Original article

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

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ABSTRACT

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 *Osperleioceras* 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* nov. 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 let 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 *Osperleioceras* 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), Morocco (Lelièvre, 1960; 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.

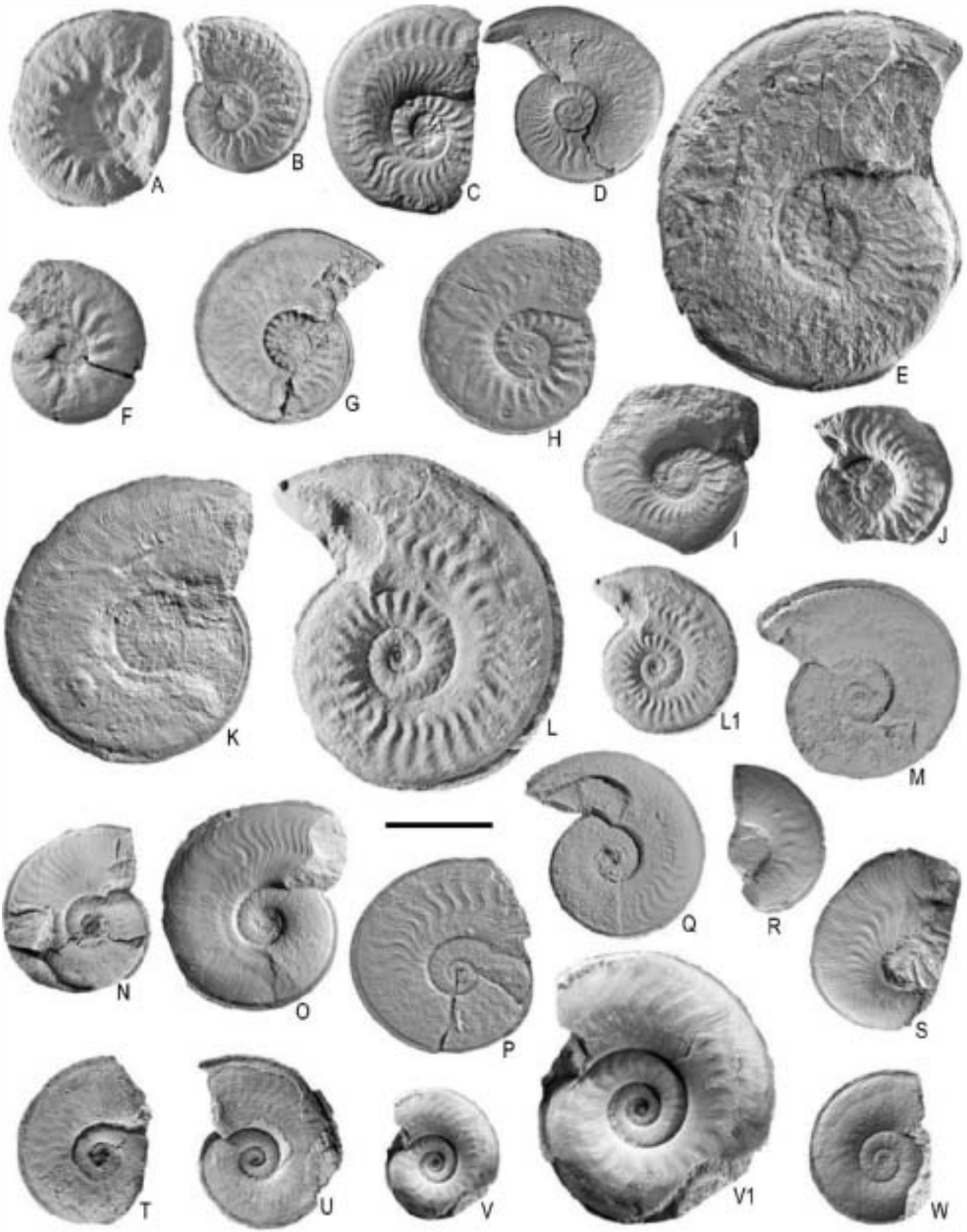

Fig. 1. A–F. *Vacekia sourensis* (Perrot, 1957): A, MP 1-3, Aalensis Zone, Mactra Subzone, Maria Pares, Lusitanian basin; B, M 33-28, ●palinum Zone, Comptum Subzone, Murtinheira, Lusitanian basin; C, D, CM.42.2 and CM.40.1, Aalensis Zone, Mactra Subzone, Cerro Méndez, Betic Cordillera; E, CM.69.3, Aalensis Zone, Buckmani Subzone, Cerro Méndez, Betic Cordillera; F, Rb16/3, ●palinum Subzone, Rabanera, Iberian Cordillera. **G–L1**. *Vacekia striata* nov. sp. Henriques: G, M 33-2 (holotype), H, M 33-4, Land L1, M 33-5 (paratype), ●palinum Zone, Comptum Subzone, Murtinheira, Lusitanian basin; I, M25-1, Aalensis Zone and Subzone, Murtinheira, Lusitanian basin; J, SG 65-20, ●palinum Zone, Comptum Subzone, São Gião, Lusitanian basin; K, M31-7 (paratype), ●palinum 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; ●, SP.LR.6, Bradfordensis Zone?,

Most Subbetic ammonites included then represent Grammoceratinae (genera *Vacekia* and *Asthenoceras*, 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 Sonniniidae, Subfamily Witchelliinae, instead of the Grammoceratinae. "*F.*" *montillanensis* clearly belongs to the Grammoceratinae and represents a new genus named here and considered by us as the last western Tethyan Grammoceratinae. 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 "*Asthenoceras vacekiformis*" 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 (southwest 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 Gião and ZA: Zambujal de Alcaria;
- Subbetic localities: SPA, SPB and SP.LR: Sierra de San Pedro, Alcalá la Real, province of Jaén; MO, MOA, MOB, MOC and 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; JAQ1: Barranco de Agua Larga, province of Jaén; JRi1: Cerro de Mahoma section, Sierra de Ricote, Province of Murcia;
- Basque-Cantabrian localities: Pu: Pujayo; Sm: San Miguel de Aguayo; Cy: Cillamayor;
- NW Iberian localities: BoII: Borobia; Al: La Almunia de Doña Godina; Ri: Ricla;
- Mallorca (Sierra Norte) localities: GB: Gorge Blau;
- Dorset (United Kingdom) localities: Be-HP: Beaminster, Horn Park Quarry (ST458022); WH-SK: Waddon Hill, Stoke Knap (ST447015); BB-b: Burton Bradstock beach (SY483892); Mp-CQ: Mapperton, Coombe Quarry (SY496998).

Codes for the UK are those used by Callomon and Chandler (1990) with additions. The UK specimens are at present in the collection of R.B. Chandler. [M] and [m] refers to macroconch and microconch, respectively. For the measurements the following parameters are used: D, diameter of the shell; H: whorl section height of the shell; U: umbilical diameter of the shell; W: whorl section width of the shell; h: H/D; u: U/D; w: W/D; N/2: number of primary ribs for a half whorl.

3. Systematic palaeontology

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily HILDOCERATACEOIDEA Hyatt, 1867
Family HILDOCERATIDAE Hyatt, 1867
Subfamily GRAMMOCERATINAE Buckman, 1904
Genus **Vacekia** Buckman, 1904
Type species: *Vacekia stephensi* Buckman, 1899.

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 Caloo-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 *Osperleioceras*, 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 *Asthenoceras*, which is possibly its descendant. *Asthenoceras* 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 *Asthenoceras*.

Vacekia sourensis (Perrot, 1957)
Fig. 1(A–F); Table S1.

1886. *Harpoceras costula* Reinecke – Vacek, S.78 (*pars*), pl. 8, figs. 10 and 11 (non pl. 8, figs. 3–9a, 12–15).

1957. *Cotteswoldia costulata* Schloth. var. *sourensis* nov. – Perrot, p. 382, fig. 1, pl. 1, figs. 1, 1a (lectotype) and 2.

1985. *Leioceras* sp. – Ureta, p. 227, pl. 2, figs. 1 and 2, pl. 30. fig. 12.

1992. *Vacekia sourensis* (Perrot) – Henriques, p. 13, pl. 2, figs. 4, 7 and 8.

1995. *Vacekia sourensis* (Perrot) – Henriques, p. 231, pl. 1, fig. 2.

Description: Discoidal specimens of medium size and moderately involute coiling (Table S1). The whorl section is high and ogival 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 specimens were figured (Perrot, 1957: pl. 1, figs. 1a, 2) but no type specimen was identified. Elmi and Caloo-Fortier (1985) designated a holotype, the specimen figured in "pl. 1, figs. 1, 1a, 1b" of Perrot (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 Aalensis Zone (Perrot, 1957). In the Iberian Range it is reported from the Pseudoradiosa Subzone to Opalinum Subzone (Ureta, 1985; Goy et al., 1988; Goy and Martínez, 1990). In the Basque Cantabrian basin it occurs in the Aalensis-Opalinum transition (Gómez et al., 2009) and on the Island of Mallorca from the base of

Sierra de San Pedro, Betic Cordillera; P, Q, MOC.12.1 and MOC.13.21, Bradfordensis Zone, Montillana, Betic Cordillera; R, S, Al22/1 and Ri379/1, Murchisonae Zone, La Almunia de Doña Godina and Ricla, Iberian Cordillera; T, WCC0019, Scissum Zone, bed 2d, horizon Aa-3b, Mapperton, Coombe Quarry, Dorset, England. **U**. *Vacekia* sp. aff. *V. stephensi*, WCC0017, Scissum Zone, bed 6a, horizon Aa-3a, Burton Bradstock beach, Dorset, England. **V, W**. *Asthenoceras* sp. A: V, V1, WCC0018, Scissum Zone, bed 6a, horizon Aa-3a, Burton Bradstock beach, Dorset, England; **W**, M 95.5, Opalinum Zone, Comptum Subzone, Murtinheira, Lusitanian basin. Scale bars: 2 cm (A–K, L1, M–V, **W**), 1 cm (L, V1).

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–L1); Table S2.

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

1957. *Cotteswoldia* sp. A – Perrot, p. 383, pl. I, figs. 3 and 4.

1985. *Vacekia (Vacekia)* sp. A – Elmi and Caloo-Forter, p. 51, pl. 2, fig. 11.

1992. *Vacekia striata* nov. sp. – Henriques, p. 5, figs. 1.1, 1.2, pl. 2, figs. 3 and 4.

1992. *Vacekia robusta* nov. sp. – Henriques, p. 9, figs. 1.3, 1.4, pl. 2, figs. 5 and 6.

1992. *Asthenoceras 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 characteristically 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 Aalensis Subzone (Upper Toarcian) to the Opalinum Zone (Lower Aalenian) (Henriques, 1995, 2000a, 2000b). In the Betic Cordillera it is restricted to the Aalensis 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 simple peristome. Innermost whorls almost smooth, progressing later to flexuous fine ribs; ornamentation weakens on the body-chamber, with simple undefined striations. Simple septal suture with a deep and wide L.

Description: Medium size discoidal shells with moderately involute coiling (O/D $\leq$ 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 the 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 lower third of the flank but deflects backwards on the ventral half of the flank. Ornamentation weakens on the body-chamber with simple ill-defined striations that may disappear completely. The 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 "*Harpoceras*" *costula* Reinecke figured by Vacek (1886: pl. 8, figs. 3, 3a, 3b, 9, 9a) from Cap San Vigilio (Italy). They differ from *V. stephensi* 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 Bradfordensis Zone (Buckman, 1899, 1904), the *obtusiformis* horizon (Callomon and Chandler, 1990), and the uppermost Comptum Subzone-Bradfordensis Zone (Linares and Sandoval, 1992).

Vacekia stephensi [M] and [m] Buckman, 1899
Fig. 1(M–Q); Table S3.

Part 1886. *Harpoceras costula* Reinecke - Vacek, p. 22, pl. 8, figs. 3–15.

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

1904. *Vacekia stephensi* Buckman – Buckman p. 157, fig. 162 in text, Table 3, fig. 156.

1960. *Vacekia stephensi* Buckman – Lelièvre, pl. 5, figs. 1–4.

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

1988. *Vacekia stephensi* Buckman – Linares et al., 1988, pl. 1, fig. 7.

1990. *Vacekia stephensi* Buckman – Fernández-López and Gómez, p. 86, pl. 3, fig. 6.

1992. *Vacekia stephensi* Buckman – Linares and Sandoval, p. 94, pl. 1, figs. 1–9.

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

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 *Asthenoceras*, 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 Bradfordensis Zone (Buckman, 1899, 1904) and Obtusiformis Horizon (Callomon and Chandler, 1990) of the type area. In the Subbetic from the upper part of the Comptum Subzone to the uppermost Bradfordensis Zone (Linares and Sandoval, 1992), from the Bradfordensis Zone in Portugal (Henriques, 1992, 1995), from the Murchisonae to Bradfordensis zones of the Iberian Cordillera (Ureta, 1985; Goy et al., 1988; Fernández-López and Gómez, 1990), and Bradfordensis Zone of Pre-Rif, Morocco (Lelièvre, 1960).

Genus **Asthenoceras** Buckman, 1899

Type species: *Grammoceras nannodes* 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 *Ancolioceras* and *Asthenoceras*, but later observed the similarity between *Asthenoceras* and *Vacekia* (Buckman, 1904). *Asthenoceras* is traditionally included in the Grammoceratinae (Buckman, 1905; Arkell et al., 1957; Westermann, 1969; Imlay, 1973, 1984; Donovan et al., 1981; Sadki, 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 evolute 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 (O/D varies from 0.32 to 0.36; see Table S4). The ovate-ogival 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 thin, high keel. Ornamentation is feeble, reduced to thin falciform striations, barely visible on the inner whorls but stronger on the outer whorls (specimen WC0018). In the adult stage the striae 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 evolute, has defined convex flanks and slightly stronger ribbing.

Asthenoceras nannodes (Buckman, 1890)

Fig. 2(A, B1); Table S5.

1890. *Grammoceras nannodes* Buckman – pl. 33, figs. 13, 14 (lectotype designed by Westermann, 1969: p. 58), 15, 16.

1899. *Asthenoceras nannodes* Buckman – Buckman, p. 49, pl. 11, fig. 28 (radial line).

?1969. *Asthenoceras* sp. aff. *A. nannodes* (Buckman) - Westermann, p. 61, pl. 14, figs. 1–7.

1992. *Asthenoceras*. sp. – Henriques, p. 22, pl. 2, fig. 12 (non fig. 13 = *Vacekia stephensi*).

Description: The coiling is evolute (U/D ~0.40) 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 ogival 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 grammoceratids. 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 Concavum Subzone, horizon Aa-14 of Horn Park Quarry, Beaminster, 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–F1); Table S6.

1988. *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.R.9 (figured in Linares and Sandoval, 1988: 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 (Concavum Zone, Limitatum Subzone).

Distribution: *Asthenoceras taverai* nov. sp. occurs in the Upper Aalenian (Concavum Zone, Limitatum Subzone) and Lower Bajocian (Discites Zone, Walkeri Subzone) of the following Median Subbetic localities: Despeñadero section (MO and MOD) in Montillana (province of Granada), Barranco de Agua 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 evolute 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 evolute with a small expansion rate. This produces a wide and shallow umbilicus (O/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 U_2 and U_3 are not retracted.

Remarks: *Asthenoceras taverai* nov. sp. is more evolute and has a smaller whorl-expansion rate than *Asthenoceras nannodes* Buckman, *A. striatum* Imlay and *A. internedium* (Imlay). It has a different style of ornament, with well developed tuberculate

Fig. 2. A, B. *Asthenoceras nannodes* (Buckman, 1890): A, A1, WCC0015, Concavum Zone and Subzone, Horn Park Quarry, Beaminster, Dorset, England; B, B1, RA 108-5, Bradfordensis Zone, Serra do Rabaçal, Lusitanian basin. **C–F**. *Asthenoceras taverai* nov. sp. Sandoval: C, C1, JAC13. R.9 (holotype, specimen figured in Linares and Sandoval, 1988: pl. 1, figs. 9, 10), Concavum Zone, Limitatum Subzone, Campillo de Arenas, Betic Cordillera; D, D1, M●.73.1, Concavum Zone, Limitatum Subzone or Discites Zone, Walkeri Subzone, Montillana, Betic Cordillera; E, E1, JA●1 (-68).1, ConcavumZone, Limitatum Subzone, Barranco de Agua Larga, Betic Cordillera; F, F1, M●.A4.71., Concavum 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 internedium* (Imlay, 1973): G–J1, M●.79.1 (specimen figured in Linares and Sandoval, 1988: pl. 1, fig. 4), M●.87.2, M●.78.1 (specimen figured in Linares and Sandoval, 1988:

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 internedium (Imlay, 1973)

Fig. 2(G–K); Table S7.

1973. *Fontannesia internedia* Imlay nov. sp. – Imlay, p. 57, pl. 4, figs. 7–15 (holotype, figs. 12–14).

1973. *Fontannesia costula* Imlay nov. sp. – Imlay, p. 57, pl. 4, figs. 16–26.

1984. *Asthenoceras* cf. *A. delicatum* Imlay – Imlay, p. 25, pl. 2, figs. 1–4.

1984. *Asthenoceras nannodes* Buckman – Sadki, p. 96, fig. 22, pl. 1, figs. 1–4.

1988. *Asthenoceras internedium* (Imlay) – Linares and Sandoval, p. 5, pl. 1, figs. 1–6.

1990. *Asthenoceras nannodes* (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. The inner whorls are almost smooth or have slightly developed spaced ridges. Mid whorls have gently falcoid faint ribs grouped in bundles of weak relief on the lower flanks. At the phragmocone end and body-chamber, the ribs gradually strengthen adorally and become more distant and more strongly projected forward. To date, specimens appear to be exclusively macroconchs. The septal suture, partially preserved in our specimens, is simple as in the holotype (Imlay, 1973: pl. 4, fig. 5).

Remarks: Studied specimens are similar to those figured by Imlay (1973), although some Oregon examples are larger. *A. nannodes* is more evolute with a smaller whorl expansion rate and less pronounced ornamentation than in *A. internedium*. *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. internedium*. Relatively involute forms figured by Sadki (1990) as *A. nannodes* (Buckman) show typical characters of the juvenile stages of *A. internedium*. In the type area (Eastern Oregon), *A. internedium* 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 Bj-2, 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 Sonniniidae (early Witchelliinae) 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* nov. sp. – Linares and Sandoval, p. 8. fig. 2c, pl. 1, figs. 12–22 (holotype: figs. 12, 13).

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 *Dumortieria 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 Meneghinii and Aalensis chrons) 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 *Geczyceras*, very abundant in the western Tethys, disappeared or became scarce. They were replaced mainly by Graphoceratinae such as *Pleydellia*, *Cotteswoldia* (dominant in the latest Toarcian), new Hammatoceratinae and the last members of the Grammoceratinae.

pl. 1, figs. 1, 2) and M●D.x.338 (juvenile), Concavum Zone, Limitatum Subzone and/or Discites Zone, Walkeri Subzone, Montillana, Betic Cordillera; K, WC0016, Discites Zone, bed 5d, Bj-2, Waddon Hill, Stoke Knap, Dorset, England. **L–O**. *Linaresites montillanensis* (Linares and Sandoval, 1988) nov. comb.: M●.83.1 (holotype, figured in Linares and Sandoval, 1988: pl. 1, figs. 12, 13), M●D.x.339, M●D.x.337 and M●.85.1 (specimen figured in Linares and Sandoval, 1988: pl. 1, figs. 21, 22), Concavum Zone, Limitatum Subzone and/or Discites Zone, Walkeri Subzone, Montillana, Betic Cordillera. Scale bars: 2 cm (A, B1, C, D, E, F, G–J, K, L, M1, N, ●), 1 cm(A1, B, C1, D1, E, F1, J1, L1, M, N1, ●1).

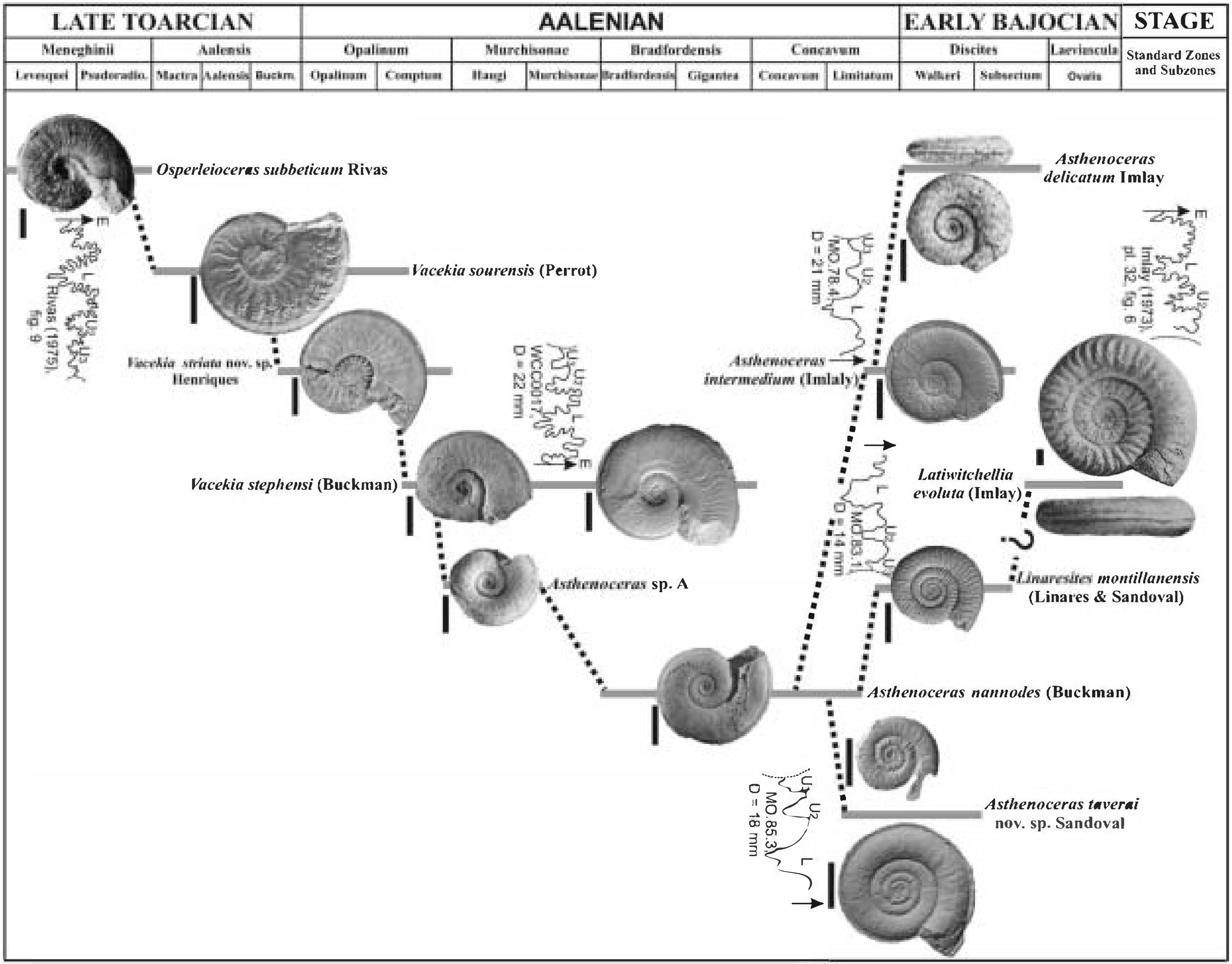

Fig. 3. Proposed phylogenetic relationships between the taxa discussed (calibrated against the Mediterranean standard zonation). Scale bars: 1 cm.

Osperleioceras, dominant in the Meneghinii 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 Meneghinii 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.

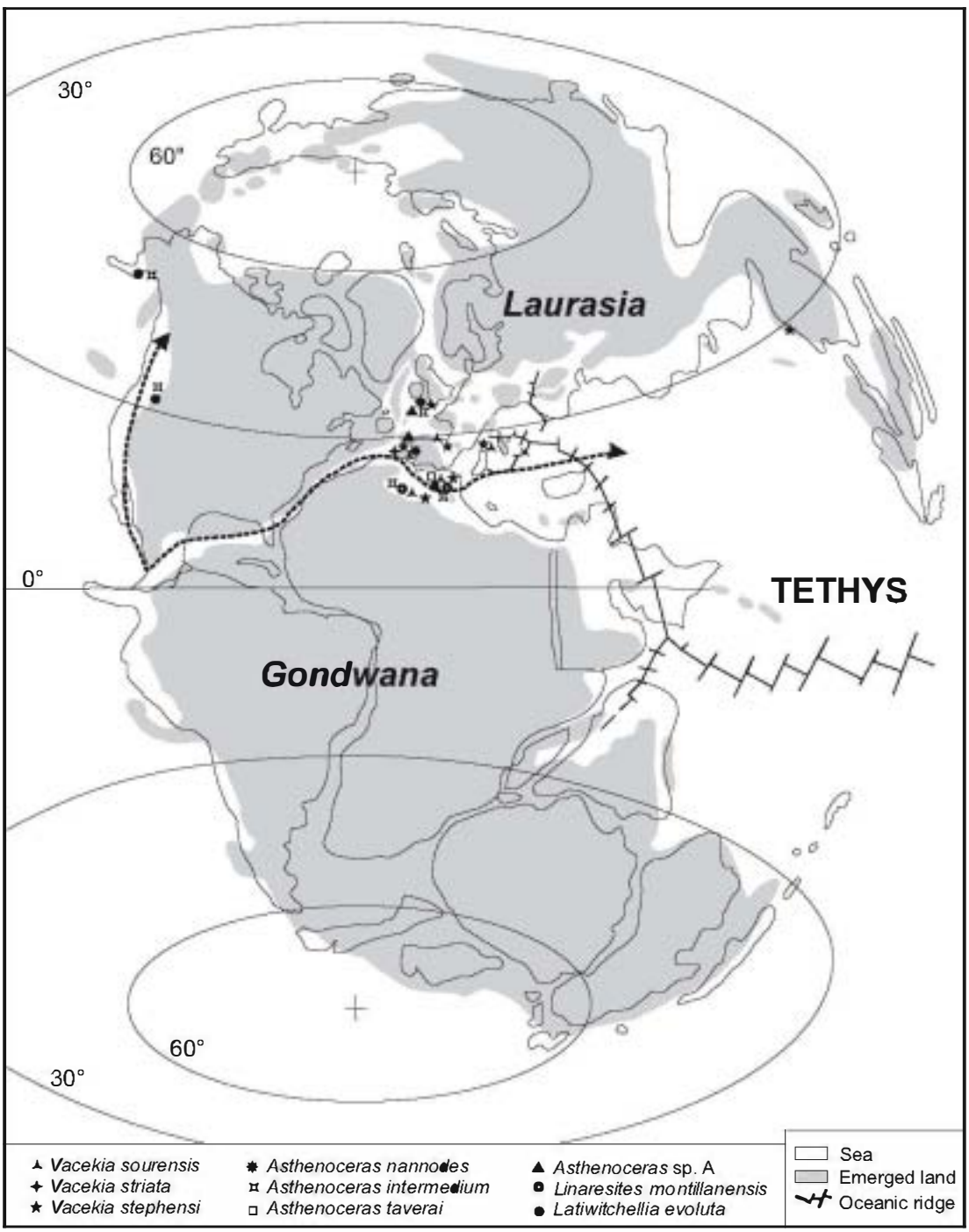

Fig. 4. Palaeogeographic distribution of some late Toarcian-early Bajocian Grammoceratinae (dotted line represents probable connections between eastern Pacific and western Tethys). Modified from Dera et al. (2009).

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*.

Asthenoceras 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. taverai* from Concavum-Discites zones). The septal suture is simple. *Asthenoceras* 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.

Linaresites nov. gen. (incl. *Fontannesia montillanensis* Linares and Sandoval, 1988) is extremely evolute and small. Ribs are well developed throughout ontogeny. The septal suture is simpler than in other Grammoceratinae (Fig. 3). This new genus is a possible progenetic form of *Asthenoceras*.

Latiwitchellia evoluta Imlay, 1973 (mainly from Oregon with rare specimens from southern Spain) shares with *Linaresites montillanensis* nov. comb. very evolute coiling, strong ribs and simple sutures, but is larger. *L. evoluta* is possibly a neotenic form of *L. montillanensis* nov. comb. and it may represent the last Grammoceratinae.

Palaeogeographical analyses of the distribution of genera and species of Grammoceratinae (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) Grammoceratinae. 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 Grammoceratinae occur in many Tethyan and eastern Pacific localities, although they dominated the ammonite assemblages only during the early Aalenian of the Lusitanian basin. *Linaresites* nov. gen. and two new species, *Vacekia striata* and *Asthenoceras taverai*, are erected and described. *V. stephensi* Buckman and *Asthenoceras nannodes* (Buckman), together with *V. sourensis* (Perrot) and *Asthenoceras internedium* (Imlay), all present in the western Tethys, are reviewed. The Toarcian genus *Osperleioceras* may represent the origin of the last Tethyan and eastern Pacific Grammoceratinae. The significant evolutionary trends of this linage 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 palaeogeographic 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).

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