

# NEW RECORDS OF *CAUDRIELLA* HAMAN AND HUDDLESTON FROM THE MIDDLE AND LATE EOCENE OF NEO-TETHYS: TAXONOMIC AND PALAEOBIOGEOGRAPHIC IMPLICATIONS

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## ABSTRACT

The middle to upper Eocene mixed carbonate-clastic and siliciclastic deposits of the Şevketiye and Keşan formations in northwest Turkey yielded unique assemblages of larger benthic foraminifera, some displaying a typical orbitoidiform test, not comparable to any known taxa in the Palaeogene of the Neo-Tethys. These specimens with a flat, discoidal test, occasionally with an indistinct central depression, possess a central layer of equatorial chambers/chamberlets displaying a cyclical (orbitoidal) growth pattern and thick lateral layers with numerous chamberlets. The megalospheric embryonic apparatus possesses three small chambers (a triconch, the chambers of which are separated by notably thin walls), followed by a large auxiliary chamberlet. These specimens closely correspond to the genus *Caudriella* Haman and Huddleston and its type-species *Margaritella ospinae* (Caudri) that has only previously been reported with confidence from the Caribbean region, notably the type locality within the middle Eocene Punta Mosquito Formation at Margarita Island off Venezuela. *Caudriella* at its type locality also possesses a trilocular embryonic apparatus, which was incorrectly interpreted as arranged in a rectilinear or slightly curved row. The diagnosis of *Caudriella* is emended and considering the similarities in their equatorial sections with closely associated *Linderina* Schlumberger, a comparison of their embryonic-nepionic stages is given from the same deposits in NW Turkey and with those from the middle Eocene of the Sulaiman Range (Pakistan) and Kutch (India). A new record of primitive *Caudriella* is presented from Jamaica. The palaeobiogeographic distribution of *Caudriella* is reconsidered, being recorded from both the American/Caribbean and the Western Neo-Tethys bioprovinces. Limited data suggest eastward directed dispersal of the genus, even though this would be counter to most of the prevailing surface currents during the Eocene.

## INTRODUCTION

*Caudriella* Haman and Huddleston, 1984, is a poorly known Eocene hyaline, bilamellar benthic foraminifer with

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a typical orbitoidiform test structure (i.e., a disc-shaped test with an equatorial layer consisting of cyclical chamberlets and lateral layers with many chamberlets). The monotypic genus and its type species *Margaritella ospinae* Caudri, 1974 were established on material from the middle Eocene Punta Mosquito Formation of Margarita Island, Venezuela (Caudri, 1974). Since then, *Caudriella* has only been recorded from a few localities, often without detailed information or illustration. These records are from middle Eocene reef limestones on the Carter Seamount, Eastern Atlantic (Jones et al., 2002), within a reworked limestone boulder in an Oligocene to early Miocene hemipelagic sequence in Nicaragua (Andjić et al., 2018), and in the Eocene shallow marine carbonates of Saint Barthélemy (Cornée et al., 2020). The genus occurs rarely in the middle Lutetian, in the lower part of the type Swanswick section (Robinson & Mitchell, 1999; Mitchell, 2004, 2013) in Jamaica. Hence, it has been interpreted as restricted to the American bioprovince (Loeblich & Tappan, 1987; Ferrández-Cañadell & Serra-Kiel, 1999; BouDagher-Fadel, 2018). Recently, Hadi et al. (2019) reported the occurrence of the genus from the Bartonian of the Alborz region in NE Iran with limited illustration and no description.

In her original description, Caudri (1974) provided excellent photographs showing the general test structure, especially of the embryonic stage of the megalospheric specimens, but failed to describe correctly the embryonic-nepionic stage of the genus. Caudri (1974) introduced the genus name *Margaritella*, but as pointed out by Haman & Huddleston (1984), this name is invalid, being preoccupied by *Margaritella* Meek & Hayden, 1860 (Mollusca); in addition, it is also preoccupied by *Margaritella* Schmidt, 1880 (Porifera), and *Margaritella* Thiele in Troschel, 1891 (Mollusca). Hence, they introduced the replacement name *Caudriella*. The original generic diagnosis for *Caudriella* was followed and repeated in subsequent works, such as the widely used treatise on foraminifera by Loeblich & Tappan (1987) and BouDagher-Fadel (2018). Ferrández-Cañadell & Serra-Kiel (1999), in their study of the test morphostructure and systematics of *Linderina* Schlumberger (with its type-species *L. brugesi* Schlumberger from France), concluded that the embryonic apparatus of *Linderina* Schlumberger consists of a triconch followed by a large fourth chamber, and this embryonic structure resembles that of *Caudriella* and that the two genera are closely related within the family Linderinidae. It is noteworthy that Ferrández-Cañadell & Serra-Kiel (1999) do not agree with the original description of the early chamber arrangement of *Caudriella* which was reported as ‘chambers generally arranged in a rectilinear or slightly curved row’ by Caudri (1974). Both Ferrández-Cañadell & Serra-Kiel (1999) and

BouDagher-Fadel (2018) indicated the necessity of further studies on the morphostructure of *Caudriella*.

We have identified some discoidal foraminifers displaying a typical orbitoidiform growth pattern (i.e., a test with distinct equatorial and lateral chamberlets) and with a trilocular embryonic apparatus, corresponding to *C. ospinae* (Caudri, 1974) in the upper Bartonian-Priabonian deposits of the Şevketiye and Keşan formations (Biga Peninsula and Thrace, NW Turkey). In the Şevketiye Formation, the foraminiferal assemblage is in-situ, but in the Keşan Formation it represents a contemporaneously redeposited assemblage from a shallow-marine environment into a deeper-marine setting. These specimens are associated with typical Tethyan larger benthic foraminifers (LBF; Özcan et al., 2010, 2018a), including the genus *Linderina*, which is common to both the Western Neo-Tethyan and the American bioprovinces, and some forms not yet described from Neo-Tethyan deposits, such as the genus *Epiannularia* (*Epiannularia pollonaisae* Caudri, 1974) which was previously only recorded from the American bioprovince. Herein we give a first detailed description of the genus *Caudriella* from the Neo-Tethys with particular emphasis on its embryonic apparatus and its early chamber arrangement. This allows us to comment on its taxonomy and palaeobiogeography. Since *Caudriella* shows some similarities to *Linderina* in equatorial sections, a comparison is carried out in detail.

#### GEOLOGICAL SETTING, STRATIGRAPHIC, AND PALAEOONTOLOGIC CONTEXT

The majority of the material described in this paper was collected from the Thrace Basin in northwestern Turkey (Fig. 1). The Thrace Basin is a middle Eocene to late Oligocene hydrocarbon-bearing, clastic depocentre, bounded by the metamorphic rocks of the Rhodope Massif to the west and the Strandja Massif to the east. In the southern part of the basin, the sedimentary rocks of the Thrace Basin extend to the Biga Peninsula south of the Marmara Sea. The sedimentary sequence of the Thrace Basin has been described by Sümengen & Terlemez (1991), Siyako & Huvaz (2007), Özcan et al., (2010, 2018a) and Okay et al. (2010, 2019). It typically begins with a diachronous middle to upper Eocene shallow-marine limestone, the Soğucak Formation, which is about 50 m thick. The Soğucak Formation is overlain by a very thick (>5 km) regressive clastic sequence of late Eocene to late Oligocene age. The clastic sequence begins with distal to medial turbidites, which pass up into deltaic shales and deltaic to paralic sandstones with lignite seams. The Thrace Basin was inverted during the late Oligocene to early Miocene by shortening and is unconformably overlain by middle Miocene and younger continental beds (Erbil et al., 2021).

The basal sedimentary rocks in the southern part of the Thrace Basin and in the Biga Peninsula are represented by the clastic beds of the Fıçitepe Formation, the carbonates of the Soğucak Formation, and the mixed carbonate-clastic sequence of the Şevketiye Formation (Siyako et al., 1989; Siyako & Huvaz, 2007; Özcan et al., 2010, 2018a; Fig. 2). These units are overlain by the deep-marine sediments of the Çeltik and/or Keşan formations (Özcan et al., 2010, 2018a; Erbil et al., 2021). The Fıçitepe Formation is a thick

unit built up of conglomerate, sandstone, siltstone, and mudstone; it is interpreted as representing a deltaic depositional system (İlgar et al., 2012). The Şevketiye Formation, cropping out only in the northern part of the Biga Peninsula, comprises sandstone, siltstone, shale, limestone, and some conglomerate beds with abundant LBF. This unit was calibrated to the Bartonian-Priabonian stages of the Eocene in the Şevketiye section based on the occurrences of nummulitids (mainly the genera *Heterostegina* and *Operculina*) and orthophragminids (Özcan et al., 2018a). Specimens of *Caudriella* were found in the upper part of the Şevketiye section (Fig. 3). The Şevketiye Formation is the time-equivalent of the regionally widespread Soğucak Formation, an important shallow-marine to reefal carbonate unit in Thrace and the Biga Peninsula. The Soğucak Formation comprises fossiliferous limestone, sandy/clayey limestone with rare thin sandstone and mudstone beds. Corals abound in some levels. Specimens of LBF occur abundantly in the limestone beds, whereas the clastic levels are mostly barren of foraminifers, but rich in mollusks and other invertebrates (Özcan et al., 2010, 2018a; Less et al., 2011; Yücel et al., 2020). The demise of shallow-marine carbonate and mixed carbonate-clastic deposition is diachronous due to subsidence of the platform when the open-marine siliciclastic and carbonate rocks of the Keşan and Ceylan formations and clastic rocks of Çeltik and İhsaniye formations were deposited. Among these, the Keşan Formation has a widespread distribution in the southern part of the Thrace Basin. This formation contains deep-marine faunal elements, as well as coeval redeposited LBFs from the shelf areas in its lower part. The distribution of LBF in the Şevketiye, Soğucak, and Keşan formations in the northern part of the Biga Peninsula (Şevketiye region) and the southern part of Thrace (Çeltik region) is given in Özcan et al. (2010, 2018a) and Yücel et al. (2020).

#### MATERIALS AND METHODS

Specimens of *Caudriella* from Turkey were collected from the Şevketiye and Keşan formations at the following two localities in the Biga Peninsula and Thrace in northwestern Turkey (Figs. 1–2). In addition, a single specimen of *Caudriella* was found in the Swanswick section in Jamaica.

#### ŞEVKETIYE SECTION, BIGA PENINSULA, TURKEY

*Caudriella* occurs only in sample ŞEV.7 of the Şevketiye Formation (40°23'59.15"N; 26°50'14.91"E; Fig. 3). This sample contains *Assilina* ex gr. *alpina* (Douvillé), *Operculina* ex gr. *gomezi* Colom and Bauzá, *Heterostegina* cf. *armenica* (Grigoryan), *Orbitoclypeus varians* (Kaufmann), *Asterocyclina stellata* (d'Archiac), *Linderina brugesi* Schlumberger, *Epiannularia pollonaisae* Caudri, *Asterigerina* sp. and *Schlosseria* sp. The sample is located below shale-siltstone beds (sample ŞEV.11) containing *Heterostegina armenica*, a species first appearing close to the Bartonian-Priabonian boundary (SBZ 18A; Less et al., 2008; Özcan et al., 2019).

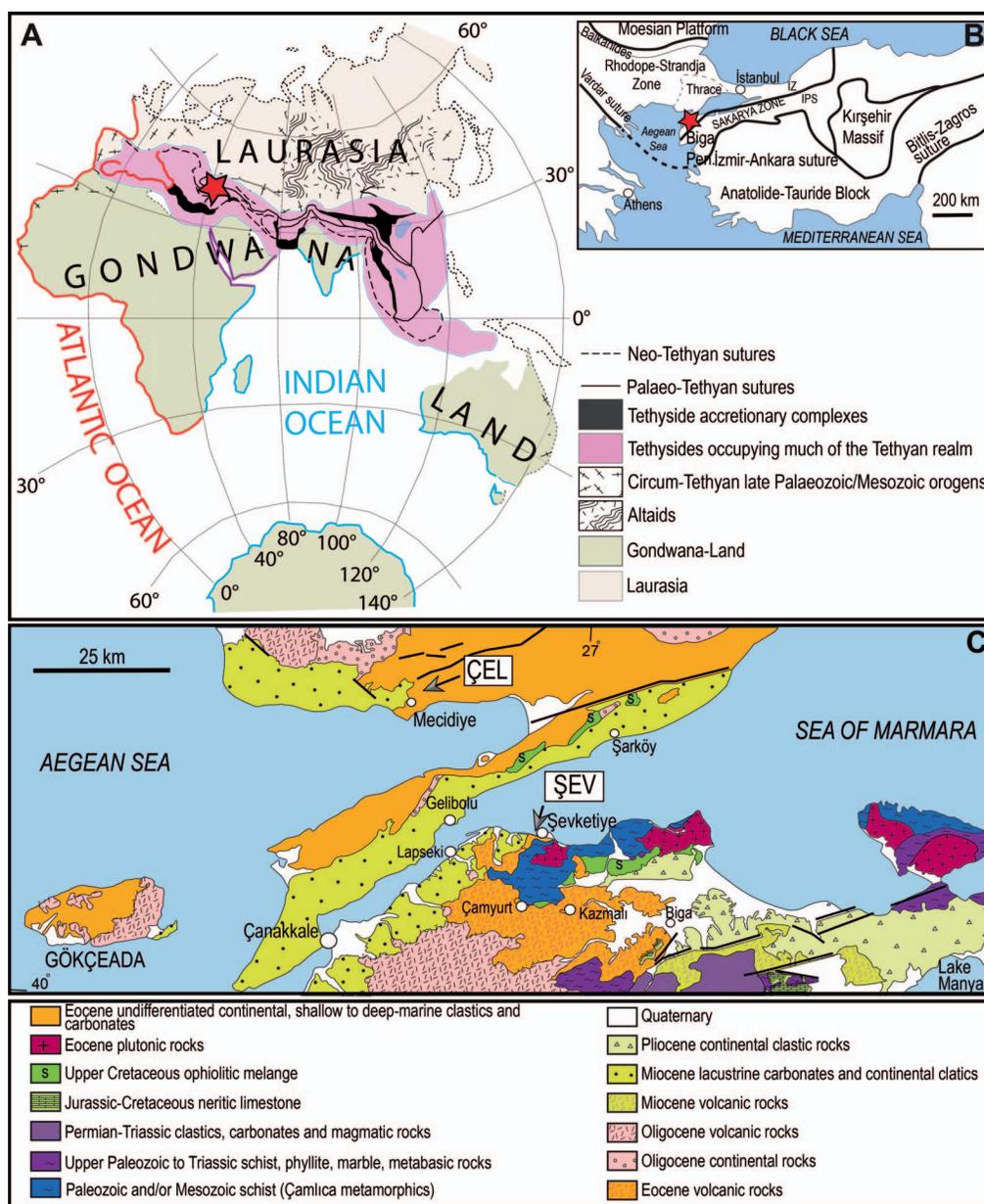


FIGURE 1. A) Tethysides in the world and location of the study area. B) Tectonic map of the northeastern Mediterranean region showing the major sutures and continental blocks (simplified from Okay & Tüysüz, 1999). C) Geological map of the northern segment of the Biga Peninsula and southern part of the Thrace with locations of the samples with *Caudriella* Haman and Huddleston (slightly modified from Akbaş et al., 2011, and Duru et al., 2012). IPS: Intra-Pontide suture, IZ: Istanbul Zone.

#### ÇELTIK SECTION, THRACE BASIN, TURKEY

Sample ÇEL.13 was collected from a sandstone bed in the lower part of the Keşan Formation (40°40'15.58"N, 26°34'14.29"E; Özcan et al., 2010). The fauna represents a resedimented assemblage with rare *Caudriella*, abundant *Heterostegina reticulata italica* Herb, *Nummulites budensis* Hantken, and *Operculina* ex gr. *gomezi* (Özcan et al., 2010). This assemblage suggests a Priabonian age (SBZ 19A).

#### SWANSWICK SECTION, JAMAICA

The type section of the Swanswick Formation at Swanswick House includes two intervals, a lower interval in the

Yellow Limestone Group and an upper level in the White Limestone Group (Robinson & Mitchell, 1999; Mitchell, 2004, 2013). The single specimen of *Caudriella* came from the lower interval. The lower intervals yield a rich LBF assemblage, including *Operculinoides jennyi*, *O. willcoxi*, *Nummulites guayabalensis*, *Pseudolepidina trimera*, *Linderrina floridensis*, and *Helicostegina gyalis*, which suggests a mid-Lutetian age.

The material consists of matrix-free specimens. Morphometric measurements and counts were carried out on axial and equatorial sections of the megalospheric specimens. The measurements and counts used in the morphometry are listed in Table 1. The measurements are illustrated in

TABLE 1. Statistical data of *Caudriella ospinae* (Caudri). TD - Test diameter, T1 - Thickness of the test at the central part of the test, T2 - Thickness of the test at the peripheral part of the test, HEL1 - Thickness of the equatorial layer in the nepionic stage, HEL2 - Thickness of the equatorial layer at the peripheral part of the test, ECH - Height of the chamberlets in the equatorial layer in nepionic stage (as measured in the equatorial section), ECW - Width of the chamberlets in the equatorial layer in nepionic stage (as measured in the equatorial section), LCH - Height of the chamberlets in the lateral layer (as measured in the axial section), LCW - Width of the chamberlets in the lateral layer (as measured in the axial section), PI - Thickness of the piles near the test surface, E1 - Length of the triconch (as measured along the axis joining the triconch and 4<sup>th</sup> chamber), E2 - Length of the triconch perpendicular to E1, E1+E2-Diameter of the triconch, E3 - Summation of the length of the triconch perpendicular E1 and height of the 4<sup>th</sup> chamber.

Specimen	TD µm	T1 µm	T2 µm	HEL1 µm	HEL2 µm	ECH µm	ECW µm	PI µm	LCH µm	LCW µm	E1 µm	E2 µm	E1+E2 µm	E3 µm
ÇEL13-9	1650										135	140	275	230
ÇEL13-24	2650										120	120	240	195
ÇEL13-25	2350										145	155	300	
ÇEL13-104	4050	610	970	90-100	170			20-30	55-80	90-140				
ÇEL13-105	3330		650		180-200	80-110	100-140	30-40			145	140	285	240
ÇEL13-106	2025				170									
ÇEL13-107	3600		700	100-110	230			20-40	50-60	80-140				
ÇEL13-108						80-90	100-135				150	150	300	
ÇEL13-109	2420					90-100	105-145				140	120	260	
ÇEL13-110						70-100	105-130				170	170	340	270
ÇEL13-117	3300	670	840	90-115				25-30	50-70	110-155				
ÇEL13-120	3950	880	1120	120	230			35-40	45-60	120				
ÇEL13-121	3150										160	150	310	
ŞEV7-102	2050			80	130-150									
ŞEV7-108	2130	550	450	90-100	150						120	140	260	210
ŞEV7-121	3300													
ŞEV7-122				70	150									
ŞEV7-127	2550										120	120	240	

Figure 4. All specimens from Turkey (prefixed 'EO/') are deposited in the palaeontological collections of the Geological Engineering Department of Istanbul Technical University. The specimen from Jamaica (prefixed 'UWIGM') is deposited in the University of the West Indies Geology Museum.

#### HISTORICAL BACKGROUND

Caudri (1974) reported the specimens of *Margaritella ospinae* (later *Caudriella ospinae*) from an assemblage of LBF including *Asterocyclina*, *Proporocyclina*, *Helicolepidina*, *Polylepidina*, *Lepidocyclina*, *Amphistegina*, *Helicostegina*, *Operculinoides*, *Nummulites*, *Sphaerogypsina*, and *Fabiania*, that suggest a middle Eocene age for the type-level. According to the above assemblage and the occurrence of *Orbulinoides beckmanni* (determined by M. Toumarkine in Caudri, 1974), the age of the type-level is constrained to the *Orbulinoides beckmanni* Zone (i.e., the early Bartonian planktonic foraminiferal zone E12/P13, 30.2–39.2Ma; Wade et al., 2011; BouDagher-Fadel, 2015), that correlates with the middle part of SBZ17 of Serra-Kiel et al. (1998). Caudri (1974) also established a further additional new genus and species from the same beds, *Epiannularia pollonaisae*, which has a completely different test architecture than orbitoidal foraminifera.

The diagnosis for *Caudriella* (as “*Margaritella*”) was given by Caudri (1974) as “test small, thick-discoidal, with a more or less pronounced central depression and a blunt edge, reminiscent of *Planorbulinella*, but without a rim of large marginal chambers. Surface pattern consisting of thick meandering ridges and knobs, obscuring all structural features.” (p. 307)

It was reported that the chambers are differentiated into equatorial (median) and lateral layers and the equatorial chambers are rounded in axial sections, with a curved somewhat embracing wall. The embryonic stage was described as consisting of three chambers, the first of which is globular in shape, generally arranged in a rectilinear or slightly curved row. This stage is followed by two symmetrical auxiliary chamberlets spanning the junction of chambers 2 and 3 on either side, and by a third one arising from the distal end of chamber 3. The periembryonic ‘spirals’, often closed by a symmetrical chamber over the protoconch, were interpreted to form a complete nepionic ring around the nucleococonch. Caudri (1974) also indicated that the genus shows a certain resemblance to *Linderina*, that lacks lateral chamberlets, thereby justifying the establishment of a new genus. Similarly, the initial chamber arrangement of *Caudriella* was interpreted by BouDagher-Fadel (2018) to consist of a small proloculus followed by two large chambers.

In their study of *Linderina brugesii* from its type-locality in France, Ferràndez-Cañadell & Serra-Kiel (1999) compared *Linderina* with *Caudriella* and concluded that the latter genus seems to differ from *Linderina* only in the presence of well-developed lateral chamberlets. These authors also stated that the embryonic apparatus of *Caudriella*, with a triconch followed by a large fourth chamber, resembles that of *Linderina*, that both genera should be classified within the Linderinidae, and that a revision of *Caudriella* is necessary.

#### SYSTEMATIC PALAEOONTOLOGY

Loeblich & Tappan (1987) assigned the genus *Caudriella* to the superfamily Asterigerinoidea d’Orbigny, 1839, and within the subfamily Lepidocyclininae Scheffen, 1932, which

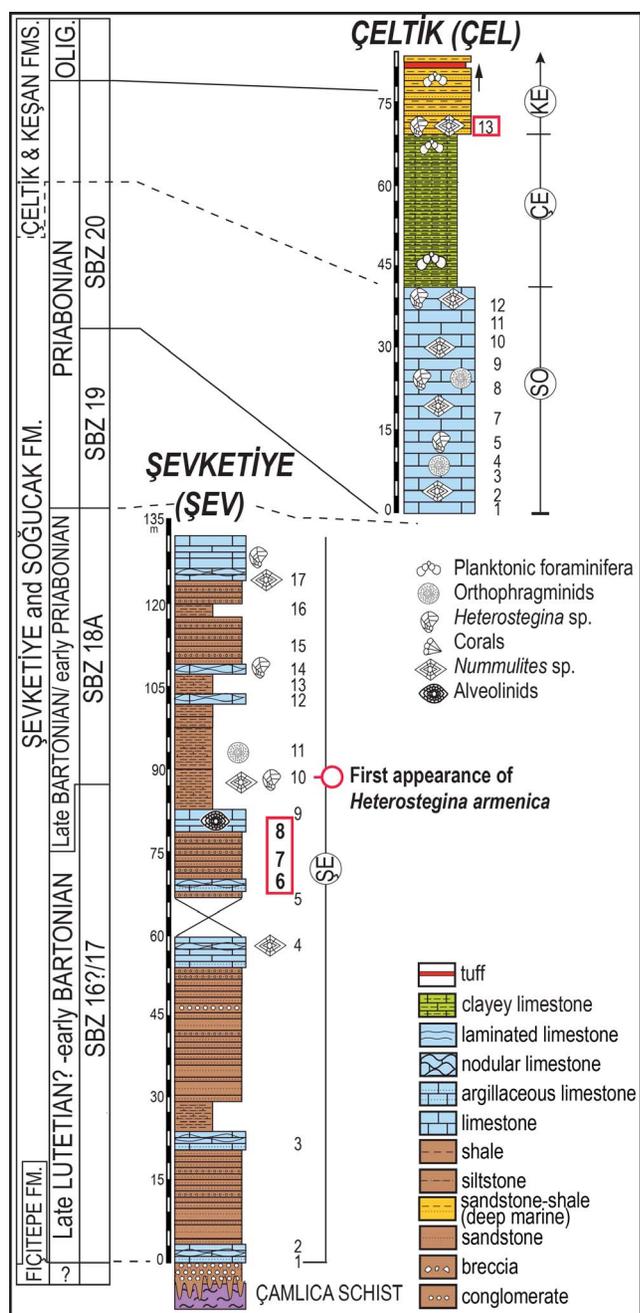


FIGURE 2. Stratigraphic columns of the Şevketiye, Soğucak and Keşan formations in the Şevketiye and Çeltik sections and position of the samples with *Caudriella*. SBZ: Shallow Benthic Zones after Serra-Kiel et al. (1998), updated by Less & Özcan (2012). ŞE: Şevketiye Fm., SO: Soğucak Fm., ÇE: Çeltik Fm., KE: Keşan Fm. Stratigraphy of both sections after Özcan et al. (2018a) and Erbil et al. (2021).

they interpreted as characterized by the presence of a ‘bilocular’ embryo, cyclical series of equatorial chamberlets and lateral chamberlets. Ferrández-Cañadell & Serra-Kiel (1999) suggested that *Caudriella* belongs to the same group as the genus *Linderina* Schlumberger and classified it in the family Linderinidae Loeblich & Tappan, 1984, because of the similarities of their embryonic apparatuses. This concept was followed by BouDagher-Fadel (2018). The Linderinidae are

considered by Loeblich & Tappan (1987, 1992) as belonging to the superfamily Orbitoidoidea Schwager, 1876. Herein, we provide an emended description of the genus based on our observations on the embryonic-nepionic stages of the genus.

Superfamily ORBITOIDOIDEA Schwager, 1876

Family LINDERINIDAE Loeblich and Tappan, 1984

Genus *Caudriella* Haman and Huddleston, 1984

*Margaritella* Caudri, 1974, p. 307, 308.

*Caudriella* Haman and Huddleston, 1984, p. 126.

**Emended diagnosis.** Test discoidal, flat to slightly biconvex or bilaterally depressed at the center. Test surface smooth with typical vermicular pattern of the lateral chamberlet walls and indistinct piles (granules). Wall hyaline-calcareous, bilamellar, with large pores (7–8 µm on average and up to 10 µm in diameter), easily visible on the exterior. The embryonic apparatus of megalospheric forms is trilocular (the size of the embryonic apparatus, corresponding to parameter E1+E2, ranging between 240 and 340 µm), with relatively thin walls. A large fourth chamber is the only epi-embryonic chamber with basal stolons; from this, two chamberlets arise in the next budding step. The equatorial chamberlets are arcuate and connected by basal stolons. Numerous lateral chamberlets form on either side of the equatorial layer.

*Caudriella ospinae* (Caudri, 1974)

Figs. 4A–B, 5A–H, 6A–H, 7A–I, 8, 9A–I, 11A–G

*Gypsina vesicularis* (Parker & Jones). Butterlin, 1970, p. 295, pl. 5, figs. 8, 9.

*Margaritella ospinae* Caudri, 1974, p. 308, 309, pl. 1, fig. 21, pl. 2, fig. 13, pl. 7, figs. 1–9.

**Description.** The test is discoidal, flat to biconvex or bilaterally indistinctly depressed at the center (Figs. 4A; 5A, B; 6A, E). Externally, the walls of the lateral chamberlets form a vermicular pattern (Figs. 5C, D; 6A, E). An umbo is absent. The walls of the lateral chamberlets show coarse pores (ca. 7–8 µm, up to 10 µm in diameter), that are visible on the surface of the test. The piles are indistinct, hardly observed externally and do not form a pattern on the test surface. The test diameter in samples ÇEL13 and ŞEV7 varies between 1.65 and 4.05 mm and 2.05 and 3.3 mm, with an average of 2.95 and 2.5 mm, respectively (Table 1). The thickness of the test in the center (T1) and near the periphery (T2) of the test ranges between 0.55 and 0.88 mm and 0.450 and 1.12 mm, respectively, being thicker near the periphery. In the studied material, only megalospheric forms were found. In these specimens, the nepionic stage does not allow us to identify any structure showing successive chamber formation [i.e., it is not possible to judge which chamber is the first (protoconch) and which one is the second (deuteroconch)]. The initial part consists of three chambers of similar dimensions and shapes (Figs. 4B, 8), encircled by a thin embryonic wall. These chambers are possibly not situated in the same plane because during the sectioning on the equatorial plane, there is a change in the configuration of the embryonic apparatus. These chambers are not circular in outline but rather sub-rounded with occasionally sharp margins and are separated by almost flat to slightly curved walls, producing an



FIGURE 3. Field photo of the upper part of the Şevketiye Formation in the Biga Peninsula (A), and close-up view of the sandy/silty beds and limestone intercalations with *Caudriella* (B). Foraminifers common in the upper part of the unit are shown alongside. 1) *Linderina brugesi* Schlumberger, ŞEV7-101. 2) *Assilina ex gr. alpina* (Douvillé), ŞEV6-5. 3) *Asterocyclina stellata* (d'Archiac), ŞEV8-10. 4) *Operculina ex gr. gomezi* Colom and Bauzá, ŞEV7-4. 5) *Sphaerogypsina globulus* (Reuss), ŞEV6-3. 6-7) *Heterostegina armenica* (Grigoryan), 6: ŞEV11-8, and 7: ŞEV11-35.

overall appearance of a 'Y' shape (Figs. 7, 8). The walls separating the embryonic chambers also look darker than the embryonic wall and other chamber/chamberlet walls in the equatorial layer (Fig. 4B). These chambers form a distinctive structural entity, an embryonic apparatus that can be rather easily distinguished from the later chambers. The chamber walls in the embryonic apparatus are always relatively thinner than the embryonic wall and may not be always traceable in equatorial sections (Fig. 8). The embryonic apparatus consists of a relatively thin wall ranging in thickness between 10–25 (generally between 10–15)  $\mu\text{m}$ . The size of the embryonic apparatus (parameter E1+E2) ranges between 240 and 340  $\mu\text{m}$  with an average of 250 to 289  $\mu\text{m}$ . The parameter E3 ranges between 195 and 270  $\mu\text{m}$ . The embryonic apparatus is usually followed by a distinctive U-shaped chamber, which is here considered to have formed at the 4<sup>th</sup> budding step. This chamber, which is usually larger than other chamberlets in the nepionic stage, connects through basal stolons to two chamberlets that form the 5<sup>th</sup> budding step. The chambers around the embryonic apparatus close at the 7<sup>th</sup> or 8<sup>th</sup> budding step and cyclical growth starts in the equatorial plane (Fig. 8). The equatorial chambers are characteristically arcuate in shape.

In axial sections, the embryonic apparatus is indistinctly observed. The equatorial chamberlets are usually arcuate in their distal parts, especially towards the marginal part of the equatorial layer (Fig. 5G, H), and occasionally may be

rounded in shape (Figs. 5H, 11B). The thickness of the equatorial layer in the center and periphery of the tests ranges between 70 and 120  $\mu\text{m}$  and 130 and 230  $\mu\text{m}$ , respectively.

The specimens from Turkey correspond to *Caudriella* Haman and Huddleston from the type-locality of the genus in Venezuela and are assigned to its only species *Caudriella ospinae* (Caudri). The only morphological difference appears to lie in the chamber arrangement in the nepionic stage, whereas the general architecture of the embryonic apparatus is the same. Our study shows that this genus possesses a trilocular embryonic apparatus (triconch), which was misinterpreted in the original publication (Caudri, 1974) and later by Loeblich & Tappan (1987). A reinterpretation of the specimens illustrated by Caudri (1974) suggests a trilocular embryonic apparatus, as already stated by Ferrández-Cañadell & Serra-Kiel (1999), who arrived at their conclusion based on the illustrations in Caudri (1974). In these specimens, there are always three chamberlets in the 5<sup>th</sup> budding step, one of which directly arises from the 4<sup>th</sup> chamber. We did not observe this feature in any specimen in our material. Nevertheless, the significance of this feature in the phylogenetic history of the genus and systematics is unknown. Caudri (1974) illustrated the embryonic-nepionic stage of only a few specimens, thus, the variation in peri-embryonic chamber arrangement (if any exists) is not known.

The single specimen (Fig. 9J) from Jamaica is referred to under open nomenclature as *Caudriella* sp. because we only

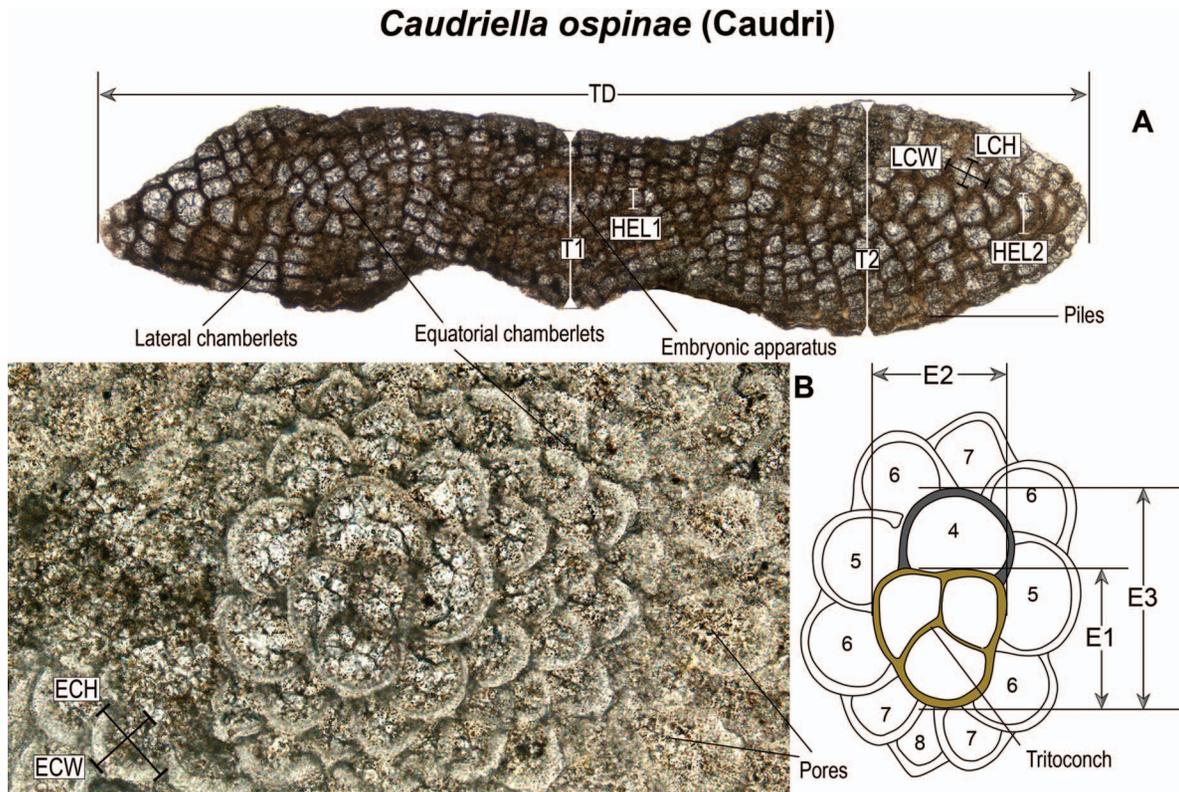


FIGURE 4. Axial (A) and equatorial (B) sections of *Caudriella* with test parameters used here in the description of the genus (see Table 1 for the explanation). The line drawing of the embryonic-nepionic stage of this specimen from Turkey shows a trilobular embryonic apparatus, a large auxiliary chamber formed at 4<sup>th</sup> budding step and following arcuate chamberlets in the equatorial layer (not all chambers formed at each growth stage are shown, only the peri-embryonic chamberlets are illustrated). A) ÇEL13-104. B) ÇEL13-105.

have a single axial section. The specimen is relatively inflated, has a well-developed equatorial layer, but only a few lateral chamberlets are developed. The relatively thick compact walls resemble *Linderina*, other for the presence of a few lateral chamberlets. More material is needed to fully describe this form and to compare it with the material from Venezuela and Turkey.

#### A COMPARISON OF *CAUDRIELLA* WITH *LINDERINA*

Essentially, *Caudriella* differs from *Linderina* in having lateral layers composed of chamberlets (Fig. 11). Moreover, *Caudriella* has a robust, thick test, the surface of which has a characteristic vermicular pattern, whereas *Linderina* has a 'pitted' surface. In equatorial sections, however, the embryonic apparatus and equatorial chambers look alike as stated by Ferrández-Cañadell & Serra-Kiel (1999). These authors further proposed that these genera are phylogenetically related because of this similarity.

The peri-embryonic chamber arrangement of *Caudriella*, however, differs from that of *Linderina* from the same deposits in Turkey because in the latter genus two auxiliary chamberlets always occur in the fourth budding step (Figs. 11I, 12). These specimens were grouped in Morphotype 2 of *Linderina*. The auxiliary chamberlets are invariably unequal in size (Fig. 12). It appears that there is a retardation

in chamber formation after the small 4<sup>th</sup> auxiliary chamberlet, and only one chamber is formed in the 5<sup>th</sup> budding step; a closing chamber is formed at the 7<sup>th</sup> or 8<sup>th</sup> budding step. This development has been observed in all specimens in the studied material from NW Turkey. Our data from the middle Ypresian of Turkey (Özcan et al., 2021) and unpublished data from the central Neo-Tethys (Pakistan and India), however, show that some specimens of *Linderina* possess only one auxiliary chamber at the 4<sup>th</sup> budding step (as in *Caudriella*, Figs. 12, 13; Özcan et al., in prep.). The specimens were grouped under Morphotype 1 of the genus *Linderina*. The material from the Pir Koh Formation in Zinda Pir (Sulaiman Range, Pakistan), the Fulra Formation in the Kutch Basin (Western India), and the Ayhan Formation in central Anatolia (Turkey) yielded both types. Among them, the specimens categorized as Morphotype 2 possess a small triconch, a large and notably smaller chamberlet both formed at the 4<sup>th</sup> budding step from which the nepionic growth starts. The closing chamberlets are usually formed at the 7<sup>th</sup> and 8<sup>th</sup> growth stages. The embryonic apparatus and following chamber formation of these specimens are the same as in *Caudriella* from northwest Turkey (compare Figs. 8 and 13). The specimens of the Morphotype 1, which is less common than Morphotype 2 in the studied material from Turkey, have a similar embryonic-nepionic stage as in *Caudriella*. We have discovered *Linderina* from the 'middle' Ypresian deposits of Ayhanlar (Nevşehir,



FIGURE 5. External views (A, B), sub-axial (H) and tangential sections (E–G) of *Caudriella ospinae* (Caudri) from the Soğucak Formation, SBZ 20, late Priabonian. Near-surface characteristics (vermicular network of lateral chamberlet walls and thin piles) of the species in slightly abraded test are shown in C and D. A, F) ÇEL13-105 (the embryonic apparatus and nepionic stage of this specimen is illustrated in Fig. 6A–C and the interpretation of the embryonic-nepionic stage is given in Fig. 7). B, E) ÇEL13-106. C, D) ÇEL13-111, G) ÇEL13-107. H) ÇEL13-104. Note that E and F were sectioned from the peripheral parts of the test, thus the test diameters of these specimens do not represent the actual diameter of the test.

*Caudriella ospinae* (Caudri)

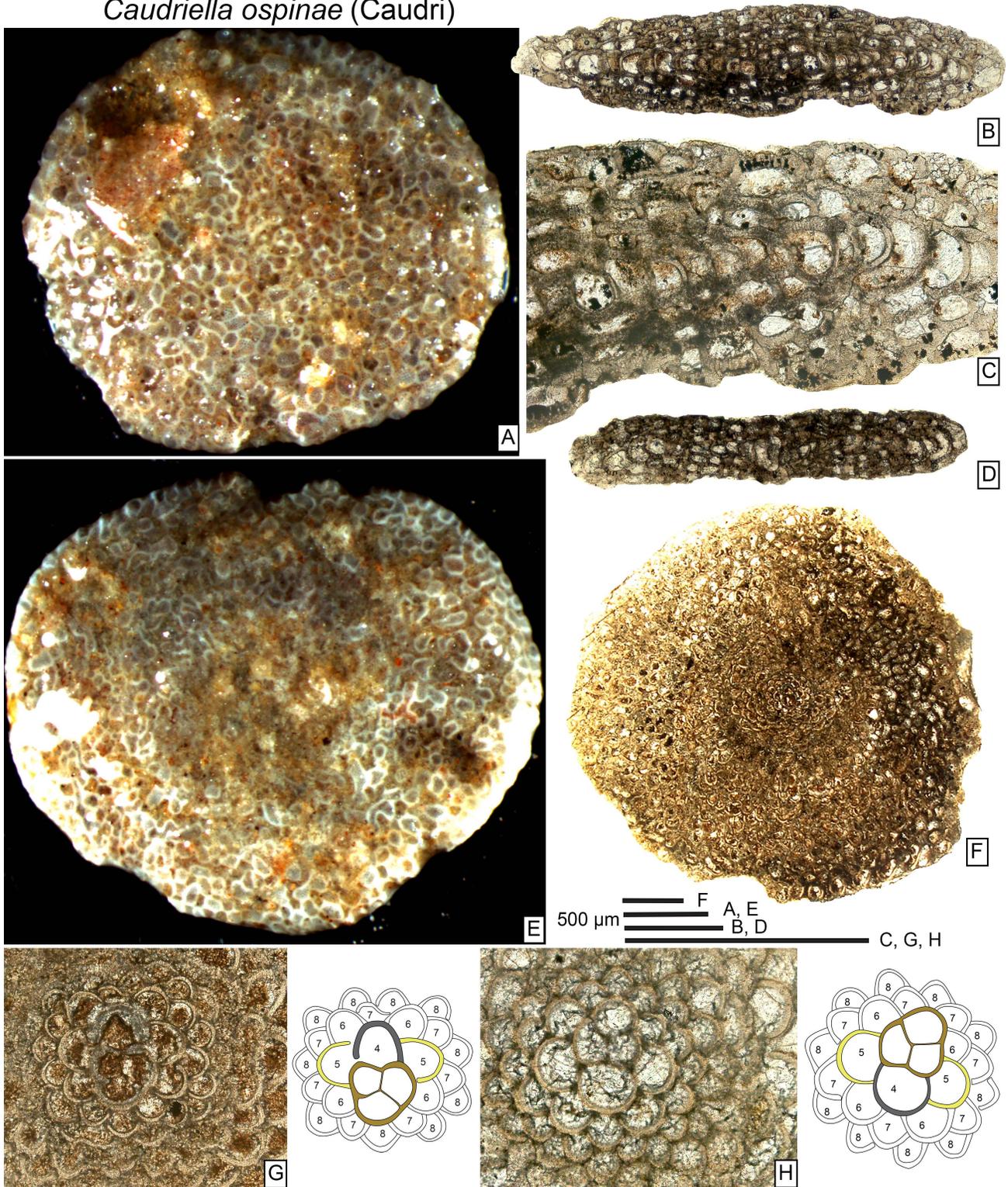


FIGURE 6. External views (A, E), axial and off-centered axial sections (B–D) and equatorial sections (F–H) of *Caudriella ospinae* (Caudri) from the Şevketiye Formation, SBZ 17/18A, Bartonian or Bartonian-Priabonian transition and the Keşan Formation, SBZ 20, late Priabonian. A–C) ŞEV7-108. D) ŞEV7-102. E–G) ŞEV7-121. H) ÇEL13-9.

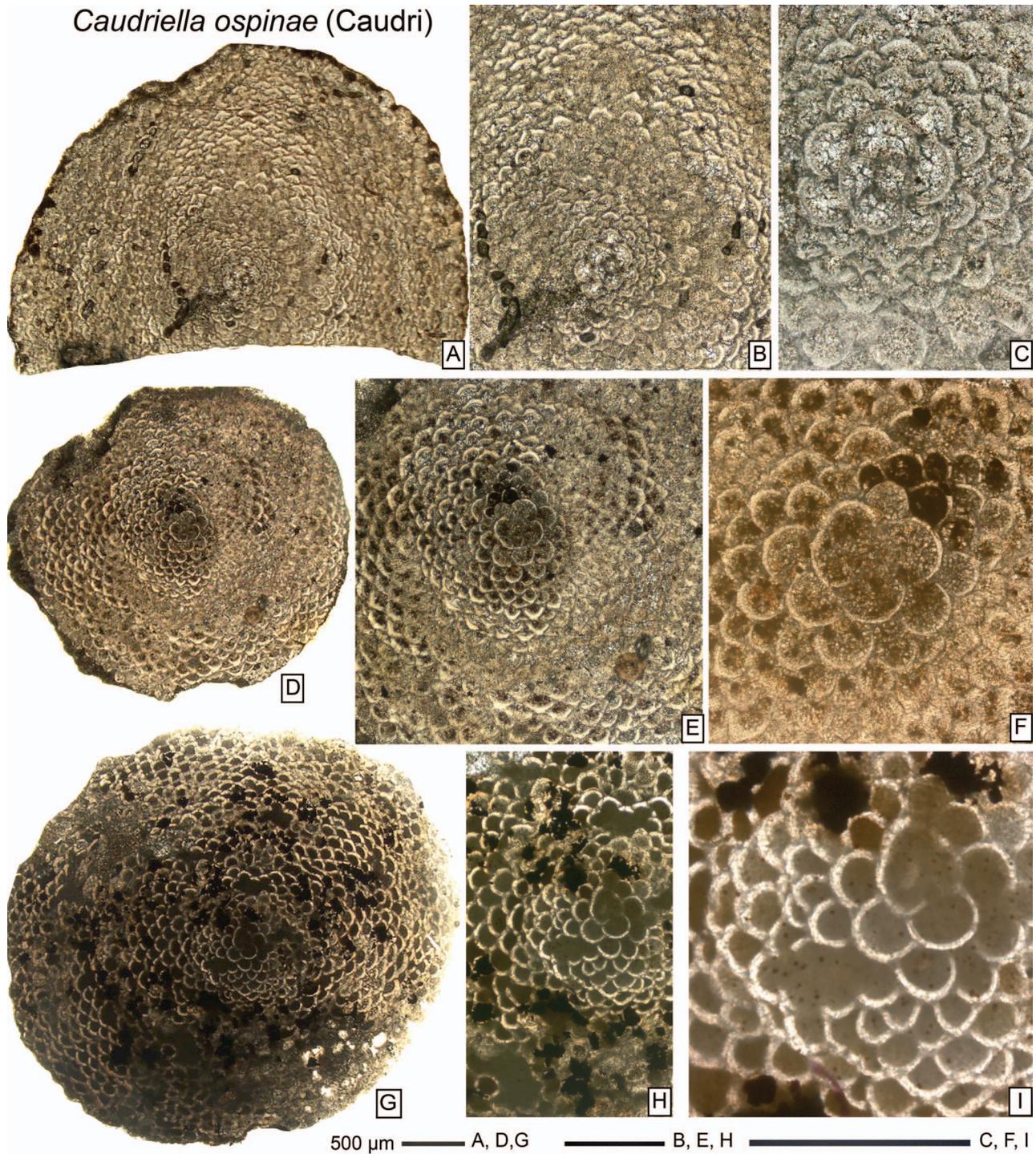


FIGURE 7. Equatorial sections showing the arcuate equatorial chamberlets and nepionic stages of *Caudriella ospinae* (Caudri) from the Keşan Formation, SBZ 20, late Priabonian. A–C) ÇEL13-105. D–F) ÇEL13-108. G–I) ÇEL13-110.

central Anatolia) in Turkey, representing the oldest record of the genus in the Tethys (Özcan et al., 2021). These specimens are represented by both morphotypes (Fig. 12), those with larger embryos belonging to Morphotype 1 and smaller ones to Morphotype 2. Thus, our data show that the peri-embryonic stage of *Linderina* is represented by two morphotypes where chamber arrangement in Morphotype 1 is

also characteristic to that in *Caudriella*. A further study of *Caudriella* and *Linderina* in the Neo-Tethys is required to trace the phylogenetic development of these genera and a possible link between them, since it appears that *Linderina* is not only restricted to the middle to late Eocene, but ranges down to the early Eocene in the Tethys. The occurrence of the genus in the Ypresian deposits of Jamaica (but with a dif-

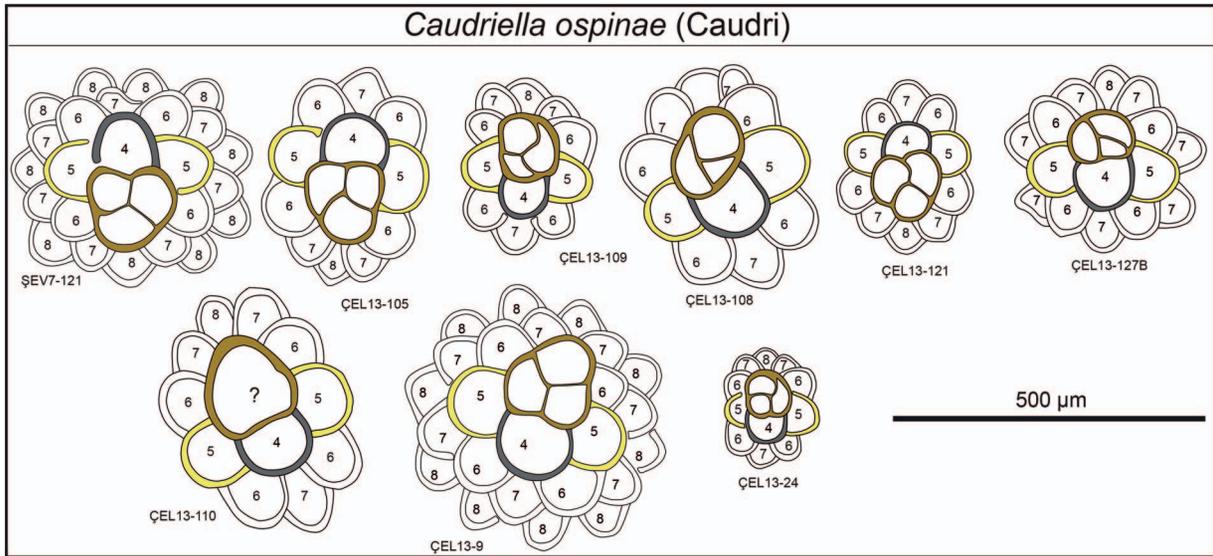


FIGURE 8. Line drawings of the embryonic and peri-embryonic chambers/chamberlets of *Caudriella ospinae* (Caudri) from the Keşan Formation, SBZ 20, late Priabonian and from the Şevketiye Formation, SBZ 17/18A. Numbers in the equatorial chamberlets denote the growth stages, accepting that auxiliary chamber is the 4<sup>th</sup> chamber after the formation of trilocular embryonic apparatus.

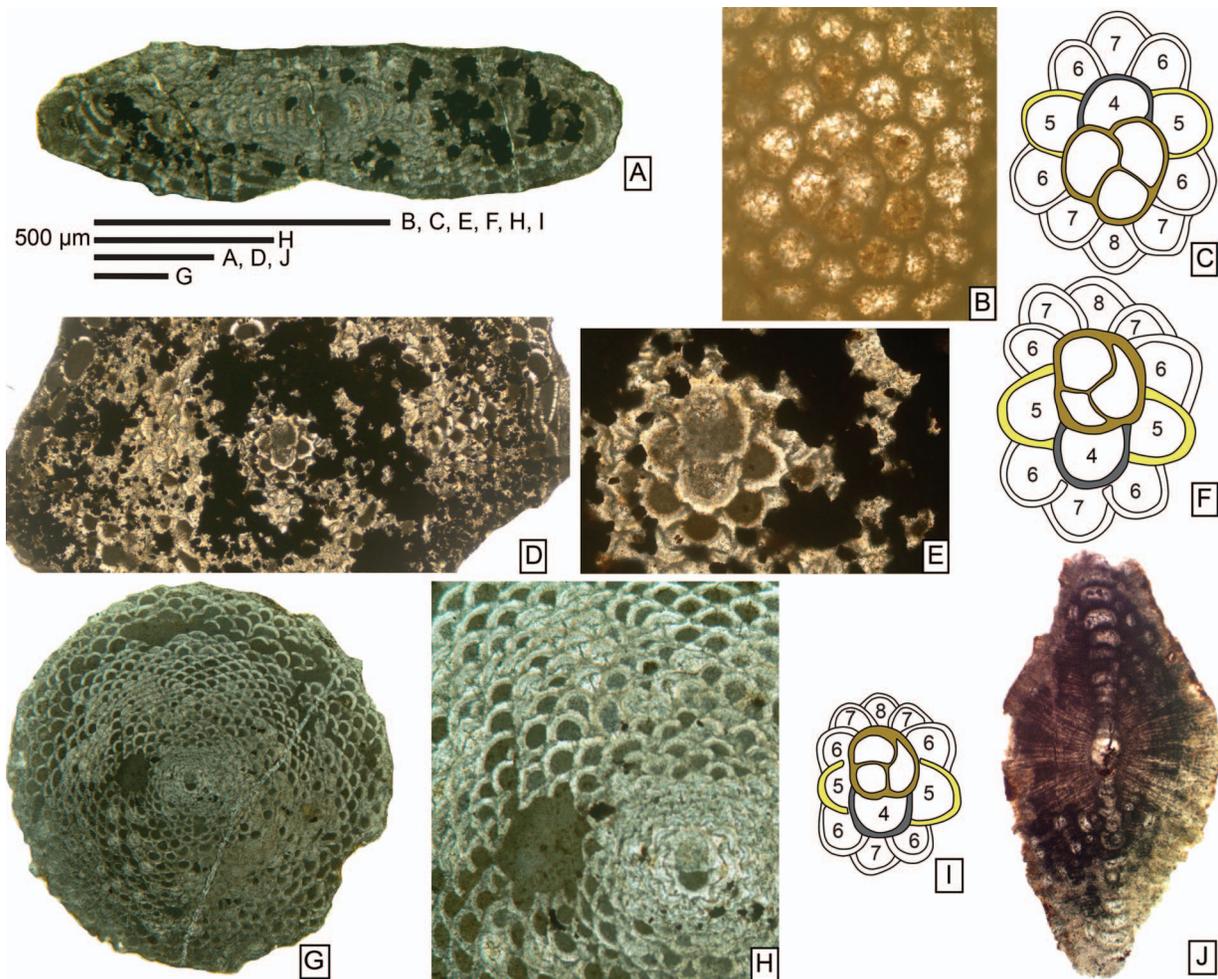


FIGURE 9. *Caudriella ospinae* (Caudri) from the Keşan Formation (A–I) and *Caudriella* sp. from Jamaica (J). Sub-axial (A) and equatorial sections (B–I), and interpretation of chamber arrangement in the nepionic stage, SBZ 20, late Priabonian and from the Şevketiye Formation, SBZ 17/18A, Bartonian/Bartonian-Priabonian transition, and a specimen with poorly developed lateral chamberlets, from the Lutetian of Jamaica. A) ÇEL13-121. B–C) ÇEL13-121. D–F) ÇEL13-109. G–I) ÇEL13-24. J) WL3275A-06.

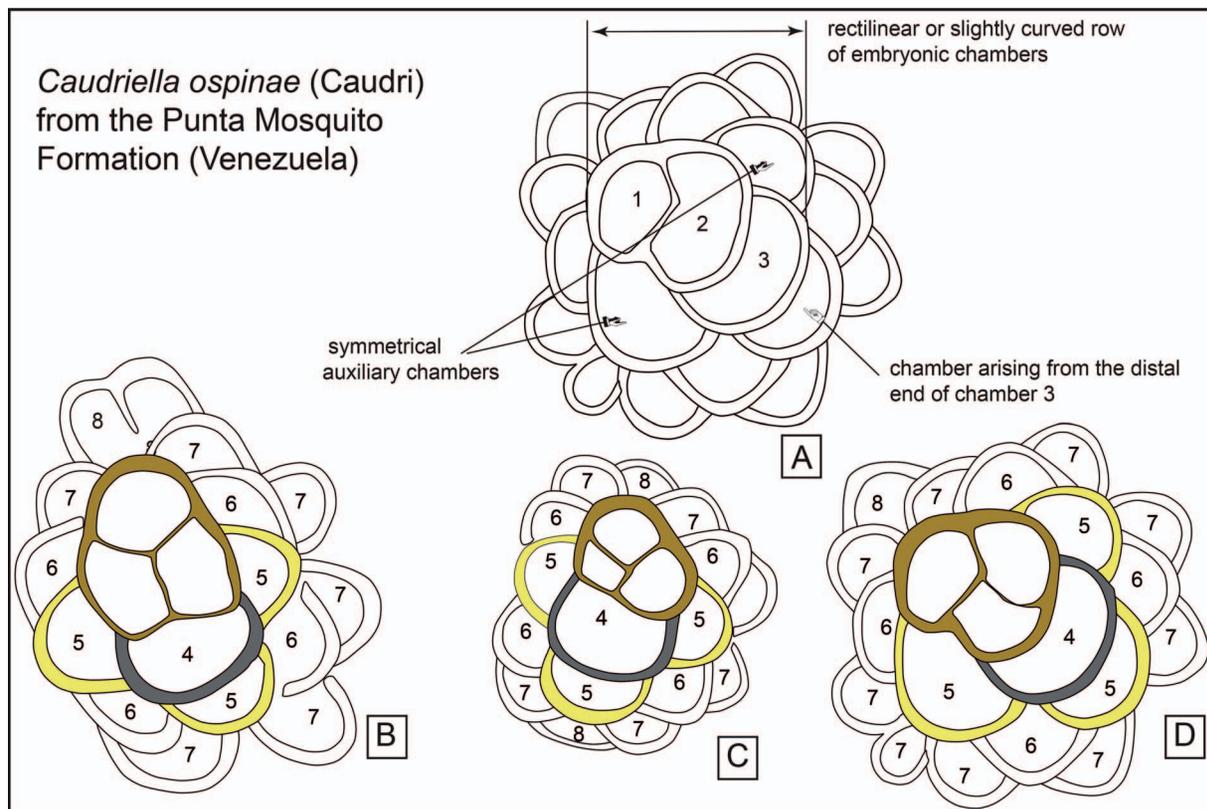


FIGURE 10. Line drawing interpretations of the nepionic stages of *Caudriella ospinae* (Caudri) as illustrated in the original description by Caudri (1974). A) interpretation of embryonic and peri-embryonic stage of the specimen illustrated in Figure 9 in Plate 7 as this chamber arrangement was explained as 'rectilinear or slightly curved row' by Caudri. Note that the thin wall of the second chamber is obliterated and is hardly seen in the original photograph. The re-interpretation of the chamber arrangement of this specimen is shown in D. In all three specimens, the large auxiliary chamber (4<sup>th</sup> chamber) give rise to the formation of three chambers at the next budding step (5<sup>th</sup> budding step). B, C) our interpretation of the embryonic and peri-embryonic stages of the specimens illustrated in figures 8 and 7 respectively in Plate 7 of Caudri (1974). Not to scale.

ferent peri-embryonic early chamber arrangement) also suggests a wider stratigraphic range of the genus in the American bioprovince.

#### PALAEOBIOGEOGRAPHY

As shown in Figure 14, the records of *Caudriella* from the Thrace Basin and Jamaica noted herein expand upon of only a handful of records from outside the type area of the genus in the southern Caribbean. Other records include:

Jones et al. (2002): Carter Seamount, eastern equatorial Atlantic. Poorly preserved specimen illustrated (identification uncertain), in supposed middle Eocene sediments.

Andjić et al. (2018): Nicaragua. Unillustrated, but noted in a block reworked into Oligocene sediments.

Cornée et al. (2020): Saint Barthélemy, Caribbean. Unillustrated, reported from lower limestone of Lutetian age (also see Robinson, 1996; Caron et al., 2019).

Hadi et al. (2019): Iranian Alborz. Recorded with limited illustration from Bartonian carbonates. If present, this is the most easterly record of the genus to date.

The closely allied genus *Linderina* is much more widespread with records from the Caribbean and across much of Tethys into South-East Asia and potentially even into low latitudes in the southern hemisphere. It is pos-

sible that *Caudriella* has been overlooked, and that new records will come to light that extend its palaeogeographic distribution.

An intriguing question is how the dispersal of Palaeogene LBF occurred during a time of major palaeogeographic re-organisation (Allen & Armstrong, 2008), with the Tethys progressively closing and the Atlantic progressively widening. The limited records of *Caudriella* are up to several thousand kilometers apart and separated by a major ocean. Whilst the records in themselves do not shed light on the means of LBF dispersal, they do serve to remind us that this question is not yet fully answered.

The classic view of Cenozoic LBF palaeobiogeography (Adams, 1967; Butterlin, 1981) is that three distinct provinces developed, centered around the American (or Caribbean), Tethyan (or Mediterranean and Middle East), and Indo-West Pacific (or South-East Asia) regions. BouDagher-Fadel (2018) has suggested an additional province in Southern Africa. Given that identical taxa are known from the various provinces, it seems unlikely, at least at the generic level, that taxa evolved through orthogenesis in each province from similar cosmopolitan ancestors, although this may be a factor at species level (Freudenthal, 1972; Matsumaru, 1991; BouDagher-Fadel & Price, 2010). The likely ancestor of *Caudriella*, plus the allied *Linderina*

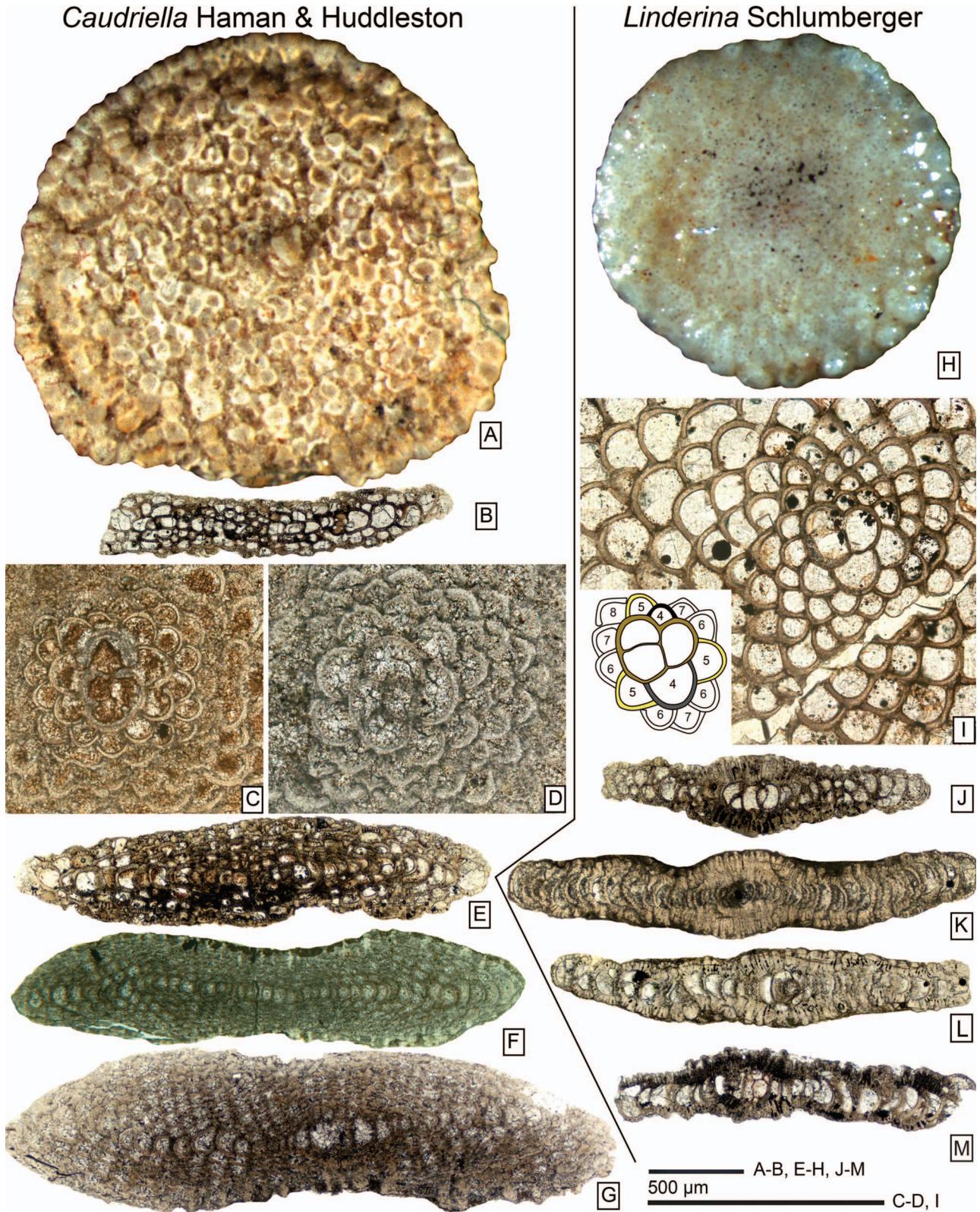


FIGURE 11. Comparison of external test features and axial, off-centered axial and equatorial sections of *Caudriella ospinae* (Caudri) (A–G) and *Linderina brugesi* Schlumberger (H–M) from NW Turkey. A–B) ŞEV7-122. C) ŞEV7-121. D) ÇEL13-105 (tangential section of this specimen is illustrated in Figure 4F). E) ŞEV7-108. F) ÇEL13-26. G) ÇEL13-117. H) ŞEV8-131. I) ŞEV8-128b. J) ŞEV7-103. K) DER10-4. L) DER2-16. M) ŞEV7-130.

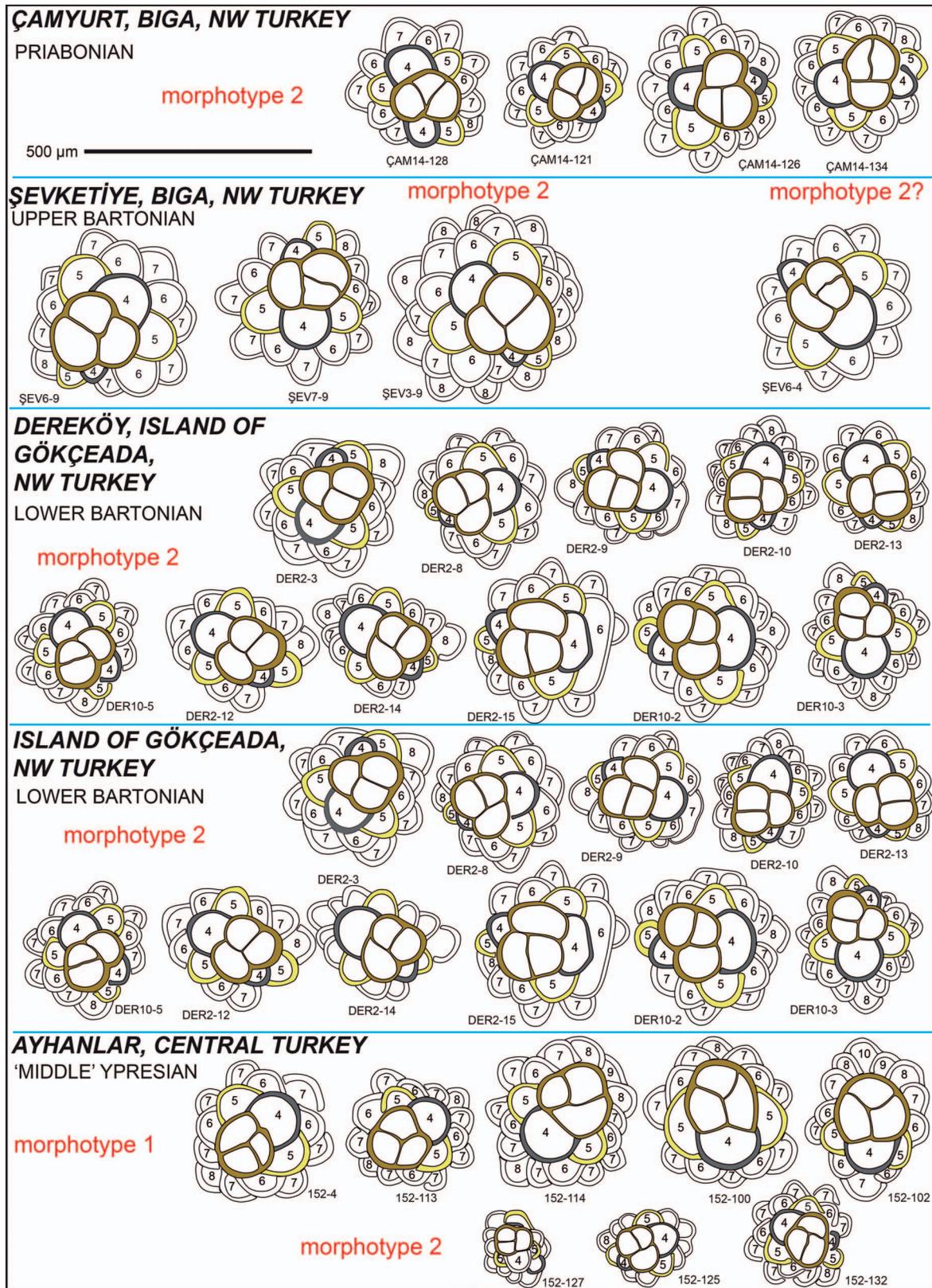


FIGURE 12. Line drawings of the embryonic and peri-embryonic chambers/chamberlets of *Linderina brugesi* Schlumberger from the Şevketiye and Soğucak formations in the Biga Peninsula and the Thrace (NW Turkey). See Özcan et al. (2018) for stratigraphic information on the Şevketiye and Çamyurt samples, and Özcan et al. (2010) for the Gizliliman section and distribution of foraminifera. The Dereköy section is located in Gökçeada where specimens were collected from a sandy carbonate sequence of early Bartonian age (note that only sample GIZA8 comes from upper Lutetian-Bartonian transitional beds, the other samples are from the Bartonian). Numbers denote growth stages assuming that the auxiliary chamber is the 4<sup>th</sup> chamber after the formation of the trilocular embryonic apparatus. SBZ zones after Less and Özcan (2012).

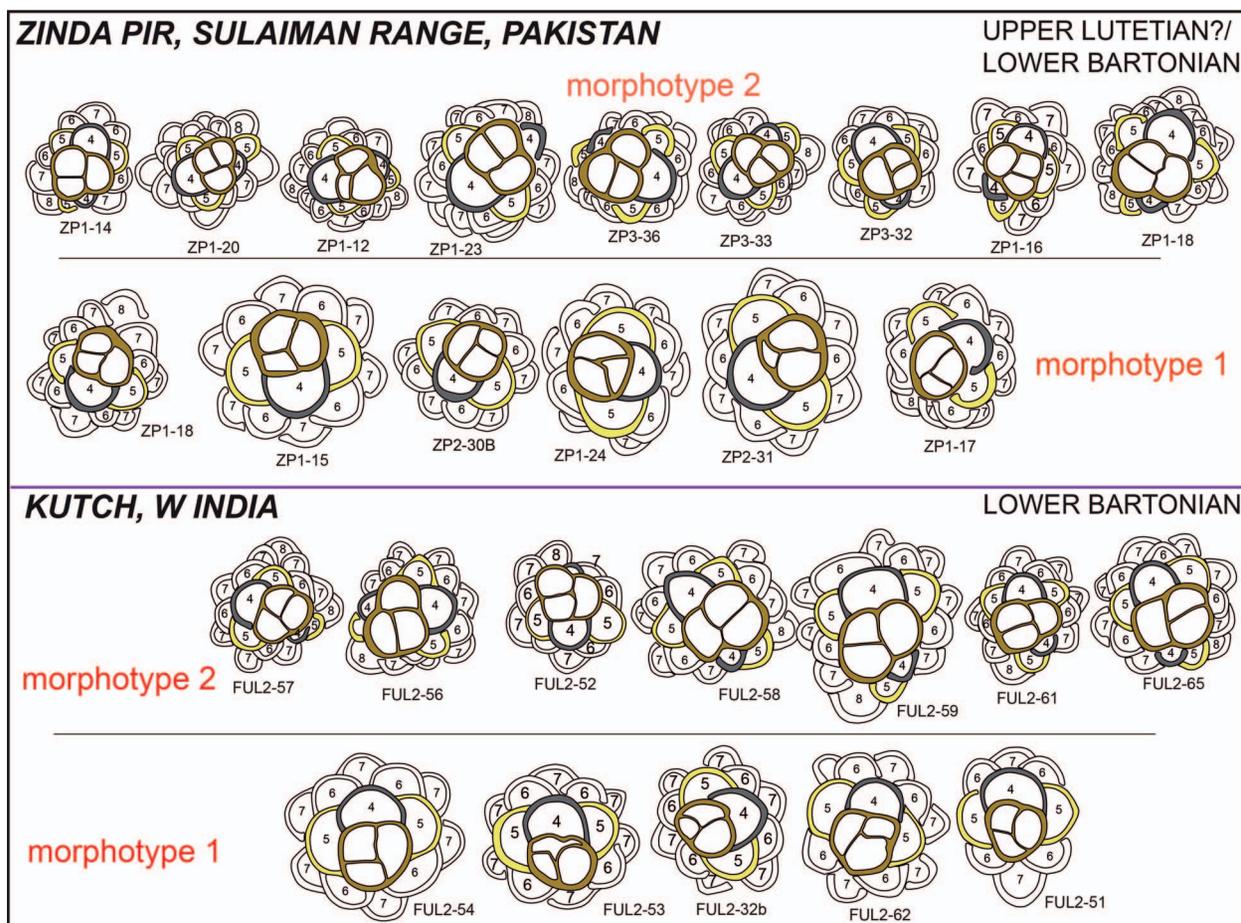


FIGURE 13. Line drawings of the embryonic and peri-embryonic chambers/chamberlets of *Linderina brugesi* Schlumberger from the Pir Koh and Fulra formations in Pakistan and India respectively. See Ali et al. (2018) for the stratigraphic information on the Pir Koh and Özcan et al. (2018b) for the Fulra formations.

and *Eoannularia*, is *Planorbulinella*, which probably arose from a *Cibicides*-like ancestor in the early Eocene (Drooger, 1993; BouDagher-Fadel, 2018). *Planorbulinella* has a cosmopolitan distribution in the Eocene, so could have formed a root stock from which various lineages of *Linderina* and *Caudriella* developed.

It seems more likely that dispersal across oceans occurred by adult foraminifera being attached to rafted material (e.g., algal grass), or that propagules became caught up in currents and were transported over large distances, possibly with the assistance of ‘island-hopping’ (Vaughan, 1933; Adams, 1967; Todd, 1976; Alve, 1999; Langer & Hottinger, 2000; Murray, 2006). In terms of transport direction, the prevalent view (Adams, 1967, 1973; Neumann et al., 1986; Butterlin, 1987; Drooger & Rohling, 1988; Renema, 2002; Mello e Sousa et al., 2003; BouDagher-Fadel & Price, 2010, 2013, 2014, 2017; Benedetti et al., 2018; BouDagher-Fadel, 2018) has been that dispersal of many LBF groups took place in an eastwards direction, from the evolutionary “incubator” of the Caribbean region, across to West Africa (especially at times of low eustatic sea-level), thence northwards into the Mediterranean region (with a possible branch southward

into southern Africa) and then into the Middle East, India and finally South-East Asia. Such a hypothesis is supported by age differences in the palaeogeographic distribution of taxa. For example, the early nummulitid which migrated across the Atlantic reached the Indo-West Pacific region 2 my after their appearance in the Western Tethys (Renema, 2002; BouDagher-Fadel & Price, 2014). *Lepidocyclus* appeared in the middle Eocene of the Americas, not achieving a circumglobal distribution until the Oligocene (Adams, 1973; Butterlin, 1987; BouDagher-Fadel & Price, 2010). By contrast, orthophragminids show no such significant diachroneity of distribution, being present in upper Paleocene rocks globally (Adams, 1973; BouDagher-Fadel & Price, 2017).

In this model *Caudriella* would have evolved in the Caribbean and then dispersed eastward through the Mediterranean and into the Thrace Basin and then possibly further eastward. Yet, as noted by Brun et al. (1982) and Butterlin (1987), such a view contrasts with views of Eocene surface current circulation patterns (e.g., Huber & Sloan, 1999; Bice et al., 2000; Huber et al., 2003), that are dominantly westwards at tropical latitudes (Fig. 14). For

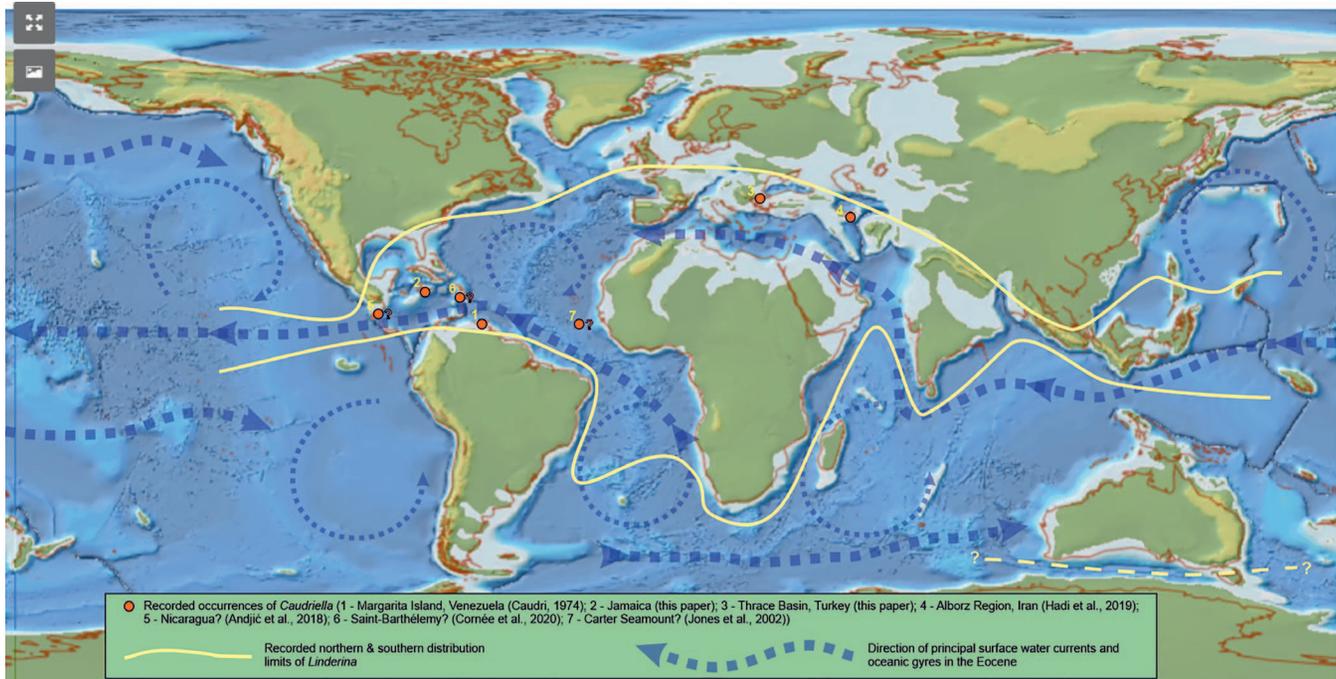


FIGURE 14. Palaeogeographic distribution of the Eocene LBF genera *Caudriella* and *Linderina*. Eocene (Lutetian) palaeogeography and palaeocurrent directions simplified after Huber & Sloan (1999), Bice et al. (2000), Huber et al. (2003), and Halliburton Neflex® product suite.

example, in the Eocene (Fig. 14), current flow through the Mediterranean region was dominantly westwards, and in the southern tropical Atlantic, currents flowed north-westward from the west African coast to the northeast coast of South America (as do the modern Guinea and South Equatorial currents), and then through the gap between North and South America into the Pacific. Such circulation patterns fit with the established controlling factors on surface current direction, such as trade winds towards the west near the equator and a clockwise gyre pattern in the North Atlantic and anti-clockwise gyre pattern in the South Atlantic (Colling, 2001; Thomas & Bowers, 2012; Garrison & Ellis, 2015). The open seaway through the Caribbean from the Atlantic to Pacific prevents equatorial counter-currents developing.

Eastward transport from the Caribbean would require initial dispersal north-eastward along the Gulf Stream (Adams, 1967), skirting the North American landmass (where there are few LBF records), and then across the Atlantic where it is wide, to Western Europe. Eustatic sea-level falls (Miller et al., 2020) are unlikely to have been of sufficient magnitude to significantly influence dispersal. This topic needs more research, including a review of the ages of occurrences of taxa at each location they are found. *Caudriella* at its Venezuelan type locality is early Bartonian in age (with primitive forms reported herein from the Lutetian of Jamaica), whilst the records from the Thrace Basin are late Bartonian or Priabonian. A possible record from the Iranian Alborz is Bartonian in age (Hadi et al., 2019). These data point to an eastward dispersal, but the data are too sparse to be conclusive. A review of the occurrences of *Linderina* and other taxa is under-

way which will hopefully provide some further information on this topic.

## CONCLUSIONS

The equatorial sections of the studied specimens show that *Caudriella* possesses a small trilocular embryonic apparatus, similar to that of the genus *Linderina*, as stated by Ferrández-Cañadell & Serra-Kiel (1999). The observations of these authors depend on the comparison of Tethyan *Linderina brugesi* (from France) with the genus from Venezuela. The *Caudriella* specimens in our material also have a similar nepionic arrangement to those from Venezuela as the embryonic apparatus at both localities is followed by a large, fourth chamber. This chamber in our specimens leads to the formation of two chamberlets in the next budding step (5<sup>th</sup> budding step), but to three chamberlets in the specimens from Venezuela. The following arcuate equatorial chamberlets are also very similar in the specimens from both localities.

The record of *Caudriella* in the Bartonian-Priabonian sequence in northwestern Turkey suggests a palaeogeographic distribution of the genus from the Caribbean region to the Neo-Tethys. *Caudriella* occurs rarely in the studied material, and this circumstance may explain why previous studies failed in identifying the genus in the well-studied Eocene deposits of the Neo-Tethys. Our data permit us to extend the stratigraphic distribution of the genus from the lower Bartonian to the end of Priabonian. A provisional record of the genus from Jamaica may imply that its lower range extends to the Lutetian. Limited data suggests eastward-directed dispersal of the genus, even though this would be

counter to most of the prevailing surface currents during the Eocene.

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