The Oxfordian ammonite genus *Passendorferia* Brochwicz-Lewiński and the Tethyan subfamily Passendorferiinae Meléndez: origin and palaeobiogeography

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Key-words: Upper Jurassic, ammonites, palaeobiogeography, West-Tethys, biostratigraphy, evolution, Mediterranean Province.

ABSTRACT: The Oxfordian ammonite group Passendorferiinae (known as "*Mediterranean perisphinctids*") forms a group of perisphinctids characterized by strongly evolute serpenticone coiling and subcircular to subquadrate whorl section, and forms a lateral divergent branch of the main stem Perisphinctidae. They originated probably from Late Callovian Grossouvriinae (*Alligaticeras*) and spread mainly in the Mediterranean (Tethyan) Province along the southern margin of Tethys, occasionally reaching the outer areas of epicontinental platforms. Their particular morphological features make them somewhat homoeomorphic with Tethyan Kimmeridgian *Nebrodites*. The phyletic link might be represented by the genus *Geyssantia* Meléndez, known from the Late Oxfordian Planula Chronozone.

Separate biogeographic distribution in relation to the Perisphinctinae might reflect a progressive differentiation of western Tethyan faunas at the Callovian-Oxfordian boundary and at the onset of the Middle Oxfordian Transversarium Chronozone. Their rapid evolution gives them a biostratigraphic value similar to that of the Perisphinctinae. At the turn of the Middle-Late Oxfordian they gave rise to early Ataxioceratinae (*Orthosphinctes*), which replaced the Perisphinctinae in epicontinental areas, and colonised the marginal epicontinental blocks of northern Tethys. The taxonomy of this group is based upon the recognition of sexual dimorphism, using a single generic and specific name for both (M) and (m), and hence rejecting the use of former subgeneric names for both dimorphs. A new species within this line: *Passendorferia nodicostata* sp. nov. from the Plicatilis Biozone (Paturattensis Subbiozone) is defined and described for the first time.

INTRODUCTION

The Oxfordian ammonite genus *Passendorferia* was erected as an independent taxon by Brochwicz-Lewiński (1973) who recognized a series of morphologically homogeneous perisphinctid assemblages ranging from the Lower Oxfordian, to the lower Upper Oxfordian. They include heavily constricted shells characterized by strongly evolute serpenticone coiling and a subcircular to subquadrate whorl section. The ribbing is "simple", radial, slightly modified, formed by mostly single and symmetrically bifurcating ribs and prominent parabolic nodes, turning into thicker, straight, "columnar" ribs, slightly elevated on the ventral margin in the adult stage of macroconchs, which made them somewhat homoeomorphic with Tethyan Kimmeridgian *Nebrodites*. These features, as well as the little apparent variation of this line with time, led Brochwicz-Lewiński (1973) to define this group as a "fairly conservative line".

Forms included

Included in *Passendorferia* are several successive links represented by forms traditionally known as "Mediterranean perisphinctids", more typically common in true Tethyan areas such as Sicily, and also present although markedly less common in southern and mid-European areas of Submediterranean Province. Some of these forms have been described ["*Perisphinctes*" *czenstochowiensis* Siemiradzki; "*Perisphinctes*" *birmensdorfensis* (Moesch); "*Perisphinctes*" *birmensdorfensis* Oppenheimer (non Moesch); "*Perisphinctes*" *regalmicensis* (Gemmellaro)] as microconchs. Among the corresponding macroconchs, have been included some taxa also traditionally assigned to "Mediterranean perisphinctids", such as "*Perisphinctes* (*Arisphinctes*)" *tenuis* Enay, "*Perisphinctes* (*Pseudarisphinctes*)" *uptonioides* Enay, or idoceratids: *Nebrodites* (*Passendorferia) ziegleri* Brochwicz-Lewiński; *"Simoceras" torcalense* Kilian; *Nebrodites* (*Passendorferia) teresiformis* Brochwicz-Lewiński. The last form was designated as the type-species for the new taxon *Passendorferia*. The origin of the group was linked to the Upper Callovian late grossouvriid-early perisphinctid genus *Alligaticeras* (type species: *Ammonites alligatus* Leckenby), comprising small-sized perisphinctids characterized by evolute serpenticone coiling, simple perisphinctoid radial ribbing, heavy constrictions and prominent parabolic nodes, and inferred to be the original synthetic form of both Oxfordian branches of *Perisphinctes* and *Passendorferia*.

Taxonomic setting

Due to the homogeneous character of this group and the sharp morphological differences in relation to typical representatives of the subfamily Perisphinctinae, as well as the strong similarity or homoeomorphy to representatives of the Kimmeridgian genera *Nebrodites* (m) and *Mesosimoceras* (M), one of us (Brochwicz-Lewiński 1973) was originally inclined to consider *Passendorferia* (M) as an Oxfordian subgenus of genus *Nebrodites,* and to place the whole group in the subfamily Idoceratinae Spath. A review of hitherto identified species of this ammonite group is presented here and their biostratigraphic value analysed, in order to discuss their dimorphic and taxonomic status (Figs 1-2; 4-5). The biogeographic distribution and biochronological importance of the group also appears relevant for understanding the phyletic history of this branch of the perisphinctids (Fig. 3). As shown below, taphonomic analysis of recorded associations of ammonites is crucial for getting a proper interpretation of the biogeographic dynamics of the group and a good understanding of their biostratigraphic succession.

The purpose of this paper is to present an updated overview of this homogeneous perisphinctid group, in order to show its biogeographic origin and spread across different areas in the Tethyan Realm, as well as its biostratigraphic value and relevance, and its phyletic relationships with other perisphinctid groups. The areas studied and collections examined correspond to the work areas of different co-authors: Transdanubian Central Range (Pilis Mountains and Gerecse Mountains) in Hungary (I.F., G.M., I.P-U), Polish Jura Chain in Central-Southern Poland (W.B-L), Western Sicily, in the provinces of Trapani (sections around Erice) and Sciacca (Contrada Diesi section: C.D'A., G.M.), Algeria, especially the reference sequence of Bou Rheddou, in the southern margin of Tellian Domain (North from Tiaret) and partly, South-Eastern France (F.A.), Betic Ranges (Southern Spain: L.S., G.M.), and the Iberian Range in Central-Eastern Spain (G.M., J.B., I.P-U., J.R.). These areas and the inferred biogeographic spread of passendorferiids are plotted in Fig. 1. Relevant supplementary data from other Submediterranean (Central Europe) or true Tethyan areas (Turkey; Tunisia) have been

taken from the abundant bibliographic material since the early monograph of Moesch (1867).

HISTORICAL BACKGROUND

Forms matching the diagnosis of the genus *Passendorferia* have been fairly often reported in the literature in the last 140 years, that is from the time when Moesch (1867) gave the first description of the species "*Perisphinctes*" *birmensdorfensis* from the Swiss Jura. This species and its close relatives were subsequently identified as a major component of the true Mediterranean faunas of the Upper Jurassic of Sicily by Gemmellaro (1875, 1877) and the Betic Ranges of southern Spain by Bertrand and Kilian (1889). Further records of ammonites assignable to this group, mainly from areas of the Submediterranean Province in southern and central Europe, were provided by Siemiradzki (1891, 1899), de Riaz (1898), and Oppenheimer (1907) thus adding new information to the knowledge of its biogeographic distribution. In more recent times, the work of Christ (1960) presented a detailed account of the stratigraphic distribution of this fauna in the Middle Oxfordian of Sicily.

Recognition of group

The first detailed revision of records of this ammonite group was carried out by Enay (1966) in his study of the Oxfordian of the French Jura (Submediterranean Province). The author also put aside the *Per. trichoplocus* Gemmellaro group of microconchs and their inferred macroconchs, the so-called "Mediterranean *Arisphinctes*" (= *Arisph. tenuis* Enay group and related forms) as a separate group of *"Mediterranean perisphinctids"* or the *"Mesogean fauna sensu stricto"*. By this differentiation, the author clearly emphasized a separate paleobiogeographic position and evolutionary history of this fauna but, nevertheless, he decided to leave the species in the genus *Perisphinctes*. Special attention should be paid to his attempt to differentiate the *Per. birmensdorfensis* (Moesch) group as a separate, typically Mediterranean phyletic unit, also including the so-called: "Mediterranean *Kranaosphinctes*" of the *cyrilii-methodii* (Neumann) groups. A new generic name *Neumannia* has been recently proposed by Głowniak (2002) for these last forms. Further studies are needed, however, to have a clear idea of the phyletic affinities of this new taxon.

The taxonomic split was completed by Brochwicz-Lewiński (1973) who showed the possibility of differentiating rather homogeneous dimorphic lines spanning the Lower Oxfordian to the lower Upper Oxfordian and proposed a new subgeneric name *Passendorferia* for this ammonite fauna. In his opinion this fauna is closer in morphology to Kimmeridgian representatives of *Nebrodites* than to contemporaneous *Perisphinctes* and, therefore, it should be placed tentatively in the genus *Nebrodites* of the subfamily Idoceratinae Spath. Evidence of dimorphism in this group was subsequently provided by Brochwicz-Lewiński and Różak (1976) who showed morphological and stratigraphical correspondence between successive macro- and microconch pairs across the Oxfordian Stage. These authors maintained the subgeneric status for this group, assigning separate sub-generic names for both dimorphs: *Nebrodites* (*Passendorferia*) (M) *and Nebrodites* (*Enayites*) (m).

Recent studies

Sequeiros (1974) was the first author to prove the presence of *Passendorferia* in Spain. He showed that the classical species *Perisphinctes torcalense,* described from the Oxfordian of the Betic Ranges by Bertrand and Kilian (1889), matches diagnosis of this subgenus. The material collected from the Betic Ranges was initially assigned by Sequeiros (1974) to different forms of the genus *Perisphinctes*. In fact, besides a few specimens assignable to *Perisphinctes (Dichotomoceras),* the bulk of the material of micro- and macroconchs turned out to be easily assignable to *Passendorferia*. In a subsequent contribution (Sequeiros 1977) the author showed that most of the species described from the Polish Jura Chain and the classic ones described from West Sicily by Gemmellaro (*loc. cit.*) are also present in this part of the southern Tethys area and he raised the status of *Passendorferia* to a full genus. Among the species described by him it is worth emphasizing the species *Pass. torcalense* (Kilian), reported from lower Bifurcatus Biozone and found to be widely spread in the Betic Ranges, and a new form, *Pass. brochwiczi* Sequeiros, characterized by markedly more involute coiling of the inner whorls than in other species hitherto assigned to *Passendorferia*, and with inner whorls not subcircular but clearly square in cross-section

and with flat flanks. This form was subsequently differentiated by Meléndez (1989) as the type species of his new genus *Sequeirosia*.

New information concerning representatives of this subfamily came from Enay (1976) who reported that *Passendorferia* was common in North Turkey, in the Pontids mountain range ("North-Anatolian biogeographic Realm"), hence characterising this region as "typically Mediterranean" (p. 535). The interval yielding the assemblage studied, which included common *Perisphinctes* (indeterminable nuclei), *Passendorferia* and *Campylites*, together with some brachiopods (*Lacunosella*), was regarded as Middle Oxfordian Plicatilis Chronozone in age.

Taxonomic definition

In the eastern Iberian Range, assigned to the Submediterranean Province, the presence of Lower Oxfordian passendorferiids, mainly *Pass. czenstochowiensis* (Siemiradzki) was reported by Meléndez *et al*. (1982). Subsequent studies (Meléndez 1984, 1989) made it possible to describe rich collections of representatives of this genus, forming a fairly complete succession of micro- and macroconchs in strata ranging in age from the lower Transversarium to the Bimammatum Biozone and showing that we deal with a well individualised phyletic unit. The studies also made it possible to differentiate the group of "*Passendorferia" brochwiczi* Sequeiros and related forms from strata of the Transversarium and Bifurcatus biozones, for which a new genus *Sequeirosia* Meléndez was proposed. The apparent dimorphic correspondence with the group of "*Perisphinctes" trichoplocus* Gemmellaro led the author to follow a trend set by other authors and to describe dimorphs under separate subgeneric names: *Sequeirosia* (*Sequeirosia*) for macroconchs and *Sequeirosia* (*Gemmellarites*) for microconchs. It is also worth noting new important links found within this phyletic line, that is the new species *Passendorferia* (*Passendorferia*) *ariniensis* Meléndez (M) from the turn of the Bifurcatus and Hypselum biozones, *Passendorferia* (*Enayites*) *rozaki* Meléndez (m), *Passendorferia* (*Enayites*) *arancensis* Meléndez (m) from lower parts of the Hypselum Biozone, *Passendorferia* (*Enayites*) *sanpedroi* Meléndez (m) from the Bimammatum Biozone and *Passendorferia* (*Enayites) wierzbowskii* Meléndez (m) from slightly higher levels (Hauffianum Biozone). From the turn of the Hauffianum and Planula biozones the author also described a new form characterized by extremely evolute coiling and thick, distant ribbing, and defined it as the new genus *Geyssantia* Meléndez. These findings showed that this Mediterranean line is fairly homogenous phyletically and may be raised to a new taxonomic category of the subfamily rank: Passendorferiinae Meléndez 1984. Subsequent studies went forward to transfer some of these new described forms from the genus *Passendorferia* into other different genera (see below).

New findings and widespread recognition of the group

The successive works by Atrops and Benest (1984, 1986, 1994) on the stratigraphy of the Upper Jurassic and on the ammonite successions in North Algeria, that is along the margins of the Tellian foreland and around Tiaret, more precisely the sections in the area of Bou Rheddou, showed the omnipresence of representatives of *Passendorferia* at the northern margins of Gondwana, that is the southern marginal parts of Tethys. These findings should be treated as predictable and confirming traditional views that the southern margins of Tethys were the cradle of this group of Mediterranean ammonites. The taxa reported by these authors included forms typical of the Hypselum Biozone such as *Pass.* (*Enayites*) *gygii* (Brochwicz-Lewiński, Różak) – *Pass.* (*Enayites*) *rozaki* Meléndez. Attention should be also paid to the fact that, unlike in the Submediterranean areas, the material figured comprises only small, juvenile (or pre-adult) micro and perhaps macroconchs, presumably forming taphonic populations of type 1 or 2, *i.e.* true colonizers of the area, according to the concept of taphonic population, as defined by Fernández-López (1995; see below, the chapter on biogeographic *vs*. taphonomic dispersal). Although the available information is still scarce, this gives further support to the hypothesis that the southern margins of Tethys were an area colonized by this group. Further relevant information on the North African margin came from Soussie *et al*. (1999) in the region of the Tunisian Dorsale (central and northeastern Tunisia) where the authors describe, in several sections (J. Zaress; J. Bent Saïdane), a rich and diversified ammonite association from the Middle and Upper Oxfordian, Plicatilis to Bimammatum biozones. This includes, in a lower association (Plicatilis Biozone) *Sequeirosia bocconii* (Gemmellaro 1875, non 1871) (M).

A middle association, characterizing the Riazi Biozone, is dominated by forms grouped in *Passendorferia birmensdorfensis* (Moesch). A third association (Fouquei Biozone) includes some undetermined *Passendorferia* (M and m), some of them still regarded as close to *Passendorferia birmensdorfensis* (Moesch). In an upper association (Bimammatum Biozone), the characteristic record of *Passendorferia rozaki* Meléndez, and *Passendorferia gygii* Brochwicz-Lewiński is especially noteworthy. This means that there is in Tunisia a Passendorferiinae succession entirely comparable to other areas of Tethys, including the reference areas of the Iberian Range (Meléndez 1989) and Sicily (D'Arpa and Meléndez 2004).

New findings from the North Italian Alps, especially from the Verona area (*Rosso Ammonitico Veronese*) showed that the same succession of species of *Passendorferia* could be found in much wider areas of the Mediterranean Province (Bennetti and Pezzoni 1986). The revision of rich material from the *Museo dei Fossili della Lessinia* (Verona, N Italy) revealed that the ammonite collections mainly comprise complete and fragmented adult specimens of macroconchs of this group.

Recent contributions to this discussion in the NE Iberian Range were made by Fontana (1990; pl. 5: 3, 4) who described a peculiar new form *Passendorferia (Enayites)* n. sp. aff. *birmensdorfensis* (Moesch) from the middle Transversarium Biozone, Schilli Subbiozone of the Iberian Range. This form was found in slightly higher levels than the true *Passendorferia birmensdorfensis* and corresponds to the specimen figured as *Passendorferia tenuis*, Meléndez, non Enay (Meléndez 1989, pl. 1: 2; pl. 2: 1; see also Meléndez and Fontana 1993, p. 203) subsequently defined as *Passendorferia erycensis* Meléndez (*in*: Pavia and Cresta 2002). Pérez-Urresti (1996) showed the omnipresence of representatives of the *Passendorferia* in the lower part of Upper Oxfordian sequences of the NE Iberian Range and confirmed the close relationships between this group and Tethyan Ataxioceratinae at the turn of the Bifurcatus-Hypselum Biozone, via *Passendorferia uptonioides* (Enay) and *Passendorferia ariniensis* Meléndez. This later form was subsequently reinterpreted as a primitive member of the subfamily Ataxioceratinae rather than as a true Passendorferiinae, being better treated as one of the presumably first representatives of the genus *Orthosphinctes*. In this way the inferred evolution of the subfamily Ataxioceratinae from the Passendorferiinae (Meléndez 1989; Atrops and Meléndez 1993) got further support. At the same time, the work of Fözy and Meléndez (1996) and Fözy *et al*. (1997) showed that the successions described across southern Europe are also traceable in Hungary (Gerecse and Pilis Mountains, Transdanubian Central Range) where good Middle-Upper Oxfordian successions appear well represented in Rosso Ammonitico facies. Ammonite records obtained for the Mecsek Mts sections (southern Hungary) include an impressive collection of early representatives of the Ataxioceratinae (*Orthosphinctes),* which show close affinities with late representatives of the Passendorferiinae, such as serpenticone coiling of the inner whorls and "simple" radial ribbing, with mainly symmetrical biplicate ribbing and only a few intercalatories. Attention should be also paid to the fact that abundant and diversified material from this southern area mainly comprises incomplete phragmocones and adult specimens of both micro and macroconchs. More recently, in Submediterranean central Europe (Switzerland) new information has become available from the type area of *Passendorferia birmensdorfensis* and closely allied Middle Oxfordian forms (Gygi 2000, 2001).

THE CURRENT STATE OF PROGRESS IN STUDIES ON THE PASSENDORFERIINAE

In recent years new data from the Oxfordian of Sicily, and an *in depth* revision of Gemmellaro's collections housed in the Geological Museum of Palermo, came from D'Arpa and Meléndez (2001, 2002b, 2004) and D'Arpa (2003). These works represent a significant contribution to the reconstruction of the succession of species of *Passendorferia* in this area and precise the stratigraphic position of several species originally described by Gemmellaro. The studies also gave further support for biostratigraphic correlations and reconstructions of biogeographic relationships with other areas within the Mediterranean and Submediterranean provinces by showing that this group of Mediterranean perisphictids has evolved at the southern margins of the Tethys, most possibly in the earliest Oxfordian, to spread widely throughout epioceanic platforms and occasionally, mostly by means of taphonomic dispersal, to more distant areas of Submediterranean epicontinental

platforms during the Oxfordian (D'Arpa and Meléndez 2002a).

From the taxonomic point of view, it is worth noting the reinterpretation of the species "*Perisphinctes" bocconii* Gemmellaro as a representative of the genus *Sequeirosia* from the lower Transversarium Biozone, Parandieri Subbiozone. On the other hand, reanalysis of the holotype of *Sequeirosia* (*Gemmellarites*) *trichoplocus* (Gemmellaro) showed that this specimen represents an incomplete phragmocone of a presumably adult macroconch. This would make its taxonomic assignation doubtful and the subgenus itself, originally defined as a "microconch subgenus", invalid.

A further remarkable point was the reinterpretation of *Per. regalmicensis* Gemmellaro, 1877 (non 1875) as a new species, *Passendorferia erycensis* Meléndez (*in*: Pavia and Cresta 2002) from the middle-upper levels of the Transversarium Biozone, Schilli Subbiozone, the type specimen of this species being an adult microconch. The corresponding macroconch would be the specimen figured by Meléndez (1984, pl. 1: 1, 2; pl. 2: 1; 1989, pl. 1: 1; pl. 2: 1). This reintepretation, based on new material from Gemmellaro's type-locality of Erice (Trapani province, North West Sicily) and from the Iberian Range (see Pl.1: 3-5) has confirmed the earlier conclusions of Fontana (1990) who figured similar micro and macroconch specimens from equivalent levels (Schilli Subbiozone) in the Iberian Range as *Passendorferia* n. sp. aff. *birmensdorfensis* (Moesch), and also of Meléndez and Fontana (1993) who referred this particular form to as a well defined assemblage in this stratigraphic interval. Finally, the analysis of the successions in western Sicily, especially those of the section of Contrada Diesi near Sciacca (SW Sicily), showed the presence in upper Bifurcatus Biozone levels, of some morphologically intermediate links between *Passendorferia* and early representatives of *Orthosphinctes,* especially those close to the *Orthosphinctes ariniensis* (*ex*: *Passendorferia ariniensis* Meléndez) group, giving further support to the inferred phyletic origin of the Ataxioceratinae in Oxfordian Passendorferiinae (D'Arpa and Meléndez 2004).

More recently, Bello (2005) has showed a detailed sequence of species of *Passendorferia* throughout the Middle Oxfordian Transversarium and Bifurcatus biozones, from early representatives of *Pass. ziegleri* (Brochwicz-Lewiński) to late representatives of *Pass. uptonioides* (Enay) and forms transitional to early *Orthosphinctes* (Ataxioceratinae) from the turn of Bifurcatus and Hypselum biozones (see Fig. 3). This author identified the dimorphic pairs at almost every stage of this evolutionary sequence. This fact has in a certain way overcome the arguments of previous authors justifing the use of subgeneric taxa for different dimorphs: *Pass.* (*Passendorferia*) Brochwicz-Lewiński (M) and *Pass.* (*Enayites*) Brochwicz-Lewiński and Różak (m); *Sequeirosia* (*Sequeirosia*) Meléndez (M) and *Sequeirosia* (*Gemmellarites*) Meléndez (m). Such nomenclatural unification means that a unique generic and specific name could be used for both dimorphs, accepting that recent findings give further support to this proposal.

PALAEOBIOGEOGRAPHIC CONTEXT

The geographical distribution of the palaeontological records of the Passendorferiinae appears to comprise wide areas of the Mediterranean Province, where these ammonites are usually found cooccuring with representatives of the Phylloceratina and Lytoceratina, and often they may represent over the 40% of the whole Ammonitina fauna and sometimes over 90 % of the Perisphinctidae. This is the reason why from the beginning of modern studies on biogeographic aspects of Jurassic ammonite faunas of Europe they started to be treated as a typical "Mediterranean" group (Fig. 1; see Brochwicz-Lewiński 1973, and references therein; Enay 1976; D'Arpa and Meléndez 2002a) in contrast to true representatives of *Perisphinctes*, mostly spread across the Submediterranean, Subboreal, partly Boreal, and Pacific provinces. These data would support the definition of the subfamily Perisphinctinae as a group expanding across areas of shallow epicontinental platforms whilst representatives of the Passendorferiinae should rather be considered as a group colonising the Tethyan, oceanic environments, spreading mainly into areas of epioceanic platform seas and deeper basin environments, and being commonly recorded in shallow platform areas across the Submediterranean Province, as a result of taphonomic dispersal (Fernández-López and Meléndez 1995; see Fig. 1).

As stated above, this ammonite group is regarded as the descendant of late Grossouvriinae of the genus *Alligaticeras* (see Brochwicz-Lewiński 1973; Brochwicz-Lewiński and Różak 1976; Me-

léndez 1989; Bello 2005). The latter ammonite taxon appears to be known mainly so far from Submediterranean and Subboreal areas such as England. However, this may be simply an effect of failure in collecting, primarily related to practically omnipresent stratigraphic gaps in the sections of the Callovian-Oxfordian transitional sequences across southern Europe, that is, in areas of the Mediterranean Province. However, in the expanded sequences of subsiding Submediterranean basins, such as the Vocontian Basin (SE France), representatives of the genus *Alligaticeras* are found to be fairly common.

BIOGEOGRAPHIC VS. TAPHONOMIC DISPERSAL (Figs 1, 2)

The geographical distribution of records of representatives of the Passendorferiinae may, however, partly reflect the effects of taphonomic dispersal, that is, post-mortem drift of empty shells, quite efficiently blurring the true biogeographical extent of the living group. As shown by the present authors (D'Arpa and Meléndez 2002a, 2004), estimations of the degree of autochthony and allochthony of recorded associations of *Passendorferia* show that the majority of hitherto described assemblages of this group, from Sicily and partly from the Iberian Range, mainly comprise adult specimens, with macroconchs clearly predominating in number over microconchs. According to Fernández-López (1995), this would correspond to what has been defined as "Taphonic populations of Type 3", *i.e.* composed of polyspecific shells of different taxa showing generally bimodal and normal distribution of size-frequencies, with a negative skew and a ratio of number of specimens to number of taxa approaching to 1; shells of mature macroconch individuals are dominant, whilst shells of juvenile individuals are virtually absent. These recorded ammonite associations clearly show signs of allochthony and represent ademic biological populations. In this analysis the author has taken into account the results of experimental studies of Chamberlain *et al.* (1981) on recent *Nautilus*, which showed the greater floating capacity of adult empty shells than juvenile ones, hence inferring large-size adult macroconchs as holding the maximum post-mortem drift capacity.

"Taphonic populations of Type 2" are formed by specimens markedly differing in size, both macro- and microconchs as well as some juvenile or pre-adult specimens. Distribution of size-frequencies shows a wide, flat topped, bell-shaped curve with high values of kurtosis. They are interpreted as comprising occasional invaders or immigrants. "Taphonic populations of Type 1" comprise monospecific assemblages formed mainly by abundant, nepionic or juvenile specimens, micro- or macroconchs, giving a size distribution of frequencies unimodal with a positive skew. They clearly represent eudemic biological populations. Specimens showing the body chamber at low diameter are indicative of juvenile individuals, hence of taphonic populations of type 1 or 2, whilst incomplete phragmocones are rather indicative of adult specimens.

Fig. 2 shows the inferred distribution of taphonic populations in the sections studied from different areas. Recorded associations composed of mostly chambered specimens (incomplete phragmocones) indicate generally taphonic populations of type 3. They display either unimodal curves with negative skew, as seen in the Betic Ranges (Sequeiros 1974, 1977; Meléndez 2006) (see here, Pl. 1: 6), Sicily-Erice Ter (D'Arpa and Meléndez 2004), Hungary in the areas of the Transdanubian Central Range (Fözy and Meléndez 1996), or bimodal curves (as in Poland).

Taphonic populations of type 2 in turn, are identified in Sicily in the section of Contrada Diesi (South west Sicily, near Sciacca, D'Arpa and Meléndez 2002a), Iberian Range (Fernández-López and Meléndez 2004; Bello 2005), and partly in Algeria, as it can be inferred from the revision of the original material referred by Atrops and Benest (1984, 1986).

As far as the degree of allochthony is concerned, the recorded abundance of specimens and the homogeneity of the recorded associations suggest little transport by post-mortem drift of shells, although it seems clear that representatives of this group would only occasionally live where they are recorded. Therefore, living representatives of the Passendorferiinae can be safely assumed to originate and spread by biogeographic dispersal throughout the Mediterranean Province, to colonize somewhat deep oceanic or outer shelf environments, and in some cases, epioceanic platform environments. In turn, the recorded associations generated by these biological entities, mainly consisting of allochthonous elements, may be treated as formed as the result of taphonomic dispersal, involving post-mortem drift concentration of empty shells in shallow platform areas. They constitute taphonic populations of type 3 (see Fig. 2). Similar

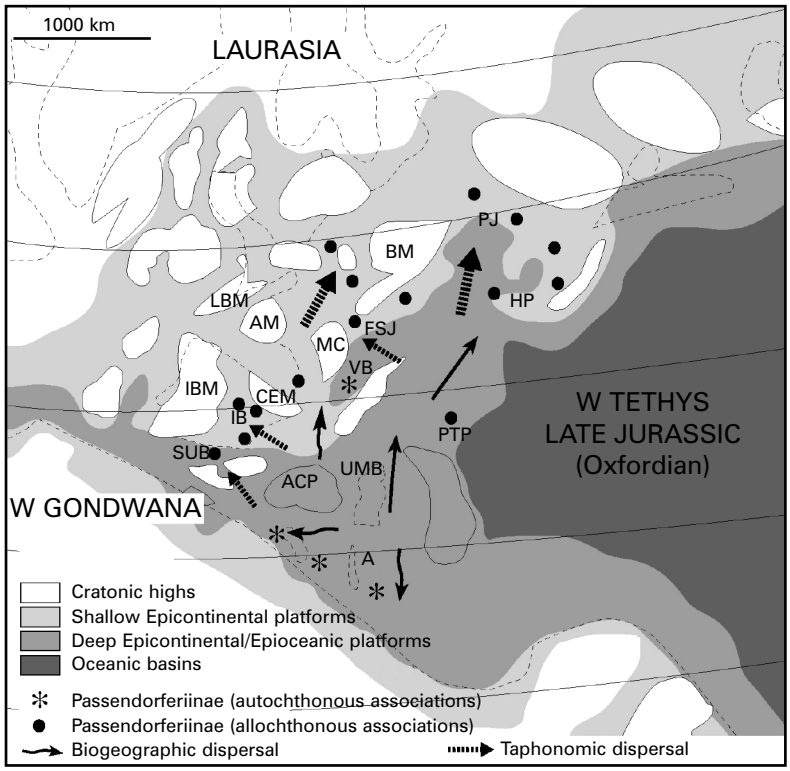


Fig.1. Geographic distribution of subfamily Passendorferiinae during Oxfordian times in the southern margin of the Tethys and their spreading to near Mediterraean and Submediterranean areas by biogeographic dispersal (black arrows). Asterisks show the areas where recorded assemblages would constitute autochthonous associations. Dots indicate the areas where recorded assemblages are mainly integrated by allochthonous associations, arrived by taphonomic dispersal (dashed arrows). Palaeogeographic sketch, after D'Arpa and Meléndez 2002a, modified: A – Apulia, IBM – Iberian Massif, IB – Iberian Basin (referred to as East-Iberian Carbonate Platform), SUB – Subbetic Basin, CEM – Catalan-Ebro Massif, ACP – Central Alpine Platform, UMB – Umbro-Marchaean Basin, PTP – Pontids Platform (Northern Turkey), HP – Hungarian Plateau, PJ – Polish Jura Basin, BM – Bohemian Massif, FSJ – French-Swiss Jura, VB – Vocontian Basin (SE France), MC – Central Massif (France), AM – Armorican Massif, LBM – London-Brabant Massif.

cases have been demonstrated by Fernández-López and Meléndez (1995) in the case of Phylloceratina Ammonoidea and, more recently, Báncora *et al.* (2005) in the case of Ataxioceratinae assemblages from the region of Calanda (East Iberian Carbonate Platform).

ORIGIN OF THE SUBFAMILY PASSENDORFERIINAE (Fig. 3)

Mediterranean perisphinctids (Passendorferiinae) have been repeatedly assumed to originate most probably in the Late Callovian, Lamberti Chron from the late grossouvriid genus *Alligaticeras* Buckman, which could possibly represent the synthetic form for both Oxfordian subfamilies Perisphinctinae (via *Properisphinctes* Spath) and Passendorferiinae (Brochwicz-Lewiński 1973; Brochwicz-Lewiński and Różak 1976; Meléndez 1989; Bello 2005). The obvious link would be the evolute serpenticone coiling typical of the genera *Alligaticeras* and *Passendorferia*, both showing fine radial "simple" ribbing, with predominance of single and symmetrically bifurcate ribs and no, or very rare intercalaries, but most of all, the persistence of parabolic ribbing, so well displayed by prominent parabolic structures in the Passendorferiinae stock but also appearing as remnant structures in some microconchs of Perisphinctinae such as those of *Otosphinctes* Buckman. However, details of the sculpture and morphology of early primitive representatives of the subfamily Passendorferiinae from the Mariae Chronozone of the lowermost Oxfordian are still very poorly known. This may be mainly due to the still unsatisfactory stratigraphic and fossil record for that part of the geological section, related to the omnipresence of stratigraphic gaps in areas of the Submediterranean and Mediterranean provinces which may locally range from the Lower or lower Middle Callovian to Middle Oxfordian, middle or even upper Tranversarium Chronozone.

EVOLUTIONARY SEQUENCE AND BIOSTRATIGRAPHIC VALUE (Figs 3, 4)

Genus Passendorferia Brochwicz-Lewiński

A description of the recorded sequence of *Passendorferia* species in the studied areas is provided in this chapter, discussing the presumable correspondence of dimorphic pairs, as presented in Fig. 5.

Lower Oxfordian

The first clearly recognized species of *Passendorferia* would be *Pass. czenstochowiensis* (Siemiradzki) coming from lower Cordatum Bio-

zone, Claromontanus Subbiozone (see Brochwicz-Lewiński 1981; Meléndez *et al*. 1982; Meléndez 1989; Bello 2005). Its precise stratigraphic position is confirmed by numerous records of co-occurring *Prososphinctes claromontanus* (Bukowski) and *Neocampylites delmontanus* (Oppel; generic name: *Neocampylites* Callomon 1973, as nom. nov. for *Ammonites delmontanus* Oppel) not to say the rich recorded associations of cardioceratids and peltoceratids in the classic sections of the Częstochowa area (southern Poland, Brochwicz-Lewiński 1981). The latter sections gave fairly large collections of representatives of *Passendorferia* and/or macro- and microconchiate forms classifiable as "Mediterranean" in appearance. Such a collection still waits for detailed study but it may be already stated that the available material shows that differentiation of this fauna may be much greater than hitherto assumed.

Middle Oxfordian Plicatilis Biozone

From the lower Plicatilis Biozone, Tenuicostatum (=Paturattensis) Subbiozone come some still poorly known specimens such as the one described by Brochwicz-Lewiński and Różak (1976,

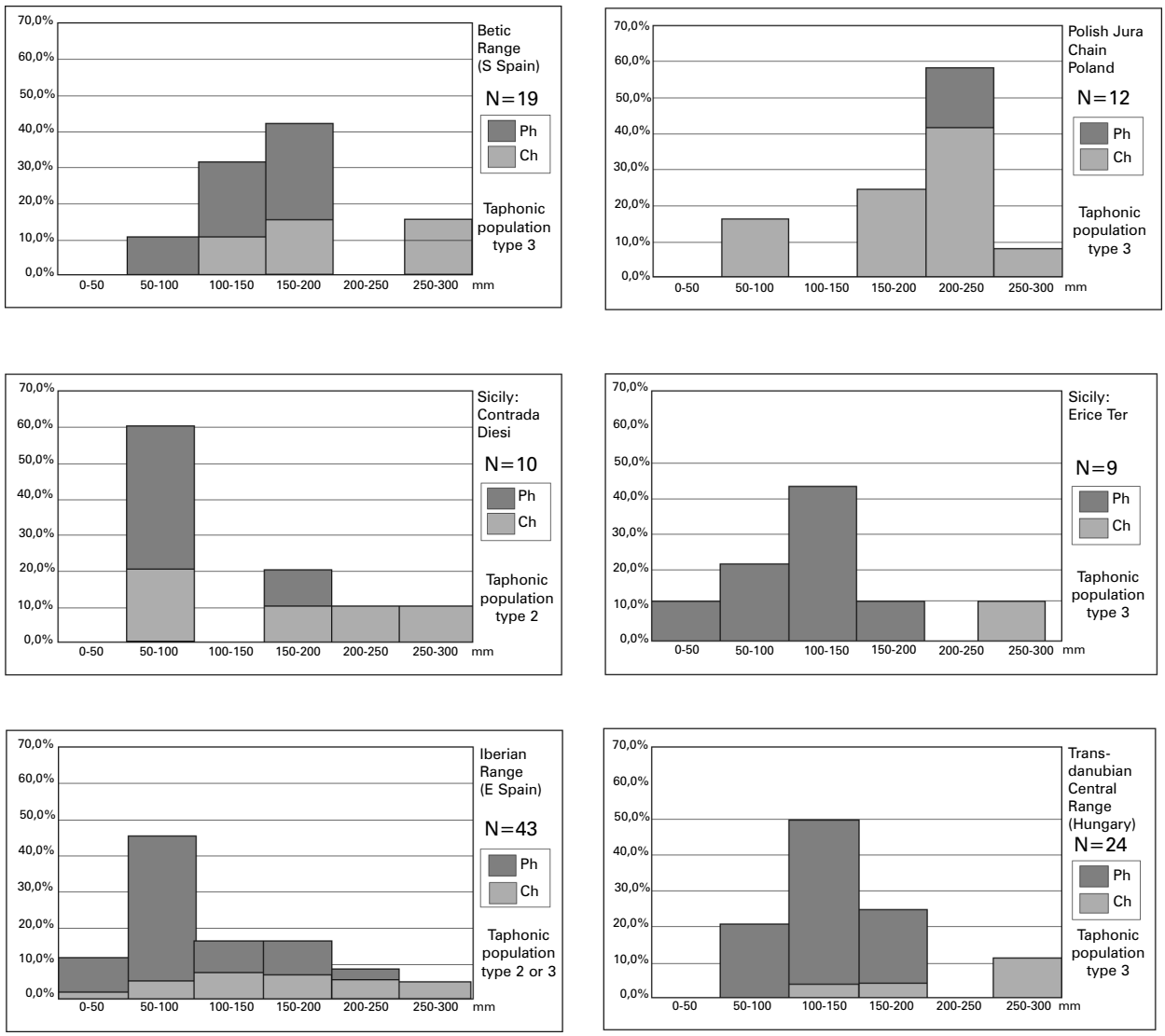


Fig. 2. Size-frequency distribution histograms of the ammonite genus *Passendorferia* from the Middle Oxfordian in the different areas studied and described in the present work, indicating the type of taphonic population. N – number of specimens measured, Ph – ratio (%) of wholly septate specimens (phragmocones), Ch – ratio (%) of specimens with body chamber.

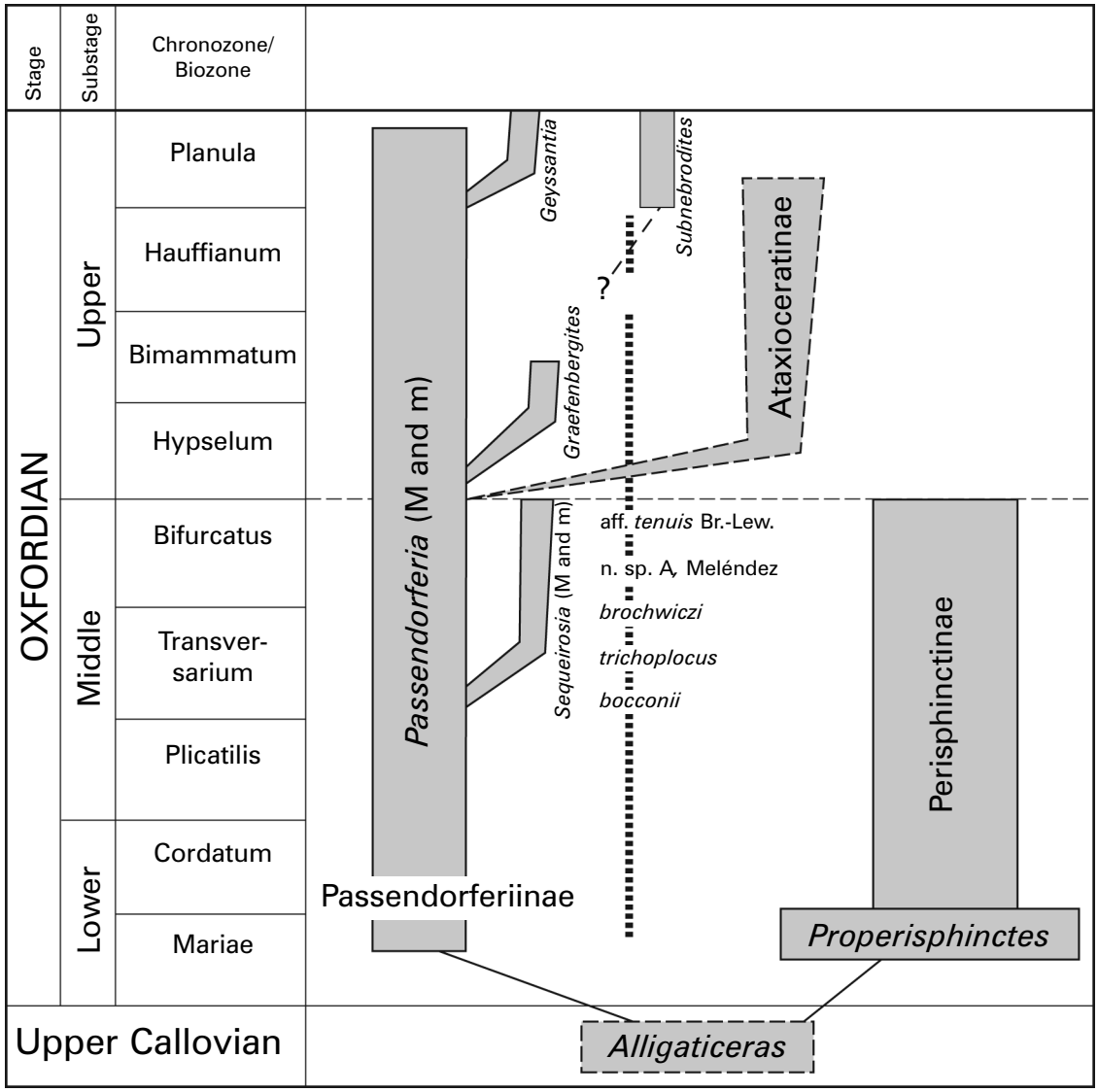


Fig. 3. Origin and inferred phyletic relationships of different genera included in the subfamily Passendorferiinae, and between this subfamily and other close Oxfordian perisphinctid groups (after Bello 2005, modified).

pl. 35: 3) from "Przybynów, near Żarki, Częstochowa area" as *Nebrodites* (?*Enayites*) sp. Similar specimens have also been described by Meléndez (1989, p. 155, pl. 11: 4) as *Passendorferia* (*Enayites*) n. sp. aff. *czenstochowiensis* (Siemiradzki) and by D'Arpa (2003, p. 173; pl. 4: 5) as *Passendorferia* (*Passendorferia*)*) czenstochowiensis* (Siemiradzki). They are characterized by evolute, rounded serpenticone (not extremely evolute) coiling, rounded whorl section and fine uniform ribbing in the inner whorls, still displaying prominent parabolic nodes and swellings, with an early trend to give thicker, rounded blunt ribs in the middle whorls in the macroconch. They show some morphological similarities with *Passendorferia tenuis* (Enay) but display prominent parabolic nodes on the ventral margin of the flank, as well as double ribs at the end of the adult phragmocone and initial part of body chamber. They also occupy a slightly lower stratigraphic position, since *Passendorferia tenuis* has been reported by this author from the upper Plicatilis Biozone, Antecedens Subbiozone (Enay 1966). The recent identification of new specimens of this form in different sections of the Iberian Range and in Sicily confirms this form as a well-defined species, occupying an intermediate horizon between *Pass. czenstochowiensis* (Siemiradzki) in the lower Cordatum, Claromontanus Subbiozone, and *Pass. tenuis* (Enay) in the Plicatilis Biozone, Ante-

cedens Subbiozone. It is hence described here as the new species: *Passendorferia nodicostata* sp. nov. (Pl. 1: 1-4).

Transversarium Biozone

A generally good stratigraphic record of the Transversarium Biozone in southern Europe, throughout the Submediterranean and Mediterranean provinces, makes biostratigraphic correlation possible across distant areas and shows the diversification of this group in Middle Oxfordian times. The species *Passendorferia ziegleri* (Brochwicz-Lewiński), created for the macroconch dimorph pair has been reported from the Polish Jura (Brochwicz-Lewiński 1973) and the Iberian Range (Meléndez 1989; Bello 2005), as well as from several other distant areas in the Mediterranean Province such as Hungary (Fözy and Meléndez 1996), Sicily (D'Arpa and Meléndez 2001) or the Betic Ranges (Sequeiros 1974, 1977) from the lower-middle levels of the Transversarium Biozone. The extremely evolute serpenticone coiling and fine ribbing displayed in the inner whorls has made some authors think it to be in fact the macroconch of *Pass. birmensdorfensis* (Moesch). However, recent findings in the Iberian Range (Bello 2005) suggest that both forms might actually constitute separate

	Meléndez and Fontana 1993, Cariou *et al.* 1997			Bello 2005	D'Arpa, Meléndez 2004
Stage	**Biozone**	**Subbiozone**	**Biohorizon**		***Passendorferia* Species sucession (modified)**
Middle Oxfordian	Bifurcatus	Grossouvrei	Bifurcatus	Malinowskae	*uptonioides teresiformis*
				Bifurcatus	
			Grossouvrei	Grossouvrei	
		Stenocycloides	Duongi	Duongi	*torcalense* (*)
			Bifurcatoides	Bifurcatoides	
	Transversarium	Rotoides	Wartae	Wartae	aff. *erycensis* (*)
			"Jelskii"	Universalis	
		Schilli	Subschilli	Subschilli	*erycensis* (*)
			Iberica	Iberica	
			Schilli	Schilli	
		Luciaeformis	Luciaeformis	Luciaeformis	*birmensdorfensis*
			Nectobrigensis	Nectobrigensis	
		Parandieri			*ziegleri*
	Plicatilis	Antecedens			*tenuis*
		Paturattensis			*nodicostata* (*)
Lower	Cordatum	Cordatum			?
		Costicardia			?
		Claromontanus			*czenstochowiensis*

Fig. 4. Comparative biostratigraphic framework for the Oxfordian Stage of subfamilies Perisphinctinae and Passendorferiinae. Standard framework for Submediterranean Province Perisphinctinae by Meléndez and Fontana (1993) and partly Cariou *et al*. (1997), recently modified by Bello (2005). Species marked with an asterisk (*) correspond to specimens illustrated in Plate 1.

groups, the species of Moesch occupying a higher biohorizon in the Luciaeformis Subbiozone. Some specimens assigned by Meléndez (1989, *e.g.* pl. 11: 5) to *Pass. birmensdorfensis* (Moesch) from the section of Aguilón (S Zaragoza) actually come from upper Parandieri Zone levels or the Parandieri-Luciaeformis junction beds. These specimens display extremely evolute serpenticone inner whorls and may in fact represent the microconch dimorph of the species *Passendorferia ziegleri* (Brochwicz-Lewiński).

The species *Passendorferia erycensis* Meléndez, *in* D'Arpa and Meléndez (2002b) (= *Perisphinctes regalmicensis* Gemmellaro 1877, non 1875), identified in material from both Sicily and the Iberian Range and re-located in its precise

Chronostratigraphic units			*Passendorferia* species sequence: proposed dimorphic pair correspondence	
	Chronozone	**Subchronozone**	**Macroconch**	**Microconch**
Middle Oxfordian	Bifurcatus	Grossouvrei	*Passendorferia uptonioides* Enay; holotype: Enay (1966), pl. 22: 1-4	*P. (Dichotomosphinctes)* n.sp. aff. *trichoplocus* (Gemm.); Enay (1966), p. 431; fig. 122: 3a-e
			Passendorferia teresiformis (Br.-Lew.); holotype: Brochwicz-Lewiński (1973), pl. XXIII: 1-2	*Passendorferia (Enayites)* sp.nov. A Meléndez (1989), p. 180; pl. 12: 16-17
		Stenocycloides	*Passendorferia torcalense* (Kilian); Pl. 1: 8; holotype: Bertrand and Kilian (1889), pl. XXV: 6	Not yet described/figured
	Transversarium	Rotoides	*Passendorferia* aff. *erycensis* Meléndez [M]; Bello (2005), pl. 6: 5; pl. 7: 1; Pl. 1: 6-7	*Passendorferia* aff. *erycensis* Meléndez [m]; Bello (2005), pl. 6: 6
		Schilli	*Passendorferia erycensis* Meléndez; Bello (2005), pl. 6: 2-4	*Passendorferia erycensis* Meléndez; holotype Gemmellaro (1887): *Perisph. regalmicensis*, pl. 4 bis: 14
		Luciaeformis	*Passendorferia birmensdorfensis* (Moesch); Bello (2005), pl. 3: 2-3; pl. 4: 2-4	*Passendorferia birmensdorfensis* (Moesch); holotype: Moesch (1867), Enay (1966) (refig.), pl. 27: 2
		Parandieri	*Passendorferia ziegleri* (Br.-Lew.); holotype: Brochwicz-Lewiński (1973), pl. XV: 1	*Passendorferia birmensdorfensis* (Moesch); Meléndez (1989), pl. 11: 5 *P. (Dichotomosphinctes)* sp. 4 (nr: KQ6/5/2) Sequeiros (1974): p. 191; pl. XIX: 3
	Plicatilis	Antecedens	*Passendorferia tenuis* (Enay); holotype: Enay (1966), pl. 19: 3	Not yet described/figured
		Paturattensis	*Passendorferia nodicostata* [M] sp. nov. Pl. 1: 4	*Passendorferia nodicostata* [m] sp. nov. Pl. 1: 1-3
Lower	Cordatum	(Cordatum +Costicardia)	???	???
		Claromontanus	Not yet described/figured with certainty	*Passendorferia czenstochowiensis* (Siemiradzki), lectotype: 1899, p. 86. (=Bukowski, 1887, pl. 30: 10)

Fig. 5. Description of the recorded sequence of *Passendorferia* species in the studied areas, from Early Oxfordian Cordatum Chronozone to Middle Oxfordian Bifurcatus Chronozone, to show the presumable correspondence of dimorphic pairs, according to the present state of knowledge as discussed in the text. The table shows a satisfactory identification of macro and microconch counterparts of the genus for each stage in the sequence. Inevitable "holes" in identified dimorphs are due to lack of clear record and/or to difficulties in re-interpreting previously illustrated specimens by former authors. No sound record of *Passendoferia* is known so far in Tethyan areas from Costicardia and Cordatum subchronozones.

stratigraphic position, is a common form in the Schilli Subbiozone. Its macroconch, wrongly identified as *Pass. tenuis* (Enay) by Meléndez (1989, pl. 1: 2; pl. 2: 1) is also normally recorded in all the above mentioned sections. It is characterized by slow, regular growth and evolute (but not extremely evolute) coiling up to the adult stage, fine and uniform ribbing and with the whorl section rounded, more inflated than in *Pass. birmensdorfensis* (Moesch). These features make it somewhat homeomorphic with *Pass. tenuis*, from the Antecedens Subbiozone.

Above the Schilli levels, in the interval from the Subschilli Biohorizon to the lower Rotoides Subbiozone (= Universalis Biohorizon), a peculiar form is recorded. It is characterized by more evolute coiling and coarser ribbing than *Pass. erycensis* Meléndez. This form, described as *Pass.* n. sp. aff. *erycensis* Meléndez by Bello (2005) seems to be the next link in this evolutionary line. However, it is also possible that this form may correspond, in fact, to the true *Pass. regalmicensis* (Gemmellaro).

Bifurcatus Biozone

In the Bifurcatus Biozone representatives of the genus *Passendorferia* form a well-known succession already described from different areas in the Mediterranean and Submediterranean provinces since the original descriptions by Brochwicz-Lewiński (1973), Brochwicz-Lewiński and Różak (1976), and Sequeiros (1977). The species *Pass. torcalense* (Kilian) is known from the first biohorizon in the lower Stenocycloides Subbiozone. This form is characterized by extremely dense ribbing, evolute coiling and a subcircular whorl section at early ontogenetic stages, changing to compressed whorl section connected with quicker growth in the middle whorls. It is very common in the Betic Ranges, S Spain; more typically so in the Subbetic units of Málaga from where comes the type specimen, but it has also been identified in almost all areas throughout Tethys. Microconchs of this species have still not been identified or described.

Passendorferia teresiformis (Brochwicz-Lewiński), the type-species of the genus, is characterized by extremely evolute serpenticone coiling in the inner whorls with sharp ribbing and a circular whorl section, turning almost suddenly into a sharp, square section with angular margins, and prominent columnar ribs, tuberculate, almost spiny on the ventral margin. The holotype of the species (Brochwicz-Lewiński 1973, pl. 13: 1) is a small size immature macroconch, rarely surpassing 220 to 250 mm diameter, in comparison with other classical forms, as it can be seen by the suture line on the type-specimen, which shows no approximation of last septa. This species occupies a well-defined horizon in the lower Grossouvrei Subbiozone within the Bifurcatus Biozone and is a common form throughout the Mediterranean and Submediterranean provinces. The specimen figured as *Perisphinctes* (*Pseudarisphinctes*) n. sp. A by Enay (1966, pl. 24: 1), from the *"Couches du Geissberg"* of Champfromier (Ain) French Jura, is a clear macroconch representative of this species, as had already been admitted by Brochwicz-Lewiński (1973). Microconchs of this species are not uncommon although they have not been regularly illustrated or described so far.

The species *Passendorferia uptonioides* (Enay) is a new link, reported by this author in the type area (French Jura) from the same stratigraphic interval, in the Bifurcatus Biozone, Grossouvrei Subbiozone (Enay 1966). The holotype, figured by Enay (1966, pl. 22: 1-4; pl. 23: 1) and paratype (loc. cit., pl. 23: 2) are characterized by the large size, up to 300 mm, and uniform slow growth with square whorl section, slightly more involute and with blunter ribbing than *Pass. teresiformis* (Brochwicz-Lewiński). The particular style of ribbing of this species, with a low point of furcation and early presence of intercalaries or trifurcations in the middle whorls, as well as the early trend to develop a more compressed whorl section, have suggested this form as the possible earliest original phyletic link of the divergent evolutionary line Ataxioceratinae Buckman.

Microconchs of this form are still not well known. However some specimens coming from the middle-upper levels of the Bifurcatus Biozone and showing the similar style of ribbing and coiling in inner and middle whorls as in macroconchs are not uncommon. The most clear could be the specimen figured by Enay (1966, p. 431, fig. 122: 3) as *Perisphinctes* (*Dichotomosphinctes*) n. sp. aff. *P. trichoplocus* (Gemmellaro), a complete adult microconch with the peristome, showing the particular evolute coiling in the inner whorls with a thick rounded whorl section, turning into a more compressed section in the middle whorls, and with somewhat thick, blunt ribbing with a trend to lower the point of furcation on the flank. The specimens figured by Meléndez (1989, pl. 12: 16, 17) as *Passen-*

dorferia (*Enayites*) n. sp. A, showing a somewhat thick, rounded whorl section and blunt ribbing, may be also accepted as microconch representatives of this species.

Specimens from the Polish Jura assigned with some reservation to this species by Brochwicz-Lewiński (1973, pl. 19-21) and referred to as *Nebrodites (Passendorferia)* cf. *uptonioides* by the author, show the style of coiling and sharp ribbing of the innermost whorls which still recall *Pass. teresiformis*, but the adult features rather correspond to the species of Enay.

Upper Oxfordian Hypselum Biozone

References to representatives of the Passendorferiinae in the Upper Oxfordian Hypselum and Bimammatum biozones are common and can be traced back as far as the lower Hypselum Biozone, Semimammatum Subbiozone (Fig. 3). The species *Passendorferia rozaki* Meléndez, a very typical form characterized by evolute serpenticone coiling with a persistent subcircular whorl section and an early trend to develop somewhat coarse ribbing, is well localised at the lower part of the Hypselum Biozone, Semimammatum Subbiozone. Subsequent references from Algeria (Atrops and Benest 1986), Hungary Pilis Mountains in the Transdanubian Central Range (Fözy and Meléndez 1996) and Sicily (Monte Inici, Cecca and Savary 2007) confirm that this species is a fairly common form. Macroconchs of this species have not yet been clearly identified so far. However, among the material studied, some wholly septate specimens showing uniform coiling (*e.g.* Meléndez 1989, pl. 13: 11, 14) might well correspond to macroconchs.

Perisphinctes birmensdorfensis Oppenheimer 1907 (non Moesch) from the Hypselum Biozone was re-defined by Brochwicz-Lewiński and Różak (1976) as *Nebrodites* (*Enayites*) *gygii*. It is characterized by fine ribbing gradually becoming somewhat thicker, and evolute coiling with a persistent subcircular whorl section. This form is only known so far by microconch representatives, but has been reported, besides from Poland, from the Transdanubian Central Range (Pilis Mountains) in Hungary (Fözy and Meléndez 1996) and from the Monte Erice sections in Sicily (D'Arpa and Meléndez 2001).

The species "*Perisphinctes" idoceroides* Dorn (1930) and *Passendorferia arancensis* Meléndez (1989), (the holotype of this species being the specimen figured by Enay, 1966, pl. 40: 7 as *?Praeidoceras* sp.) from this same stratigraphic interval, were first placed in the genus *Passendorferia* by Meléndez (1989) with some reservations. They have been recently placed in the new genus *Graefenbergites* by Schairer and Schlampp (2003). This new taxon could be (with some logical reservation) accepted as a new taxon within the subfamily Passendorferiinae, divergent from the main *Passendorferia* line (Fig. 3).

Bimammatum-Hauffianum Biozone

Further successive links within this main line would be assignable to *Passendorferia sanpedroi* Meléndez (1989) from the Bimammatum Biozone levels of Ariño (Ventas de San Pedro section), the holotype of which is a complete adult microconch. From the same stratigraphic levels and the same locality of Ariño, there were also reported and figured some incomplete macroconchs: *Passendorferia* (*Passendorferia*) n. sp. A (Meléndez 1989, p. 151, pl. 9: 1-2; non 3) which perfectly match the macroconch of this species. The later form *Passendorferia wierzbowskii* Meléndez (= *Idoceras? Nebrodites (Enayites*?) aff. *gygii* Brochwicz-Lewiński, *in:* Wierzbowski 1978, pl. 2: 17) is a somewhat thickly ribbed *Passendorferia* with a rounded "massive" to early compressed whorl section. These forms, as well as the evolute crassicostate form described as *Passendorferia* sp. ind. by Meléndez (1989, pl. 10: 1-7) from higher levels in the Hauffianum to lower Planula Biozone seem to prove that the main *Passendorferia* line goes up through the Upper Oxfordian and is phyletically linked with *Nebrodites* from the Lower Kimmeridgian. However, an alternative interpretation was put forward by Pérez-Urresti (1996), according to whom these Upper Oxfordian forms may represent microconch counterparts of representatives of *Orthosphinctes*.

Genus Sequeirosia Meléndez

Middle Oxfordian Transversarium Biozone

The genus *Sequeirosia* was erected as a new taxon by Meléndez (1984, 1989) on the basis of the type-species: "*Passendorferia" brochwiczi* Sequeiros 1977. It is characterized by relatively involute serpenticone coiling in the inner whorls, unlike the typical representatives of *Passendorferia*, and a persistent subquadrate whorl section with angular umbilical and ventral margins in the

inner whorls (see above). Since its definition, some forms first described as "*Perisphinctes*" or *Passendorferia* have been transferred to this new genus expanding throughout the Transversarium and Bifurcatus biozones as a series of still poorly known forms. However, the available material shows that these forms represent a fairly complete succession of dimorphic pairs (Fig. 3).

In the lower Transversarium Biozone, Parandieri Subbiozone, the species *Sequeirosia boccoonii* (Gemmellaro) seems to be the earliest known representative of this genus (D'Arpa 2003, p. 183, pl. 9:1). Only macroconch specimens of this species have been described so far. From the middle Transversarium Biozone, Luciaeformis to lower Schilli Subbiozone, comes the form *Sequeirosia trichoplocus* (Gemmellaro). The type specimen of this species, first interpreted as an adult microconch, is, in fact, after detailed examination of the specimen, a wholly septate, incomplete phragmocone; most probably of a macroconch. Microconch specimens of this form are not uncommon in the lower-middle part of Transversarium Biozone, Luciaeformis Subbiozone of the Iberian Range (Meléndez 1989, pl. 14: 2-5; pl. 15: 3-4) characterized by evolute coiling, flat sided square whorl section and extremely fine ribbing, slightly prorsiradiate on the flank. It should be noted that the "Wartae Subbiozone" (Meléndez 1989) was subsequently changed to "Luciaeformis Subbiozone" (see Cariou *et al*. 1991).

The species *Sequeirosia brochwiczi* Sequeiros comes from the Schilli to (?) the lower Rotoides Subbiozone. Its ribbing is somewhat dense and fine (although not as fine as in *S. trichoplocus*), rectiradiate and uniform on the flank, with single ribs predominant, and parabolic nodes becoming less prominent than in *Passendorferia*. The species is relatively common in the Betic Ranges, Torcal de Antequera, Málaga province (from where the type specimen comes), the Iberian Range and in Sicily, where a well-preserved specimen has been recently collected from the section of Roccapalumba (D'Arpa *et al*. 2006). A remarkable specimen from the Iberian Range, Calanda region, figured by Meléndez (1989, pl. 14: 1), an almost complete adult phragmocone, was first reported from the "Wartae" (= Luciaeformis) Subbiozone. However, it comes from bed 2 of the outcrop Calanda-2. In this particular section, the Oxfordian sequence appears extremely condensed, and specimens of *Larcheria* have already been collected from beds 4 and 6. So it is fairly possible that the basal levels do already belong to the Schilli Subbiozone. The rest of the known specimens of this species clearly come from the Schilli Subbiozone, having been collected together with *Passendorferia erycensis* Meléndez; *Larcheria* spp., and above the levels with *Gregoryceras riazi* (De Grossouvre).

Several forms clearly belonging to *Sequeirosia* have been described in the past under various different names. The specimens described as *Perisphinctes melmorei* Arkell by Enay (1966; pl. 24: 2 non 3) and *Perisphinctes inmutabilis* Enay (1966; pl. 24: 4) presumably from strata of the Transversarium Biozone ("*Couches à spongiaires*") of the French Jura, may be easily assigned to the genus *Sequeirosia* Meléndez.

Bifurcatus Biozone

In the Bifurcatus Biozone, the form figured by Brochwicz-Lewiński (1973, pl. 22: 1) as *Perisphinctes* n. sp. aff. *tenuis* Enay, from middle Bifurcatus Biozone levels from Biskupice (Polish Jura Chain) shows the typical "involute" serpenticone coiling of the inner whorls and square whorl section, in contrast with the comparable ontogenetic stage in *Passendorferia*, as illustrated by this author (*loc. cit*., pl. 22: 1). Also, the form figured by Meléndez (1989, pl. 16: 1), presumably from Bifurcatus Biozone levels of La Mierla (province of Teruel, SW Iberian Range) shows these peculiar features in coiling, whorl section and ribbing. It seems therefore that, although still poorly known, *Sequeirosia* appears as a clear, diversified taxon throughout the Middle Oxfordian.

Genus Geyssantia Meléndez

The hypothesized phyletic connection between Oxfordian Passendorferiinae and Kimmeridgian Idoceratinae (genus *Nebrodites*) is probably represented by the genus *Geyssantia* Meléndez 1989 (see Fig. 3). The latter comprises forms recorded in lower Planula levels and characterized by extremely evolute serpenticone coiling, the umbilical parameter (U/D ratio) ranging up to 0.7, rounded subcircular whorl section and crassicostate ornamentation with coarse and large ribs on the flank and venter, becoming smooth at an early stage. The form described from southern Germany (Heidenheim; Franconian Alb) by Nitzopoulos (1974, pl. 10: 5) as *Nebrodites (Mesosimoceras) evolutus* (Gemmellaro) from bed S.25 of the "Schneider Profil" (= Planula-Galar Biozone

transition beds, see fig. 18, p. 111) well matches the diagnosis of this genus, as do the specimens reported from Algeria by Atrops and Benest (1984, 1986). A further specimen assigned to *Geyssantia geyssanti* Meléndez has been recently reported from NW Sicily, Monte Inici section by Cecca and Savary (2007; p. 524, fig. 7c). The available information seems to indicate that this taxon comprises relatively small-sized specimens, that is microconchs 50-80 mm in diameter and macroconchs probably not exceeding 150 mm in diameter. The specimen illustrated by Nitzopoulos (1974) seems to be wholly septate, most probably an incomplete phragmocone of a macroconch, despite the remark of the author (p. 78: "suture line not preserved"). Such features support its phyletic position as a forerunner of Lower Kimmeridgian *Nebrodites* of the group *hospes-agrigentinum*, as already noted by Callomon (*in*: Donovan *et al*. 1981).

CONCLUSIONS

The Oxfordian ammonite subfamily Passendorferiinae forms a homogeneous phyletic branch of the Perisphinctidae arising from Late Callovian Grossouvriinae of the genus *Alligaticeras*, diversifying and spreading in Tethyan areas during the Lower and especially Middle Oxfordian and giving rise to early representatives of the genus *Nebrodites* at the turn of the Oxfordian and Kimmeridgian stages (Fig. 3). A diverging branch of the main *Passendorferia* line probably gave rise to early representatives of the Ataxioceratinae at the turn of Middle-Upper Oxfordian (Bifurcatus-Hypselum Chronozone interval) as it appears by the intermediate features shown by some transitional forms from these levels, such as *Passendorferia uptonioides* (Enay) and *Orthosphinctes ariniensis* (Meléndez). The geographical distribution of the Passendorferiinae gives them the character of a "pure Tethyan" fauna as they appear omnipresent throughout the Mediterranean and the marginal parts of the Submediterranean Province. This along with the fairly constant association with Rosso Ammonitico facies suggest biogeographic and evolutionary segregation from main stem Perisphinctinae in more favourable open oceanic and epioceanic platform environments along the southern margin of Tethys. Although their geographic spread throughout the Mediterranean Province and the marginal parts of the epicontinental platform seas of Southern Europe appears explainable in terms of biogeographic dispersal, the arrival of shells in proximal platform areas where they are found in associations best interpreted as allochthonous was, in most cases, due to taphonomic dispersal by post-mortem drift of adult shells (Fig. 1). Biogeographic and taphonomic data indicate that true biological populations inhabitated more distal, deeper areas of the platforms. The evolutionary succession of *Passendorferia* species has supplied a high-resolution biostratigraphic framework for the Mediterranean Province comparable and correlatable with that provided by representatives of the Perisphinctinae in the Submediterranean Province. The evolutionary history of the Passendorferiinae also appears crucial for reconstructing and understanding the origin of the perisphinctid subfamilies Ataxioceratinae and Idoceratinae.

APPENDIX: TAXONOMIC NOTE

Passendorferia nodicostata nov. sp.
Pl. 1: 1-4

1989. *Passendorferia* (*Enayites*) n. sp. aff. *czenstochowiensis* (Siemiradzki), Meléndez, p. 155, pl. 11: 4 a, b; fig. 31 (= Holotype).
2003. *Passendorferia* (*Passendorferia*) *czenstochowiensis* (Siemiradzki), D'Arpa, p. 173, pl. 4: 5 (= Paratype).
2004. *Passendorferia* cf. *tenuis* (Enay), D'Arpa and Meléndez, p. 257, fig. 2.

MATERIAL: 5 specimens (M and m) more or less complete, from the Iberian Range, Sicily, and the Polish Jura, Some further 10 incomplete specimens, preserved as incomplete nuclei.

HOLOTYPE: Pl. 1:1. Specimen nr. KA1.110.1 Coll. L. Sequeiros. Aguilón, section AG.1 Iberian Range, level A.110 (microconch). First figured by Meléndez (1989, p. 155; pl. 11: 4a-b). Palaeontological Museum of Zaragoza, Spain. Lower Plicatilis Biozone, Paturattensis Subbiozone.

PARATYPE: Pl. 1: 2 Specimen nr. MGUP/C.D.28. Sicily. Coll: C. D'Arpa. Contra da Diesi section (near Sciacca). level: 3 (complete adult microconch) Callovian-Oxfordian transitional interval. First figured by D'Arpa (2003, p. 173; pl. 4: 5). Museo Geo-

logico G. G. Gemmellaro, Univ. Palermo, Italy. Lower Plicatilis Biozone, Paturattensis Subbiozone.

OTHER SPECIMENS ASSIGNED:

(1) Specimen nr: WBL.Wr2/15 Coll. W. Brochwicz-Lewiński (microconch). Wrzosowa section (Polish Jura): Pl. 1: 3. Geological Institute, Warsaw, Poland. Lower Plicatilis Biozone, Paturattensis Subbiozone, or (?) Cordatum Biozone.

(2) Specimen nr: WBL.Wr2/13 Coll. W. Brochwicz-Lewiński (macroconch). Wrzosowa section (Polish Jura): Pl. 1: 4. Geological Institute, Warsaw, Poland. Lower Plicatilis Biozone, Paturattensis Subbiozone, or (?) Cordatum Biozone.

DERIVATIO NOMINIS: The name *nodicostata* refers to prominent parabolic nodes appearing as double ribs or umbilical bifurcations on the flank, and swellings at the ventral margin in microconchs at the end of phragmocone and the beginning of body chamber in adult specimens, and also in the inner whorls of macroconchs.

TYPE HORIZON: Lower Middle Oxfordian: Plicatilis Biozone, Paturattensis Subbiozone. Specimens of this species are common in Submediterranean and Mediterranean Province areas, within the Callovian-Oxfordian transition levels, generally associated with *Perisphinctes paturattensis* Loriol. Due to frequent processes of stratigraphic gaps and taphonomic re-elaboration at this interval in the sections of the Submediterranean Province studied, it is not excluded that further findings might cast some light and modify the stratigraphic position of this species, between the Claromontanus and Paturattensis subbiozones.

REMARK: The Polish specimens might cast some doubt on the stratigraphic position of this species since, according to Głowniak and Matyja (*in*: Dembicz *et al*. 2006 a, b) they could in fact come from the Lower Oxfordian, Cordatum Biozone). They are, hence, accepted into synonomy with some reservation due to some uncertainty on their stratigraphic position.

DIAGNOSIS: Small to middle size species of *Passendorferia* (M) and (m), characterized by evolute serpenticone coiling with subcircular whorl section in inner whorls, turning into slightly more massive in adult stage of microconchs and with prominent parabolic nodes or double ribs and deep constrictions. Macroconchs turning to subquadrate, slightly compressed whorl section.

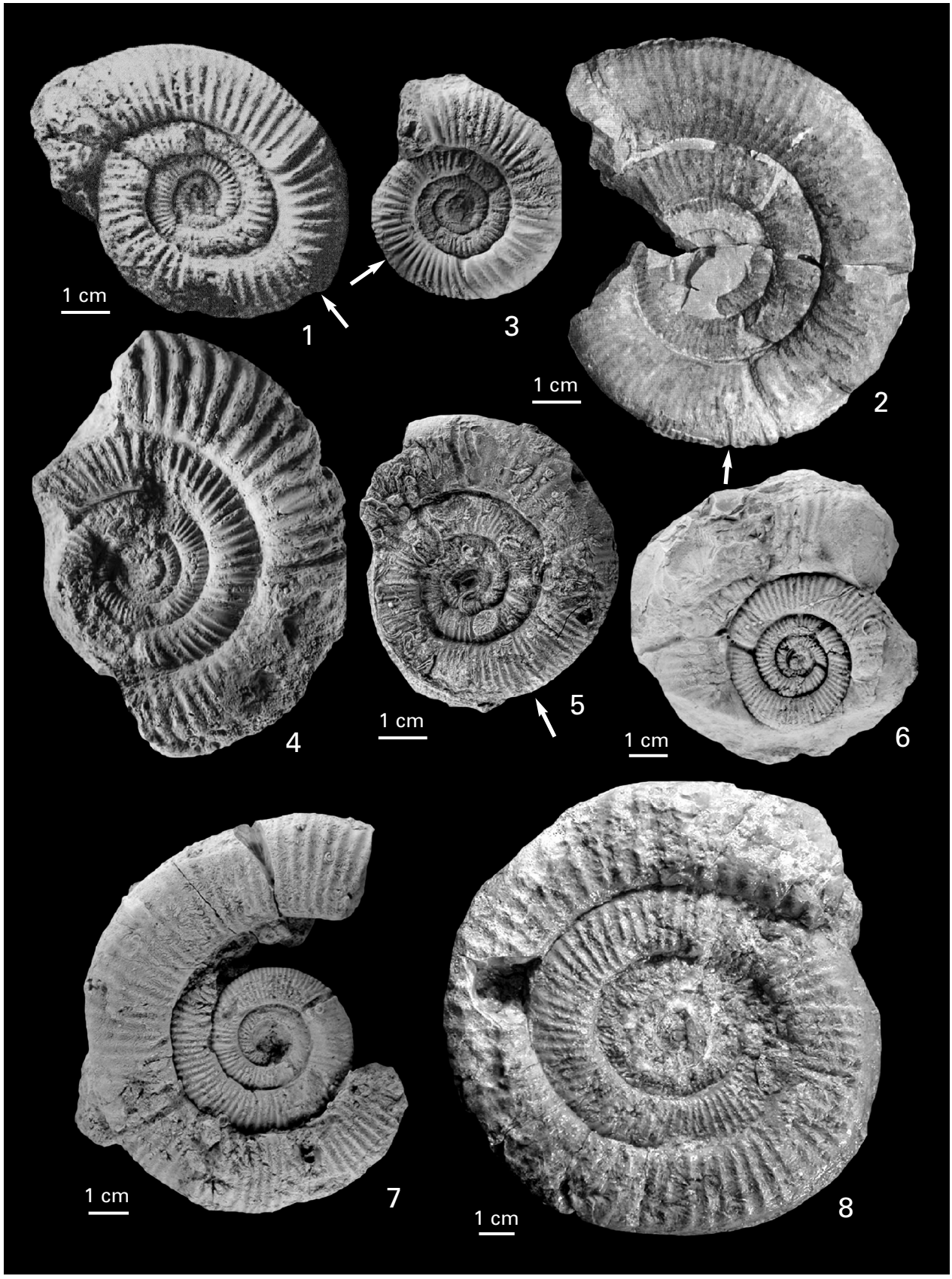
DESCRIPTION: The available material of this new species comprises only a few complete specimens. The holotype is a complete adult microconch from the Iberian Range (Aguilón). This seems to be a small to medium size species of *Passendorferia*, the microconchs reaching 70-80 mm diameter and macroconchs ranging between 150 and 200 mm.

The shell comprises evolute to extremely evolute serpenticones in the early stages of development with circular whorl section, turning sharply more "massive" with slightly more involute coiling in the adult stage in microconchs, and subquadrate with almost angular margins in macroconchs. Ribbing uniform and dense, not extremely fine, with rounded, blunt somewhat thick, radial primaries, thicker than in the close relatives *Passendorferia czenstochowiensis* (Siemiradzki) or *Passendorferia tenuis* (Enay) with deep, radial or slightly prorsiradiate constrictions. The ribs are regularly biplicate. In the inner whorls single ribs may be common and alternate with bifurcations. However, from the ephebic stage and in the adult body chamber, bifurcate ribs predominate. In macroconchs the primary ribs become progressively thicker from a diameter of 80-100 mm giving rise to typical straight columnar ribs, distally enlarged and prominent or even slightly projected on the ventral margin.

Parabolic structures or nodes are clearly visible on the whorl side as double ribs, umbilical bifurcations or lateral nodes, and as typical swellings at the ventral margin, mostly visible at the end of the adult phragmocone and first portion of the adult body chamber.

RELATIONSHIPS AND DIFFERENCES: The closest relative of this new form is the presumable forerunner, *Passendorferia czenstochowiensis* (Siemiradzki) generally reported from the lower Cordatum Biozone, Claromontanus Subbiozone. This species also possesses prominent parabolic nodes on the whorl side but differs from *nodicostata* by its finer ribbing and more evolute coiling with slower growth and persistent square whorl section.

Passendorferia tenuis (Enay) from the Plicatilis Biozone, Antecedens Subbiozone, is characterized by the remarkably uniform "soft" blunt ribbing, with slow growth, persistently rounded, subcircular whorl section and virtual absence of parabolic nodes on the flank, which makes it clearly different from *Passendorferia nodicostata* nov.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STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: The scarce specimens of this species are found so far in the Callovian-Oxfordian transition beds, from the same recorded ammonite association as *Perisphinctes* of the *P. paturattensis-montfalconensis* Loriol groups, Middle Oxfordian, Plicatilis Biozone, Paturattensis Subbiozone. The species is widespread across the Iberian Range (the best specimens come from the sections of Aguilón-Tosos, and in Sierra de Albarracín). It is also found in the same stratigraphic levels in Sicily, Erice sections (see D'Arpa 2003) and Polish Jura wherefrom come two of the specimens assigned to this new species (see remark above).

Acknowledgements

This paper is a contribution to the research projects: CGL 2004/ 02694/BTE (MEC-CSIC, Spain) and OTKA 68453 (Hungary). Warm thanks are also due to Dr. R. Enay, for numerous comments supplying information on neighbour areas to the here studied and for constructive refereeing of the manuscript.

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Plate 1

1-4 – *Passendorferia nodicostata* sp. nov.: 1 – Holotype (m). Complete adult microconch preserving the final peristome and lappets. Iberian Range, Spain. Aguilón. Specimen: KA1.110.1 Aguilón (coll. L. Sequeiros). Figured in Meléndez (1989, p. 155, pl. 11: 4) Callovian-Oxfordian transition bed (Fe-ooid: Arroyofrío Bed). Middle Oxfordian, Plicatilis Biozone; Paturattensis Subbiozone. D = 56 mm. Palaeontological Museum, University of Zaragoza, Spain. 2 – Paratype: Specimen MGUP/C.D.28. Sicily, Contra da Diesi section (near Sciacca). level: 3 (complete adult microconch) coll: C. D'Arpa. Figured in D'Arpa (2003, p. 173, pl. 4: 5) Callovian-Oxfordian transitional interval. Middle Oxfordian, Plicatilis Biozone; Paturattensis Subbiozone. D = 75 mm. Museo Geologico G.G. Gemmellaro, Univ. Palermo, Italy. 3 – Specimen WBL.Wr2/15. Wrzosowa quarry, Polish Jura Chain. Complete, presumably immature microconch, with the beginning of the peristome. Geological Institute, Warsaw (Poland). 4 – Specimen: WBL.Wr2/13. Same locality and level as Nr. 3. Middle Oxfordian, Plicatilis Biozone; Paturattensis Subbiozone. (?) Immature macroconch, preserving the beginning of the body chamber. Geological Institute, Warsaw (Poland). 5 – *Passendorferia erycensis* Meléndez: (m). Adult microconch, incomplete, preserving *c*. one third of whorl of body chamber. Specimen nr: WMo.1/18/2. Moneva (coll. J. Bello). Middle Oxfordian, Transversarium, Biozone, Schilli Subbiozone. D = 50 mm. Palaeontological Museum, University of Zaragoza, Spain. 6-7 – *Passendorferia* aff. *Pass. erycensis* Meléndez. 6 – (M). Wholly septate macroconch. Specimen nr: WRi.1/48/1 Ricla (coll. J. Bello). D = 61 mm. Figured by Bello (2005), p. 257, pl. 7: 1. Middle Oxfordian, Transversarium Biozone; Rotoides Subbiozone. D = *c*. 60 mm. 7 – (M). Wholly septate macroconch. Specimen, nr: WBE.1/24/14 Barranco de las Estacas (Ariño). Col. G. Meléndez. Figured by Bello (2005) p. 257, pl. 6: 5. Middle Oxfordian, Transversarium Biozone; Rotoides Subbiozone. D = *c*. 82 mm. Palaeontological Museum, University of Zaragoza, Spain. 8 – *Passendorferia torcalense* (Kilian): (M). Wholly septate adult macroconch. Specimen nr: CUM/4/10. Subbetic Ranges (S Spain), Canuto de Utrera (Málaga). Middle Oxfordian, Bifurcatus Biozone; (?) Stenocycloides Subbiozone. D = *c*. 155 mm. Palaeontological Museum, Estepona, Málaga (Spain).

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