

4. Size changes with time in ataxioceratids

Adult size change with time in Oxfordian perisphinctids has been recognised by many authors and been considered as a taxonomically important characteristic. It has been the subject of detailed studies by Brochwicz-Lewinski & Rozak (1974) and Meléndez (1984), who inferred a relationship with evolutionary process. Atrops (1982) has demonstrated the existence of similar but "cyclic" time-size changes representatives of the subfamily Ataxioceratinae during the Lower Kimmeridgian in southeastern France.

Current available data suggest a cyclic distribution of observed size changes during the Lower Kimmeridgian beyond the purely random distribution of adult size within a population. As is the case in Oxfordian Perisphinctids, size changes in ataxioceratids during the Lower Kimmeridgian seem to be an important factor

leading to morphological changes both for macro and microconchs (i.e., many "evolutionary" changes in shell morphology and ornamentation may be explained as a result of increase or decrease in size).

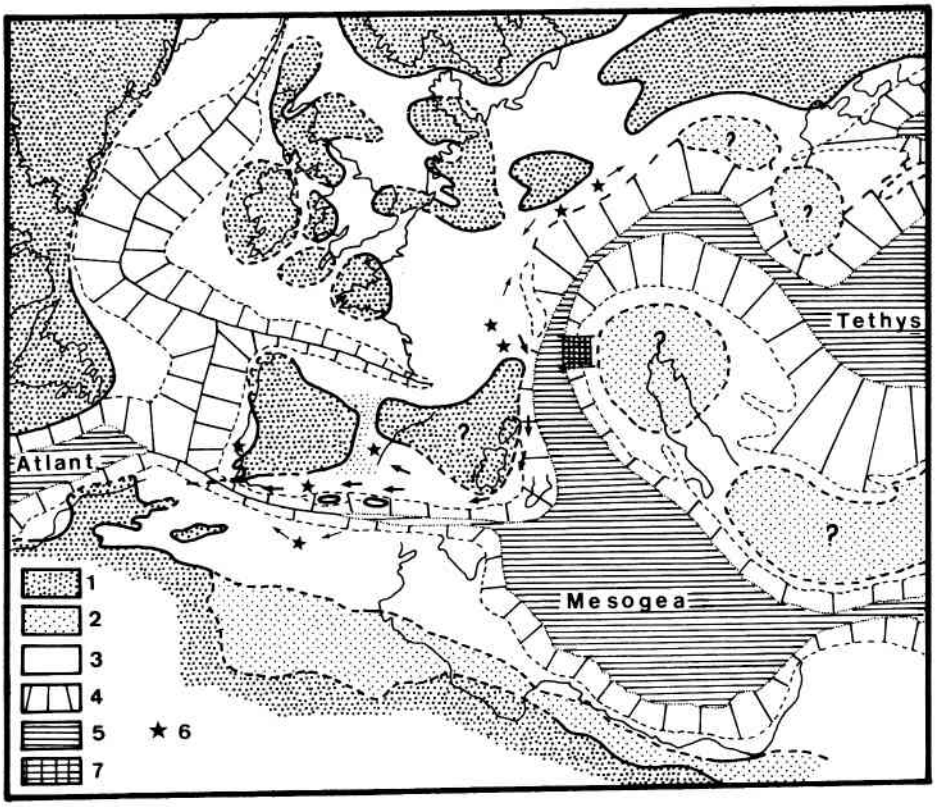
At this point the question of whether size changes are in any way related to environmental or paleogeographic factors (such as bathymetry) is still to be answered. However, it should be noted that, as in the case of Oxfordian perisphinctids, the periods of maximum reduction in adult size normally coincide with the time at which a mass occurrence of typically mesogean elements is recorded. This is what happens at the Bifurcatus-Bimammatum boundary (= M/U Oxfordian boundary). This can also, be observed at the Platynota-Hypselocyclum and Hypselocyclum-Divisum boundaries. In the first case (top of Platynota Zone), there is a mass occurrence of *Nebrodites* also in the Iberian Chain. Similarly, in the Uppermost Hypselocyclum Zone, there is a general arrival of representatives of *Taramelliceras* from the *compsum* group, together with several species of *T. (Metahaploceras)*. The sudden arrival of *T. compsum* (Oppel) at this level makes its previously supposed origin from the species *Tar. strombecki* (Opp.) hardly justifiable. The Hypselocyclum-Divisum boundary is sharply marked not only by representatives of Taramelliceratinae, but by the sudden occurrence of the genera *Crussoliceras* and *Garnierisphinctes* and by the extinction of *Ataxioceras*. As stated above, more evidence is needed to settle the question of whether these time-size changes are environmentally dependent and whether reduction in adult size is a pedomorphic process which results within a population at a period of increase in depth and the arrival of new invaders.

5. Iberian ataxioceratids and migration paths

The Iberian Chain is a large mountain range extending throughout central and eastern Spain in a general NW-SE direction. Jurassic sediments consist mostly of carbonate fairly rich in ammonite fauna. However, Upper Jurassic material from the Lower Kimmeridgian onwards has a higher detrital content, while the faunal content is markedly scarce. The region of Calanda in the northeastern part of the Iberian Chain constitutes a fortunate exception to this rule, the Upper Jurassic being well-represented by a carbonate succession highly rich in ammonites, ranging in age from the Lower Kimmeridgian (Platynota Zone) to Lower Tithonian (Hybonotum Zone).

As already stated, studies carried out by the present authors in this region have led to the recognition of a similar ammonite succession and, therefore, the same biostratigraphic scheme as that established for southeastern France (Atrops 1982) and southern Germany. Some peculiarities affecting the Iberian populations should, however, be stressed:

(1) Ammonite faunal spectra from the Calanda region appear much closer to those known from southeastern France and Southern Germany than to those described for more southerly areas, such as the Betic Range (Subbetic Zone) by



Text Fig. 1. Paleogeographic reconstruction of the western Tethys for the Upper Jurassic. (M. Oxf.-L. Kimm.) showing the inferred position of land areas and marine platforms around the Iberian Massif. Arrows indicate the assumed migration paths for representatives of Ataxioceratinae. (Modified after Thierry & Charpy 1982). 1) Emerged areas 2) Eventually emerged, epicontinental seas, 3) Epicontinental seas, 4) Continental margin, 5) Supposed area of oceanic crust, 6) Records of Ataxioceratinae and 7) 'Italian' population.

Olóriz (1978), or any other typically Tethyan area. Differences from such areas mainly concern the abundance of ataxioceratids, very scarce in Tethyan regions, and the extreme scarcity of simoceratids and Taramelliceratinae in the Iberian Chain, so abundant in the Betics.

(2) Faunal differences with southeastern France, though few are by no means negligible. At this point the scarcity of some elements is worth noting; at certain stratigraphic levels, some types may be quite common in Central Europe, such as *Sutneria,* Taramelliceratinae, haploceratids, and simoceratids (*Nebrodites*).

(3) Ataxioceratids, though basically similar to those in Central Europe, display some striking peculiarities mainly affecting the mode of coiling and ornamentation, that would most probably fall within the intraspecific, geographic variability

(Atrops & Meléndez, in prep.). These features, such as coarser ribbing, large, deep constrictions, a less-marked trend to involuteness in microconchs, and some variations in adult size, make them distinct from both French, Betic, Algerian, and Portuguese representatives.

All this evidence supports the idea of the Calanda region being a restricted, ?isolated area with good geographic connections to Central Europe, but probably with some particular ecologic conditions. The striking scarcity of some "typically Tethyan" faunal elements, such as *Nebrodites, Taramelliceras,* etc., once more indicates bathymetry as a main controlling factor; this is in accord with the paleogeographic reconstructions recently made by some authors (Gómez 1978, Alvaro et al. 1979) for the Upper Jurassic in the Iberian Chain.

This same reasoning speaks against the studied region and the central and southern part of the Iberian Chain as forming a continuous faunal migration path during the Upper Jurassic (Lower Kimmeridgian onwards). As already stated, in the central and southern part of the Iberian Chain the sparse ammonite fauna above the Lower Platynota Zone (i.e., from the Desmoides Subzone) may be regarded as exceptional. The special character of such occurrences, i.e., irregular ocurrence of single, normally adult individuals or occasional accumulations, makes it unlikely that the difficulty of fossilization is the only controlling factor. On the contrary, various aspects of the faunal record (isolated adults at different levels and in different provenances) give support to the hypothesis of an occasional immigration of floating individuals rather than *in situ* populations (see Fernández-López 1985).

Therefore, communication seems best established with southeastern France through the northeastern extreme of the Iberian Chain and Catalanian Mountains, where good Kimmeridgian faunal successions are reported (Salas, oral com.). Communication with more southerly areas, such as with the Betics, northern Africa and Portugal, would most likely have been along Iberia, i.e., the western slope of the Tethys and around the Corso-Sardinian Massif (Text Fig. 1). This situation appears even more certain from the Upper Platynota Zone onwards in the northwestern central, and southern Iberian Chain, where evidence for a marine regression is commonly recorded (see Gómez 1978, Alvaro et al. 1979). On the other hand, the peripheral migration between southeastern France and the Betic-Algerian area may be better understood now that recent paleogeographic reconstructions (Dercourt et coll. in press) have reinterpretated the formerly assumed "southern Tethys" or "mesogean" oceanic trough as a shallower carbonate shelf area, where faunal movements in both directions would likely have taken place.

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