Original article

Latest Toarcian-earliest Bajocian (Jurassic) Grammoceratinae (Hildoceratidae, Ammonitina) of the western Tethys: Their palaeobiogeographic and phylogenetic significance

José Sandoval a,*, Maria Helena Henriques b, Robert B. Chandler c, Soledad Ureta d

a Departamento de Estratigrafía y Paleontología, Universidad de Granada, Av. Fuentenueva s/n, 18002, Granada, Spain
b Departamento de Ciências da Terra e Centro de Geociências, Universidade de Coimbra, 3049 Coimbra codex, Portugal
c Shirley High School, Shirley Church Road, CM6 1EF, Croydon, United Kingdom
d Departamento de Paleontología, Facultad de Ciencias Geológicas (UCM) and Instituto de Geología Económica (CSIC-UCM), 28040, Madrid, Spain

Keywords:
Grammoceratinae
Ammonitina
Jurassic
Western Tethys
Taxonomy
Palaeobiogeography

A B S T R A C T

Grammoceratinae (Hildoceratidae, Ammonitina) abound in the Toarcian strata of many western Tethyan localities, especially the Subbetic and Lusitanian basins (of southern Spain and central western Portugal, respectively). They decline through the Aalenian and disappear by the lowermost Bajocian. The genera Asthenoceras, Vacekia (subgenera Vacekia and Nadorites) and Fontannesia are traditionally considered as the last Grammoceratinae, with species of Osperloiceras occurring in the uppermost Toarcian. Grammoceratinae are common in the eastern Pacific, especially Oregon and Alaska where Asthenoceras is abundant. They also occur in the eastern Tethys (Thailand). Although studies of Toarcian to early Bajocian Subbetic and Lusitanian grammoceratins already exist, new material from these and other palaeogeographic areas (England, Portugal and Spain) is revised here. A new genus, Linaresites novo gen. (for Fontannesia montillanensis Linares and Sandoval) and two new species (Vacekia striata Henriques, and Asthenoceras taverai Sandoval) are described. Another form, "Asthenoceras" sp. A is described and kept in open nomenclature. Temporal analysis of Aalenian to early Bajocian Grammoceratinae demonstrates a progressively more evolute morphology through time, sometimes coupled with size reduction. Palaeogeographic evidence suggests that during the early Middle Jurassic, western Tethys and eastern Pacific were temporarily well connected, possibly through the Hispanic Corridor, as demonstrated by the similarity between Tethyan and eastern Pacific Grammoceratinae.

1. Introduction

Grammoceratinae (Hildoceratidae, Ammonitina) abound in Toarcian rocks of many western Tethyan localities where they are primary biostratigraphic tools. They become progressively scarcer in the Aalenian and disappear in the Lower Bajocian. The genera Asthenoceras Buckman, 1889, Vacekia Buckman, 1899, Fontannesia Buckman, 1892 and Nadorites Elmi and Caloo-Fortier, 1985 (here considered synonymous of Vacekia) are traditionally cited among the latest Toarcian-earliest Bajocian Grammoceratinae. Additionally, "species" of Osperloiceras Krimholz and Tazikhin, 1957, occur in the late Toarcian. Linares and Sandoval (1988, 1992) presented detailed monographic studies on some of these taxa, figuring Subbetic ammonites included in the genera Vacekia, Asthenoceras and Fontannesia, all assigned by these authors to the Subfamily Grammoceratinae (Hildoceratidae, Ammonitina). Grammoceratinae are also abundant in the uppermost Toarcian-Aalenian interval of the Lusitanian basin. Henriques (1992) described three new "species" of Grammoceratinae from the region: Vacekia striata, V. robusta, Asthenoceras vacekiformis and one Asthenoceras sp.

Latest Toarcian to early Bajocian Grammoceratinae are known from other regions of western Tethys, e.g., England (Buckman, 1887-1907; Callomon and Chandler, 1990), Iberian Cordillera (Ureta, 1985; Fernández-López and Gómez, 1990; Goy and Ureta, 1990), Cantabrian Cordillera (Gómez et al., 2009), Mallorca (Goy and Ureta, 1988; Alvaro et al., 1989), Italy (Vacek, 1886, 1988, 1990; Sadki, 1984, 1990, 1994, 1996), and Algeria (Elmi and Caloo-Fortier, 1985). They are common in the eastern Pacific, especially in Oregon (Imlay, 1973, 1984) and Alaska (Westermann, 1969), and present in the eastern Tethys (Thailand; Kozai et al., 2010). Here, Subbetic and Lusitanian material studied by Linares and Sandoval (1988, 1992) and Henriques (1992, 2000a) is reviewed and new data from other palaeogeographic areas added.
Fig. 1. A–F. *Vacekia sourensis* (Perrot, 1957): A, MP 1-3, Aalensis Zone, Macrata Subzone, Maria Pares, Lusitanian basin; B, M 33-28, Opalinum Zone, Comptum Subzone, Murtinheira, Lusitanian basin; C, D, CM.42.2 and CM.40.1, Aalensis Zone, Macrata Subzone, Cerro Méndez, Betic Cordillera; E, CM.69.3, Aalensis Zone, Buekmani Subzone, Cerro Méndez, Betic Cordillera; F, Rb16/3, Opalinum Subzone, Rabanera, Iberian Cordillera. G–L. *Vacekia striata* nov. sp. Henriques: G, M 33-2 (holotype), H, M 33-4, Land Ll, M33-5 (paratype), Opalinum Zone, Comptum Subzone, Murtinheira, Lusitanian basin; I, M25-1, Aalensis Zone and Subzone, Murtinheira, Lusitanian basin; J, SG 65-20, Opalinum Zone, Comptum Subzone, São Giao, Lusitanian basin; K, M31-7 (paratype), Opalinum Zone and Subzone, Murtinheira, Lusitanian basin. M–T. *Vacekia stephensi* Buckman, 1889: M, MP 100-1, Bradfordensis Zone, Maria Pares, Lusitanian basin; N, RA111-12, Bradfordensis Zone, Serra do Rabaçal, Lusitanian basin; O, SPLRS, Bradfordensis Zone?.
Most Subbetic ammonites included then represent Grammoceratinae (genera *Vacekia* and *Astheneoceras*, and “Fontannesia” *montillanensis* Linares and Sandoval), excluding rare *Fontannesia* (e.g., *F. tortiva* Buckman). These differ morphologically from *Fontannesia*. Chandler et al. (2006) regarded *Fontannesia* as the probable ancestor of *Witchellia* and placed it in the Family Sonnninidae, Subfamily Witchelliinae, instead of the Grammoceratinidae. “F.” *montillanensis* clearly belongs to the Grammoceratinidae and represents a new genus named here and considered by us as the last western Tethyan Grammoceratinidae. Most Aalenian specimens from the Lusitanian basin described by Henriques (1992) as *Vacekia* are members of this genus; some Upper Toarcian examples may be juvenile forms of the genus *Cotteswoldia*. The “type” of “Astheneoceras vacekiiformis” from the Opalinum Subzone is a primitive *Vacekia*, here included in *V. striata* nov. sp.

2. Origin of the studied material

The specimens described here come primarily from the Lusitanian basin (central Portugal) and the central part of the Subbetic basin, Betic Cordillera (southern Spain), along with examples from the Iberian Cordillera (NW-SE belt, Spain), Basque-Cantabrian basin (northern Spain), Island of Mallorca, and Dorset (southern England). Localities are abbreviated to alpha-numeric codes for brevity:

- Lusitanian localities: M: Murtinheira section; MP: Maria Pares section; PCS: Poço Central Sul; RA: Serra do Rabaçal; SBVII: Serra da Boa Viagem; SG: São Gian and ZA: Zambujal de Alcara;
- Subbetic localities: SPA, SPB and SPLR: Sierra de San Pedro, Alcalá la Real, province of Jaén; MO, MOA, MOB, MOD: sections of Montillana area, Montillana, province of Granada; JAC13: Alta Coloma, Campillo de Arenas, Province of Jaén; MTT: la Torquilla, Noalejo, province of Jaén; JAI1: Barranco de Agu, Lusitanian basin. Scale bars: 2 cm (A-K, L1, M-V, W), 1 cm (L, V1).

Codes for the UK are those used by Callomon and Chandler (1985; Goy et al., 1988; Goy and Martinez, 1990). In the Basque-Cantabrian localities: Pu: Pujayo; Sm: San Miguel de Aguayo; Cy: Cillamayar; NW Iberian localities: Rl: Borobia; AI: La Almunia de Doña Godina; Ri: Ricla;
- Mallorca (Sierra Norte) localities: CB: Gorge Blau;
- Dorset (United Kingdom) localities: HE-BP: Beaminster, Horn Park Quarry (ST458022); WH-SK: Waddon Hill, Stoke Knop (ST447015); H: Burton Bradstock beach (SY483892); Mp-CQ: Mapperton, Coombe Quarry (SY496998).

3. Systematic palaeontology

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINAE Hyatt, 1889
Superfamily HILDOCERATAEOIDEA Hyatt, 1867
Family HILDOCERATIDAE Hyatt, 1867

Subfamily GRAMMOCERATINAE Buckman, 1904
Genus *Vacekia* Buckman, 1904

Type species: *Vacekia stephensi* Buckman, 1889.

Diagnosis: The genus *Vacekia* includes discoidal shells of medium size with moderately involute coiling. The umbilical wall is vertical, or near so, with flat or slightly convex flanks and high thin keel. Three developmental stages of ornamentation can be identified: the innermost whorls are smooth, sometimes with feeble ribbing; intermediate whorls are ribbed; the adult stage is finely striated. Septal sutures are simple with a deep, broad lateral lobe.

Remarks: *Vacekia* has been included in Leioceratinae (Arkell et al., 1957) and in Graphoceratinae (Donovan et al., 1981). Elmi and Callo-Fortier (1985), Henriques (1992) and Linares and Sandoval (1992) placed *Vacekia* in the Grammoceratinae due to a marked difference in morphology (ribbing style, keel, etc.) and septal suture compared to graphoceratids and consider it best placed with typical late Toarcian Grammoceratinae.

*Vacekia* shares similarities with *Ocerleioceras*, a possible ancestor, but *Vacekia* is slightly more evolute and smaller, with flat or almost flat flanks, a vertical or sub-vertical umbilical wall and a higher keel. It also shows similarities with *Astheneoceras*, which is possibly its descendant. *Astheneoceras* is more evolute, has an ogival rather than ovate or sub-rectangular whorl section and an oblique or curved umbilical wall. The three growth stages typical of *Vacekia* are not well differentiated in *Astheneoceras*.

*Vacekia sourensis* (Perrot, 1957) - Ureta, p. 227, pl. 2, figs. 1 and 2, pl. 30, fig. 12.

Description: Discoidal specimens of medium size and moderately involute coiling (Table S1). The whorl section is high and ovigal with convergent flanks and a thin keel. Specimens possess a shallow umbilicus with a straight wall and rounded umbilical edge. There are pairs of slightly flexuous, fine, simple ribs projecting orally at the umbilical margin. They deflect slightly adorally on the inner third of the flank and curve slightly before disappearing just before the ventral margin. Through ontogeny the ribs weaken into feeble striations. The body-chamber occupies at least half a whorl. The relatively simple septal suture has a deep, wide and typically indented lateral lobe.

Remarks: Perrot (1957) described specimens from the Northern and Central Lusitanian basin. Two species were figured (Perrot, 1957: pl. 1, figs. 1a, 2) but no type specimen was identified. Elmi and Callo-Fortier (1985) designated a holotype, the specimen figured in “pl. 1, figs. 1a, 1b,” of *Vacekia* (1957). This imprecise reference probably corresponds to specimen number 95, figured by Perrot (1957) on pl. 1, figs. 1, 1a. It is therefore the lectotype by definition. The species was originally recorded as *Aalenia* (Perrott, 1957). In the Iberian Range it is reported from the Pseudoradosa Subzone to Opalinum Subzone (Ureta, 1985; Goy et al., 1988; Goy and Martínez, 1990). In the Basque-Cantabrian basin it occurs in the Aalenia-Opalinum transition (Gómez et al., 2009) and on the Island of Mallorca from the base of
the Aalensis Zone to the base of the Opalinum Zone (Goy and Ureta, 1988). In the Lusitanian basin, it is recorded from the Mactra Subzone to the base of the Comptum Subzone (Zbyszewski et al., 1974; Henriques, 1992, 1995, 2000a). In the Betic Cordillera, the species occurs in the Aalensis Zone.

*Vacekia striata* nov. sp. [M] and [m] Henriques

Fig. 1(G–I); Table S2.

1886. *Harpcoceras costula* Reinecke - Vacek, p. 78 (pars), pl. 8, figs. 3, 3a, 3b, 9 and 9a (non pl. 8, figs. 4–8, 10–15).


1992. *Vacekia robusta* nov. sp. - Henriques, p. 9, figs. 1, 1.4, pl. 2, figs. 5 and 6.

1992. *Asthénoceras vacekiformis* nov. sp. - Henriques, p. 9, figs. 1.5, 1.6, 1.7, pl. 2, figs. 9 and 10.

2000a. *Vacekia* sp. - Henriques, p. 33, pl. 1, fig. 16.

**Derivation of the name** - Based on the characteristic fine, weakly defined striations distinctive of this species.

**Holotype**: Specimen M 33-2 (Fig. 1(G)); dimensions [mm]: D = 36.3, H = 16.8, U = 11.2; D = 29.0, H = 13.2, U = 9.1) stored in the Department of Earth Sciences, Faculty of Sciences and Technology, University of Coimbra (Portugal). Specimens M 33-5, M 33-7, M 33-8 and M 33-9 are paratypes.

**Type locality and occurrence**: The holotype was obtained from bed 33 of Murtinheira section (Cap Mondego, Northern Lusitanian basin, Central Portugal) and comes from the base of the Comptum Subzone (Lower Aalenian). The species is recorded from different localities in the Lusitanian basin and ranges from the Aalenian Subzone (Upper Toarcian) to the Opalinum Zone (Lower Aalenian) (Henriques, 1995, 2000a, 2000b). In the Betic Cordillera it is restricted to the Aalenian Zone.

**Diagnosis**: Discoidal shell with moderately involute coiling. Whorl section high, ogival to sub-rectangular, with high and thin keel. Body-chamber occupies about half a whorl and terminates in a peristome (specimen SG 119-3). The innermost whorls are almost smooth, progressing later to flexuous fine ribs; ornamentation weakens on the body-chamber. Intraspecific variability includes: weak ribbed, ribbed, angular-ribbed and striated morphotypes. Adult microconchs (Fig. 1(H, J)) are slightly more evolute than macroconchs, with a reduced striate stage. The simple septal suture possess a deep and wide L.

**Description**: Medium size discoidal shells with moderately involute coiling (O/D ≤ 0.35; see Table S1). The whorl section is high, ogival to sub-rectangular, with sub-parallel flanks and a high, thin keel. The umbilicus is shallow and narrow with a straight, sloping umbilical wall, with a rounded edge on inner whorls that becomes acute on the body-chamber, which occupies about half a whorl and terminates in a peristome (specimen SG 119-3). The innermost whorls are almost smooth, progressing later to bunches of flexuous fine ribs, irregularly grouped and of variable relief. The ribbing is strongly projected forwards on the inner third of the flank, weakening to fine dense striations on the body-chamber. Intraspecific variability includes: weak ribbed, ribbed, angular-ribbed and striated morphotypes. Adult microconchs (Fig. 1(H, J)) are slightly more evolute than macroconchs, with a reduced striate stage. The simple septal sutures possess a deep and wide L with typical indentation.

**Remarks**: Specimens of *V. striata* nov. sp. from the Lusitanian basin have morphologies resembling specimens of "*Harpcoceras* costula" Reinecke figured by Vacek (1886; pl. 8, figs. 3, 3a, 3b, 9, 9a) from Cap San Vigilio (Italy). They differ from *V. striata* Buckman, 1899 (suppl., pl. 10, figs. 17–19; 1904: p. 157, suppl.fig. 156, p. 167, fig. 162 in text) from Dorset (England) upon which the ornamentation sharpens on the outer whorls. Biometry demonstrates a close relationship, with a gradual transition between *V. striata* nov. sp. from the uppermost Toarcian-Lower Aalenian, and *V. stephensi*, recorded from the Bradfordens Zone (Buckman, 1899, 1904), the obustiformis horizon (Callomon and Chandler, 1990), and the uppermost Comptum Subzone-Bardfordens Zone (Linares and Sandoval, 1992).

*Vacekia stephensi* [M] and [m] Buckman, 1899

Fig. 1(M–Q); Table S3.


1899. *Vacekia stephensi* Buckman - pl. 10, figs. 16–19, holotype by monotypy.

1904. *Vacekia stephensi* Buckman - pl. 157, fig. 162 in text, Table 3, fig. 156.


1985. *Vacekia* sp. - Ureta, pl. 5, fig. 5.


1992. *Asthénoceras*. sp. - Henriques, p. 22, pl. 2, fig. 13 (non fig. 12 = *Asthénoceras*).

2010. *Vacekia* sp. - Kozai et al., fig. 5c.

**Description**: Ammonites of medium size (maximum 50 mm diameter) with moderately involute coiling (O/D from 0.27 to 0.35) and relatively rapid whorl-expansion (H/D from 0.39 to 0.45; see Table S3). The whorl section is sub-rectangular to ogival with a vertical to oblique umbilical wall and with a rounded edge on inner whorls becoming acute on the body-chamber. A tabulate venter possesses a high and thin keel. The inner and middle whorls are almost smooth or ornamented by flexuous very feeble ribs. Later in ontogeny, ribs develop singularly or infrequently into irregular groups, becoming thicker, of variable relief and more distantly spaced. Ribbing is falciform and strongly projected forwards on the inner third of the flank, weakening to fine dense striations on the body-chamber. Intraspecific variability includes: weak ribbed, ribbed, angular-ribbed and striated morphotypes. Adult microconchs (Fig. 1(S)) possess a peristome with short, narrow, mid-lateral lappets. The septal suture is simple.

**Remarks**: Some specimens of *V. stephensi* have similarities to primitive *Asthénoceras*, but species belonging to this genus are more evolute, display an ovate-ogival, rather than sub-rectangular whorl-section and have taller keel. The species is recorded from the Bradfordens Zone (Buckman, 1899, 1904) and Obtusiformis Horizon (Callomon and Chandler, 1990) of the type area. In the Subetic from the upper part of the Comptum Subzone to the uppermost Bradfordens Zone (Linares and Sandoval, 1992), from the Bradfordens Zone in Portugal (Henriques, 1992, 1995), from the Murchisonae to Bradfordens zones of the Iberian Cordillera (Ureta, 1985; Goy et al., 1988, Fernandez-Lopez and Gomez, 1990), and Bradfordens Zone of Pre-Rif, Morocco (Lelièvre, 1960).

Genus *Asthénoceras* Buckman, 1899

**Type species**: *Grammoceras nanodes* Buckman, 1890.

**Diagnosis**: Small Grammoceratinae with evolute coiling, a slow to median whorl-expansion rate and wide, shallow umbilicus. The ovate to ogival whorl-section is compressed with a thin, hollow and very high keel. Scarce pronounced ribs and striate growth lines ornament the shell. The septal-suture is simple.

**Remarks**: Buckman (1899) remarked on the affinities between the graphoceratids *Anclloceras* and *Asthénoceras*, but later observed the similarity between *Asthénoceras* and *Vacekia* (Buckman, 1904). *Asthénoceras* is traditionally included in the Grammoceratinae (Buckman, 1905; Arkell et al., 1957; Westermann, 1969; Imlay, 1973, 1984; Donovan et al., 1981; Sadik, 1990; etc.).
but research is currently inadequate regarding the relationship between Asthenoceras and Vacekia. Linares and Sandoval (1988) and Henriques (1992) demonstrated a close relationship between them. They share a similar general shell morphology, ornamentation, septal-suture and high, slim keel. Asthenoceras is more evolve and has a more ogival whorl section with different ribbing and a simpler suture.

“Asthenoceras” sp. A
Fig. 1(V, W); Table S4.

Distribution: The Lusitanian specimens come from the Lower Aalenian (Opalinum Zone, Comptum Subzone) of the Murtinheira and São Gião sections (Henriques, 1992, 1995, 2000a). The single English specimen has a similar stratigraphic position in the Leioceras lineatum horizon (Aa-2) of Burton Bradstock (Dorset).

Description: Discoidal, depressed shells of small size and moderately involute coiling (0/D varies from 0.32 to 0.36; see Table S4). The ovate-ovigal whorl section has convex flanks and a rounded umbilical edge. The maximum whorl breadth is at about two-fifths of the whorl height from the umbilical edge. The venter has a high, thin keel. Ornamentation is feeble, reduced to thin falconiform striations, barely visible on the inner whorls but stronger on the outer whorls (specimen WC0018). In the adult stage the flanks are bunched at the point of inflection from which they develop radiating groups separated by feeble distant ribs. In the studied specimens the peristome is not preserved and the suture line is only partially visible in some.

Remarks: The described specimens show intermediate characters between Vacekia and Asthenoceras, but coiling, in particular, and the section and ornamentation are closer to that of Asthenoceras. A. nannodes (Buckman), from later strata, is possibly a descendent of “Asthenoceras” sp. A, but is more evolve, has defined convex flanks and slightly stronger ribbing.

Asthenoceras nannodes (Buckman, 1890)
Fig. 2(A, B); Table S5.

Description: The coiling is evolute (U/D ~0.4) with a moderately small whorl-expansion rate (H/D ~0.33). The umbilicus is wide and shallow. The whorl-section is sub-circular on the innermost whorls, rapidly becoming ovigal and compressed with an oblique to rounded umbilical wall and gently convex flanks. The venter has a hollow very high keel. The body-chamber is slightly less than half a whorl. Ornament is feeble or absent on the inner whorls. Later stages have gentle falcoid-sigmoid, faint ribs, grouped in weakly developed bundles on the lower third of the flanks. The primary ribs on the body-chamber become progressively stronger, but this character is weakly developed in our specimens. The septal suture (partially preserved in the English specimen) is simple.

Remarks: Westermann (1969: p. 58) considered Buckman’s specimens to be microconchs. However, a study of Buckman’s (1890) specimens provides no evidence, other than small size to support this interpretation. The dimorphic status of the new specimens and Buckman’s presently remains unresolved. None of the specimens so far placed in Asthenoceras nannodes Buckman has been shown to possess lappets, a feature characteristic of microconch grammatoceratids. The lectotype of Asthenoceras nannodes, from Stoford, Somerset, England, comes from an unknown horizon (Westermann, 1969). The other specimen figured by Buckman (1890) comes from the “Paving Bed”. Recent studies by R.B. Chandler show that in the Yeovil-Bradford Abbas (Somerset-Dorset, England) area the Paving Bed is of variable age spanning parts of the Murchisonae-Bradfordensis zones. The only new English specimen comes from the Concaum Subzone, horizon AA-14 of Horn Park Quarry,Beamish, Dorset. The Lusitanian specimens are less like the type and come from the Bradfordensis Zone.

Asthenoceras taverai nov. sp. [M] and [m] Sandoval
Fig. 2(C-F); Table S6.
1888. Asthenoceras sp. A – Linares and Sandoval, p. 6, pl. 1, figs. 7–10.

Derivation of name: In honour of our friend, Dr. J.M. Tavera, professor of Palaeontology, University of Granada.

Holotype: Specimen JAC13.R9. (figured in Linares and Sandoval, 1888; pl. 1, figs. 9 and 10; here refigured in Fig. 2(C, C1); dimensions [mm]: D = 35.0, H = 9.0, U = 18.0; D = 28.0, H = 7.5, U = 14.0); stored in the Department of Stratigraphy and Palaeontology, Faculty of Sciences, University of Granada (Spain).

Type locality: The holotype is from the Torquilla section, province of Jaén, southern Spain (Central sector of the Median Subbetic, Betic Cordillera) and comes from the uppermost Aalenian (Concaun Zone, Limitatum Subzone).

Distribution: Asthenoceras taverai nov. sp. occurs in the Upper Aalenian (Concaum Zone, Limitatum Subzone) and Lower Bajocian (Discites Zone, Walken Subzone) of the following Median Subbetic localities: Despefiadero section (MO and MOD) in Montillana (province of Granada), Barranco de Auqa Larga section (JAQ1), Montejícar (province of Granada) and Torquilla section (JAC13) in Campillo de Arenas (province of Jaén).

Diagnosis: Shells of small size, particularly the microconchs, with very evolve coiling and a low whorl expansion rate. Whorl section ovate with gently convex flanks and a very elevated thin keel. Spaced ribs with ventrolateral nodes occur on the inner whorls; about the penultimate whorl, this ornamentation is replaced by curved-forward costula that occupy the external half of the flanks. The septal suture is simple; E and L have almost the same length.

Description: The size is small, particularly of the microconchs (maximum: 35 mm diameter in the probable [M] and 22 mm in [m]). Coiling is very evolve with a small expansion rate. This produces a wide and shallow umbilicus (0/D varies from 0.50 to 0.53; see Table S6). The whorl section varies from ovate, with gently convex flanks and elevated keel in macroconchs, to an oblique umbilical wall and less convex flanks in microconchs. Ornamentation varies between dimorphs and throughout ontogeny. Rib-shaped spaced ridges (flares) occur on the inner whorls of macroconchs. They are better developed on the upper flanks where ventrolateral nodes may also occur. About half way round the penultimate whorl the ornament is replaced by inwardly-curved forward-projecting costula that occupy the external half of the flanks and become progressively stronger. The costula are grouped into a few bundles in the lower flanks. In microconchs the rib-shaped ridges are more pronounced than in macroconchs. These progressively weaken through ontogeny and can either be limited to the external half of the flank or fade completely. One specimen has a complete peristome with well developed lateral lappets. The septal suture is extremely simple in both dimorphs, E and L have almost the same length; the saddle E-L is wide and bipartite, and lobes U2 and U3 are not retracted.

Remarks: Asthenoceras taverai nov. sp. is more evolve and has a smaller whorl-expansion rate than Asthenoceras nannodes Buckman, A. striatum Imlay and A. intermediun (Imlay). It has a different style of ornament, with well developed tuberculate
Fig. 2. A, B. *Asthenoceras nannodes* (Buckman, 1890): A, A1, WCC0015, Conavum Zone and Subzone, Horn Park Quarry, Beaminster, Dorset, England; B, B1, RA 108-5, Bradfordensis Zone, Serra do Rabacal, Lusitanian basin. C-F. *Asthenoceras taverai* nov. sp. Sandoval: C, C1, JACl3. R9 (holotype, specimen figured in Linares and Sandoval, 1988: pl. 1, figs. 9, 10), Conavum Zone, Limitatum Subzone, Campillo de Arenas, Betic Cordillera; D, D1, MO·73-1, Conavum Zone, Limitatum Subzone or Discites Zone, Walkeri Subzone, Montillana, Betic Cordillera; E, E1, JA01 (-68), 1, Conavum Zone, Limitatum Subzone, Barranco de Agua Larga, Betic Cordillera; F, F1, MO·A4-71, Conavum Zone, Limitatum Subzone or Discites Zone, Walkeri Subzone, Montillana, Betic Cordillera (specimen figured in Linares and Sandoval, 1988: pl. 1, fig. 7). G-K. *Asthenoceras intermedium* (Imlay, 1973): G-J1, MO·79-1 (specimen figured in Linares and Sandoval, 1988: pl. 1, fig. 4), MO·77-2, MO·78-1 (specimen figured in Linares and Sandoval, 1988: pl. 1, fig. 6).
rib-shaped ridges on inner whorls. *Linaresites montillanensis* (Linares and Sandoval) nov. comb. displays similar coiling but has a less ovate whorl-section and stronger ribbing throughout ontogeny.

*Asthenoceras intermedium* (Imlay, 1973)
Fig. 2(G-K); Table S7.
1973. *Fontannesia intermedia* Imlay nov. sp. – Imlay, p. 57, pl. 4, figs. 7–15 (holotype, figs. 12–14).
1990. *Asthenoceras namnodes* (Buckman) – Sadki, p. 207, pl. 1, figs. 1, 2.

**Description:** Small discoidal, compressed shells with moderately evolute coiling (O/D from 0.37 to 0.42; see Table S7) and ogival to ovate sections that are much higher than wide. The umbilical wall varies from nearly vertical to gently oblique merging evenly into gently convex flanks. The fastigate venter has a very high hollow keel. The body-chamber occupies a little more than half a whorl. A simple peristome is preceded by a narrow sinuous and finely striated band. Sigmoid ribs arise from the base of the flanks and are first radiate or merging evenly into gently convex flanks. The septal suture is very simple (Fig. Imlay, 1973: pl. 4, fig. 5).

**Remarks:** Studied specimens are similar to those figured by Imlay (1973), although some Oregon examples are larger. *A. namnodes* is more evolute with a smaller whorl expansion rate and less pronounced ornamentation than in *A. intermedium*. *A. striatum* Imlay, of similar age in the type area (Imlay, 1973), is more evolute and has finer, more defined and more regular ornament than *A. intermedium*. Relatively involute forms figured by Sadki (1990) as *A. nameodes* (Buckman) show typical characters of the juvenile stages of *A. intermedium*. In the type area (Eastern Oregon), *A. intermedium* probably occurs in the Upper Aalenian to lowermost Bajocian (Imlay, 1973; Taylor, 1988). The Subbetic specimens come from the Upper Aalenian (Limitatum Subzone) to lowermost Bajocian (Walkeri Subzone). The English specimen is from the Lower Bajocian (horizon B2, Walkeri Subzone). Moroccan specimens are from the Discites Zone (Sadki, 1990).

**Linaresites** nov. gen. Sandoval

**Derivation of name:** In honour of Dr. Asunción Linares, professor of Palaeontology of the University of Granada from 1947 to 2003.

**Type species:** *Fontannesia montillanensis* Linares and Sandoval, 1988: pp. 8–10, figs. 12–22 (by original designation). Only the type species is included in the new genus.

**Occurrence:** Upper Aalenian (Concavum Zone) and lowermost Bajocian (Discites Zone). To date, *Linaresites* nov. gen. has been recorded only in the Central Sector of the Subbetic, southern Spain (Linares and Sandoval, 1988) and the High Atlas, Morocco (Sadki, 1994, 1996).

**Diagnosis:** Very small Grammoceratinae with very evolute coiling and a low whorl expansion rate. The ovate whorl section possesses a well developed thin keel. Sigmoid ribs are well developed and strongly retroverse. The septal-suture is very simple.

**Remarks:** Originally the type species was placed in *Fontannesia* because the genus was included in the Grammoceratinae (Linares and Sandoval, 1988). Studies of numerous *Fontannesia*, mainly from southern England, show that it is not a grammoceratid: the suture is more complex, the ribbing style different and the keel is weakly defined or absent. These characters are closer to the Sonninidae (early Witchellinidae) than to typical Aalenian Grammoceratinae such as the genera *Vacekia* and *Asthenoceras*. *Linaresites* nov. comb. shares. Similarities with *Asthenoceras*, but retains well marked ribbing throughout ontogeny, is slightly more evolute, and has a slightly different whorl-section and weaker keel.

*Linaresites montillanensis* (Linares and Sandoval, 1988) nov. comb.
Fig. 2(L–O1); Table S8.
1988. *Fontannesia montillanensis* Linares and Sandoval, p. 8, fig. 2c, pl. 1, figs. 12–22 (holotype: figs. 12, G).
1996. *Fontannesia montillanensis* Linares and Sandoval – Sadki, p. 152, pl. 1, fig. 5.

**Description:** Very small-sized shells (maximum diameter < 30 mm). Coiling is very evolute with a very low whorl expansion rate and a wide (O/D > 0.51; see Table S8) shallow umbilicus. The ovate whorl section has a rounded umbilical wall, slightly convex flanks and venter and a thin and high keel, occasionally bordered by two very shallow sulci. The innermost whorls are smooth with dense and relatively strong ribs developed on the second whorl. The inner and middle whorls have single ribs and on the body-chamber some ribs are grouped in pairs. Sigmoid ribs arise from the base of the flanks and are first radiate or retroverse, becoming strongly projected forward on the upper flanks. The septal suture is very simple (Fig. 3). The peristome is not well preserved in the available material and the dimorphic status of *L. montillanensis* nov. comb. is presently not resolved.

**Remarks:** “*Fontannesia* curvata” (Buckman, 1802, for *Dumorteritia grammoceroides* in Buckman, 1892: pl. 47, figs. 1–5), a microconch with lappets, shows morphological similarities with *Linaresites montillanensis* nov. comb., but Buckman’s specimens are slightly more involute, have a higher whorl expansion rate, flanks that are slightly more parallel and less dense ribbing. *L. montillanensis* nov. comb. occurs in the Upper Aalenian and lowermost Bajocian (Discites Zone) of Subbetic (Linares and Sandoval, 1988) and in the High Atlas (Sadki, 1994, 1996).

4. Discussion

During late Toarcian times (between the Meneghini and Aalenian chron) an important change occurred involving a turnover in ammonite taxa, probably related to palaeoceanographic events (Sandoval et al., 2002, 2008). At this time, typical Upper Toarcian genera such as *Polyplectus*, *Osperleioceras* and *Geczyveria*, very abundant in the western Tethys, disappeared or became scarce. They were replaced mainly by Graphoceratinae such as *Pleydella*, *Cotteswoldia* (dominant in the latest Toarcian), new Hammatoceratinae and the last members of the Grammoceratinae.
Osperleioceras, dominant in the Meneghini Chron of many western Tethyan areas, was replaced by Vacekia together with species of Asthenoceras and the new genus Linaresites, that continue to the latest Toarcian to earliest Bajocian.

In western Tethys Osperleioceras from Meneghini Zone has high variability in both size and ornamentation (Morard and Guex, 2003). Some of the more involute Osperleioceras (e.g., O. authelini [Monestier], O. subbeticum [Rivas]) from the upper part of the Reynesi biozone (Rivas, 1975) have ribbed inner whorls and a striated body-chamber similar to primitive Vacekia (e.g., V. sourensis and V. striata) and may represent its origin (Fig. 3). If this hypothesis is correct, an analysis of morphology and temporal succession of genera and species of latest Toarcian to earliest Bajocian Grammoceratinae demonstrates common trends: progressive uncoiling through time (tending to more evolute forms) coupled with size reduction and simplification of the septal suture (Fig. 3).

The morphs cited here from the late Toarcian genus Osperleioceras are semi-involute, showing slight convex flanks but not such a high keel. The innermost whorls are almost smooth, later a ribbed stage and a body-chamber in adults that maybe striated. In general Vacekia is slightly more evolute and smaller than the last Osperleioceras and has flat or sub-flat flanks, a vertical umbilical wall, higher keel and simpler septal sutures.

Fig. 4. Palaeogeographic distribution of some late Toarcian-early Bajocian Grammoceratinae (dotted line represents probable connections between eastern Pacific and western Tethys). Modified from Dera et al. (2009).
The oldest Vacekia (subgenus Nadorites of some authors) display intermediate characters between the youngest Osperleioceras and typical early middle Aalenian Vacekia (V. stephensi) with strong, spaced rib pairs on intermediate whorls and a striated or finely ribbed body-chamber. Generally, three stages of ornamentation can be differentiated in Vacekia: innermost whorls smooth or weakly ribbed, intermediate stages ribbed, and striations on adult shells. In the latest Vacekia (e.g., V. stephensi from Bradfordensis Zone) the costulate stage may be much reduced or absent. Septal sutures are simpler than in Osperleioceras.

Astenoceras is generally smaller and more evolute than Vacekia. The whorl-section is gently ovate and the keel highly developed. Some species are smooth throughout ontogeny, but others are striated or ribbed at the external flanks of the last whorl. More evolute specimens may have spaced, rib-shaped tubercles on the inner whorls (A. vateri from Concavum-Discites zones). The septal suture is simple. Astenoceras descends from Vacekia but the underlying evolutionary processes remains elusive. An early innovation involving the production of new characters in the inner whorls coupled with progenesis may be more likely.

Linairesites nov. gen. (incl. Fontanites montanallensis Linares and Sandoval, 1988) is extremely evolute and small. Ribs are well characters in the inner whorls coupled with progenesis may be more likely. In the latest Vacekia (e.g., V. stephensi from Bradfordensis Zone) the costulate stage may be much reduced or absent. Septal sutures are simpler than in Osperleioceras.

Latitricheilla evoluta Imlay, 1973 (mainly from Oregon with rare specimens from southern Spain) shares with Linairesites montanallensis nov. comb. very evolute coiling, strong ribs and simple sutures, but is larger. L. evoluta is possibly a neotenic form of L. montanallensis nov. comb. and may represent the last Grammocerataceae.

Paleogeographical analyses of the distribution of genera and species of Grammocerataceae (Fig. 4) supports the hypothesis that during the Early-Middle Jurassic transition, the western Tethys and eastern Pacific were at least temporally well connected, perhaps through the Hispanic Corridor. This is supported by the similarity between Tethyan (especially Subbetic and Lusitanian) and eastern Pacific (Oregon and Alaska) Grammocerataceae. The main evolutionary processes probably took place in western Tethys, but some taxa may have their centre of origin in the eastern Pacific (Oregon or Alaska), subsequently migrating to the western Tethys through the Hispanic Corridor.

5. Conclusions

Latest Toarcian to earliest Bajocian Grammocerataceae occur in many Tethyan and eastern Pacific localities, although they dominated the ammonite assemblages only during the early Aalenian of the Lusitanian basin. Linairesites nov. gen. and two new species, Vacekia striata and Astenoceras vateri, are erected and described. V. stephensi Buckman and Astenoceras nanmodes (Buckman), together with V. souensis (Perrot) and Astenoceras intermedium (Imlay), all present in the western Tethys, are reviewed. The Toarcian genus Osperleioceras may represent the origin of the last Tethyan and eastern Pacific Grammocerataceae. The significant evolutionary trends of this lineage are a progressive uncoiling through time, coupled with a size decrease and simplification of the septal suture.

The simultaneous occurrence of typical western Tethyan species and some eastern north Pacific forms (Oregon and Alaska) demonstrates that these paleogeographic realms were at least briefly well-connected during the late Toarcian-early Bajocian. This connection is likely to have been via the Hispanic Corridor (Proto-Atlantic).

Acknowledgements

We express our gratitude to Prof. F. Cecca (Université Pierre-et-Marie-Curie, Paris-VI) and Prof. S.R. Fernández-López (Universidad Complutense, Madrid) for constructive criticisms and advices that improved the manuscript. We thank Antonio P. Jiménez for producing the images, M. J. Higgins, D. Tolley, R. Condiffe, E. Seal (the English site owners), D. T. Sole for providing one of the specimens from Burton Bradstock, and A. Cowap for cleaning the British material. The Wessex Cephalopod Club and notably the late J. H. Callomon are thanked for support in the field. Carol Payne made important corrections to the English of the final manuscript. This study forms part of the results obtained in Research Projects: CG12005-04574/BTE, CG2008-03112, GCL2008-00533/BTE, GCL2008-03112/BTE and CG2008-01273/BTE, financed by the DGI (Dirección General de Investigación, España) and by the EMMI and RNM-200 Research Groups (Junta de Andalucía, España).

References


