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The bivalve *Anopaea* (Inoceramidae) from the Upper Jurassic-lowermost  
Cretaceous of Mexico

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Abstract

In Mexico, the Upper Jurassic to lowermost Cretaceous La Casita and coeval La Caja and La Pimienta formations are well-known for their abundant and well-preserved marine vertebrates and invertebrates. The latter include conspicuous inoceramid bivalves of the genus *Anopaea* not formally described previously from Mexico. *Anopaea bassei* (Lecolle de Cantú, 1967), *Anopaea* cf. *stoliczkai* (Holdhaus, 1913), *Anopaea* cf. *callistoensis* Crame and Kelly, 1995 and *Anopaea* sp. are rare constituents in distinctive Tithonian-lower Berriasian levels of the La Caja Formation and one Tithonian horizon of the La Pimienta Formation. *Anopaea bassei* was previously documented from the Tithonian of central Mexico and Cuba, while most other members of *Anopaea* described here are only known from southern high latitudes. The Mexican assemblage also includes taxa which closely resemble *Anopaea stoliczkai* from the Tithonian of India, Indonesia and the Antarctic Peninsula, and *Anopaea callistoensis* from the late Tithonian to ?early Berriasian of the Antarctic Peninsula. Our new data expand the palaeogeographical distribution of

the high latitude *Anopaea* to the Gulf of Mexico region and substantiate faunal exchange, in the Late Jurassic-earliest Cretaceous, between Mexico and the Antarctic Realm.

Keywords: *Anopaea*, Late Jurassic, earliest Cretaceous, La Caja/La Pimienta formations, palaeobiogeography.

## 1. Introduction

Late Jurassic to earliest Cretaceous marine sediments are widespread in northeastern and central Mexico, but inoceramid bivalves are only mentioned occasionally (e.g., Burckhardt, 1930; Burckhardt and Mülleried, 1936; Cantú-Chapa, 1967; Mora et al., 2000; Buchy et al., 2003). A few taxa were illustrated (Cantú-Chapa, 1989; López-Caballero, 2009) but formal descriptions are rare to date (Felix, 1891; Lecolle de Cantú, 1967; Villaseñor et al., 2005).

Here we document 19 inoceramid bivalves of the genus *Anopaea* from the La Caja Formation of Coahuila, Nuevo León and San Luis Potosí, and from the La Pimienta Formation of Puebla (Fig. 1). The specimens were collected from different stratigraphic levels and were assigned to *Anopaea bassei* (Lecolle de Cantú, 1967), *A. cf. stoliczkai* (Holdhaus, 1913), *A. cf. callistoensis* Crame and Kelly, 1995 and *Anopaea* sp. The Late Jurassic-Early Cretaceous genus *Anopaea* is a characteristic constituent in both the Boreal and the Austral realms (e.g., Crame, 1981; Kelly, 1984; Dhondt, 1992; Crame and Kelly, 1995; Sha, 1996; Damborenea et al., 2013), but isolated occurrences include the Tithonian of the Carpathian Alps (Boehm, 1883), the late Tithonian of Cuba (Myczyński, 1999), the Tithonian of Mexico (Cantú-Chapa, 1967; Lecolle de Cantú, 1967; Cantú-Chapa, 1989) and the late Tithonian of

Indonesia (Westermann et al., 1978). Here we document *Anopaea* from northeastern and central-east Mexico and discuss the palaeobiogeographic and palaeoclimatic implications of their presence in Mexico.

## FIGURE 1

### 2. Depositional environments and stratigraphic ages

Late Jurassic to earliest Cretaceous sediments occur widely in northeastern, eastern and central Mexico and are known as the La Pimienta Formation (Cantú-Chapa, 1967; Goldhammer, 1999; Goldhammer and Johnson, 2001; Pessagno et al., 2009) deposited under hemipelagic conditions, and the La Caja Formation (Imlay, 1936; Longoria, 1984; Pessagno et al., 2009), which is regarded as the time-equivalent proximal to distal shelf facies (e.g., Goldhammer, 1999; Goldhammer and Johnson, 2001). Overall, the sedimentary succession is transgressive in the two lithostratigraphic units, with strong transgressional pulses during the middle Kimmeridgian, the early and late Tithonian, and the early Berriasian (Goldhammer and Johnson, 2001; Olóriz et al., 2003; Jenchen, 2007; Ocampo-Díaz et al., 2008; Pessagno et al., 2009). Lithologies are predominantly siliciclastic and composed of conglomerate, sandstone, shale and marl, while the Kimmeridgian-Tithonian part of the La Caja Formation yields additional phosphatic sediments (e.g., Imlay, 1936, 1938; Rogers et al., 1956; Michalzik, 1988; Goldhammer and Johnson, 2001; Zell et al., 2013, 2014b). The La Caja and the coeval, comparatively more distal La Pimienta formations are widely known for their abundant and well-preserved marine vertebrate and invertebrate assemblages. Most taxa are endemic to the ancient Gulf of Mexico but some show affinities with the European Tethys (e.g., Cantú-Chapa, 1967; Lecolle

de Cantú, 1967; Verma and Westermann, 1973; Buchy et al., 2003; Buchy, 2010; Zell et al., 2014a, b; Frey and Stinnesbeck, 2014a, b). On the other hand, belemnites assigned to *Cylindroteuthis* and the bivalve *Buchia* are of Boreal origin (Seibertz and Spaeth, 1999, 2008; Mora et al., 2000; López-Caballero, 2009; Pessagno et al., 2009; Zell et al., 2013).

The bivalves described here were collected in the upper La Caja and the upper La Pimienta formations of northeastern and central Mexico. For locations see Figure 1; for the stratigraphic position of bivalves within the sediment unit see Figure 2. Shells are mostly preserved three-dimensionally, but a few are flattened and one is preserved with both their valves in “butterfly position” (see *Anopaea* cf. *callistoensis* Crame and Kelly, 1995; Fig. 6a).

## FIGURE 2

### 3. Systematic palaeontology

Bivalve classification follows Bieler et al. (2010), morphological terms used in the text are shown in Figure 3, discussion of higher taxonomic levels follows Cox et al. (1969) and Lazo (2006). Measurements are taken at the maximum axial altitude (al) where a complete set of data is possible, maximum al preserved is also indicated as  $al_{max}$ . All specimens described here are housed in the *Colección de Paleontología de Coahuila* (CPC), at the Museo del Desierto, Saltillo, Coahuila, Mexico.

## FIGURE 3

Class BIVALVIA Linné, 1758 (Buoanni, 1681)

Subclass PTERIOMORPHA Beurlen, 1944

Order PTERIOIDA Newell, 1965

Suborder PTERIINA Newell, 1965

Superfamily PTERIOIDEA Gray, 1847

Family INOCERAMIDAE Zittel, 1881

Genus *Anopaea* Eichwald, 1861

**Type species:** *Inoceramus lobatus* Auerbach and Frears, 1846

*Anopaea bassei* (Lecolle de Cantú, 1967)

Fig. 4

1967. *Inoceramus bassei* sp. nov. – Lecolle de Cantú, p. 31-32, pl. 9, figs. 1-6.

1989. *Inoceramus bassei* Lecolle – Cantú-Chapa, pl. 1, fig. 1.

1999. *Anopaea* sp. aff. *Anopaea callistoensis* Crame and Kelly – Myczyński, p. 85, pl. 4, figs. 1, 2, 4, 7.

**Material:** One incomplete specimen from La Peñita, Nuevo León (CPC-1443), one incomplete right valve from a phosphate pit at Puerto Piñones, Coahuila (CPC-1444, Fig. 4f), one incomplete right valve from Sierra El Jabalí, Coahuila (CPC-1445, Fig. 4a), one incomplete left valve (CPC-1446, Fig. 4b) and four incomplete right valves (CPC-1447, Fig. 4c; CPC-1448, Fig. 4d; CPC-1449, Fig. 4e; CPC-1450, Fig. 4g) from Mazatepec, Puebla. Dimensions are provided in the table below and abbreviations used therein are explained in Figure 3.

**Description:** Large-sized *Anopaea* with a rounded-wedge shaped outline and a prominent posterior and anterodorsal region. The dorsal margin is straight; the

anterior, ventral and dorsal margins are widely rounded. The gently anteriorly-curved, small pointed beak is situated slightly below the hinge (Fig. 4f<sub>2</sub>). The anterior side of the umbo drops sharply away in a deeply excavated curve; a prominent lunule is present (Figs. 4f<sub>2</sub> & 4e<sub>2</sub>). Our specimens are weakly inflated with maximum degree of convexity in the umbonal region. An anterior sulcus is not present. Corrugations are regularly spaced and narrow; they reach maximum widths of about 3 mm (2.8 corrugations per 10 mm height in specimen CPC-1448, Fig. 4d). They have rounded summits and a symmetrical cross-profile. The interspace width gradually increases from 0.6 mm across the umbo to 1.6 mm near the ventral margin (CPC-1448, Fig. 4d). Ribs weaken towards the dorsal, posteroventral and anterodorsal margins. Traces of six oval to nearly rectangular ligament pits are seen on the internal mould and reach to 0.8 mm in width (CPC-1449, Fig. 4e<sub>2</sub>).

Specimens CPC-1445 (Fig. 4a; shell preservation) and CPC-1450 (Fig. 4g; internal mould) are associated with prominent tubes situated at the transition between the anterior and dorsal, and between the posterior and dorsal margins; they are accompanied by siphonal gapes. The tubes are about 10 mm in width in both the large-sized ( $H_{\text{preserved}}=82.5$  mm) specimen CPC-1445 (Fig. 4a) and the smaller-sized ( $H=27.1$  mm) specimen (internal mould) CPC-1450 (Fig. 4g); their preserved length reaches 25 mm in CPC-1445. The tubes are projected postero- and anterodorsally; they curve upwards in the well-preserved right valve of specimen CPC-1450 (Fig. 4g). The shell of valve and of both tubes is preserved in specimen CPC-1445 (Fig. 4a), but tubes are flattened due to lithologic overburden. They are unornamented, without any evidence of growth lines or any other type of structures. A direct connection between the valve and accompanying tubes cannot be observed, but both tubes move into their associated siphonal gapes. The internal mould of a right valve

(CPC-1444, Fig. 4f) exhibits a downward directed, tube-like structure projecting through the lunule.

**Dimensions:**

**TABLE 1**

**Discussion:** The rounded-wedge shaped outline, the presence of a prominent lunule and the prominent, regular narrow-spaced corrugations characterize the genus *Anopaea* (Crame, 1981; Crame and Kelly, 1995). Although Myczyński (1999) and Pszczółkowski and Myczyński (2003) suggested that *Inoceramus bassei* should be assigned to *Anopaea stoliczkai*, we agree with Lecolle de Cantú (1967) that *Anopaea bassei* is a valid species, which closely resembles *A. stoliczkai* but differs by stronger ribbing across the umbo, more regularly spaced ribs, slightly stronger inflation of valves and smaller-sized ligament pits (*A. bassei*: 0.8 mm; *A. stoliczkai*: <2 mm in width, see Crame, 1981, p. 212). *Anopaea stoliczkai* described by Crame (1981, pl. 1, fig. a-f) has a more rounded outline, and is less obviously pyriform. There is also a more prominent, flattened postero-dorsal area on both, left and right valves. The internal moulds of *Anopaea* sp. aff. *Anopaea callistoensis* from the upper Tithonian of Cuba were described by Myczyński (1999), are here interpreted to belong to *Anopaea bassei*. The Cuban specimens are morphologically inseparable from *Anopaea bassei* described by Lecolle de Cantú (1967), and from the present specimens. Prominent tubes and their siphonal gapes are here described for *Anopaea* for the first time. The two prominent, upward-projected, calcified tubes are interpreted as siphons and indicate that the bivalve was buried in the substrate. Modern deep burrowing bivalves such as *Mya* and *Lutraria* are characterized by long



siphons. They are de facto sessile endobenthonic elements, living at >300 mm depth (Cox, 1969). *Anopaea bassei* had two siphons, possibly inhalant and exhalant, providing access to the bottom water, similar perhaps to the modern *Loripes lucinalia* (Lamarck) (Cox, 1969, p. N4, fig. 1.1). The orientation of *Anopaea bassei* may thus have resembled that of Recent Tellinidae, which are placed immediately below surface, with the commissure horizontal and the right valve representing the upper one (Cox, 1969). The function of the prominent downward-directed structure in specimen CPC-1444 (Fig. 4f<sub>2</sub>) is not known and cannot be determined due to insufficient preservation (internal mould) of the single specimen.

**Occurrence:** *Anopaea bassei* was first described by Lecolle de Cantú (1967) from the middle Tithonian La Pimienta Formation at Mazatepec, Puebla, southern Mexico, associated with the ammonites *Kossmatia victoris* and *Pseudolissoceras zitteli* (described by Cantú-Chapa, 1967), but also occurs in upper Tithonian sediments in the subsurface of Nuevo León (Pozo Corral 1), northeastern Mexico (Cantú-Chapa, 1989). Myczyński (1999) reported *Anopaea* sp. aff. *Anopaea callistoensis* from the upper Tithonian of Cuba. These specimens are here interpreted to represent specimens of *Anopaea bassei*. At Sierra El Jabalí (Fig. 1), *Anopaea bassei* occurs in a lowermost Berriasian (Calpionella Zone, Zone B), 8 mm-thick, dark grey marl at approximately 2.5 m below the La Caja-Taraises formations boundary. The belemnite *Rhaphibelus aciculiformis* Zell et al. 2013 is present 10 mm below the horizon under consideration and was also interpreted to be of earliest Berriasian age (Zell et al., 2013).

Stratigraphic assignment of the horizon is based on calpionellids identified by Adatte et al. (1994) at Sierra El Jabalí. At La Peñita (Fig. 1), *Anopaea bassei* was identified at the base of a 1.8 m-thick dark grey limestone of the lowermost Berriasian Calpionella Zone B at 11 m below the top of the La Caja Formation and from a

phosphate pit at Puerto Piñones assigned to the Tithonian. At Mazatepec, *Inoceramus bassei* was sampled from the riverbed of the Rio Tecolutla (Fig. 1) and we cannot provide a precise horizon of origin. However, our sampling site can be correlated to approximately the middle Tithonian point 4 of the La Pimienta section illustrated by Cantú-Chapa (1967, p. 15), slightly below the “*Suarites* beds” (point 3). Lecolle de Cantú (1967) identified the species at Mazatepec which was there assigned to the middle Tithonian.

#### FIGURE 4

*Anopaea* cf. *stoliczkai* (Holdhaus, 1913)

Fig. 5

**Material:** Two incomplete, flattened right valves (CPC-1452, Fig. 5b; CPC-1453, Fig. 5c) and one incomplete, slightly flattened left valve (CPC-1451, Fig. 5a) from El Verde, San Luis Potosí. Dimensions are provided in the table below and abbreviations used therein are explained in Figure 3.

**Description:** Large-sized *Anopaea* with a prominent posterior region. The valve margins are not completely preserved in our material, but a rounded wedge-shaped outline is indicated. The dorsal margin is straight; the posterior margin is moderately convex and is only partially preserved in one specimen (CPC-1452, Fig. 5b). The ventral and posterior margins seem to be widely rounded. The beak is small and pointed, gently anteriorly curved; it is situated slightly above the hinge (Fig. 5a<sub>2</sub>). The anterior side of the umbo drops sharply away in a deeply excavated curve; a prominent lunule is present (Fig. 5a<sub>2</sub>). Our specimens are only weakly inflated with maximum degree of convexity in the umbonal region. An anterior sulcus is not

present. Regularly to irregularly spaced narrow corrugations reach maximum widths of about 4 mm (1.5 corrugations per 10 mm height in specimen CPC-1452, Fig. 5b). They have rounded summits and are symmetrical in cross-profile. The interspace width gradually increases from 1.4 mm across the umbo to 6.7 mm near the ventral margin (CPC-1453, Fig. 5c). Ribs become finer towards the dorsal margin and weaken towards the posterior margin. The umbo is unornamented.

**Dimensions:**

**TABLE 2**

**Discussion:** Our material lacks the genus-characteristic anterior sulcus. Even though, specimens assigned to *Anopaea* by Crame (1981) also lack an anterior sulcus; this author also included specimens described by Holdhaus (1913) and he discussed the variable strength of ribs and their interspaces, similar to the individuals described here. Due to the low quality of preservation, the shape and the outline of our valves are not conclusively determinable, but preserved features are indistinguishable from characteristics seen in *Anopaea stoliczkai* (Holdhaus, 1913, p. 418, pl. 98, figs. 10-11; Crame, 1981, p. 212, pl. 1, figs. a-f).

**Occurrence:** The most similar species, *Anopaea stoliczkai*, was first described from the lower Tithonian of India by Holdhaus (1913), but the taxon was also reported from the Tithonian of eastern Alexander Island, Antarctic Peninsula (Crame, 1981) and the upper Tithonian of Indonesia (undescribed and unfigured in Westermann et al., 1978; discussed by Crame, 1981). At El Verde (Fig. 1), two horizons yielding *Anopaea cf. stoliczkai* are situated within the upper middle to lower upper Tithonian *Kossmatia* Beds, in a 4 m-thick silty limestone unit within an interval rich in

phosphatic horizons. Stratigraphic assignment of both horizons is based on ammonites identified by Verma and Westermann (1973), and on data summarized by Villaseñor et al. (2012).

## FIGURE 5

*Anopaea* cf. *callistoensis* Crame and Kelly, 1995

Fig. 6

**Material:** One almost complete right valve, one incomplete right valve (CPC-1454, Fig. 6a) and one incomplete, deformed left valve (CPC-1455, Fig. 6c) from Puerto Piñones, Coahuila, and two complete right valves (CPC-1456a & b, Fig. 6b) from Sierra El Jabalí, Coahuila. Dimensions are provided in the table below and abbreviations used therein are explained in Figure 3.

**Description:** Medium-sized, equivalve *Anopaea* with an elongate-rectangular outline and a weak posteroventral sulcus with a subrectangular outline. The dorsal margin is straight; the anterior margin is moderately convex and slightly shorter than the more convex posterior margin. The ventral margin is widely rounded in the largest-sized specimen (CPC-1455, Fig. 6c) and short and convex in the smaller-sized specimens. The umbones are prominent and prosogyrous; the beaks are situated slightly above the hinge. The lunule is well developed. Our specimens are weakly (CPC-1456, Fig. 6b) to moderately (CPC-1454, Fig. 6a) inflated, with maximum convexity reached in the umbonal and central regions and a considerable flattening towards the anterodorsal and posterodorsal regions. Regularly spaced fine growth lines are present as well as low irregular commarginal folds. Specimen CPC-1454 (Fig. 6a) is

ornamented by regularly spaced corrugations reaching maximum widths of about 0.9 mm. They have acute summits and are symmetrical in cross-profile. A small, “ear-like” anterior buttress is present in specimen CPC-1454 (Fig. 6a).

**Dimensions:**

**TABLE 3**

**Discussion:** Specimens described here are relatively small ( $H_{\max.}=31.4$  mm; CPC-1455) and are interpreted to represent juveniles, as also suggested by their typically more erected outline as compared to adult specimens (cf. Crame and Kelly, 1995). *Anopaea callistoensis* is characterized by very fine concentric ribs, which are superimposed on low folds (Crame, 1981, p. 213, pl. 2, figs. e-j; Crame and Howlett, 1988, p. 15, fig. 6a; Crame and Kelly, 1995, p. 93, pl. 1, figs. 1-7, text-figs. 3a-b, d-e, 4b). This distinctive ornament pattern is not present in our material, possibly due to poor preservation and lack of adult specimens. Thus, a precise assignation of our specimens to *Anopaea callistoensis* is not possible. Crame (1981) and Crame and Kelly (1995) discussed the similarities between *Anopaea callistoensis* and the coeval Russian *A. brachowi* (Rouillier) and *A. sphenoides* (Gerasimov). From these species, *A. callistoensis* and our specimens are distinguished by a subrectangular posterior margin and by less regularly spaced commarginal folds.

**Occurrence:** *Anopaea callistoensis* is known from the lower Tithonian (Crame, 1981; Butterworth et al., 1988; Crame and Howlett, 1988) to possibly lower Berriasian (Crame and Kelly, 1995) of Alexander Island, Antarctic Peninsula. At Puerto Piñones (Fig. 1), *Anopaea* cf. *callistoensis* occurs rarely close to the formational top, 3 m below the base of the overlying Taraises Formation in a lowermost Berriasian (cf.

Adatte et al., 1991, 1996; López-Caballero, 2009; Zell et al., 2013) marl of 10 to 20 mm thickness. At Sierra El Jabalí (Fig. 1), close to the village Gomez Farías, *Anopaea* cf. *callistoensis* occurs in a lowermost Berriasian (lower Calpionella Zone B), 10 mm-thick marly siltstone at approximately 33 m below the La Caja-Taraises formations boundary. Stratigraphic assignment of the horizon is based on calpionellids identified by Adatte et al. (1994) at Sierra El Jabalí.

## FIGURE 6

*Anopaea* sp.

Fig. 7

**Material:** Three incomplete left valves (CPC-1457, Fig. 7a; CPC-1458, Fig. 7b; CPC-1459, Fig. 7c) and one incomplete right valve (CPC-1460, Fig 7d) from El Chorro, Coahuila. Dimensions are provided in the table below and abbreviations used therein are explained in Figure 3.

**Description:** Small to medium sized *Anopaea*. The dorsal margin is straight; the anterior margin is moderately convex and shorter than the posterior margin, which is also more convex. The ventral margin is not preserved but the ventral-most ribs indicate that it is straight to moderately convex. The umbo is prominent and situated anteriorly, at one third of the dorsal margin (CPC-1459, Fig. 7c). A lunule is seen in CPC-1457 (Fig. 7a). Our specimens are moderately inflated, with a maximum degree of convexity in the umbonal region and notable flattening posteroventrally. Growth lines are regularly spaced, fine and low. In addition, irregular concentric commarginal folds are present. Regularly spaced fine corrugations are seen in CPC-1457 (Fig. 7a)

and reach maximum widths of about 0.6 mm. Corrugations exhibit rounded summits and are symmetrical in cross-profile.

**Dimensions:**

**TABLE 4**

**Discussion:** Due to insufficient preservation, a specific assignation is not possible. However, the Mexican specimens exhibit the species-characteristic regularity of ornamentation of *Anopaea trapezoidalis* (Thomson and Willey, 1972), which is unknown from other taxa of *Anopaea* (Crame, 1981, p. 215). However, ornamentation in *A. trapezoidalis* (Thomson and Willey, 1972) differs from the present specimens in comparatively deep interspaces with a U-shaped profile, which separate even, regular, sub-parallel ribs.

**Occurrence:** The El Chorro site is situated on the southwestern flank of the Sierra de Los Chorros (Fig. 1). *Anopaea* sp. was sampled there from the upper portion of the La Caja Formation (Tithonian-lowermost Berriasian). We cannot assign the specimens to a specific horizon of origin.

**FIGURE 7**

**4. Discussion**

Most taxa known to date of the genus *Anopaea* were reported from the Boreal and Austral realms, and Tethyan occurrences are rare (e.g., Crame, 1981, 2002). The presence of four different *Anopaea* species (*Anopaea bassei*, *A. cf. stoliczkai*, *A. cf. callistoensis* and *Anopaea* sp.) in the Gulf of Mexico region of northeastern and

central Mexico is therefore unexpected. The high diversity is even more surprising when the palaeobiogeographic relationship and distribution of these taxa is considered. The *Anopaea* taxa from northeastern and central Mexico are most closely related to species known from the Antarctic Peninsula (Thomson and Willey, 1972; Crame 1981, 1982; Crame and Howlett, 1988; Butterworth et al., 1988; Crame and Kelly, 1995), where they are relatively abundant, and to taxa from northern India (Holdhaus, 1913), Indonesia (Westermann et al., 1978) and eastern Cuba (Myczyński, 1999) (Fig. 8), where occurrences are rare.

*Anopaea stoliczkai* is documented from Antarctica (Crame, 1981) and was also reported from the lower Tithonian of India (Holdhaus, 1913) and the upper Tithonian of Indonesia (Crame, 1981). The Mexican occurrences are from two sediment horizons in the upper middle to lower upper Tithonian in northern San Luis Potosí.

*Anopaea callistoensis* was documented from the lower Tithonian to possible lower Berriasian of the Antarctic Peninsula (summarized by Crame and Kelly, 1995).

*Anopaea cf. callistoensis* is here described from the lowermost Berriasian of southern Coahuila and *Anopaea* sp. from the upper part of the Tithonian or lowermost Berriasian of southern Coahuila. The Mexican *Anopaea* spp. therefore add important evidence to the hypothesis that a faunal connection existed during the latest Jurassic (Tithonian) and earliest Cretaceous (Berriasian) between the Antarctic Realm and the Gulf of Mexico. This migratory pathway was previously suggested by Myczyński (1999) based on the presence of *Anopaea* in the upper Tithonian of eastern Cuba.

Based on ammonites, Khudoley (1974) and Salazar (2012) also suggested that the faunal connections between the eastern Pacific and the Gulf of Mexico were stronger than expected. At Mazatepec, *Anopaea bassei* appears slightly below the Tithonian “*Suarites* beds” (point 3; Cantú-Chapa, 1967, p. 15). Based on ammonites, this unit,



which was also identified at Sierra de Catorce, Chihuahua (Cantú-Chapa, 1976), shows closest resemblance to the Interspinosum Zone of the Andes (Hillebrandt et al., 1992). Inoceramids and buchiids from the upper Tithonian of Sierra de los Organos, Cuba, are associated with ammonites of Pacific origin (Myczyński, 1989; Pszczólkowski and Myczyński, 2003). *Anopaea bassei* here described from the Tithonian of Coahuila and Nuevo León, was previously reported only from the middle Tithonian of central Mexico (Lecolle de Cantú, 1967), the upper Tithonian of northeastern Mexico (Cantú-Chapa, 1989), and from the upper Tithonian of eastern Cuba (Myczyński, 1999). The species is thus known only from the Gulf of Mexico and here regarded to be endemic to this region.

The Late Jurassic “circum-Tropical marine Current” was directed westward, transporting water from the Atlantic through the ancient Gulf of Mexico into the Pacific (Iturralde-Vinent, 2003, and references therein). This situation changed during the Berriasian, when northward-directed surface currents established along the western margin of South America. These currents entered the ancient Gulf of Mexico and water masses were transported in a northeastern direction into the ancient Atlantic (Scotese and Moore, 2014). *Anopaea* likely originated in the Antarctic Realm or India (e.g. Spiti Shales of Himalayas; Holdhaus, 1913) but migrated westwards into the ancient eastern Pacific during the Middle Jurassic plate margin re-organisation of Antarctica (e.g., Elliot, 2013). This opening, accompanied by a global transgression, led to the formation of a shallow intermittent epicontinental seaway between east Africa and southern Patagonia during the Tithonian-Berriasian (Riccardi, 1991) and was likely accompanied by changing environmental conditions and the generation of a new oceanic current system with intermittent transport of cold water from the Antarctic Realm into the eastern Pacific, and from there across the Balsas Portal

(Imlay, 1940; Arkell, 1956; López-Ramos, 1981) into the Gulf of Mexico. The expansion of Antarctic cold-water currents into the tropics and subtropics could have been a driving factor for the intermittent expansion of Antarctic bivalve faunas into northeastern and central Mexico and eastern Cuba. Crame (1981) suggested that the distribution of *Anopaea* was controlled predominantly by facies rather than the result of climatic zonation. Nevertheless, the intermittent presence of cool nutrient-rich water masses is indicated in northeastern Mexico by the repeated occurrence of phosphate-rich sediment units (e.g., Rogers et al., 1956; Zell et al., 2013, 2014b) and is likely related to upwelling (e.g., Michalzik, 1988; Zell et al., 2014b). Thus, the presence of *Anopaea* in Mexico may be related to upwelling, offering cold-water environments at least at or near the seafloor.

## FIGURE 8

*Anopaea* species identified here are rare and restricted to specific intervals of the La Caja and La Pimienta formations. Even in these units the diversity of *Anopaea* is low and restricted to only a single taxon per horizon. In addition, no other benthic elements are associated with *Anopaea* in these horizons.

The genus *Anopaea* was largely, but not exclusively, a deep-water taxon (e.g., Crame, 1981; Crame and Kelly, 1995; Myczyński, 1999). This interpretation coincides with facies interpretations of the La Caja and La Pimienta formations, which are considered to represent hemipelagic depositional environments (e.g., Michalzik, 1988; Michalzik and Schumann, 1994; Adatte et al., 1994; Goldhammer and Johnson, 2001). In the Southern Hemisphere, the occurrence of *Anopaea* is linked to deep-water facies associated with the circum-Pacific volcanic arcs, along with buchiids,

oxytomids, certain ammonites and belemnites (among others). Our record and the Cuban occurrences (Myczyński, 1999), indicate that *Anopaea* increased in numerical importance within benthic assemblages from low to high latitudes.

Cold-water intervals were recently documented from the Upper Jurassic La Casita and La Caja formations of northeastern Mexico and are characterized by the intermittent presence of Boreal elements, such as the bivalve *Buchia* (e.g., Mora et al., 2000) and the belemnite *Cylindroteuthis* (Zell et al., 2013), and by the abundance of phosphorite-rich sediments (e.g., Rogers et al., 1956; Zell et al., 2013, 2014b). The latter were likely the result of upwelling of nutrient-rich cold bottom waters (Michalzik, 1988; Michalzik and Schumann, 1994; Zell et al., 2014b). The presence of *Anopaea* in the La Caja and La Pimienta formations therefore supports the occurrence of cold bottom-water intervals in the subtropical Gulf of Mexico region. However, the presence of the Boreal elements *Buchia* and *Cylindroteuthis* provides strong evidence for the ingression of cold water from the northeast via the Hispanic Corridor (e.g., Zell et al., 2013), while identified *Anopaea* species represent Austral elements that must have immigrated to Mexico via the Pacific ocean. This alternating intermittent presence of Boreal and Austral elements thus relates to profound changes in the Gulf of Mexico current system, with short-term ingressions from east to west through the Hispanic Corridor, and from west to east, from the Pacific through the Balsas embayment. These conditions ended near the Jurassic-Cretaceous boundary as a result of rising seawater temperatures and transgression (e.g., Abbink et al., 2001; Lécuyer et al., 2003; Gröcke et al., 2003; Olóriz et al., 2003; Ocampo-Díaz et al., 2008; Pessagno et al., 2009), which allowed for long-term access of faunal elements from the European Tethys (e.g., Adatte et al., 1994, 1996, 2001; Buchy et al., 2003).

The Antarctic immigrants (e.g. *Anopaea*) were among the first elements to disappear from the ancient Gulf of Mexico.

The palaeobiology of Upper Jurassic-lowermost Cretaceous inoceramids is poorly understood. Taxa are distributed widely from inner shelf to abyssal depths (Schneider et al., 2013), and abundance was higher close to continental landmasses and oceanic islands than in distal equivalents (Crampton, 1996 and sources mentioned therein). Likely, they were epifaunal to semi-infaunal suspension feeders using a wide range of substrate types (Schneider et al., 2013). Many Cretaceous inoceramids were tolerant to low oxygen conditions (e.g., Sageman, 1989), which would explain their presence in horizons lacking other benthic elements. In the Mexican localities discussed here low oxygen sea-floor conditions are indicated by the mono-specific benthic assemblages of *Anopaea* sp. and *Anopaea bassei* and by high  $C_{org.}$ -content in the limestone containing *Anopaea* sp. and *Anopaea bassei*, indicated by dark-color and a foul smell when split with a hammer. Crame (1981, p. 208, fig. 2) discussed the life position of *Anopaea* based on the general morphology of their valves (e.g. equivalve nature and rounded-elongated outline). He suggested that *Anopaea* was an epifaunal, endobyssally-attached surface-dweller rather than an infaunal burrower.

## 5. Conclusions

Here we discuss new and relatively complete material of the bivalve *Anopaea* from central and northeastern Mexico. The individuals were collected in the Upper Jurassic-lowermost Cretaceous (mid Tithonian-lower Berriasian) La Caja and La Pimienta formations. *Anopaea stoliczkai* (Holdhaus, 1913) and *A. callistoensis* Crame and Kelly, 1995, were previously reported from Antarctica, while *A. bassei* (Lecolle de Cantú, 1967) is here considered to be endemic to the ancient Gulf of Mexico. The

presence of Austral *Anopaea* species reflects periods of cold bottom-water ingression from the Pacific into the Gulf of Mexico and may either be related to geotectonic changes associated with the opening of the Balsas Portal in southwestern Mexico, to short intervals of global cooling, or to distinct periods of upwelling of cold and nutrient rich bottom water system. Our new findings from Mexico extend the palaeogeographic distribution of all three *Anopaea* species and provide evidence for an intermittent latest Jurassic-earliest Cretaceous faunal pathway between the Antarctic Realm, the Pacific Realm and into the Gulf of Mexico.

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### Figure captions

**Fig. 1.** Map of Mexico with insets of Upper Jurassic-lowermost Cretaceous localities studied here. Base map of Mexico simplified after Instituto Nacional de Estadística y Geografía (2013).

**Fig. 2.** Lithostratigraphic columns of the La Caja Formation showing horizons from which bivalves of the genus *Anopaea* were collected. *Anopaea* cf. *stoliczkai* is recorded from the lower upper Tithonian Kossmatia beds at El Verde; *Anopaea* cf. *callistoensis* is documented from the earliest Berriasian Calpionella Zone B at Puerto



Piñones and at Sierra El Jabalí, *Anopaea bassei* from the early Berriasian Calpionella Zone B at Sierra El Jabalí and from the earliest Berriassian Calpionella Zone B at La Peñita.

**Fig. 3.** Morphologic terms used here are illustrated for an idealized right valve of the genus *Anopaea*. They are based on Crame (1981), Walaszczyk (1992), Tröger and Summesberger (1994), Crame and Kelly (1995), Harries et al. (1996) and Walaszczyk and Cobban (in Kennedy et al., 2000). H: height; L: length; al: axial length; sa: secondary axis; bh: beak height; u: distance between two ribs; b: beak; h: hinge; l: lunule; ab: anterior buttress; as: anterior sulcus;  $\alpha$ : apical angle;  $\iota$ : inclination;  $\pi$ : posterodorsal angle.

**Fig. 4.** *Anopaea bassei* (Lecolle de Cantú, 1967). a, right valve (CPC-1445) from the lowermost Berriasian portion at Sierra El Jabalí; b, internal mould of left valve (CPC-1446) from the middle Tithonian portion of the La Pimienta Formation at Mazatepec; c, internal mould of right valve (CPC-1447) from the middle Tithonian portion of the La Pimienta Formation at Mazatepec; d, internal mould of right valve (CPC-1448) from the middle Tithonian portion of the La Pimienta Formation at Mazatepec; e, right valve view (e<sub>1</sub>) and internal view (e<sub>2</sub>) of an internal mould (CPC-1449) from the middle Tithonian portion of the La Pimienta Formation at Mazatepec; f, right valve view (f<sub>1</sub>) and dorsal view (f<sub>2</sub>) of an internal mould (CPC-1444) from a phosphate pit of Tithonian age at Puerto Piñones; g, internal mould of right valve (CPC-1450) from the middle Tithonian portion of the La Pimienta Formation at Mazatepec.

**Fig. 5.** *Anopaea cf. stoliczkai* (Holdhaus, 1913) from the upper middle to lower upper Tithonian portion of the La Caja Formation at El Verde. a, left valve view (a<sub>1</sub>) and dorsal view (a<sub>2</sub>; CPC-1451); b, right valve (CPC-1452); c, right valve (CPC-1453).

**Fig. 6.** *Anopaea cf. callistoensis* Crame and Kelly, 1995. a, two internal moulds of juvenile right valves (CPC-1454) from the earliest Berriasian portion of the La Caja Formation at Puerto Piñones; b, two juvenile right valves (CPC-1456) from the earliest Berriasian portion of the La Caja Formation at Sierra El Jabalí; c, internal mould of a left valve (CPC-1455) from the earliest Berriasian portion of the La Caja Formation at Puerto Piñones.

**Fig. 7.** *Anopaea* sp. from the Berriasian portion of the La Caja Formation at El Chorro. a, internal mould of a left valve (CPC-1457); b, internal mould of a left valve (CPC-1458); c, internal mould of a left valve (CPC-1459); d, internal mould of a right valve (CPC-1460).

**Fig. 8.** Palaeogeographic map of the Late Jurassic world (Blakey, 2014). An asterisk marks the study area. The distribution of *Anopaea* species discussed here is based on several sources mentioned in the text. Dashed lines indicate probable migration routes (including interpretations of Myczyński, 1999).

### Table captions

**Table 1.** Dimensions:

**Table 2.** Dimensions:

**Table 3.** Dimensions:

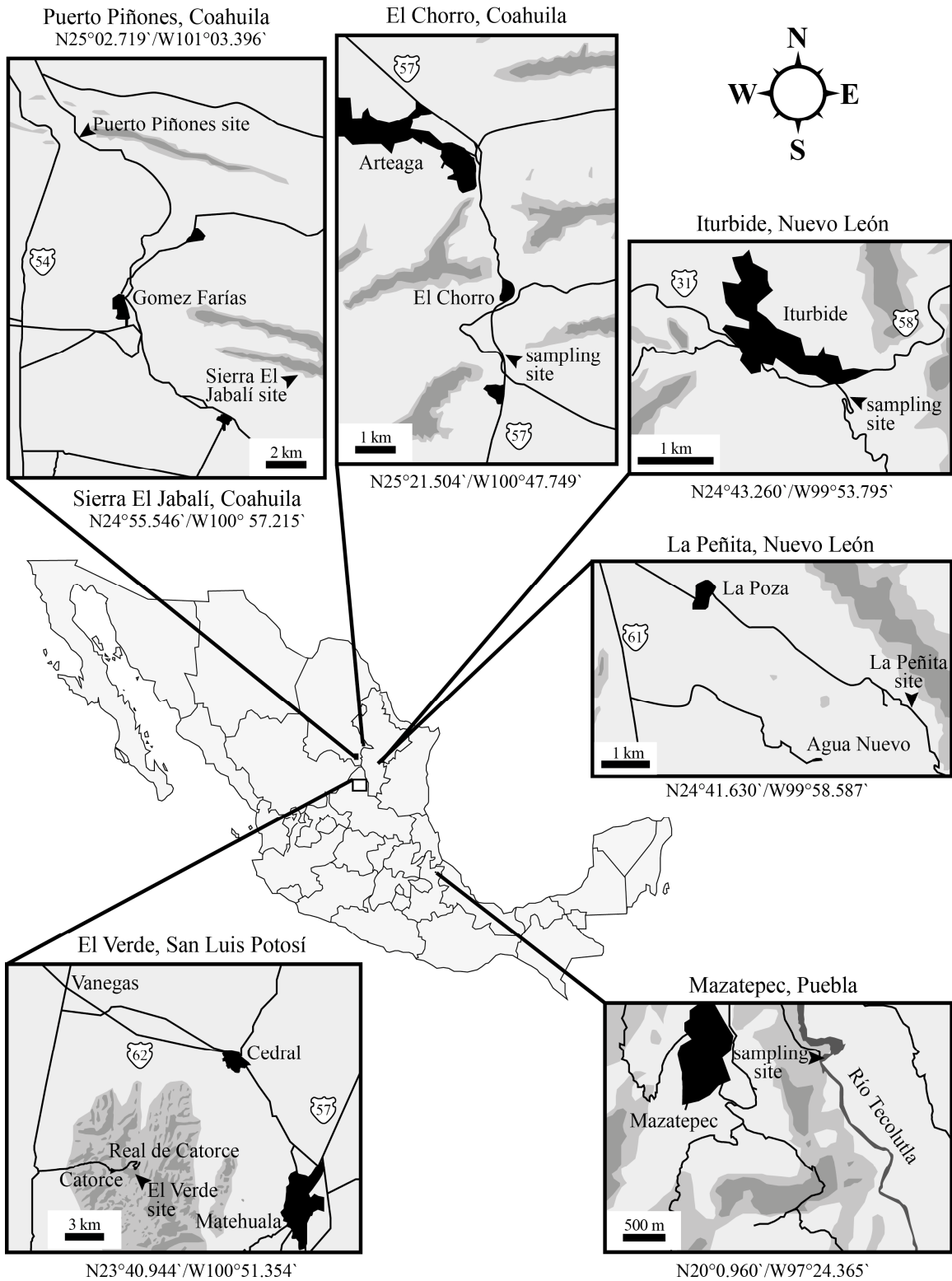
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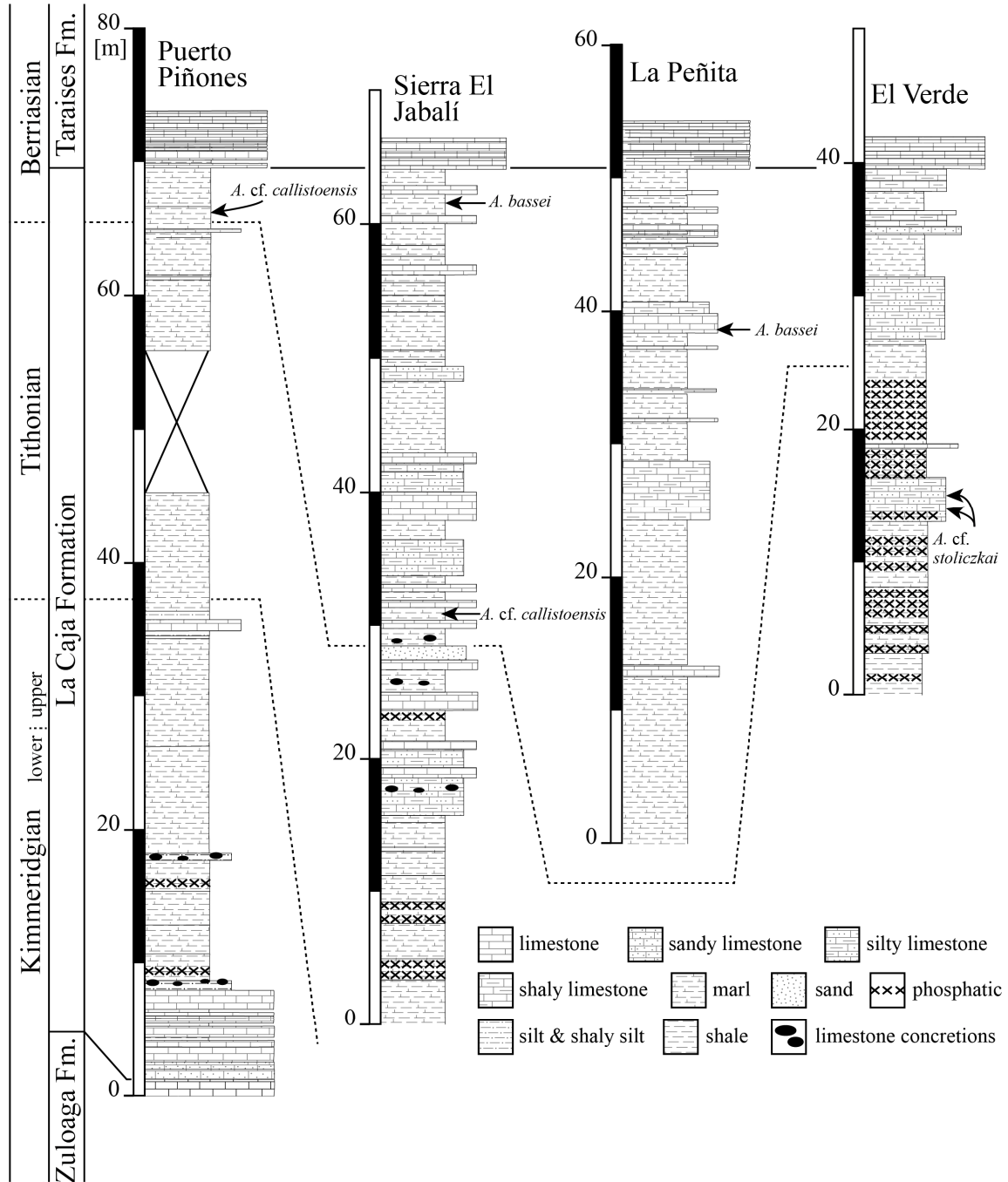
	al	sa	al/sa	H	L	H/L	bh	u	$\alpha$	t	$\pi$	$a_{\max}$
CPC-1443		104.3						2.3 to 3.0				47.2
CPC-1444	48.4	48.8	0.99	47.7	47.3	1.01	5.5	1.5 to 4.7	96	42	136	
CPC-1445		103			101.3			1.7 to 3.8				80.3
CPC-1446	80.3			76.8	82.9	0.93	6.7	1.4 to 3.1	96	53	128	
CPC-1447				45.6			4.4	0.9 to 3.5	78		119	42.6
CPC-1448	65.2			62.7	73.9	0.85	4.1	0.9 to 4.3	94	39		
CPC-1449							4.3	1.1 to 4.0	98	57		42.1
CPC-1450	27.9			27.1			3	1.3 to 2.2	72	32	96	

	al	sa	al/sa	H	L	H/L	bh	u	$\alpha$	$\iota$	$\pi$	$al_{\max}$
CPC-1451							6.1	2.8 to 5.3	94	48		50.3
CPC-1452	21.4	38.5	0.56	21	36.1	0.58	1.8	1.3 to 2.2	132	38	103	
CPC-1453							25.2	1.4 to 6.7	107	25		96.1

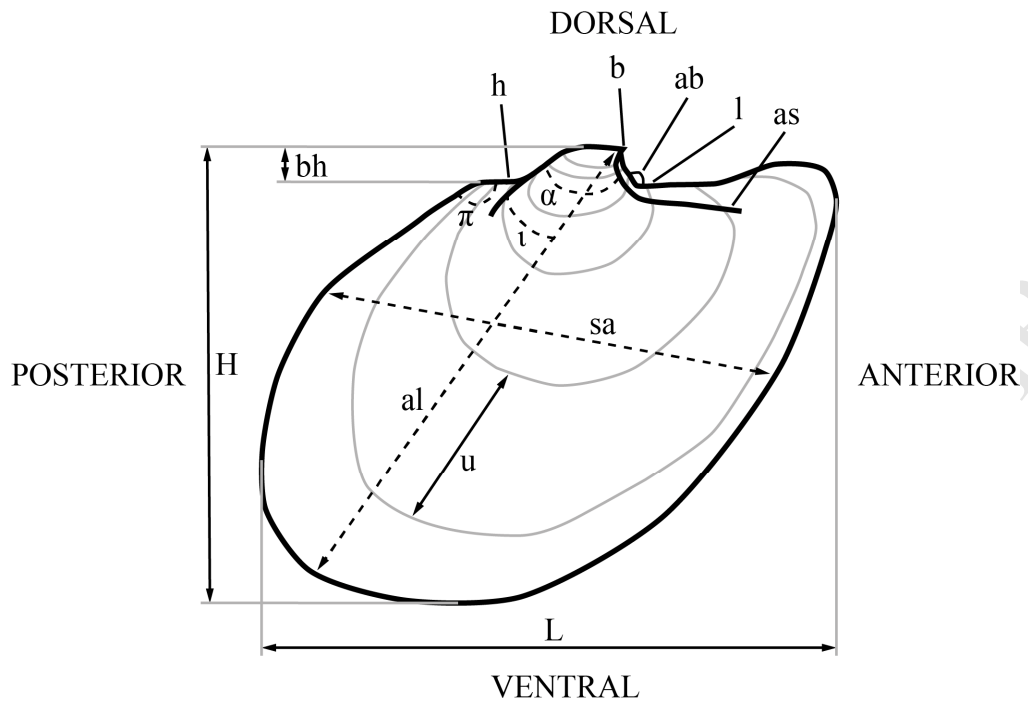
	al	sa	al/sa	H	L	H/L	bh	u	$\alpha$	$\iota$	$\pi$
CPC-1454	20.1	17.5	1.15	20	16.7	1.2	1.5	0.9 to 1.6	68	23	114
CPC-1455	33.6	35.4	0.95	31.4	33.8	0.93	24.1	0.8 to 1.1			
CPC-1456a	10.5	10.8	0.97	10.2	10.1	1.01	1.2	0.3 to 0.9	54	41	115
CPC-1456b	10.4	7.8	1.33	10.3	7.7	1.34	1.6	0.2 to 0.6	46	19	

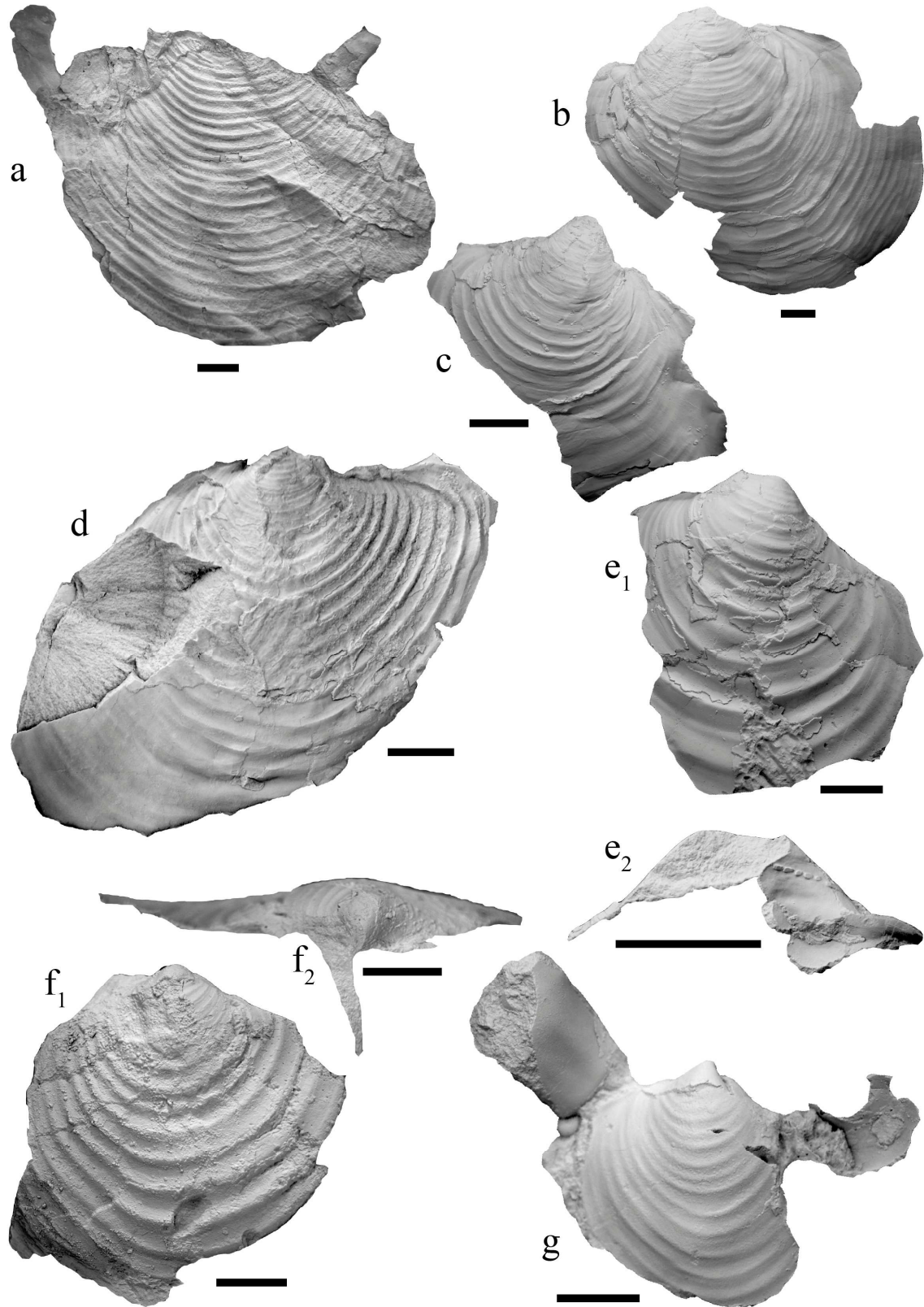
	al	H	L	bh	u	$\alpha$	t	al <sub>max</sub>
CPC-1457		19.6		23.1	0.2 to 0.6	76	36	20.5
CPC-1458					0.1 to 2.3			50.6
CPC-1459			35		0.1 to 0.9			26.5
CPC-1460	41.1	40.9			0.3 to 10	292	241	

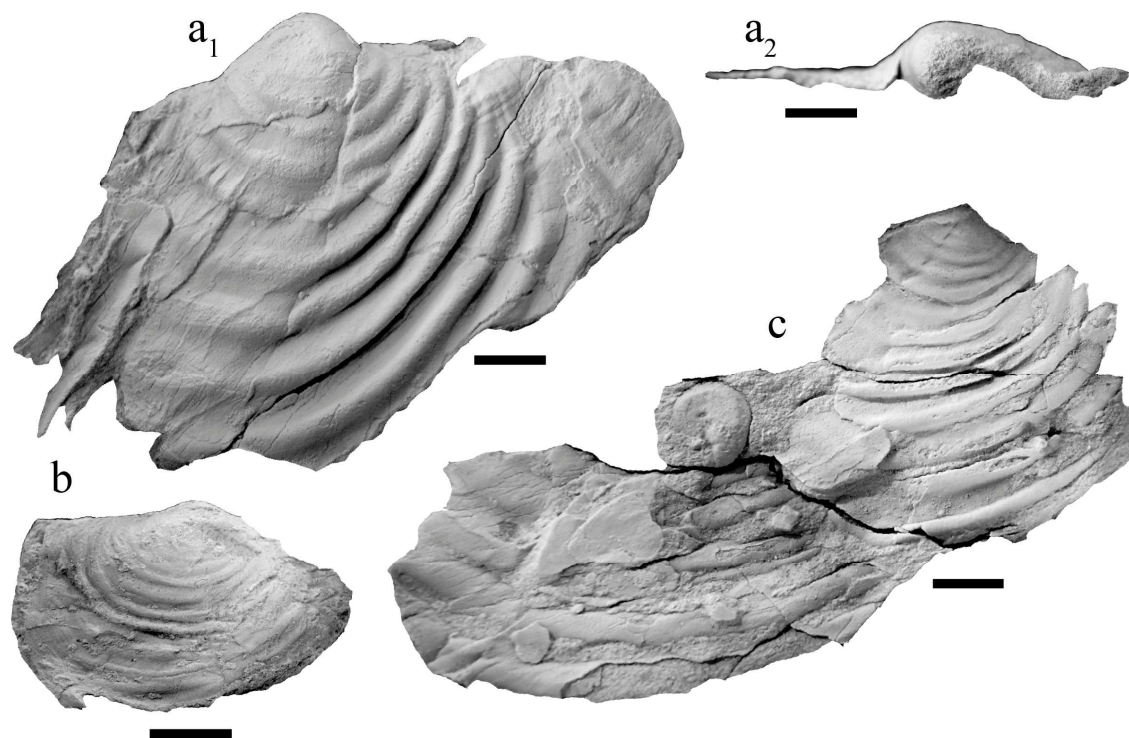




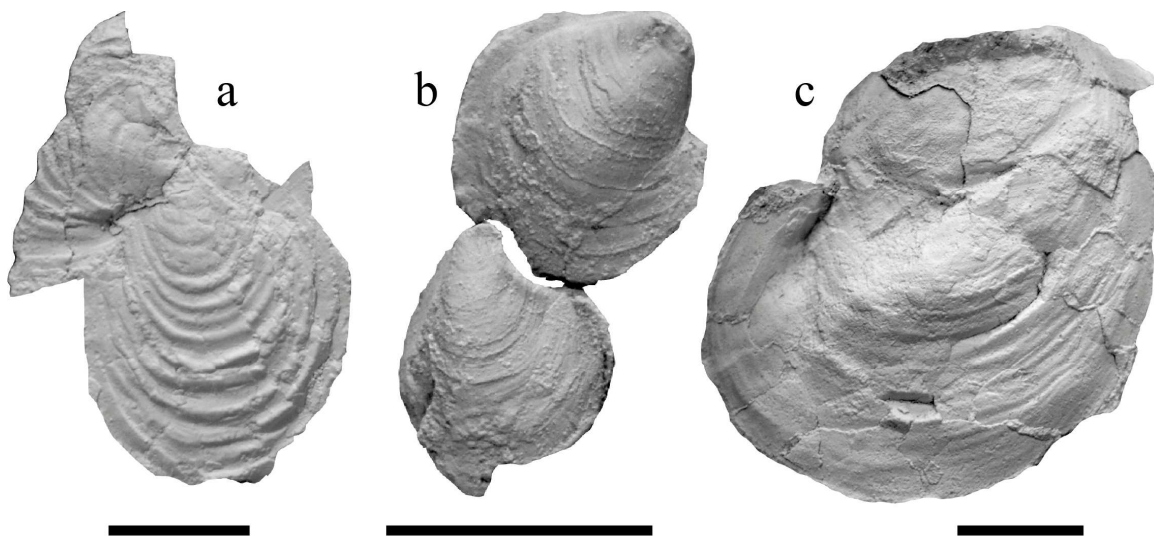




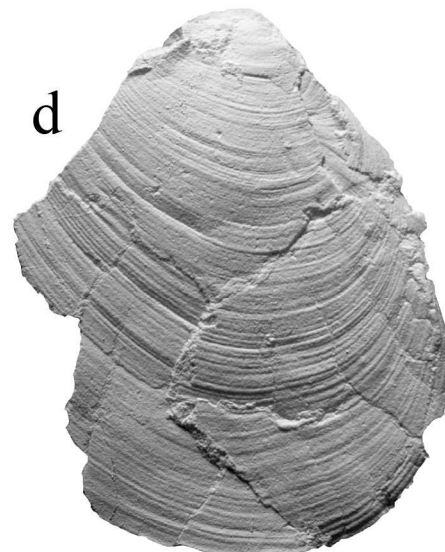
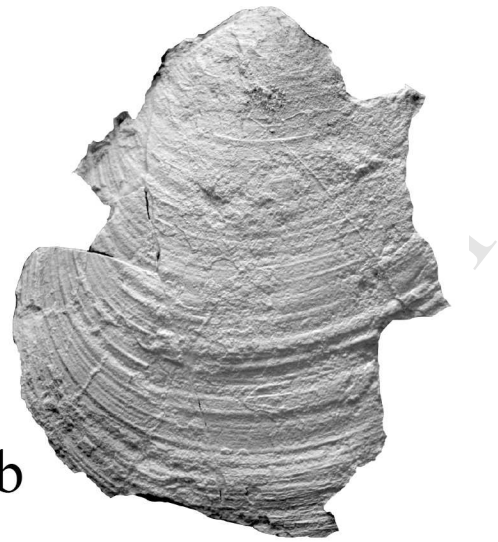
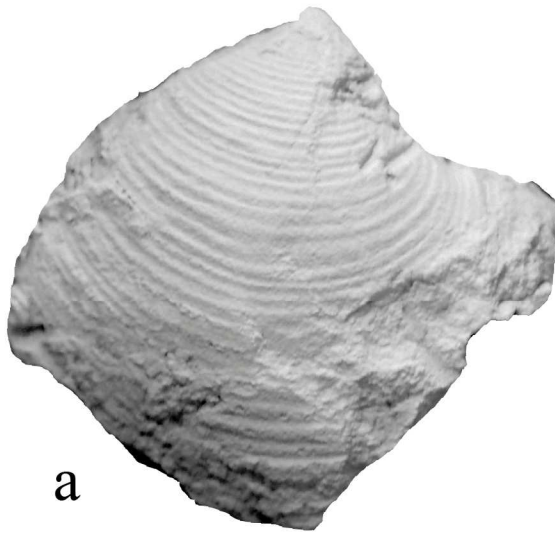




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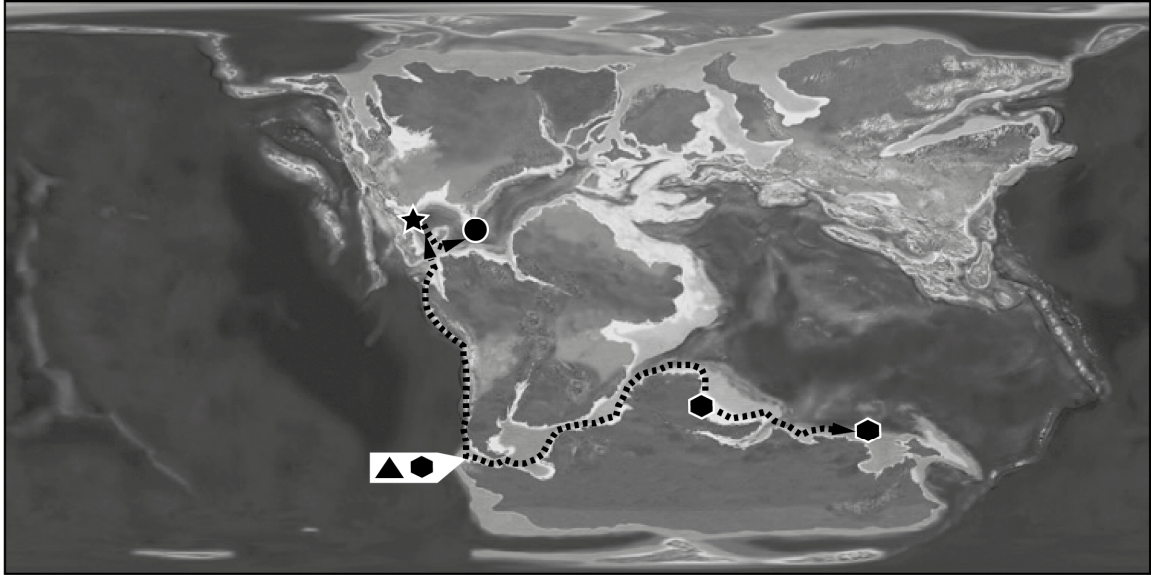


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- *Anopaea bassei* (Lecolle de Cantú, 1967) (late Tithonian)    ● *A. stoliczkai* (Holdhaus, 1913) (Tithonian)  
▲ *A. callistoensis* Crame & Kelly, 1995 (early Tithonian-early Berriasian)

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We provide data about stratigraphy and palaeogeography of the bivalve *Anopaea* (Inoceramidae) from the uppermost Jurassic-lowermost Cretaceous of northeastern and central-east Mexico

We identified four species

Two species indicate a faunal connection between the ancient Gulf of Mexico and the southern high latitudes

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