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Jaeniceras, a new genus of Tithonian ammonites based on *Perisphinctes ponti* Fallot & Termier

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Key words: *Jaeniceras ponti* nov. gen., females and males, homoeomorphy, *Djurjuriceras*, "*Burckhardticeras*", Tithonian, Betic Range.

Abstract. Based on the holotype of *Perisphinctes ponti* Fallot & Termier and new well-preserved specimens from southern Spain, the new genus *Jaeniceras* is introduced. The genus includes a group of distinctive Tethyan ammonites the females of which have been considered as belonging to the genus *Djurjuriceras* Roman, and the males to "*Burckhardticeras*" Olóriz . The partial homoeomorphy between these ammonites is here resolved by the study of their sexually-dimorphic sculpture ontogeny and morphology. *Jaeniceras* nov. gen. was distributed along the Central Tethys during the late Early Tithonian Ponti Zone. It seems possible that the new genus originated from some representative of the Andean lineage *Catutosphinctes* Leanza & Zeiss migrating along the Caribbean-North Atlantic seaway during the Fallauxi Zone.

INTRODUCTION

The species *Perisphinctes ponti* Fallot & Termier, 1923 remained scarcely cited in the literature until Enay and Geyssant (1975) used its name to label the Ponti Zone (late Early Tithonian) and provisionally assigned the species to the genus *Micracanthoceras* Spath, 1925. Olóriz (1978) reassigned the species to the genus *Djurjuriceras* Roman, 1936, based on the similarity of the sculpture of the adult female bodychamber of *P. ponti* and *Djurjuriceras djurjurense* Roman, 1936. *Djurjuriceras* has been recently assigned to the family Himalayitidae by Énay & Howarth (2019), and according to the Algerian fauna described by Roman (1936) the age of *D. djurjurense* is Microcanthum-Durangites zones.

Recent stratigraphically controlled collections (ERA, FGA) from the Ponti Zone in southern Spain (Fig. 1) have yielded several adult ammonites perfectly matching the holotype of *P. ponti* (Fig. 2). These specimens, as well as the holotype, show strong differences with repect to *D. djurjurense*, especially in the phragmocone, reducing the similarity to a resemblance of the sharp and widely spaced primary ribs of the adult female bodychamber. *P. ponti* and *D. djurjurense* would appear to be homoemorphs of different ages. The phragmocones are so different that the Spanish ammonites can be assigned to the Subfamily Torquatisphinctinae Tavera, 1985 and *Djurjuriceras* very likely to the Subfamily Paraboliceratinae Spath, 1928 as already discussed by Parent and Garrido (2021).

Close resemblance between ammonoid taxa which are not closely related, or homoeomorphy, lacking phyletic or palaeobiogeographic relevance, is a well known phenomenon (*e.g.*, Buckman, 1895, 1898; Reyment, 1955; Kennedy, Cobban, 1976; Donovan *et al.*, 1981; Dommergues *et al.*, 1989; Scherzinger *et al.*, 2010). Homoeomorphy has produced misidentifications and/or biased time-correlations and palaeobiogeographic distributions, and, especially, wrong

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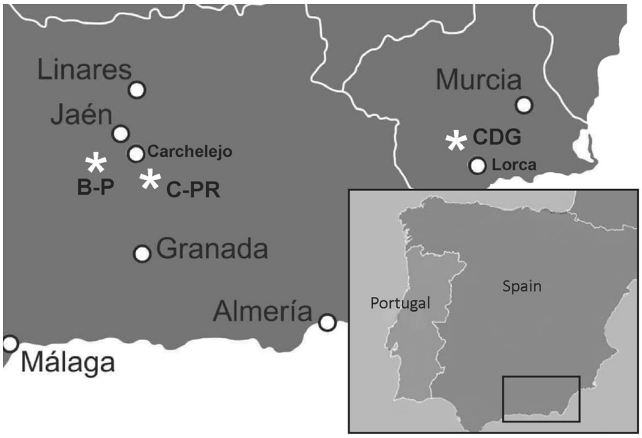

Fig. 1. Localities of provenance of the studied material in southern Spain

B-P – Barranco de la Parrilla, west of Carchelejo, Jaén; C-PR – Barranco de Cazalla-Puerto Rico, southeast of Carchelejo, Jaén; CDG – Cerro de Don Gonzalo, Lorca, Murcia

phyletic reconstructions, or even hampered them. Resolution of these (partial) resemblances between ammonites, usually of different ages and/or biogeographic distributions, may be easy to figure out by adding stratigraphic information to the study of the ontogeny (Donovan *et al.*, 1981). The most difficult cases of homoeomorphy may be resolved by:

1. The study of the ontogeny of well preserved specimens from stratigraphically well controlled collections. The whole ontogeny of homoemorphic taxa cannot be the same. The most reliable distinction comes from the sculpture ontogeny. Similarites in the whorl section and the involution must be considered with caution since they tend to be extremely variable in most ammonite species. The septal suture line could be useful if the homoeomorphs belong to different families or higher taxa.
2. Comparison of the sexual dimorphism. It would be very rare (say impossible) that different species have identical females and males, or show the same patterns of morpho-sculptural differentiation.

The recently collected specimens assignable to *P. ponti* studied here are well-preserved, including almost complete females and complete males, which allows description of the ontogeny and sexual dimorphism, and so resolves the homoeomorphy with *D. djurjurense*. The Spanish ammonites are the basis for revision of the species *P. ponti* which is taken as the type species for the new genus *Jaeniceras*.

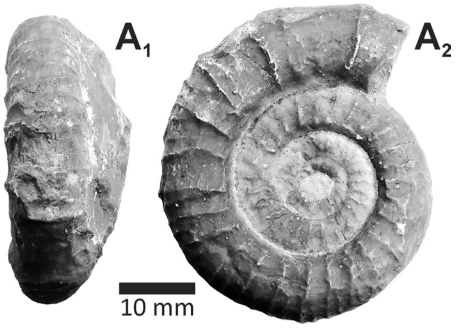

Fig. 2. *Perisphinctes ponti* Fallot & Termier, 1923

Holotype (UJF-ID.11586) refigured. Middle Tithonian of Bendinat, near Palma de Majorque. Natural size (×1)

STRATIGRAPHIC FRAMEWORK

The studied ammonites were collected from three small outcrops of the so-called Ammonitico Rosso Superior Formation in southern Spain (Fig. 1). These outcrops are small and in part temporary, or mostly covered by debris. The collection of the abundant ammonites in the sediments was made from some thin strata. The age of the collected fauna is inferred by the association of species confidently recognized from the more complete, well preserved specimens. We have collected from the following outcrops:

1. Barranco de la Parrilla, west of Carchelejo, Jaén Province. The stratigraphy has been studied by Olóriz (1978) and Tavera (1985). The collected assemblage associated with *Jaeniceras ponti* nov. gen., indicating the Ponti Zone, was already discussed in Parent *et al.* (2023) and Parent, Ramos-Agustino (2024).
2. Barranco de Cazalla-Puerto Rico, southeast of Carchelejo, Jaén Province. The stratigraphy has been studied by Olóriz (1978) and Tavera (1985). Fauna and lithology very similar (identical in chronostratigraphical terms) to those of Barranco de la Parrilla. The Ponti Zone fauna associated with *Jaeniceras ponti* nov. gen. is very abundant, including:

- *Volanoceras volanense* (Oppel, 1863),
- *Lytogyroceras subbeticum* (Olóriz, 1978),
- *Protetragonites* gr. *quadrisulcatus* (d'Orbigny, 1841),
- *Haploceras* cf. *carachtheis* (Zejszner, 1846),
- *Lemencia* sp.,
- *Simplisphinctes*? sp.,
- abundant biplicate perisphinctoid ammonites which are often reported in the literature as *Aulacosphinctes*, *Subdichotomoceras* and *Parapallasiceras*,
- *Lytoceras* sp.,
- Scarce phylloceratoids belonging to *Ptychophylloceras*, *Holcophylloceras*, and *Calliphylloceras*.

From the upper part of the bed(s) there was collected a large, incomplete female specimen of *Volanoceras perarmatiforme* (Schauroth, 1865) – a species with large adult females which mostly occurs in the upper Ponti Zone (see Schweigert *et al.*, 2002).

3. Cerro de Don Gonzalo, Lorca, Murcia. The stratigraphy and ammonite fauna of the region of Murcia have been studied by Barthel *et al.* (1966), Seyfried (1978), and Olóriz (1978). The ammonites which are associated with *Jaeniceras ponti* nov. gen. indicate the Ponti Zone, include:

- *H.* cf. *carachtheis*,
- *V. volanense*,
- *L. subbeticum*,
- *Lemencia* sp. (incomplete females and a lappeted male).

SYSTEMATIC PALAEONTOLOGY

Conventions. Bodychamber is abbreviated as Bc and phragmocone Ph. In this paper we consider the females to be the so-called macroconchs and the males the microconchs, according to the abundant evidence and discussions summarized by Klug *et al.* (2015, with references) and Parent, Zatoń (2016, with references). Measurements: diameter (D), diameter at last septum (D_{ls}), diameter at adult peristome (D_{p}), all given in millimetres (mm). Umbilical width (U), width (W) and height (H_1) of whorl section, are given either in mm or as dimensionless indexes of the ratio to D. Length of bodychamber (L_{Bc}) in degrees [°]. Number of primary ribs per half whorl: P. In the synonymy list a doubtful assignation is marked with ?, and the holotype figuration with *.

Repositories. The Spanish specimens are housed in the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS). Casts of the specimens figured by Roman (1936) are housed in the Paleontological-Geological Collection of the University Claude Bernard Lyon 1 (UCBL-FSL). The collection of Fallot, Termier (1923) is in the Collections géologiques de l'Observatoire des Sciences de l'Univers de Grenoble. OSUG – COLLECTIONS, a database of rocks, minerals and fossils [https://web.collections.osug.fr/; https://web.collections.osug.fr], OSUG, UGA. doi:10.5072/OSUG-COLLECTIONS.all. (UJF-ID).

Order **Ammonitida** Haeckel, 1866

Suborder **Ammonitina** Fischer, 1882

Superfamily **Perisphinctoidea** Steinmann, 1890

Family **Ataxioceratidae** Buckman, 1921

Subfamily **Torquatisphinctinae** Tavera, 1985

Genus ***Jaeniceras*** nov.

Type species. *Perisphinctes ponti* Fallot & Termier, 1923.

Derivation of the name. After Jaen (southern Spain), a region where the genus is well represented.

Diagnosis. *Female*. Evolute from the innermost whorls; whorl section rounded to subrectangular, wider than high. Phragmocone ribbing narrow and high; primary ribs bifurcating widely splayed in the upper flank; few trifurcates and simple ribs intercalated. Adult bodychamber with more distant, simple or bifurcate primaries that tend to set in pairs. *Male*. Smaller, half-size or less; phragmocone and bodychamber like the female phragmocone; lateral lappets.

Species included. *Perisphinctes ponti* Fallot & Termier, 1923, *Djurjuriceras anularium* Olóriz, 1978, and *Djurjuriceras armonicum* Olóriz, 1978.

Distribution. For the time being as the type species.

Remarks and comparison. The shell-shape (whorl section and involution) is that of many different perisphinctoids. The diagnostic feature of the new genus is the sculpture ontogeny, combining characters typical of the subfamily Torquatisphinctinae in the phragmocone, and distinctive in the adult female bodychamber.

Djurjuriceras Roman, 1936, as represented by its type species *D. djurjurense*, shows slight similarity with *Jaeniceras ponti* nov. gen. in the ribbing of the bodychamber, but the phragmocone is completely different (further discussion below).

Jaeniceras ponti (Fallot & Termier, 1923) nov. gen.
Figs. 2–4

?1890. *Simoceras* aff. *Albertinus* Catullo – Bogdanovitsch: 143, pl. 5: 5

*1923. *Perisphinctes Ponti* n. sp. – Fallot & Termier: 9, pl. 1: 4 (holotype)

1978. *Djurjuriceras* sp. gr. *ponti* (Fallot & Termier, 1923) – Olóriz: 646, pl. 53: 1–3

1978. *Djurjuriceras armonicus* n. sp. – Olóriz: 648, pl. 53: 4

1978. *Djurjuriceras anularius* n. sp. – Olóriz: 649, pl. 53: 5

1978. *Burckhardticeras peroni* (Roman, 1936). – Olóriz: 625, pl. 53: 6–12

?1978. *Aulacosphinctes quadri* n. sp. – Olóriz: 638, pl. 53: 15

1997. "*Djurjuriceras*" *ponti* (Fallot & Termier) – Cariou & Hantzpergue: pl. 25: 11

2008. *Djurjuriceras* – Reolid-Perez: 105, fig. 31c and pl. 5 (both the same specimen)

2010. *Burckhardticeras peroni* (Roman) – Benzaggagh *et al.*: 303, fig. 5C

Holotype (Fig. 2). *Perisphinctes ponti* was established from a single specimen with at least part of its bodychamber. As this latter does not show clear signs of uncoiling, the specimen must be a subadult female. The actual measurements of the specimen are slightly smaller than those given

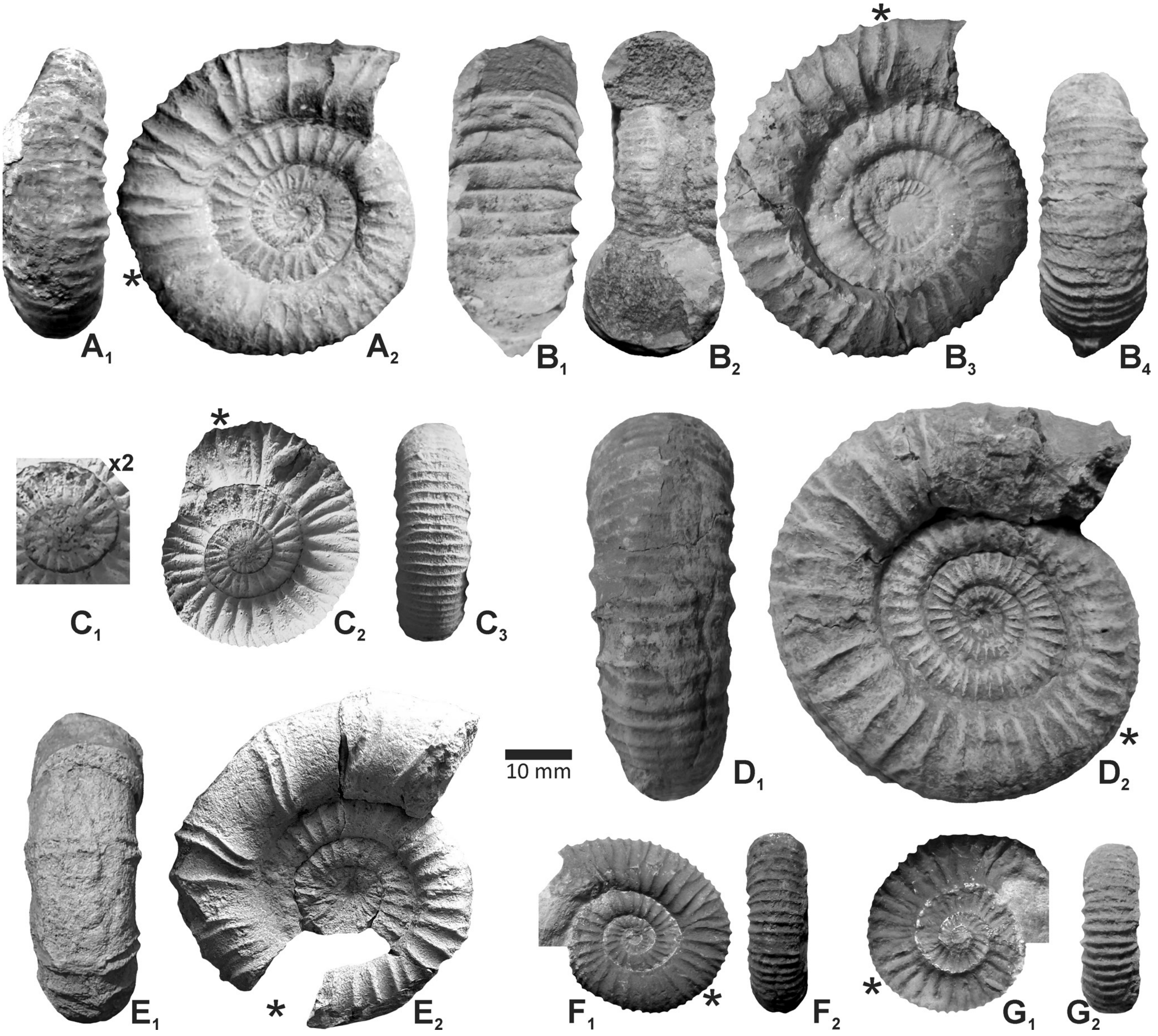

Fig. 3. ***Jaeniceras ponti*** **(Fallot & Termier, 1923) nov. gen. Ponti Zone, Southern Spain**

A. Almost complete adult female (SMNS 70740/1) from the Barranco de Cazalla-Puerto Rico. **B.** Adult female phragmocone with beginning of bodychamber (SMNS 70740/2) from the Barranco de Cazalla-Puerto Rico. **C.** Small adult female phragmocone (SMNS 70740/3) from the Barranco de la Parrilla, showing detail of the inner whorls (C_1, ×2). **D.** Almost complete adult female (SMNS 70740/4) from the Barranco de Cazalla-Puerto Rico. **E.** Almost complete subadult female (SMNS 70740/5) from Cerro de Don Gonzalo. **F, G.** Complete adult males (SMNS 70740/6 and 70740/7) from the Barranco de Cazalla-Puerto Rico. All natural size (x1) except C_1 (×2). The asterisk indicates the last septum

by Fallot & Termier (1923: 8), actually: maximum D = 43.2 mm with U = 22.9 mm, W = 11.2 mm, and H_1 = 10.9 mm. Since the lithology of the specimen contains a high proportion of clay, some contraction by loss of water since the date of collection seems possible.

The horizon and location of the holotype were not very accurately defined; according to the authors it came from the middle Tithonian of Bendinat, near Palma de Majorque. Enay, Geyssant (1975) identified the species from specimens collected with the assemblage from which they defined the Ponti Zone. Olóriz (1978) described as *Djurjuriceras* gr. *ponti* several specimens from the Ponti Zone which match the holotype. Our specimens, most of them perfectly matching the holotype, were collected associated (in the same bed) with most of the guide assemblage of ammonites of the Ponti Zone. Furthermore, there are no records of the species in the literature neither in our collections, in older or younger levels than the Ponti Zone. Thus, it is very likely that the type horizon of *Jaeniceras ponti* nov. gen. is in the Ponti Zone.

Material. Five well-preserved, more or less complete adult or subadult female macroconchs: three from Barranco de Cazalla-Puerto Rico (SMNS 70740/1-2, 4), one from Barranco de la Parrilla (SMNS 70740/3), and one from Cerro de Don Gonzalo (SMNS 70740/5). Two complete adult male microconchs from Barranco de Cazalla-Puerto Rico (SMNS 70740/6-7). Southern Spain. Ammonitico Rosso Superior Formation. Upper Lower Tithonian, Ponti Zone.

Description (based on the holotype and the new material). *Female*. All the specimens are serpenticonic and evolute from the innermost whorls up to the adult bodychamber. The phragmocone whorls have U/D = 0.40–0.50, and the bodychamber about 0.45–0.55 (Fig. 4A). The whorl section is rounded to subrectangular, with proportions between W/H_1 = 1.0 and 1.5 (Fig. 4B). The sculpture shows two developmental stages (Fig. 4C):

1. In the the phragmocone, from about D = 10 mm, the primary ribs originate in the umbilical wall, cross the flank radially or slightly prosocline, and in the upper third they bifurcate, widely splayed, in equally strong and sharp secondaries. Sporadic primaries remain simple, and some trifurcate, in most specimens about one or two per whorl; in a small adult female (Fig. 3C) three to five trifurcate in some whorls. All ribs cross the venter unchanged; only in one specimen (Fig. 3B_4) it can be noted a slight midventral weakening in a short portion of whorl of the adult phragmocone. In the inner (most) whorls, at about D = 10 mm, the specimens develop one constriction preceeded by a primary rib bifurcated in the umbilical shoulder.
2. From the end of the adult phragmocone (D_{ls} = 35 to 48 mm) the primary ribs become progressively more distant (lowering P), many of them bifurcating in the upper third of the flank like in the inner whorls, while some others remain simple. In some specimens a few ribs ribs are set in pairs, well-spaced each other (Fig. 3A, E).

Our largest specimen (Fig. 3D) is an almost complete adult with maximum preserved D = 66 mm and D_{ls} = 48 mm; it has three-quarters of whorl of bodychamber, but no signs of peristome can be discerned.

Male. Identical to the inner whorls of the female at comparable diameters. In the bodychamber the ribbing remains unchanged. The peristome bears subtriangular lappets, rather short and wide. The adult phragmocone varies within D_{ls} = 22–23 mm, and the diameter at peristome is D_{p} = 29–30 mm; L_{BC} = 180°.

Remarks and comparison. The history of the classification of the species is mostly summarized in the synonymy given above. A few years after establishing the species, Fallot (1931) reported its occurrence in a section near Barranco Grande (southern Spain), among a collection of Tithonian to Berriasian ammonites. Arkell (1956) cited the species in reference to the holotype, as probably belonging to *Aulacosphinctes* Uhlig, 1910. Enay and Geyssant (1975) reported the species as "*Micracanthoceras*" *ponti* from the collections they studied from southern Spain, and designated this as index-species of the Ponti Zone. As Enay and Geyssant (1975: 49) themselves explain (rather unclearly) it is just the index-species (not abundant) of the zone; as is

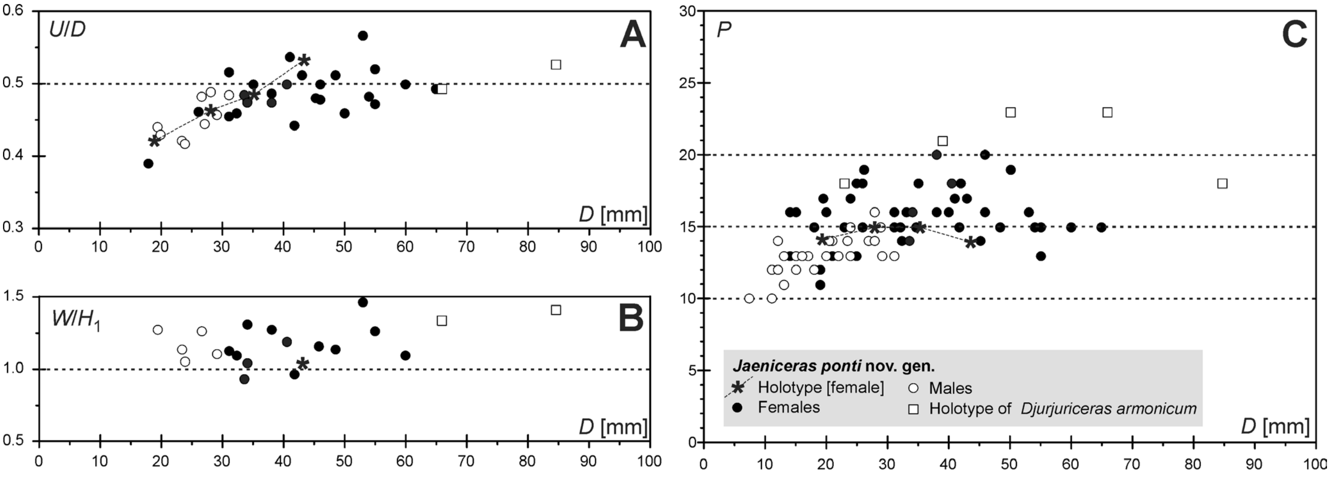

Fig. 4. ***Jaeniceras ponti*** **(Fallot & Termier, 1923) nov. gen. Biometric characterization by involution (*U/D-D*), whorl section (*W/H_1-D*), and ribbing (*P-D*)**

Female and male specimens including the present material and Olóriz (1978: pl. 53) typical of any individual species it has a locally and contingently variable stratigraphic range, and the zone is recognized by the assemblage of the guide-species, not just by the index which in most collections is not present. Olóriz (1978) described a large collection of females and males under different names (discussed below). Cariou and Hantzpergue (1997) figured a sexual dimorphic pair from southern Spain. The most recent figured specimen seems to be the adult male from Msila (Morocco) in Benzaggagh *et al.* (2010), among a Ponti Zone ammonite-assemblage.

Djurjuriceras armonicum Olóriz, 1978 is larger and more densely ribbed than the holotype of *Jaeniceras ponti* nov. gen. (Fig. 4C), but with the same style of ribbing and shell-shape. In our material there are transitional forms in a continuous range of intraspecific variation: from large and densely ribbed specimens (Fig. 3A, D), like the holotype of *D. armonicum*, towards smaller and less densely ribbed ones (Fig. 3E). Thus, *D. armonicum* is here considered an intraspecific variant of *Jaeniceras ponti* nov. gen.

Djurjuriceras anularium Olóriz, 1978 is a very incomplete specimen resembling to some extent the outermost whorl of the variants of the species shown in Figure 3B, E. Assuming the unknown inner whorls could be comparable also, it is here considered another synonym of *Jaeniceras ponti* nov. gen.

Aulacosphinctes quadri Olóriz, 1978 could belong to *Jaeniceras ponti* nov. gen., because it has a very similar style of ribbing and whorl section, but it bears a wide ventral groove at least in the beginning of the last whorl preserved. The ventral groove in perisphinctoids is a very variable feature (Guex, 1970; Donovan *et al.*, 1981; Parent, 2001; Frau *et al.*, 2016), and could represent extreme intraspecific variation.

The ammonite from the Shemiran Mountains, northern Iran figured by Bogdanovitsch (1890: pl. 5: 5) as *Simoceras* aff. *albertinus* Catullo, 1855 (see Scherzinger *et al.*, 2010: 201) seems to be an adult of similar size to that of of adult females of *Jaeniceras ponti* nov. gen., and it shows a similar sequence of sculpture stages. In the phragmocone the ribbing is rectiradiate to slightly prosocline and ends with some trifurcated, widely splayed ribs, passing to well-spaced primaries in the bodychamber, some of them set in pairs. The phragmocone ribbing seems to be denser than in *Jaeniceras ponti* nov. gen. Unfortunately the exact age of the specimen is not accurately known further than Tithonian.

As noted above the adult female bodychamber of *Jaeniceras ponti* nov. gen. (Fig. 3A, D) shows some similarity with that of the holotype of *D. djurjurense* (Fig. 5) because of the large and sharp primary ribs, but the phragmocones are completely different, as well as the adult size. In *D. djurjurense* the penultimate whorl (adult phragmocone) of the holotype is subrectangular, higher than wide in whorl section, as noted by Roman (1938). The ribbing is fine and dense on the flanks and venter, with more than 39 primaries per half-whorl, nearly three-fold the number in *Jeaniceras ponti* nov. gen. This is at a similar diameter, but more importantly at a similar growth stage, the adult/preadult phragmocone. The primary ribs are slightly prosocline to slightly flexuous; many bifurcate, narrowly splayed, in the upper flank. One of each four or five primary ribs has a tiny bulla just below the ventrolateral shoulder (Fig. 5A_2). The ventral view of the bodychamber of the paratype (Fig. 5B_3) shows

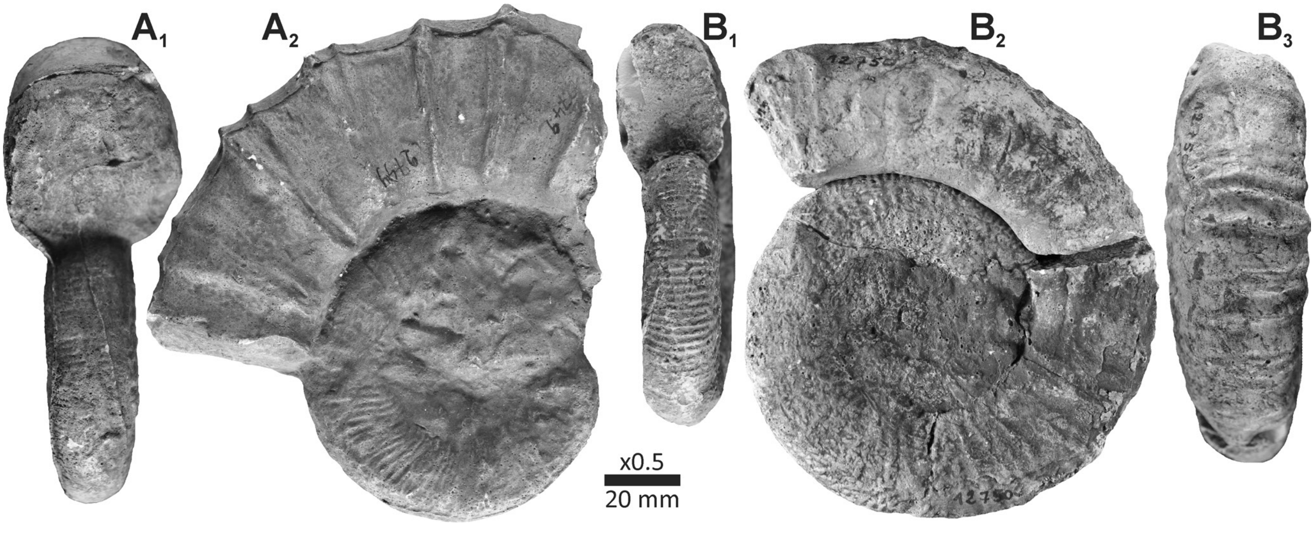

Fig. 5. ***Djurjuriceras djurjurense*** **Roman, 1936**

Casts of the holotype (**A**) and paratype (**B**), originally figured by Roman (1936: pl. 2: 5 and 3: 4, respectively). Holotype: UCBL-FSL-12749; paratype: UCBL-FSL-12750. All half-natural size (×0.5) the "gemination" sensu Enay, Howarth (2019: 108) of the secondary ribs, forming a ventral loop. These differences are not very evident from the original illustrations in Roman (1936), but were better exposed by Roman (1938: 298) and are seen in the photographs of the casts in our Figure 5. Thus, the superficial resemblance of the ribbing of the adult female bodychamber is considered homoeomorphy, lacking any phylogenetic or palaeogeographic relevance. *Djurjuriceras* has been considered a member of the Virgatosphinctinae Spath, 1923 (*e.g.*, Roman, 1936, 1938; Arkell *et al.*, 1957), the Himalayitidae Spath, 1925 (*e.g.*, Olóriz, 1978; Donovan *et al.*, 1981; Tavera, 1985; Enay, Howarth, 2019; Szives, Fözy, 2022), or the Lithacoceratinae Zeiss, 1968 (*e.g.*, Sarti 2020). Because of the ribbing and morphology, especially in the phragmocone, Parent, Garrido (2021) suggested it could be assigned to the Lithacoceratinae or to the Paraboliceratinae Spath, 1928. However, the small bullae in the ventrolateral shoulder of the phragmocone of the holotype, suggest it is more likely a late member of the Paraboliceratinae.

The Andean genus *Catutosphinctes* Leanza & Zeiss, 1992 (Subfamily Torquatisphinctinae) forms a long-lived lineage from the basal Andean Tithonian Picunleufuense Zone up to at least the Late Tithonian Koeneni Zone, and has been recorded in eastern S America from the Neuquén and Tarapacá basins (*e.g.*, Parent *et al.*, 2011, 2015; Salazar, Stinnesbeck, 2016; Parent, 2022), and Venezuela (MacDonald, 1968: fig. 5b). The species *Catutosphinctes proximus* (Steuer, 1897) of the Proximus Zone (rather equivalent to the Fallauxi Zone), and *Catutosphinctes araucanensis* (Leanza, 1980), *Catutosphinctes americanensis* (Leanza, 1980), and the subjective junior synonym *Catutosphinctes catutosensis* (Leanza, Zeiss, 1990) of the Internispinosum Zone (nearly equivalent to the Ponti Zone), show sculptural similarities in the adult female bodychamber: they have prominent primary ribs, sometimes arranged in well spaced sets of pairs in the style of *Jaeniceras ponti* nov. gen. (*e.g.*, Parent, 2022: fig. 21A). *C. catutosensis* was originally described as a *Djurjuriceras* but later cast in doubt in Leanza, Zeiss (1992). However, there are also significant differences, beyond the different palaeogeographic distributions, that distinguish *Catutosphinctes* from *Jaeniceras* nov. gen.: (1) the former includes larger to much larger adult females and males, (2) has higher rib-density in the phragmocone, and (3) does not develop the trifurcate ribs, other than rarely, which are consistently developed at about one or two per whorl in *Jaeniceras* nov. gen. These differences seem to us enough for distinction between *Jaeniceras* nov. gen. and *Catutosphinctes*. However, the characters in common like the predominant serpenticonic shell-shape with sharp and straight ribs, regularly bifurcating in widely splayed secondaries, make them part of the Torquatisphinctinae and both genera could be closely related as discussed below.

Sexual dimorphism. In our material there are several small lappeted specimens (Fig. 3F, G) which, at a comparable diameter, are identical to the inner whorls of the females (Fig. 3A–E), and are thus considered males of the species. In this form the sexual dimorphism of *Jaeniceras ponti* nov. gen. is the typical for most ataxioceratids. The males mature and halt their growth at a smaller size than the females which develop the complete ontogeny of the species. Females and males have the same growth rate as indicated by their similar rib density (Fig. 4C). The early maturation of the males can be described as a paedomorphic pattern produced by an intraspecific developmental heterochronic process of progenesis (McNamara, 1986; Parent, 1997; Neige *et al.*, 1997; Klug *et al.*, 2015).

Among his large collections from southern Spain, Olóriz (1978) described as "*Burckhardticeras peroni*" (Roman, 1936) several small male specimens from the Ponti Zone (= Burckhardticeras Zone) which are identical to our specimens in Figure 3F, G. Enay, Cecca (1986: 48) considered the Spanish specimens assigned to *B. peroni* by Olóriz (1978) as the microconchs of *Perisphinctes ponti*.

The type species of "*Burckhardticeras*" Olóriz, 1978 [name pre-occupied by *Burckhardticeras* Flores-Lopez, 1967] is *Himalayites peroni* Roman, 1936, established with no designation of holotype. The mention of a holotype by Villaseñor (2024: 283) is erroneous since Roman (1936) did not designate that. We designate the specimen figured by Roman (1936: pl. 4: 14) as the lectotype of *Himalayites peroni* Roman, 1936. This specimen, as well as three paralectotypes (Roman, 1936: pl. 4: 10, 11, 13), are moderately involute and compressed with relatively high flanks, and densely ribbed with prosocline, mostly bifurcate ribs. This configuration is very different from that of the specimens of Olóriz (1978: pl. 53: 6–12) which are evolute serpenticones (lower flanks) with stronger and less dense ribbing. Moreover, the fauna described by Roman (1936) must belong to the Microcanthum and Durangites zones of the Upper Tithonian, in contrast with the Ponti Zone age of the mentioned specimens from southern Spain described by Olóriz (1978). "*Burkchardticeras*" Olóriz, 1978 remains as a monotypic genus of Microcanthum-Durangites zones age. Among the paralectotypes there is one specimen (Roman, 1936: pl. 4: 12) which could be assigned to *Durangites* Burckhardt, 1912/*Protacanthodiscus* Spath, 1923 by its fine ribbing with small periodic ventral tubercles.

Distribution. There are in the literature relatively few figurations of *Jaeniceras ponti* nov. gen. to our knowledge; those are (see synonymy) in Fallot, Termier (1923), Olóriz (1978), Cariou, Hantzpergue (1997), and Benzaggagh *et al.*, (2010). Vígh (1984) has cited the occurrence of *Djurujuriceras* ex gr. *ponti* among large assemblages from the Bakony and Gerecse Mountains in Hungary. In nominal terms these

Hungarian assemblages indicate the Ponti Zone (as Burckhardticeras Zone in Vígh, 1984); unfortunately the specimens could not be located (Ottilia Szives, pers. comm. 30/04/25). Frau *et al.* (2016) cited the occurrence of the species (as "*Burckhardticeras*" *ponti*) in the Ponti Zone of Drôme, France.

Thus, the distribution of the species, and so the genus for the time being, includes, at least southern Spain, Mallorca, Morocco, southern France, and Hungary. However, it could be much expanded if the specimen of Bogdanovitsch (1890) from northern Iran could be confirmed as belonging to the species. It would be not very surprising for the Ponti Zone in the Tethys is poorly recorded in large areas (Mazenot, 1939; Cecca, Enay, 1991; Benzagaggh *et al.* 2010), as was also noted for the case of the genus *Pseudhimalayites* Spath, 1925 in Parent *et al.* (2023).

Origin and evolution. We have not found any Tethyan ammonite in the Fallauxi Zone or below that could be attributed to, or closely compared with *Jaeniceras* nov. gen. to be considered as a plausible ancestor. Therefore, considering the similarities between *Catutosphinctes* and *Jaeniceras* nov. gen., this latter could be an off-shot of the lineage *Catutosphinctes* from late representatives of *C. proximus* (Fig. 6).

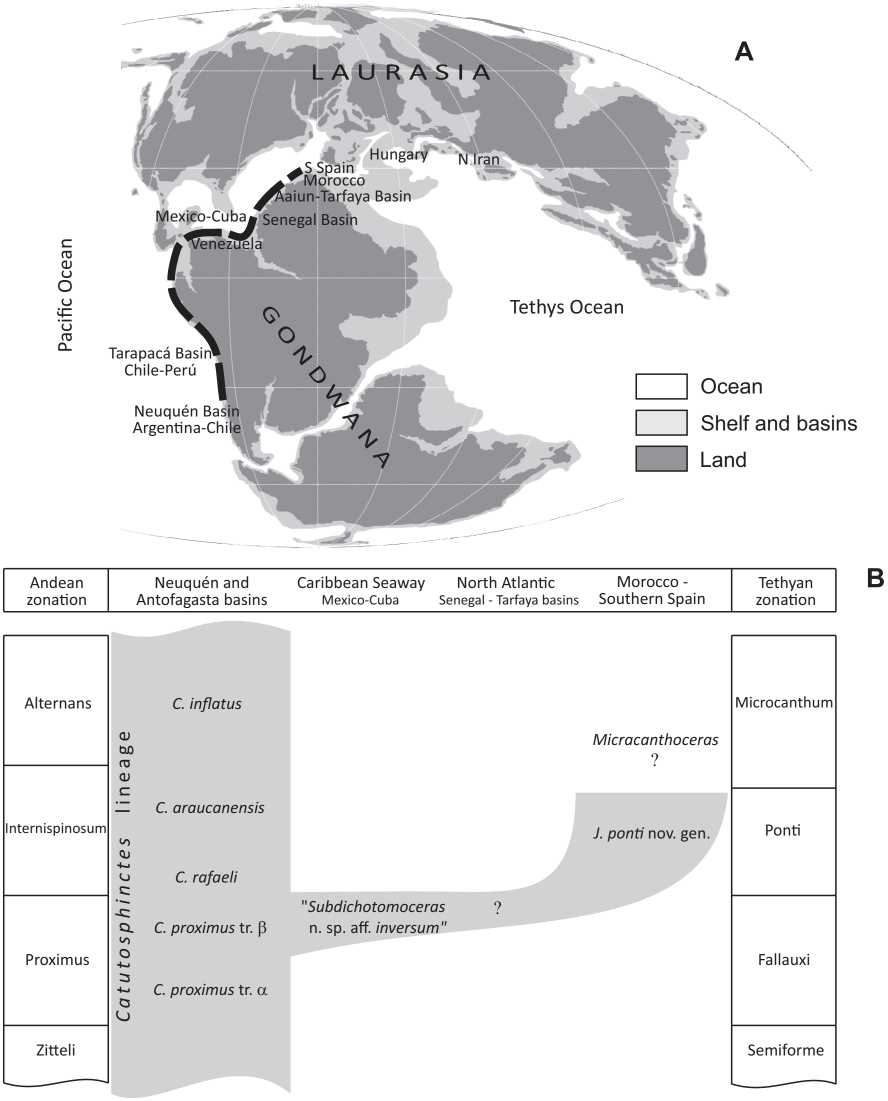

Fig. 6A. Possible migration route of *Catutosphinctes* (heavy black broken line) through the Caribbean Seaway and the North Atlantic towards southern Spain-Morocco in a Tithonian geography based on Parent *et al.* (2017a; see references therein) and complemented with data from Wilhem (2014). The regions and basins mentioned in the text are indicated. **B.** Spatio-temporal evolutionary model proposed for the origin of *Jaeniceras* nov. gen. from the *Catutosphinctes* lineage (see text) through an excursion of *Catutosphinctes proximus* transient β via forms such as "*Subdichotomoceras* n. sp. aff. *inversum*" (in Verma, Westermann, 1973). The possible origin of *Micracanthoceras* from *Jaeniceras* is indicated

However, there are few comparable ammonites from Mexico which would be the intermediate step for an excursion of *Catutosphinctes* towards the region of southern Spain-Morocco via the Caribbean Seaway and the North Atlantic. There are a few ammonites recorded from Mexico which could be assigned to *Catutosphinctes*. One is the specimen figured as *Perisphinctes corona* Burckhardt by Peña-Muñoz (1964: pl. 4: 1, 2), but unfortunately with unknown stratigraphic position in the La Caja Fm. The important ones are those adult female phragmocones that Verma, Westermann (1973: pl. 30: 1, 2) figured as *Subdichotomoceras* n. ap. aff. *inversum* Spath, 1931, coming from the so-called Virgatosphinctinae beds, Early Tithonian Fallauxi-?Ponti zones (Callomon, 1992; Villaseñor *et al.*, 2012: 4). They are almost identical in shell-shape and sculpture to the phragmocone of the large females of *C. proximus* transient β (sensu Parent, 2003) from the upper Proximus Zone of Cerro Lotena (see Parent, 2022: fig. 21A, B). These Mexican specimens can be safely assigned to Torquatisphinctinae and very likely to *Catutosphinctes*. Due to the scarcity of *Catutosphinctes*-like reports in Mexico (none in Cuba) it seems that they did not develop persistent populations in the Caribbean region. There are no (published at least) ammonite records in the Senegal and Aaiun-Tarfaya basins in northwestern Africa (see Wilhem, 2014) where the Upper Jurassic sediments (mostly evaporites) are offshore and covered by Cretaceous and Quaternary deposits (Davison, 2005).

Olóriz (1978) reported the occurrence of sporadic specimens of *Micracanthoceras* sp. in the upper part of the Ponti Zone. These specimens resemble the male of *Jaeniceras ponti* nov. gen., differing by the presence of incipient tubercles ("lamelliform" sensu Olóriz, 1978) in the rib bifurcation points. According to Olóriz (1978) it seems very likely that *Micracanthoceras* evolved from *Jaeniceras ponti* nov. gen. (as *Burckhardticeras peroni* in his paper) in the late Ponti zone. This hypothesis has been supported by Parent (2001) and was considered a possibility by Frau *et al.* (2016). On the other hand, the earliest Andean Tithonian Himalayitids, *Windhauseniceras internispinosum* (Krantz, 1926) and *Corongoceras huarpense* Parent, Garrido, 2021, originated from late representatives of *Catutosphinctes proximus* in the late Proximus Zone (see Parent *et al.*, 2015, 2017b, Parent, Garrido 2021). If *Jaeniceras* nov. gen. originated from *Catutosphinctes* as we suggest, then the Andean and the European himalayitids would have a common origin in this latter genus.

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