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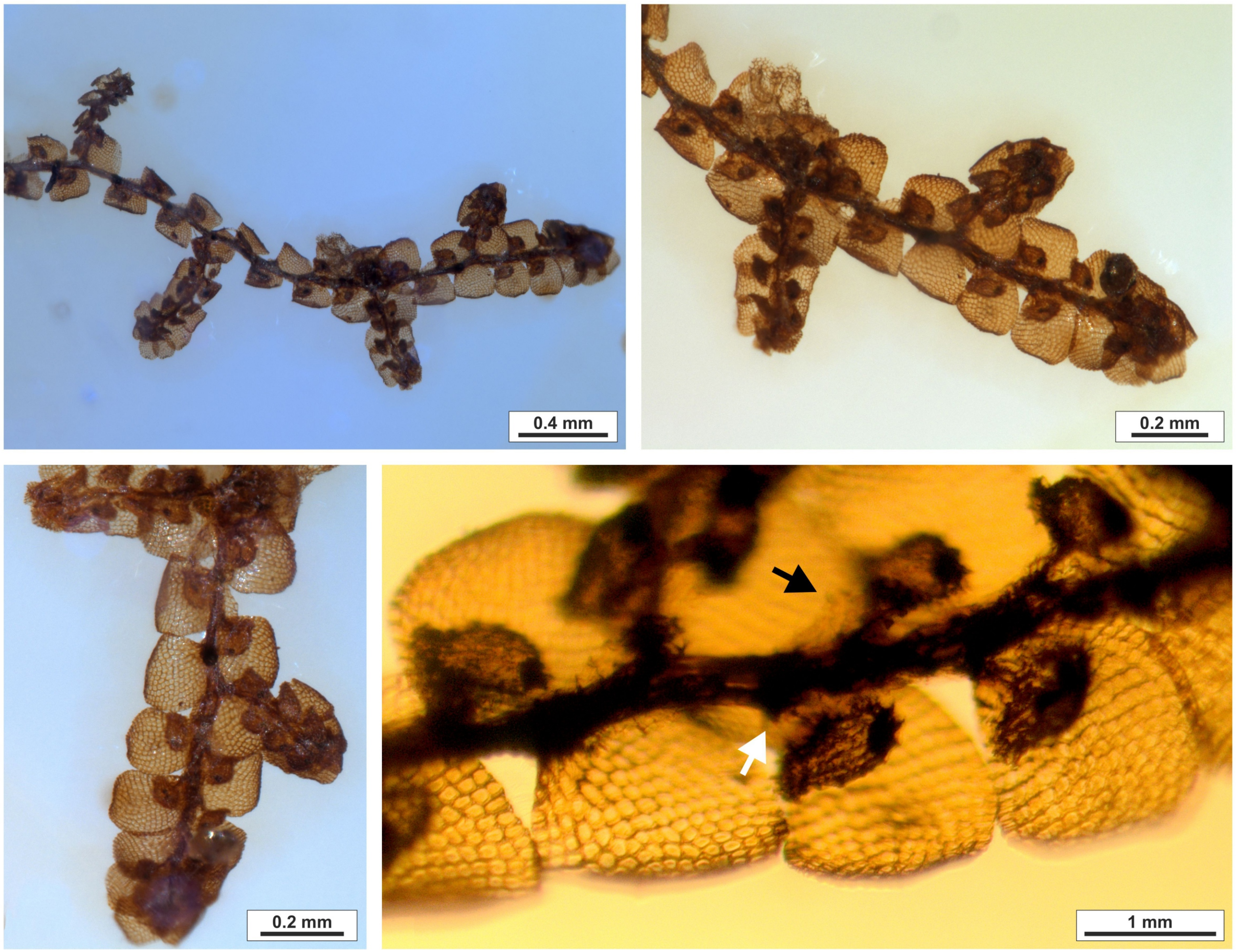

Frullania sp. Tallo mostrando diferentes partes y detalles de las hojas. La flecha negra muestra los anfigastrios y la flecha blanca la forma de las células de la hoja.

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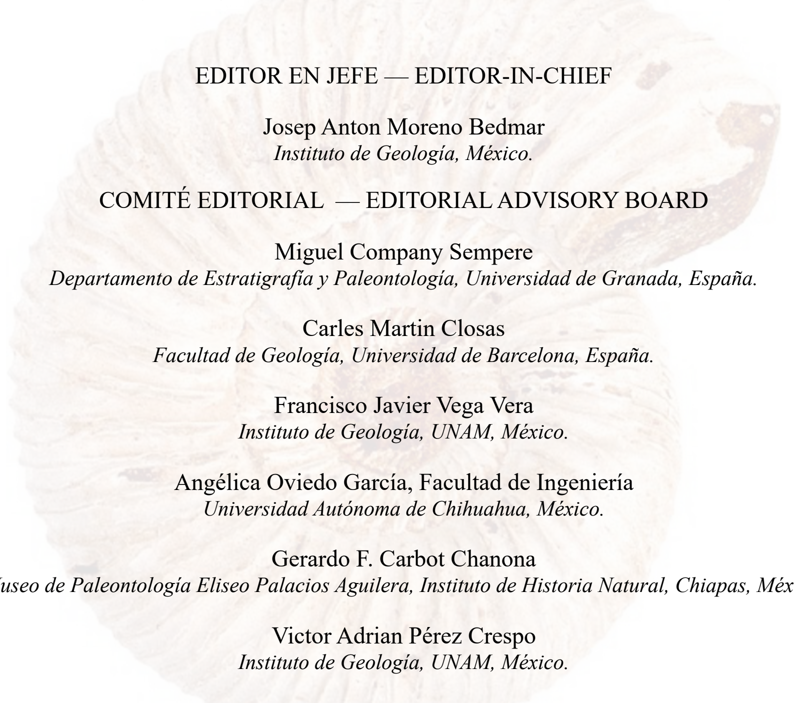

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First record of the collared peccary *Dicotyles tajacu* (Artiodactyla, Tayassuidae), in the Gliptodonte locality, Villaflores municipality, Chiapas

Primer registro del pecarí de collar Dicotyles tajacu (Artiodactyla, Tayassuidae), en la localidad de Gliptodonte, municipio de Villaflores, Chiapas.

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Abstract

Tayassuidae (peccaries) is a family of artiodactyls exclusively of America, that was widely distributed in North America during the Pleistocene. Nevertheless, records of this family are scarce in Mexico. The only valid species reported from the Late Pleistocene in Mexico were *Platygonus compressus* and *Dicotyles tajacu*, based on a few specimens. In this study, we report a new peccary specimen from the Gliptodonte locality (Late Pleistocene, Rancholabrean NALMA), Villaflores municipality, in the southern State of Chiapas. The new specimen consists of a distal part of the left humerus, which shows morphological differences from other North American Pleistocene and recent peccaries (*Mylohyus*, *Platygonus*, and *Tayassu*), allowing positive identification of the collared peccary *D. tajacu*. Thus, a new record of the species for the State of Chiapas and the first record of the Gliptodonte locality in the municipality of Villaflores is added, expanding the distribution range of the species during the Late Pleistocene in Mexico.

Keywords: collared peccary, Pleistocene mammals, Rancholabrean NALMA, southern Mexico.

Resumen

Tayassuidae (pecaríes) es una familia de artiodáctilos exclusiva de América, que se distribuyó ampliamente en América del Norte durante el Pleistoceno. Sin embargo, los registros de esta familia son escasos en México. Las únicas especies válidas reportadas para el Pleistoceno Tardío de México son Platygonus compressus y Dicotyles tajacu, con base en muy pocos especímenes. En este estudio reportamos un nuevo ejemplar de pecarí de la localidad Gliptodonte (Pleistoceno Tardío, NALMA Rancholabreano), municipio de Villaflores, en el sureño Estado de Chiapas. El nuevo espécimen consiste en la parte distal del húmero izquierdo, que muestra diferencias morfológicas con otros pecaríes del Pleistoceno y del Reciente de América del Norte (Mylohyus, Platygonus y Tayassu), lo que permitió la identificación del pecarí de collar D. tajacu. Se suma así un nuevo registro de la especie para el Estado de Chiapas y el primer registro de la localidad Gliptodonte en el municipio de Villaflores, ampliando el rango de distribución de la especie durante el Pleistoceno Tardío en México.

Palabras clave: *Mamíferos pleistocénicos, NALMA Rancholabreano, pecarí de collar, sureste de México.*

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1. Introduction

Tayassuidae Palmer, 1897, is a New World family of artiodactyls that diverged in the Eocene from a common Asian ancestor with the family Suidae, but has radiated successfully in North America, with a chronological range from the late Eocene to the present (Harris and Li-Ping, 2007; Prothero, 2009, 2021). This family was one of the first to cross South America during the Great American Biotic Interchange in the middle Pliocene (GABI 1; Woodburne, 2010).

Tayassuidae were very diverse at the end of the Neogene and the beginning of the Quaternary, with the Pleistocene being the geological epoch with most genera and species. During this time interval, six genera were recognized in South America and five in North America. The genera *Brasiliochoerus* Rusconi 1930; *Catagonus* Ameghino, 1904; *Parachoerus* Rusconi, 1930; *Dicotyles* Cuvier, 1816; *Platygonus* Le Conte, 1848 and *Tayassu* Fischer, 1814 are present in South America (Gasparini *et al.*, 2013; Parisi Dutra *et al.*, 2017). The genera *Mylohyus* Cope, 1889; *Platygonus*, and *Dicotyles*, have been recognized in the Pleistocene of North America, but *Tayassu* does not have a fossil record until now (Kurtén and Anderson, 1980; Mayer and Wetzel, 1987; Hulbert *et al.*, 2009; Czaplewski, 2012; Prothero, 2021). Recently, a new taxon, *Muknalia minima*, was established based on an almost complete mandibular ramus, recovered from the Muknal cave (Late Pleistocene-early Holocene), which is part of the Ox Bel Ha system, in Quintana Roo, Yucatán (Stinnesbeck *et al.*, 2017). However, *M. minima* were relegated as a junior synonym of *Pecari tajacu* (=*Dicotyles tajacu* [Linnaeus, 1758]) by Schubert *et al.* (2020). Another Pleistocene Mexican record of peccaries is the flat-headed peccary *Platygonus compressus* Le Conte, 1848, documented for El Cedazo, Aguascalientes; Tequixquiac, State of Mexico; Valsequillo, Puebla and the Chapala Basin, Jalisco (Lucas, 2008; Ferrusquía-Villafranca *et al.*, 2010). Other described species from the Pleistocene of Mexico are *P. ticuli* Mones, 1974 from Chapala and Zocoalco, Jalisco (Mones, 1974) and *P. alemanii* Dugès, 1891 from Moroleón, Guanajuato (Dugès, 1891). However, *P. ticuli* has been synonymized with *P. vetus* Leidy, 1882 by Lucas (2008), while *P. alemanii* does not differ from *P. compressus*, so it can be synonymized with this species. The collared peccary *Dicotyles tajacu* has been documented for the Loltún and Actún Spukil caves in Yucatán (Arroyo-Cabrales and Álvarez, 2003), and for the Santa Marta shelter in Ocozocoautla, Chiapas, based on cranial and appendicular material from the layer XVI, corresponding to the Pleistocene (García-Bárcena, 1976; Acosta *et al.*, 2018).

The fossil record of peccaries in Mexico is poorly known. Therefore, the aim of this work is to report for the first time the presence of the collared peccary *Dicotyles tajacu* in the Gliptodonte locality, Villaflores municipality, based on the distal part of a humerus collected from the Late Pleistocene (NALMA Rancholabrean) fluviolacustrine sediments that crop out in that locality. This discovery contributes to the knowledge of the Late Pleistocene fauna in southern Mexico.

2. Study area and geological setting

The Gliptodonte locality (locally named Rancho Argentina) is located in the vicinity of the town Villaflores, at 16°12'55"N and 93°16'20"W (Figure 1). This locality is registered with the code 2PSP00000134 in the National Database of Paleontological Monuments in the Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos of Instituto Nacional de Antropología e Historia (INAH).

The sedimentary sequence is formed by alternating fluvial sediments of 8.0 m thick (Figure 2). The base is 1.6 m thick and is formed by olive silt, thin sand, and brown clay organic. Over the base section, there is a 0.30 m layer of brown silty clay. In this section, fossil remains of the glyptodont *Glyptotherium cylindricum* (Brown, 1912), the ground sloth *Eremotherium laurillardi* (Lund, 1842), the horses *Equus mexicanus* (Hibbard, 1955), *E. conversidens* Owen, 1869, and the with-tailed deer *Odocoileus virginianus* Zimmermann, 1780 have been recovered (Montellano-Ballesteros and Carbot-Chanona, 2010; Gómez-Pérez and Carbot-Chanona, 2012; Jiménez-Hidalgo *et al.*, 2019; Carbot-Chanona *et al.*, 2022). The next section is a 1.0 m layer composed of dark brown clay and brown clay-silt. Above this section, there is a 0.40 m layer of fine sand to silt section without boulders. The next layer is formed by 0.70 m of brown fine clay. Above

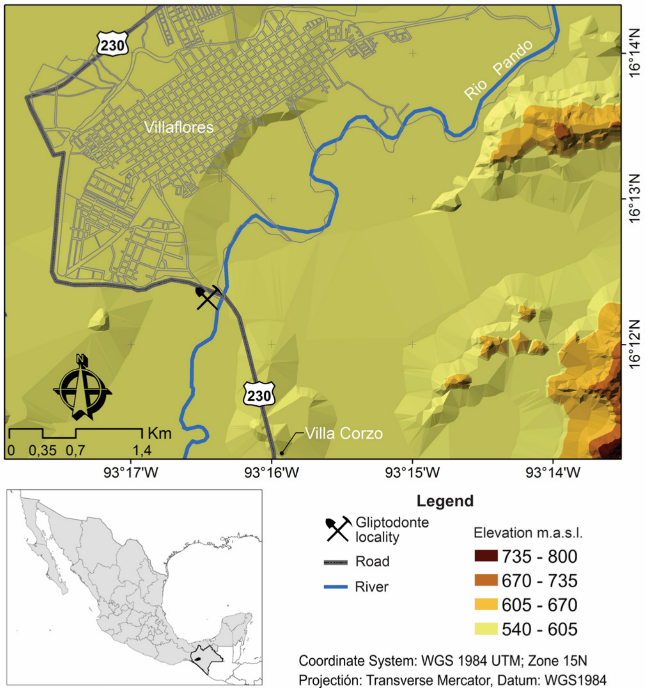

Figure 1. Location of the Gliptodonte locality, in Villaflores, Chiapas, southern Mexico.

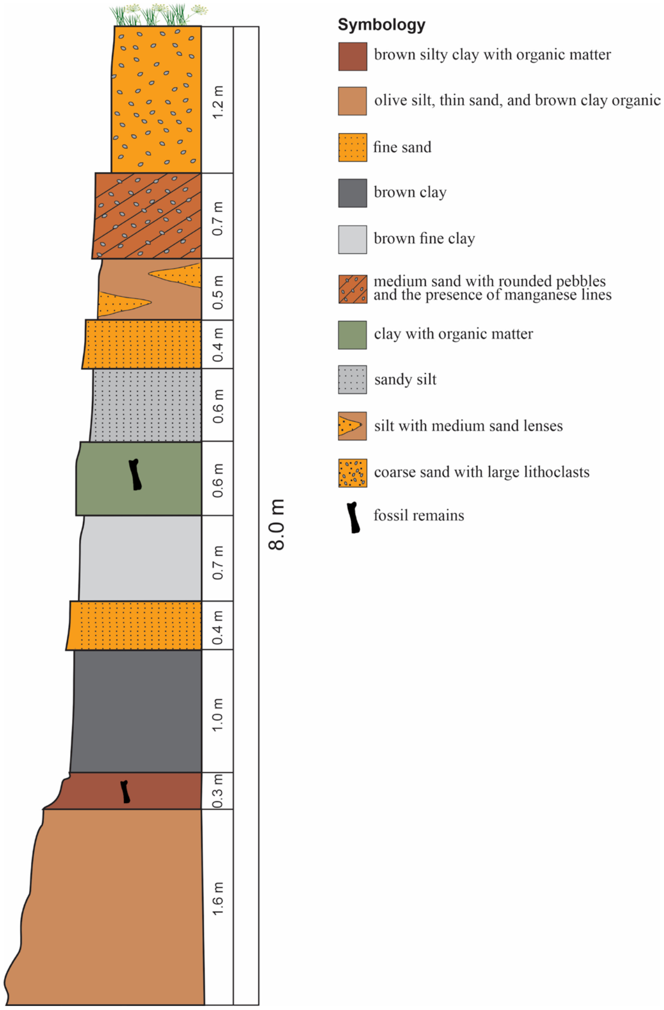

Figure 2. Generalized stratigraphic section of the Gliptodonte locality, Villaflores, Chiapas, southern Mexico

this section is a 0.6 m of clay with organic matter; in this section there are *G. cylindricum*, *E. conversidens*, and *O. virginianus* fossil remains (Gómez-Pérez and Carbot-Chanona, 2012; Jiménez-Hidalgo *et al.*, 2019). The next layer is formed by 0.60 m of sandy silt. Above there is a 0.40 m of fine-grained sand. Over this section, there is a 0.50 m layer of silt with medium sand lenses. The next layer is formed by 0.70 m medium sand with rounded pebbles and the presence of manganese lines. Finally, the upper part of the sequence consists of 1.2 m coarse sand with large lithoclasts.

The faunal association present in the locality has been referred to Rancholabrean NALMA (Gómez-Pérez and Carbot-Chanona, 2012).

3. Material and methods

The specimen described here consists of the distal half of a completely permineralized left humerus that presents a median state of conservation and was recovered from horizontal fluvial sediments that crop out in the Gliptodonte locality in the municipality of Villaflores, Chiapas.

The anatomical terminology used in this study is based on Schmid (1972) and Bortolami and Callegari (1995). The measurements were obtained with a digital caliper with an error range of 0.1 mm and were taken as shown in Figure 3. This study follows the proposal of Acosta *et al*. (2020), who argue that the valid binomina for the collared peccary is *Dicotyles tajacu*, and not *Pecary tajacu*, *Tayassu tajacu*, or *Dicotyles crassus*.

Since artiodactyl taxa of similar sizes existed in the Late Pleistocene of North America, such as deer (Cervidae Gray, 1821), antilocaprids (Antilocapridae Gray, 1866), and peccaries (Tayassuidae), a first comparison was conducted with recent specimens of these groups to assign the material studied here to a particular family. For this purpose, osteological material of the withe-tailed deer *Odocoileus virginianus* (specimens IHNCR-001 and IHNCR-007), the pronghorn *Antilocapra americana* Ord, 1815 (DP 1555), the with-lipped peccary *Tayassu pecari* (Link, 1975) (IHNCR-042) and the collared peccary *Dicotyles tajacu* (specimens DP 638, DP 5099, DP 7779 and IHNCR-048) was used. Subsequently, the fossil material was compared in detail morphologically and meristically with the tayasuid species present in the North American Rancholabrean NALMA, *Mylohyus fossilis* (Leidy, 1860) and *P. compressus*, and with the living *T. pecari* and *D. tajacu* (Figures 5 and 6, Table 1).

3.1. Institutional abbreviations

DP, Osteological Collection, Laboratorio de Arqueozoología “M. en C. Ticul Álvarez Solórzano” (historically Departamento de Prehistoria), Instituto Nacional de Antropología e Historia, Ciudad de México, México. **IHNFG**, Instituto de Historia Natural, Fósil Geográfico (acronym historically used for the paleontological collection now housed at Secretaría de Medio Ambiente e Historia Natural), Tuxtla Gutiérrez, Chiapas, México. **IHNCR**, Instituto de Historia Natural, Reference Collection, Museo de Paleontología “Eliseo Palacios Aguilera”, Secretaría de Medio Ambiente e Historia Natural, Tuxtla Gutiérrez, Chiapas, México.

3.2. Morphological abbreviations

afc, articulation of the flexor complex; **lc**, lateral condyle; **mc**, medial condyle; **le**, lateral epicondyle; **me**, medial epicondyle; **of**, olecranon fossa; **rf**, radial fossa; **stf**, supratrochlear foramen, **tr**, trochlea.

3.3. General abbreviations

NALMA, North American Land Mammal Age.

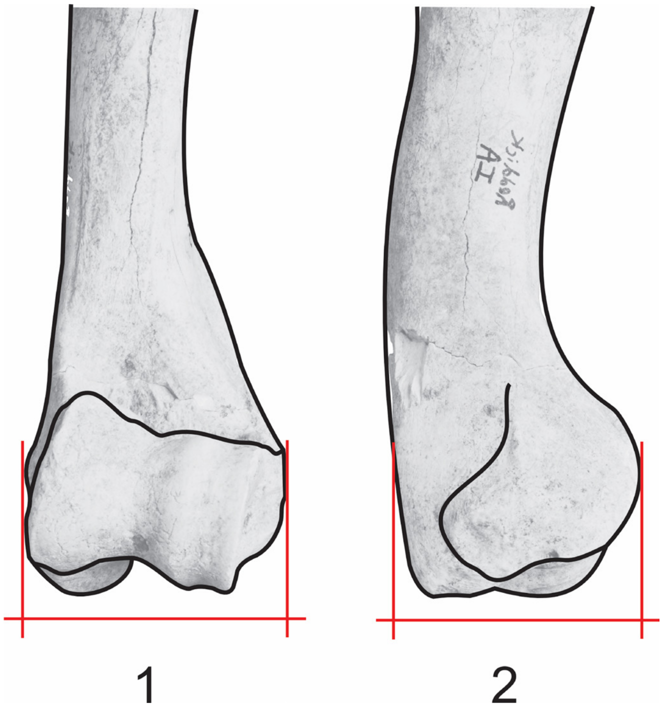

Figure 3. Schematic drawing of the humerus showing the measurements taken. 1) Lateral-medial length through the epicondyles, and 2) anteroposterior width.

4. Results

4.1. Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Suborder Suiformes Jaekel, 1911
Family Tayassuidae Palmer, 1897
Genus *Dicotyles* Cuvier, 1816

Dicotyles tajacu (Linnaeus, 1758)
Figures 4 (3D model), 5, and 6, Table 1

4.2. Referred material

IHNFG-2718, distal half of left humerus (Figure 4), collected by Valente Villanueva in 2003 and later donated to the Museo de Paleontología “Eliseo Palacios Aguilera”. The specimen is housed in the paleontological collection of the Secretaría de Medio Ambiente e Historia Natural, State of Chiapas, southern Mexico.

4.3. Location and horizon

Gliptodonte locality, Villaflores, Chiapas, southeastern Mexico. Late Pleistocene, Rancholabrean NALMA.

4.4. Description

The IHNFG-2718 specimen corresponds to the distal half of the left humerus (Figure 4). The diaphysis-epiphysis suture was completely ossified, indicating that it was an adult specimen. The lateral and medial borders of the articular end as well as the borders of the articular condyles were rounded, indicating that the material underwent a process of dragging after fossilization. In the anterior view, it can be seen that the medial condyle is slightly wider than the lateral condyle. The medial epicondyle projected slightly medially, whereas the lateral epicondyle extended laterally. The articulating surface of the flexor complex lies distally on the medial epicondyle and is projected distally. In the medial view, the flexor complex joint extends from the posterior part of the medial epicondyle to the medial part of the epicondyle. The olecranon fossa is wide and shallow, and the supratrochlear foramen is located inside. In the posterior view, the lateral supracondylar crest was observed to be incipiently protruding.

5. Discussion

5.1. Comparison of IHNFG-2718 with medium-sized artiodactyls

Medium-sized artiodactyls of the families Antilocapridae (*Stockoceros conklingi* Stock, 1930), Cervidae (*Odocoileus virginianus* and *Navahoceros fricki* Schultz and Howard, 1935), and Tayassuidae (*Platygonus compressus, Mylohyus fossilis,* and *Dicotyles tajacu*) inhabited North America during the Rancholabrean (Kurtén and Anderson 1980). Therefore, a first comparison was made between IHNFG-2718 and living representatives of these families, to include the specimen in one of them.

IHNFG-2718 is an adult specimen because the epiphysis-diaphysis suture was completely ossified. Its dimensions are smaller than those of the humeri of *Antilocapra americana* (DP 1555) and *Odocoileus virginianus* (IHNCR-001 and IHNCR-007). Both *A. americana* and *O. virginianus* were approximately 15% larger than IHNFG-2718. In contrast, the dimensions of IHNFG-2718 were comparable to those of an adult specimen of *T. pecari* and *D. tajacu* (Table 1).

Detailed morphological comparisons between IHNFG-2718, *O. virginianus, A. americana,* and *T. pecari* revealed distinctive features in the humerus of these species. In anterior view, the medial condyle and the lateral condyle in IHNFG-2718 were of similar proportions, as observed in the humerus of *T. pecari* and *D.*

Figure 4. 3D model of the IHNFG-2718 left humerus. To see the model with better resolution, access in https://sketchfab.com/3d-models/humero-fosil-de-pecari-de-collar-40207bbe0d3d46b4a45550ea2aca46bf

tajacu, whereas in the humerus of *O. virginianus* and *A. americana*, the medial condyle was wider laterally-medially than the lateral condyle (Figure 5). In the posterior view, IHNFG-2718 presents the supratrochlear foramen in the olecranon fossa, which is present in *T. pecari* and *D. tajacu*, but not in *O. virginianus* or *A. americana*. Additionally, the inner lower border of the olecranon fossa in *T. pecari* and *D. tajacu* was almost horizontal, a feature observed in IHNFG-2718. In contrast, in *O. virginianus* and *A. americana*, the border was lateromedially inclined (Figure 5). Another striking feature is that the articulating surface of the flexor complex is more distally prominent in *T. pecari, D. tajacu*, and IHNFG-2718 than in *O. virginianus* and *A. americana*. Additionally, the olecranon fossa is wider and deeper in IHNFG-2718 than in *O. virginianus* and *A. americana*, but is similar to the olecranon fossa of *T. pecari* and *D. tajacu*.

All the morphological and meristic features of IHNFG-2718 indicate that it is a tayasuid, similar to *T. pecari* and *D. tajacu*.

5.2. Comparison of IHNFG-2718 to another North American tayasuids

The genera of tayasuids present in the Rancholabrean of North America, *Platygonus,* and *Mylohyus,* and the living *Tayassu* and *Dicotyles,* differ from each other mainly by craniomandibular features and size (see Prothero, 2021). Of the four taxa, *Mylohyus* is the largest, a trait that is reflected in the postcranial bones, which are slightly larger than those of *Platygonus*, *Tayassu*, and *Dicotyles* (Figure 5, Table 1). In addition to size, there were morphological differences between the humeri of the four genera. The humerus in *Mylohyus*, *Tayassu*, and *Dicotyles* is similar in general morphology and proportion and is slenderer than the humerus of *Platygonus* (Lundelius, 1960). In *Mylohyus,* the crest on the lateral border of the olecranon fossa is farther from the fossa and lies on the lateral surface of the humerus (Lundelius, 1960). This feature is similar in *Tayassu* and *Dicotyles*, while in *Platygonus* the crest is located on the back of the humerus (Lundelius, 1960). Additionally, the medial border of the olecranon fossa is narrower and more angular in *Mylohyus* than in *Platygonus,* a feature that is similar in *Tayassu* and *Dicotyles* (Lundelius, 1960). In the specimen IHNFG-2718, the morphological characteristics present in *Tayassu* and *Dicotyles* are observed, in addition to the fact that its measurements fall within the size range of these two genera (Table 1), so it is ruled out that it belongs to *Mylohyus* or *Platygonus*.

Although there are differences in size between the extant species of peccaries, *Tayassu pecari* (total length= 905-1,390 mm; height at shoulders= 400-530 mm; body mass= 25-40 kg; Mayer and Wetzel, 1987) and *Dicotyles tajacu* (total length= 870-940 mm; height at shoulders= 400-480 mm; body mass= 18-27 kg; Hall, 1981), these differences in size are not noticeable in the dimensions of the humeri compared in this study (Figure 6, Table 1). However, a detailed comparison between the humeri of these species allowed us to identify some morphological differences.

In the posterior view, the humerus of *T. pecari* presents a slight elevation on the internal lateral border of the olecranon fossa, which extends distally to the middle part of the lateral epicondyle, forming a small “ridge” (Figure 6). In contrast, in the *D. tajacu* humerus, the medial lateral border of the olecranon fossa, this “ridge” is not present. In the specimen IHNFG-2718, the “ridge” of *T. pecari* humerus was not observed either, but the internal lateral edge of the olecranon fossa was similar to that of *D. tajacu* (Figure 6). Based on this morphological characteristic, the specimen IHNFG-2718 is assigned to *Dicotyles tajacu*, thereby adding a new record of the species for the state of Chiapas and the first record for the Gliptodonte locality, in the municipality of Villaflores, thus expanding the distribution range of the species during the Late Pleistocene in Mexico.

5.3. Paleoenvironmental significance

Today, *D. tajacu* inhabits deserts, arid woodlands, oak woodlands, and tropical areas from the southern U.S.A. through to northern Argentina (Grubb and Groves, 1993). This species has unusual climatic tolerance, because it occurs in forests where average temperatures are around 27 °C, but some populations have also been found in desert areas where temperatures reach 45 °C (Bodmer and Sowls, 1993). The distribution of *D. tajacu* is clearly tropical and semi-tropical, and agrees with the presence of neotropical mammals in the Gliptodonte locality, such as *E. laurillardi* and *G. cylindricum* (Gómez-Pérez and Cabot-Chanona, 2012; Carbot-Chanona *et al.*, 2022), and with the palynological fossil record, that includes Compositae, Mimosoideae, Gramineae, Solanaceae, and Pinaceae (Carbot-Chanona *et al.*, 2008), indicating that this was the main type of environment in Chiapas during the final Pleistocene.

6. Conclusions

Although the material described here consists only of a distal fragment of the left humerus, an exhaustive morphological comparison with the humeri of various species of living and fossil North American medium-sized artiodactyls allowed us to refer the specimen IHNFG-2718 as belonging to the collared peccary *Dicotyles tajacu*, a species that lives in several regions of the State of Chiapas. With this finding, we document a new record of this species for the Late

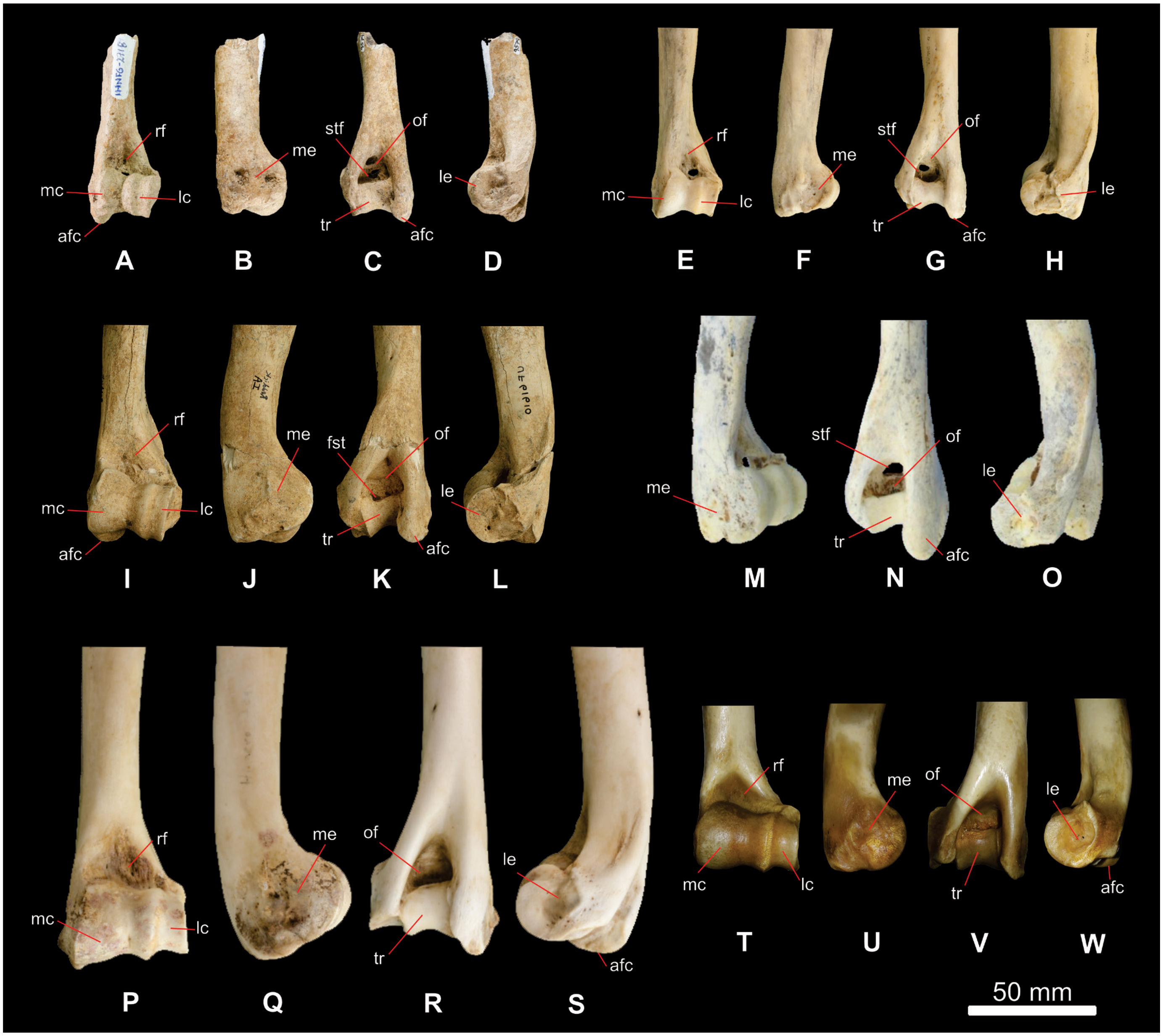

Figure 5. Comparison between North American medium-sized artiodactyls. A–D, left humerus (IHNFG-2718), in anterior (A), medial (B), posterior (C), and lateral (D) view. E–H, left humerus of *Tayassu pecari* (IHNCR-042), in anterior (E), medial (F), posterior (G), and lateral (H) view. I–L, right humerus (flipped images) of *Platygonus compressus* (UF-61610), in anterior (I), medial (J), posterior (K), and lateral (L) view. M–O, right humerus (flipped images) of *Mylohyus fossilis* (RMM 4567), in anteromedial (M), posterior (N), and posterolateral (O) view. P–S, left humerus of *Odocoileus virginianus* (INHCR-001), in anterior (P), medial (Q), posterior (R), and lateral (S) view. T–W, left humerus of *Antilocapra americana* (DP 1555), in anterior (T), medial (U), posterior (V), and lateral (W) view. Scale bar equal 50 mm.

Pleistocene in Mexico, as well as the first record of the species for the Gliptodonte locality.

The presence of *D. tajacu* in Chiapas allows us to know the fauna present in southeastern Mexico during the Late Pleistocene. In future studies, these findings could provide data to understand which taxa managed to prevail over the extinction caused in the Pleistocene-Holocene interval as a consequence of climate change.

Conflicts of interest

The authors declare that they have none.

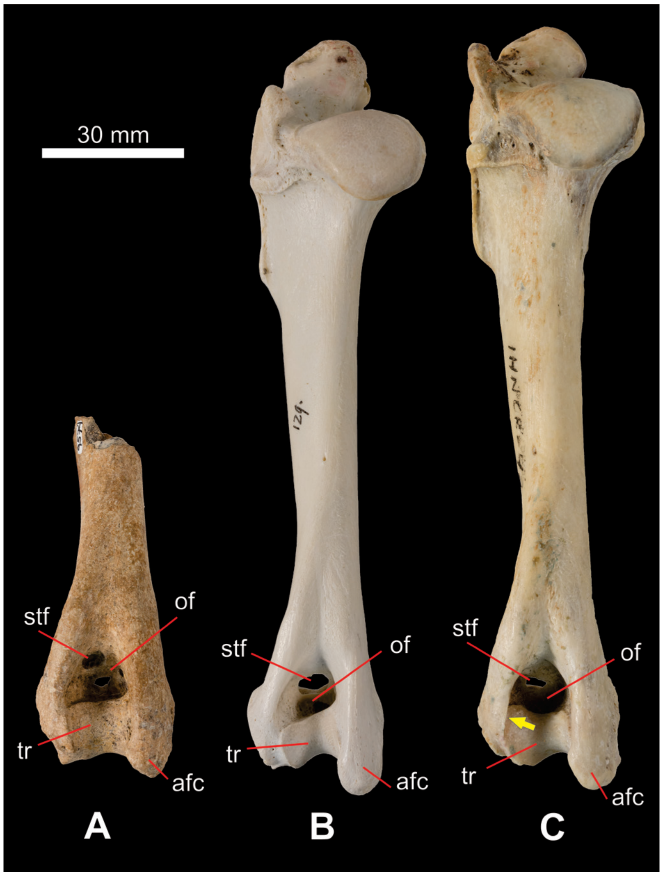

Figure 6. Comparison between (A) IHNFG-2718, (B) *Dicotyles tajacu* (IHNCR-048), and (C) *Tayassu pecari* (IHNCR-042) in posterior view. Scale bar equal 30 mm. The yellow arrow shows the slight elevation on the internal lateral border of the olecranon fossa present in *T. pecari*, but not in *D. tajacu* and IHNFG-2718.

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Table 1. Comparative measurements (in mm) of tayassuids during the Late Pleistocene in North America. Data were taken from Finch *et al.* (1970)[a] and Lundelius (1969)[b].

Specimens	Lateral-medial length through the epicondyles	Anteroposterior width
IHNFG-2718	29	26
Tayassu pecari IHNCR-045	27	24
Dicotyles tajacu DP 608	27.5	23
Dicotyles tajacu DP 5099	25.4	22.2
Dicotyles tajacu DP 7779	29	24.8
Dicotyles tajacu IHNCR-048	27	23
[a]*Platygonus compressus* USNM 26098	42	--
[a]*Platygonus compressus* USNM 26100	45	--
[a]*Platygonus compressus* USNM 26102	40.5	--
Platygonus compressus UF 61610	38.6	36.6
Mylohyus nasutus (=*M. fossilis*) RMM 4567	46.7	33
[b]*Mylohyus nasutus* (=*M. fossilis*) TMM 933-3232	42.5	45.6

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The genus *Zuercherella* Casey, 1954 in the Upper Aptian (Lower Cretaceous) of the Cottonwood District, Northern California

El género Zuercherella Casey, 1954 en el Aptiano superior (Cretácico Inferior) del Distrito de Cottonwood, en el norte de California

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Abstract

The presence of the Tethyan species *Zuercherella zuercheri* (Jacob, 1906) in the Upper Aptian of the Cottonwood district, northern California, is documented for the first time, allowing confirmation of an affinity between the Tethyan and Northeast Pacific biota during the Upper Aptian, *Eotetragonites wintunius* and *Acanthohoplites gardneri* Zones. The paleontological study of very well-preserved material also allows a better knowledge of the adult morphology of *Zuercherella zuercheri*.

Keywords: Ammonites, Aptian, California, Cretaceous, Paleobiogeography.

Resumen

Se reporta por primera vez la presencia de la especie tetisiana Zuercherella zuercheri (Jacob, 1906) en el Aptiano superior del distrito de Cottonwood, en el norte de California, lo que permite confirmar la existencia de afinidades entre la biota tetisiana y la del Pacífico nororiental durante el Aptiano superior, en las biozonas Eotetragonites wintunius y Acanthohoplites gardneri. El estudio paleontológico de material muy bien conservado también permite tener un mejor conocimiento de la morfología del adulto de Zuercherella zuercheri.

Palabras clave: *Cretácico, Ammonites, Aptiano, California, Paleobiogeografía.*

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1. Introduction

The upper Aptian ammonite fauna of northern California has been long recognized for its endemism (Anderson, 1902, 1938; Murphy, 1956, 1967a and b; Amédro and Robaszynski, 2005; Murphy and Rodda, 2006; Rodda and Murphy, 2022).

Zuercherella zuercheri (Jacob, 1906), a distinctive species known from South America, and Europe, and reported here for the first time in western north America, allows us to highlight a connection between the Tethys and the Northeast Pacific Province during the lower part of Upper Aptian.

Most of the material herein investigated has been collected in the 1950' by one of us (M.A.M.) in the Upper Aptian of northern California, *Eotetragonites wintunius* Zone and base of the *Acanthohoplites gardneri* Zone. These specimens were previously identified as *Puzosia* sp. A and/or *P*. sp. B in Murphy (1956).

2. Systematic paleontology

Conventions. Dimensions are given in millimeters: D = diameter; W = whorl breadth; H = whorl height; U = umbilicus.

We follow the descriptive categories established by Rodda and Murphy (2022).

Abbreviations used.

- CASG - California Academy of Sciences, Geology Collection.
- UCLA - University of California, Los Angeles.
- UJF-ID - Université Grenoble-Alpes, ex Institut Dolomieu collections.

Order Ammonitida Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Desmoceratoidea Zittel, 1895
Family Desmoceratidae Zittel, 1895
Subfamily: Uhligellinae Latil, Murphy and Rodda, 2023

Definition of the subfamily. The subfamily Uhligellinae, as herein understood, is probably polyphyletic and brings together the genera *Zuercherella* Casey, 1954, *Uhligella* Jacob, 1907, *Pseudorbulites* Casey, 1961, *Grantziceras* Imlay, 1961, *Roberticeras* Latil, Murphy and Rodda, 2023, *Leconteites* Casey, 1954, *Brewericeras* Casey, 1954, and provisionally *Boliteceras* Whitehouse, 1928 and *Cophinoceras* Whitehouse, 1928. This subfamily comprises constricted desmoceratids that derive from the genera *Zuercherella* and *Pseudorbulites* with a suture line with symmetrical to feebly asymmetrical, trifid L. We do not follow Wright (1996) and maintain the genera *Leconteites* and *Brewericeras* within the Uhligellinae because of their symmetrically trifid suture.

Discussion. The genus *Uhligella* has been extensively discussed by Riccardi and Medina (2002, p. 306) who follow the Treatise classification.

The genus *Pseudorbulites* Casey, 1961 (type species: *Desmoceras* (*Uhligella*) *convergens* Jacob, 1908, p. 29, pl. 2, figs. 24–26, by the original designation of Casey, 1961, p. 145) was considered by Wright (*in* Wright *et al.*, 1996, p. 81) as a possible synonym of *Beudanticeras* (*Grantziceras*) Imlay, 1961, without any discussion. Kennedy (2000, p. 165) regarded it as a synonym of *Beudanticeras* s.s., considering that Jacob's species differs little from early *Roberticeras*. As pointed out by Riccardi and Medina (2002, p. 298), *Pseudorbulites* and *Grantziceras* have both a stout section and funnel-shaped umbilicus, but *Grantziceras* differs from *Pseudorbulites* by its less involute coiling, more numerous strongly biconcave constrictions and its rather broader ventral area. In spite of that, Riccardi and Medina considered that *Pseudorbulites* and *Grantziceras* were probable synonyms. We agree with Casey (1961, p. 145) statement: 'I am of the opinion that *Pseudorbulites* should be established as an independant genus rather than as a subgenus of *Beudanticeras*. The outstanding features of *Pseudorbulites* are its stout, elliptical whorls, funnel-shape umbilicus, striated test and highly dissected suture-line.' Furthermore, *Grantziceras* is a typical pacific boreal genus of a rather elevated Lower Albian age (*Brewericeras hulenense* Zone). Because of its stratigraphic range just below and above the Aptian-Albian boundary, and because of its tethyan origin, *Pseudorbulites* is regarded herein as a distinct genus and as a possible ancestor of the Lower-basal Middle Albian tethyan lineage *Roberticeras africana* (Pervinquière, 1907), *R. dupinianum* d'Orbigny, 1841, *R. arduennense* Breistroffer, 1947 and the still enigmatic *R. subparandieri* Spath, 1923.

The genus *Boliteceras*, a rather involute, with funnel-shaped umbilicus, and inflated ammonite, with broad, shallow, sinuous constrictions, fine, feeble ribs and broadly rounded venter, is in need of further study. The suture, not figured, is said to have wide-stemmed saddles and regularly trifid first lateral lobe. This genus has been regarded as a doubtful genus by Wright (1996) without further explanation. Riccardi and Medina (2002) regarded it as a synonym of *Beudanticeras* (now *Roberticeras*). Whitehouse (1928) assigned an Upper Albian age to the genus *Boliteceras* on the basis of the occurrence of Upper Albian ammonites within the same formation. Both *Boliteceras daintreei* (Etheridge, 1872) and *Boliteceras perlatum* (Whitehouse, 1928) are known from Hughenden, Queensland, Wallumbilla Formation and possibly Allaru Mudstone (Rozefelds *et al.*, 1990). The Wallumbilla Formation has been redefined by Vine *et al.* (1967) and Gray *et al.* (2002) and both authors give it an Aptian to Albian age. The Allaru Mudstone, doubtfully considered as a lateral equivalent of the Oodnadatta Formation, is probably Albian-Cenomanian (Gray *et al.*,

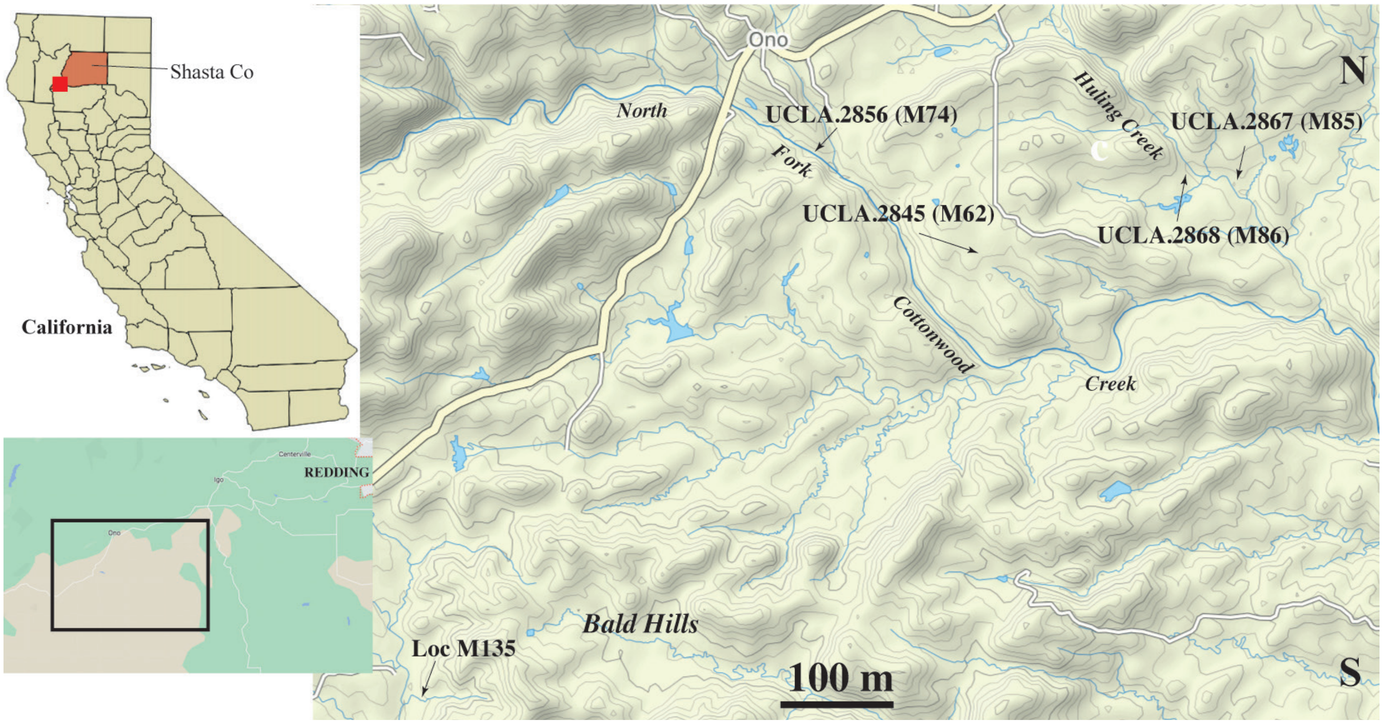

Figure 1. Map of the studied area, with location of the localities that yielded *Zuercherella zuercheri* (Jacob, 1906).

2002). According to Day (1968) *Politeceras daintreei* co-occurs with ?*Falciferella* and is of Lower Albian age while McKenzie (personal communication) gives a Middle Albian age. The genus *Boliteceras* is herein excluded from the synonymy of the genus *Roberticeras* and, pending a revision of the australian material, *Boliteceras* is herein considered as a distinct genus and provisionally maintained in the Uhligellinae.

The monospecific genus *Cophinoceras* was created for Upper Albian ammonites (Tambo series) of eastern Australia, with elliptical whorl section, narrow funnel shape umbilicus, straight prorsiradiate primary ribs (constrictions covered by the test), each pair of such ribs being separated by 8–12 short straight intercalatories. The suture is said to have wide-stemmed saddles and regularly trifid first lateral lobe. *C. ogilviei* has been collected near the mouth of Bynoe River, on Normanton-Burketown Road, N Queensland, Autralia, in the Normanton Formation which is considered Albian and more recently Cenomanian (Rawlings *et al.*, 1997). According to Day (1968), this species comes from the Upper Albian.

Day (1968, unpublished dissertation) described a new Upper Albian species: “*Beudanticeras*” *vinei*, for several large ammonites, saying that it could be referred to *Cophinoceras*. He adds: «“*Beudanticeras*” *vinei* sp. nov. is referred to the genus *Beudanticeras* with some reservation. The species attains an exceptionally large size for a *Beudanciceras* and approaches the dimensions of many species of Puzosia Bayle. However, typical *Puzosia* has a more depressed whorl section. The deep ventral lobe of the suture is also unusual for a *Beudanciceras*. The suture of *Desmoceras* Zittel is very similar, but that form also has a depressed whorl section. ». This species co-occurs with *Myloceras*, *Labeceras* and *Appurdiceras* and is of Late Albian age.

In our opinion, «*Beudanticeras*» *vinei* probably represents the adult stages of *Cophinoceras ogilviei*. The taxonomic position of the genus *Cophinoceras* remains uncertain but is in no way related to the european Lower Albian *Roberticeras*. As for *Boliteceras*, it is provisionally maintained within the Uhligellinae, keeping in mind that it seems to be more closely related to the Puzosiinae.

Genus *Zuercherella* Casey, 1954
(= *Corteziceras* Etayo Serna, 1979, p. 27; type species
C. cortezi by original designation)

Type species. *Desmoceras zuercheri* Jacob, 1906, p. 9, by the original designation of Casey, 1954, p. 112.

Diagnosis. Medium-sized high-whorled shell with oval or subquadrate whorl-section, venter narrowly rounded; constrictions shallow, sinuous; between the constrictions are several ribs. Main ribs begin slightly above or at the umbilical rim; intercalatory ribs occur only in the upper half of the flanks. Outer whorls appear to be feebly ornamented based on a single specimen.

Zuercherella zuercheri (Jacob 1906)
Figures 2a–d, 3a–c, 4a-c, 5, 6

Synonymy.

1906 *Desmoceras zürcheri* Jacob, p. 9, pl. II, fig. 1–3.
?1907 *Desmoceras* (*Uhligella*) cf. *zürcheri* Jacob; Pervinquière, p. 137, pl. 5, fig. 26.
1910 *Uhligella zürcheri* Jacob and Tobler; Kilian, pl. 10, fig. 3.
1920 *Uhligella zürcheri* Jacob and Tobler; Fallot, p. 261, pl. 3, fig. 7.
Non 1933 *Uhligella zuercheri* Jacob and Tobler; Rouchadze, p. 183, pl. 2, fig. 4, 5.
1949 *Uhligella zürcheri* Jacob; Luppov et al., p. 211, pl. LX, fig. 1a, 1b, text-fig. 37.
1954 *Zuercherella zuercheri* (Jacob and Tobler); Casey, p. 112.
1956 *Puzosia* sp. A; Murphy, fig. 6.
1956 *Puzosia* sp. B; Murphy, fig. 6.
1957 *Zurcherella zurcheri* Jacob; Wright p. L368, fig. 481: 1a, b.
1958 *Zürcherella zürcheri* Jacob; Luppov and Drushchits, p. 109, pl. 50, fig. 8.
?1964 *Zürcherella zürcheri* (Jacob); Fülöp, pl. 4, fig. 1, 2.
1964 *Zürcherella zürcheri* Jacob; Kemper, p. 39, pl. 4, fig. 1; pl. 15, fig. 1; pl. 17, figs 1–3.
1966 *Zürcherella zürcheri* (Jacob); Schindewolf, p. 623.
1968 *Beudanticeras* (*Zuercherella*) *zuercheri* (Jacob); Wiedmann and Dieni, p. 130, pl. 12, fig. 1.
1969 *Zurcherella zurcheri* Jacob; Egoian, p. 177, pl. 15, fig. 8, 9; pl. 25, fig. 64.
1971 *Zuercherella zuercheri* Jacob; Kvantaliani, p. 98, pl. 15, fig. 1.
1971a *Zürcherella zürcheri* (Jacob); Kemper, pl. 4, fig. 7.
1971b *Zürcherella zürcheri* (Jacob); Kemper, pl. 29, fig. 1.
1976 *Zürcherella zürcheri* (Jacob); Kemper, pl. 4, fig. 7.
1980 *Zurcherella zurcheri* (Jacob); Thomel, p. 124, fig. 246.
1982 *Beudanticeras* (“*Zuercherella*”) *zuercheri* (Jacob); Renz, p. 22, pl. 1, fig. 20; text-fig. 10c, d.
?1986 *Zurcherella alpina* Demay and Thomel, p. 34.
1993 *Zuercherella zuercheri* (Jacob); Sharikadze, p. 135, text-fig. 6.
1995 *Zürcherella zürcheri* Jacob; Kemper, pl. 5, fig. 5.
1996 *Zuercherella zuercheri* (Jacob); Wright, p. 80, fig. 61: 2.
1996 *Zuercherella zuercheri* (Jacob); Mutterlose, p. 51, pl. 3, fig, 2, 3.
1996 *Zürcherella zürcheri* (Jacob); Weber, p. 79, pl. 3, fig. 1, 2, pl. 8, fig. 2, 3, pl. 9, fig. 4.
? 2004 *Zuercherella* cf. *zuercheri* (Jacob and Tobler, 1906); Bogdanova and Hoedemaeker, p. 245, pl. 41, fig. 2.
2005 *Zuercherella zuercheri* (Jacob and Tobler); Dutour, pl. 17, fig. 1-6, fig. 12.
2005 *Zuercherella zuercheri* (Jacob); Kvantaliani in Kotetishvili *et al.*, p. 322, pl. 61, fig. 2.
? 2007 *Zuercherella zuercheri* Jacob et Tobler; Szives, p. 55, pl. 3, figs 21, 22, 23.
2008 *Zurcherella zurcheri* (Jacob & Tobler); Joly & Delamette, fig. 6L.
2011 *Zuercherella zuercheri* (Jacob); Klein and Vašiček, p. 113 (pars).

Type material. The species is based on four syntypes, juveniles, less than 50 mm of diameter. Two of the four syntypes are in the collections of the University Grenobles Alpes (*ex* Dolomieu collections), both from the Upper Aptian of Chaudon (Alpes de Haute Provence, France). We were unable to trace the syntypes figured by Jacob (1906, pl. 2, fig. 1 and text-fig. 3) from the Upper Aptien of Luitere Zug (Switzerland). No type specimen was designated by Jacob. Dutour (2005, unpublished) considers the specimen figured by Jacob (1906, pl. 2, fig. 1) as the holotype. Consequently, the specimen figured by Jacob (pl. 2, fig. 3) is herein selected as the lectotype. The lectotype UJF-ID.1064 *Desmoceras* (*Uhligella*) *zürcheri* Jacob, 1906, pl. 2, fig. 3, is herein refigured (Fig. 2a, b).

N°	D	H	W	U	W/H
UJF-ID.1064	39.0	18.0 (.46)	12.7 (.33)	7.8 (.20)	0.71

UJF-ID.1064 is a juvenile preserved as a pyritized internal mold. The coiling is involute (U/D = 0.20) with low, broadly convex umbilical wall and shoulder, feebly convex flanks, and narrow feebly convex venter. There are seven radial, feebly flexuous constrictions on the last half-whorl, with adapical rib on the outer part of the flanks and venter. There are about six feeble, fine riblets between each constriction, that arise on the inner third of the flanks. The suture shows a trifid, symmetrical L (Fig. 2d).

UJF-ID.1065 *Desmoceras* (*Uhligella*) *zürcheri* Jacob, 1906, pl. 2, fig. 2 : paralectotype

N°	D	H	W	U	W/H
UJF-ID.1065	43.0	19.0 (.44)	14.5 (.34)	10.5 (.24)	0.76

An oxidized limonitic juvenile specimen, differing only from the previous specimen by its flatter flanks.

The original figure of one of the syntypes from Luitere Zug (Jacob, 1906, pl. 2, fig. 1) is herein refigured (Fig. 2c), showing the differences of ornamentation owing to the kind of preservation.

Material. Eight specimens from Northern California:

- CASG70778 of unknown origin (Figs 5, 6);
- CASG70779 (UCLA loc. 2845, = M62: 40°27’30.91”N, 122°35’47.96W): *Acanthohoplites gardneri* Zone (Figs 4a-c);
- CASG70781 (including CAS70784: UCLA loc. 2867, = M85: 40°27’51.16”N, 122°34’13.61W): from Huling Creek, co-occurs with ‘*Acanthohoplites*’ *aegis* at the base of the *Acanthohoplites gardneri* Zone;
- CASG70783 (UCLA loc. 2856, = M74: 40°27’57.73”N, 122°36’45.15W), from North Fork of Cottonwood Creek, where it co-occurs

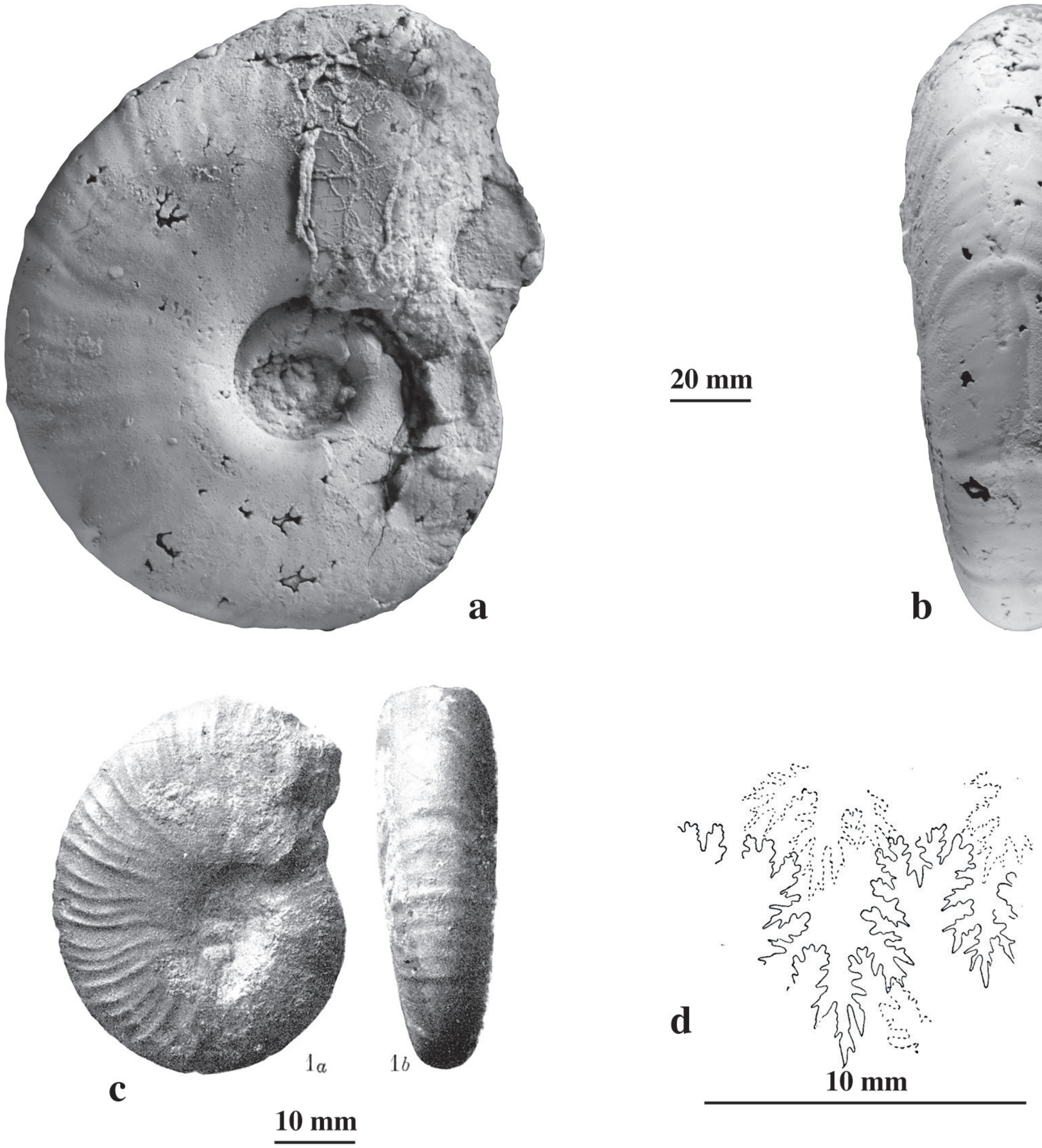

Figure 2. *Zuercherella zuercheri* (Jacob, 1906). a, b, the lectotype, a juvenile from the Upper Aptian of Chaudun (Alpes de Haute Provence, France); c, one of the syntypes from the Upper Aptian of Luitere Zug (Switzerland), the original figure of Jacob (1906, pl. 2, fig. 1); d, suture line one of the syntypes from the Upper Aptian of Luitere Zug (Switzerland), the original figure of Jacob (1906, text-fig. 3).

with *Acanthohoplites gardneri* at the base of the *Acanthohoplites gardneri* Zone (Figs 3a–c);

- CASG70784 (UCLA loc. 2868, = M86: 40°27’55.79”N, 122°34’30.11W): from Huling Creek section, where it co-occurs with *Eotetragonites wintunius* (Anderson, 1938), *Eotetragonites wintunius* Zone;
- CASG70785 of unknown origin;
- an unnumbered specimen (loc. M135: 40°25’23.87”N, 122°39’13.78W), from the Bald Hills, Barr section where it co-occurs with *Eotetragonites wintunius* (Anderson, 1938), *Melchiorites indigenes* (Anderson, 1938), *Hypophylloceras onoense* (Stanton, 1895) and *Argonauticeras argonautarum* (Anderson, 1902), *Eotetragonites wintunius* Zone;
- an unnumbered specimen of unknown origin.

These specimens have been collected within the *Eotetragonites wintunius* Zone and at the base of the *Acanthohoplites gardneri* Zone, Upper Aptian of Shasta Co, California (Murphy, 1956). They are preserved as calcareous internal molds, partially covered by aragonitic shell.

N°	D	H	W	U	W/H
Unnumbered	38.5	18.0 (.47)	14.5 (.38)	8.5 (.22)	0.81
CASG70781	44.0	19.5 (.44)	15.0 (.34)	8.5 (.19)	0.77
M135	54.5	23.5 (.43)	21.0 (.39)	15.0 (.28)	0.89
CASG70783	80.0	34.0 (.43)	26.5 (.33)	20.0 (.25)	0.78
CASG70779	98.5	41.0 (.42)	33.5 (.34)	28.5 (.29)	0.82

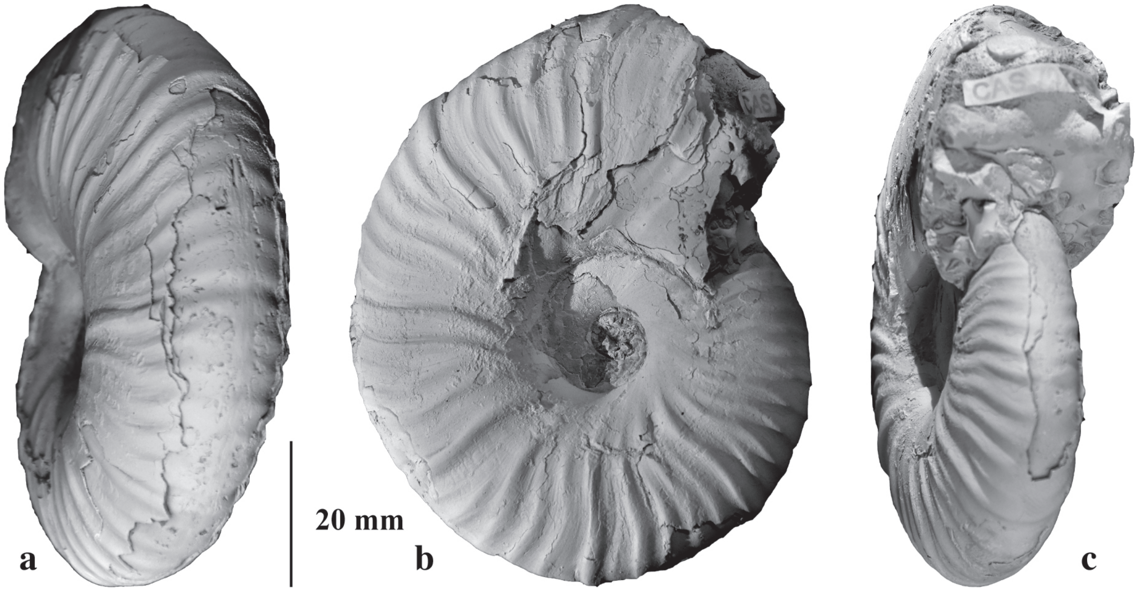

Figure 3. *Zuercherella zuercheri* (Jacob, 1906). a–c, CASG70783, UCLA locality 2856 (= M74), Huling Creek, base of the *Acanthohoplites gardneri* Zone, Upper Aptian.

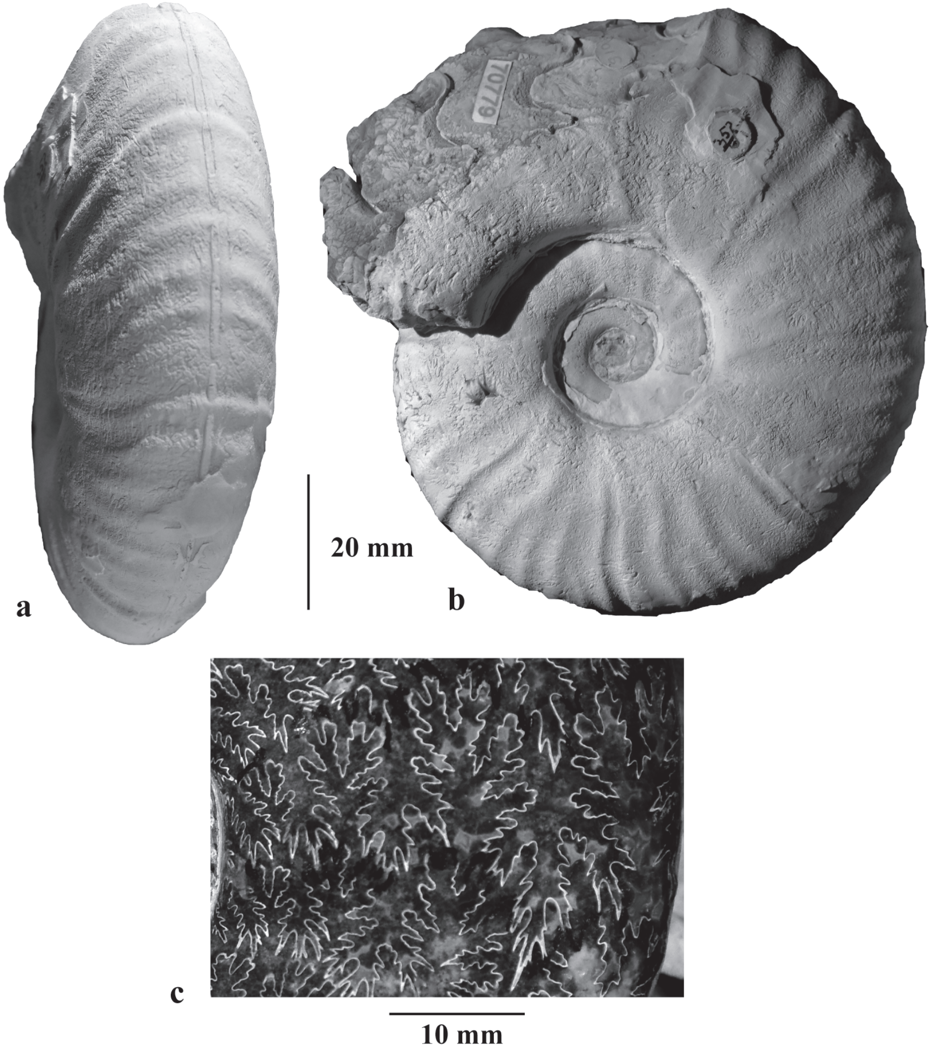

Figure 4. *Zuercherella zuercheri* (Jacob, 1906). a–c, CASG70779, UCLA loc. 2845 (= M62), *Acanthohoplites gardneri* Zone, Upper Aptian.

The coiling is involute on the juvenile (U/D between 0.19 and 0.22), becoming moderately involute with age with (U/D between 0.25 and 0.29). The whorl section is compressed (W/H between 0.77 and 0.89), oval to elliptical, with funnel-shape, moderately deep umbilical wall, broadly rounded umbilical shoulder, slightly convex flanks, with a maximum of width at the inner third. The outer part of the flanks converge to a narrowly rounded venter. The inner whorls, up to a diameter of 30 mm, show inconspicuous coarse ribs on the outer part of the flanks of the internal mold, and numerous falcoid growth lines on the shell that are strongly prorsiradiate on the inner part of the flanks. Beyond 30 mm, there are 9–10 prorsiradiate, coarse, wide, shallow constrictions, that are slightly projected forward on the ventral area where they are feebly collared backward. The internal mold bears almost inconspicuous, fine, sinuous, prorsiradiate ribs on the less ornamented specimens (unnumbered, M135) to coarse, low, prorsiradiate, biconcave ribs, arising at the umbilical seam and tending to branch at mid flanks on strongly ornamented specimens (CASG70781-85). When the shell is preserved, the constrictions are replaced by slightly biconcave, strong, prorsiradiate ribs that cross the venter without diminution, where they are slightly projected forward. The intercalatories arise at the umbilical seam or at the inner third of the flanks and are mostly attenuated on the siphonal area. With age, the costation becomes coarser and feebler on both internal mold and shell. The largest available specimen (CASG70778: Figs 5, 6), has an estimated diameter of 180 mm, comprising a 80° sector of body chamber, which is crushed and weathered, seeming to retain only inconspicuous ribbing and feeble growth striae on the shell. The suture (Fig. 4c) is moderately divided, having a deep L and a strongly retracted suspensive lobe, and it is very close to the partial suture figured by Jacob (1906, text fig. 3) (fig. 2d).

Discussion. The measurements given by Dutour (2005) for the material from south-east France, and those of the Californian material are consistent. The Californian ammonites differ from the lectotype of *Zuercherella zuercheri* (Jacob, 1906, pl. 2, fig. 1), by their narrowly convex venter, wider constrictions that are slightly projected forward on the venter, stronger, broader, coarser ribs and a slightly wider umbilicus. *Zuercherella latecostata* (Riedel, 1938) from the Upper Aptian of Colombia, differs from our material by the presence of numerous strong collared ribs that tend to bifurcate on the outer part of the flanks and its lower whorl section. *Zuercherella etayosernay* Bogdanova

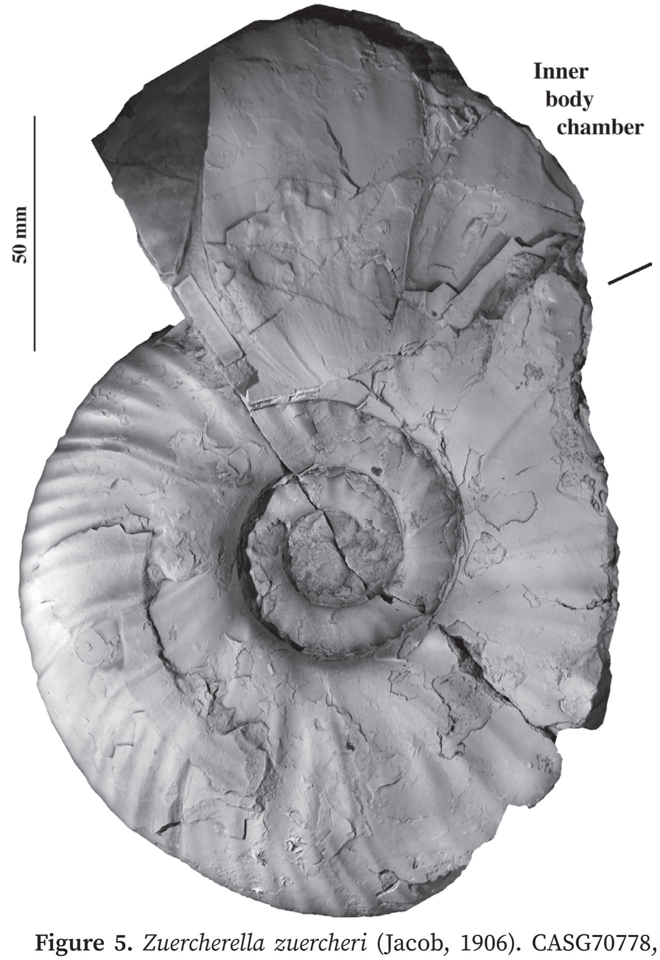

Figure 5. *Zuercherella zuercheri* (Jacob, 1906). CASG70778, locality and age unknown, Upper Aptian.

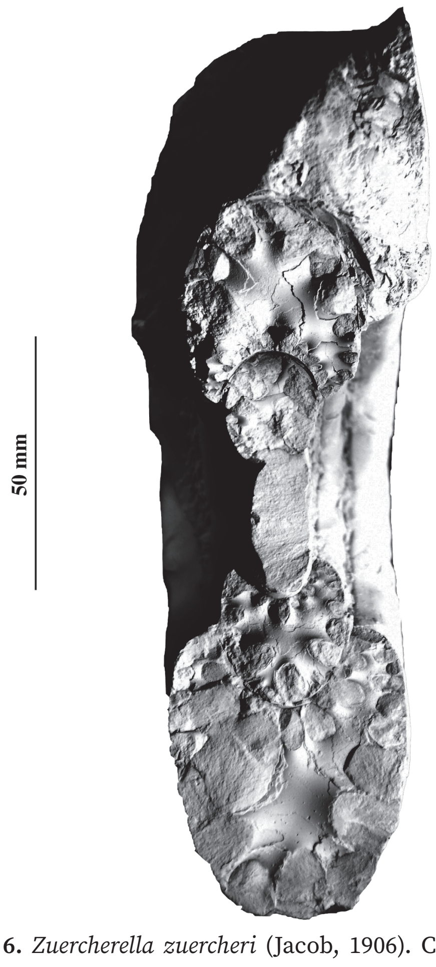

Figure 6. *Zuercherella zuercheri* (Jacob, 1906). CASG70778, locality and age unknown, Upper Aptian.

and Hoedemaeker, 2004, from the Aptian–?Albian of Colombia, is characterized by its narrow umbilicus and feeble ornament.

The specimen figured as *Zuercherella* cf. *zuercheri* (Jacob, 1906) by Bogdanova and Hoedemaeker (2004, p. 245, pl. 41, fig. 2) is very close to the syntype figured by Jacob (1906, pl. 2, fig.1), herein refigured (fig. 2c).

Demay and Thomel (1986) proposed to assign specimens figured by Fallot as *Uhligella zurcheri* (1920, p. 261, pl. 3, fig. 7) to *Zuercherella alpina* (Demay and Thomel, 1986). These authors recognize three distinct species in the upper Aptian of the south-east of France, *Zuercherella alpina* occurring in lower part of the interval (*Dufrenoyia furcata* zone and base of the *Epicheloniceras subnodosocostatum* Zone), *Zuercherella impressa* and *Z. zuercheri* occurring in the upper part of the interval (*Epicheloniceras subnodosocostatum* Zone and *Parahoplites melchioris* Zone). The morphological differences between those three species concern the strength of the ornamentation on the juvenile growth stages but this material was neither described nor figured.

According to Dutour (2005, p. 144), it might be conceivable that the morphologies of the *Dufrenoyia furcata* Zone and those of the *Parahoplites melchioris* Zone belong to distinct species, but such an approach has still to be supported by further studies.

Occurrence. According to Dutour (2005), the species occurs with certainty from the *Dufrenoyia furcata* Zone to the upper part of the *Parahoplites melchioris* Zone (first half of Upper Aptian). The species has been reported from France, Switzerland (Jacob, 1906; Dutour, 2005), Germany (Kemper, 1964), Italy (Wiedmann and Dieni, 1968), Morocco (Rey *et al.*, 1988), Georgia (Kvantaliani, 2005) and Venezuela (Renz, 1982). It occurs also in the *Eotetragonites wintunius* Zone and the base of the *Acanthohoplites gardneri* Zone, Upper Aptian of Shasta Co, California.

3. Conclusion

Zuercherella zurcheri is well-documented for a long time from North Tethyan margins and Germany (see the synonymy above). It has been sporadically reported from the south margin of Atlantic regions, in Morocco (Rey *et al.*, 1988) but without any illustration, in Venezuela (Renz, 1982), and its presence is suspected in Colombia (Bogdanova and Hoedemaeker, 2004, see above) (Fig. 7). The species is reported for the first time in north California, and it is the first known record of a Tethyan ammonite species in the upper Aptian of northern California. Affinities between Tethyan and Northeast Pacific biota have been already suggested by Iba and Tanabe (2007), and Iba *et al.* (2011) during Upper Aptian time, based on the record of bivalvs. It is reasonable to assume that a migration path existed along the south Atlantic margin through the Colombian sea.

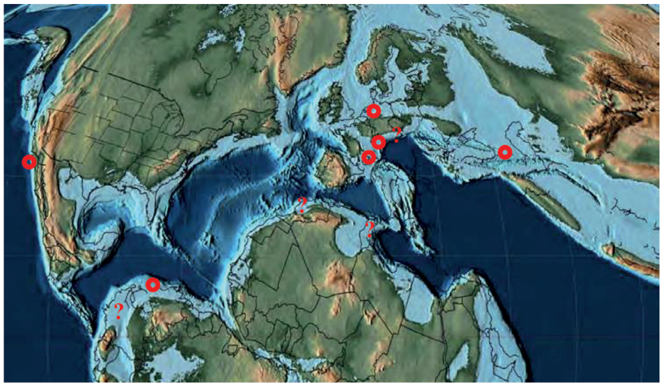

Figure 7. Paleogeographic map at the Upper Aptian with the distribution of *Zuercherella zuercheri* (Jacob, 1906) (map after Scotese, 2014).

Further investigations among the abundant material housed in the California Academy of Sciences, San Francisco, would be required to better understand the affinities between Northeast Pacific, south Atlantic margin and Colombian biota.

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Zittel, K.A. von (1895). *Grundzüge der Palaeontologie (Palaeozoologie)* [Book]. R. Oldenbourg, München/Leipzig, vii + 972 p.Figure 7. Paleogeographic map at the Upper Aptian with the distribution of *Zuercherella zuercheri* (Jacob, 1906) (map after Scotese, 2014).

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A review of *Beudanticeras* Hitzel, 1902 (Cretaceous Ammonitida), and its occurrence in the Cottonwood District of Northern California

Una revisión de Beudanticeras Hitzel, 1902 (Ammonitida del Cretácico), y su presencia en el Distrito de Cottonwood en el norte de California

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Abstract

Beudanticeras Hitzel is a distinctive but relatively rare Upper Albian (Cretaceous) ammonite that has been reported from the southeast France and the Cottonwood District of northern California coastal ranges. In both iterations of the Treatise (Wright, 1957 and 1996), it has been placed in the Desmoceratidae even though the type species has none of its characteristics. We classify it as the sole genus in the Family Beudanticeratidae Breistroffer, 1953 (*nomen translatum* herein, *ex* Beudanticeratinae Breistroffer, 1953) which is characterized by its discoidal shape, narrow umbilicus with an angulate shoulder, sickle-shaped ornamentation, and strongly asymmetrically bifid L. Most discoidal ammonites identified as "*Beudanticeras*" have features characteristic of the Desmoceratidae, such as, constrictions and trifid L, and are classified in *Roberticeras,* new genus. *Beudanticeras* and *Cleoniceras* are similar with respect to shell shape and strongly asymmetrically bifid suture but significantly different with respect to ornament, and shell shape. Four species are assigned to *Beudanticeras*: *B. beudanti* (Brongniart, 1822) and *B. sphaerotum* (Seeley, 1866) from Europe, *B. haydeni* (Gabb, 1864) from California, and *B. sutherlandbrowni* (McLearn, 1972) from British Columbia. *B. haydeni* (Gabb, 1864), based on a specimen from the Cottonwood district, occurs only in uppermost Albian strata, and can be distinguished from the similar *B. beudanti* by differences of degree in the umbilicus and ornament.

Keywords: Albian, ammonites, biostratigraphy, California, Cretaceous.

Resumen

Beudanticeras Hitzel es una ammonite del Albiano Superior (Cretácico) muy característico, pero relativamente escaso que ha sido reportado en el sureste de Francia y el distrito de Cottonwood en las cordilleras costeras del norte de California. En las dos versiones del Treatise (Wright, 1957 y 1996), se ha ubicado este género en Desmoceratidae a pesar de que la especie tipo no tiene ninguna de sus características. Nosotros lo clasificamos como el único género de la Familia Beudanticeratidae Breistroffer, 1953 (nomen translatum, ex Beudanticeratinae Breistroffer, 1953)*, que se caracteriza por su forma discoidal, ombligo angosto con pared angulada, ornamentación en forma de hoz y sutura L bífida fuertemente asimétrica. La mayoría de los ammonites discoidales identificados como "Beudanticeras" tienen rasgos característicos de Desmoceratidae, como constricciones y L trífida, y aquí se clasifican como el nuevo género Roberticeras. Beudanticeras y Cleoniceras son similares con respecto a la forma de la concha y la sutura bífida fuertemente asimétrica, pero significativamente diferentes con respecto a la ornamentación y la forma de la concha. Se asignan cuatro especies a Beudanticeras: B. beudanti (Brongniart, 1822) y B. sphaerotum (Seeley, 1866) de Europa, B. haydeni (Gabb, 1864) de California y B. sutherlandbrowni (McLearn, 1972) de Columbia Británica. B. haydeni (Gabb, 1864) está basado en un espécimen del distrito de Cottonwood, estando solo presente en los estratos de la parte más alta del Albiano superior y puede distinguirse de la especie similar B. beudanti por diferencias en la región umbilical y la ornamentación.*

Palabras clave: *Albiano, ammonites, bioestratigrafía, California, Cretácico.*

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1. Introduction

In the Treatise classification (Wright, 1996), the Beudanticeratinae, a subfamily of Desmoceratidae, is broadly characterized to encompass varied morphologies of presumed affinity. The diagnostic characteristics of the type species of *Beudanticeras, B. beudanti,* we believe excludes it from the Desmoceratidae. Below we support this exclusion, suggest a different classification, and discuss the implications of this change. The systematic part reviews the species we assign to *Beudanticeras* Hitzel, 1902, the sole genus in the Family Beudanticeratidae.

The *Beudanticeras haydeni* studied herein were collected near the junction of Huling Creek and North Fork of Cottonwood Creek, near Ono, Shasta Co, California (Figure 1).

2. Systematic paleontology

Conventions. Dimensions are given in millimeters: D = diameter; W = whorl breadth; H = whorl height; U = umbilicus. We follow the descriptive categories established by Rodda and Murphy (2022).

Specimens examined are housed in the following collections:

UCLA	University of California, Los Angeles (Now at CASG).
CASG	California Academy of Sciences, Geology Collection.
CS	Clarence Schuchman at CASG
GSC	Geological Survey of Canada
LACMIP	Los Angeles County Museum, Invertebrate Paleontology Collection.
MNHNP	Muséum National d'Histoire Naturelle de Paris
UCMP	University of California, Berkeley, Museum of Paleontology
UJF-ID	Université Grenoble-Alpes, ex Institut Dolomieu collections.

Order Ammonitida Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Desmoceratoidea Zittel, 1895
Family Beudanticeratidae Breistroffer, 1953

(*nomen translatum* herein, *ex* Beudanticeratinae Breistroffer, 1953)

Diagnosis. Same as for *Beudanticeras*.

Genus *Beudanticeras* Hitzel, 1902

Synonomy

1902 *Beudanticeras* Hitzel, p. 875.
1923 *Beudanticeras,* Hitzel, 1905 (sic), Spath, p. 49 (pars).
1932 *Beudanticeras* Hitzel, 1902, Seitz, p. 392 (pars).
1960 *Beudanticeras* Hitzel, 1905 (sic), Murphy and Rodda, p. 851.
1979 *Beudanticeras* Hitzel, 1902, Scholz, p. 68.
1988 *Rapidoplacenticeras* Alabushev, p. 110.

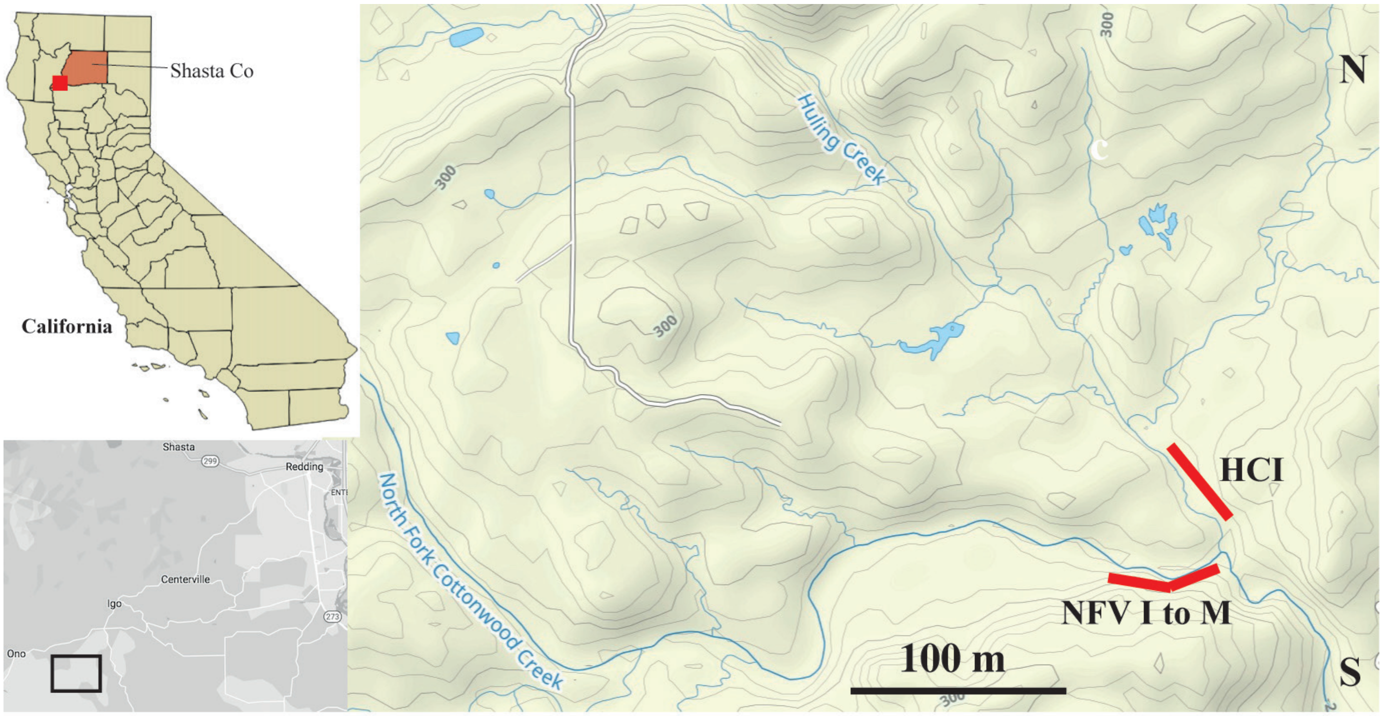

Figure 1. Map of the studied area, with location of the sections that yielded *Beudanticeras haydeni* (Gabb, 1864).

1993 *Beaudanticeras* Hintzel, 1905 (sic), Kennedy, p. 235.

2002 *Beudanticeras* Hitzel, 1905 (sic), Riccardi and Medina, p. 299 (pars).

Type species. *Ammonites beudanti* Brongniart, 1822 (in Cuvier and Brongniart, p. 95, 99, 394) by original designation and tautonomy.

Generic diagnosis. Involute, discoidal, gradumbilicate shells with falcoid growth lines, ornament of ribs on the outer flank, and a suture line with broad, strongly asymmetrical bifid L with E shorter than L.

Discussion. *Beudanticeras* has long been associated with the Desmoceratidae, an assignment that needs to be changed, because the diagnostic characteristics of the type species, *B. beudanti,* (lack of constrictions, suture with strongly asymmetrically bifid L, gradumbilicate shell) excludes it from the Desmoceratidae. We propose to consider *Beudanticeras* as the sole genus of Beudanticeratidae

Beudanticeras Hitzel as emended by Spath (1923) is based on a specimen in the collection of the Muséum National d'Histoire Naturelle, Paris (MNHN-F-J07792), from Rochers de Fiz, Haute-Savoie, France designated as the lectotype by Spath (1923, p. 49; Kennedy, 1993, p. 237). Examination of the figure of the lectotype (Kennedy, 1993, fig. 2) and other specimens from the type region in the Delamette Collection at the Muséum d'Histoire Naturelle, Geneva and the Muséum d'Histoire Naturelle, Paris shows that the lectotype and remaining specimens have neither the constrictions nor collars typical of desmoceratids. Only a single specimen in the Geneva collection shows a constriction and that specimen shows only one on one side of the specimen (the feature on this specimen is regarded as an aberrant variant unrelated to the genetics of the Desmoceratidae). The umbilical edge is acutely rounded or angular and the umbilical wall steep, but not perpendicular to the flank. The ornamentation of most specimens is confined to spaced, crescent-shaped ribs on the outer flank that do not cross the venter. Falcoid growth lines rather than sigmoidal or biconvex ones typical of desmoceratids are present, a distinctive suture line with an asymmetrically bifid L as opposed to the trifid L in typical desmoceratids (Jacob, 1908, fig. 14; Spath, 1923, fig. 12c; Seitz, 1932, fig. 1; Wright, 1957, fig. L482-2c), and an E shorter than L. To our knowledge, the ontogenetic development of the suture line of *B. beudanti* has been reported only by Jacob (1908, fig. 10) and Schindewolf (1966, Figs. 383, 384). In both cases, the specimens used by these authors are not correctly identified. The suture figured by Jacob (1908, fig. 10) has been drawn on an unidentified ammonite from La Balme de Rencurel (Isère, France). The age of this condensed level is lower Albian to basal middle Albian (Breistroffer, 1931) and the ammonite used by Jacob should be assigned to some species of the new genus described below. The material figured by Schindewolf, 1966) comes from the condensed Albian of Escragnolles. The age of Escragnolles material is lower to basal upper Albian but *B. beudanti* has never been reported from Escragnolles, even in the very detailed study of Gebhard (1979). A suture drawn from a juvenile specimen of *B. beudanti* from Entrèves-en-Bauge (Savoie, France), with a whorl height of 7 mm (Figure 2a), clearly shows that L is more strongly asymmetrical than the L of Jacob's figure at a similar size.

Two of us accepted Spath's (1923, p. 50) interpretation of this genus (Murphy and Rodda, 1960) and we all feel his analysis of its history, particularly Jacob's (1908) misidentification of the type species, *Beudanticeras beudanti* (Brongniart) is correct. However, most of the taxa he has placed in the genus are distinct from *Beudanticeras* and should be assigned elsewhere.

Two types of discoidal conchs have traditionally been assigned to *Beudanticeras*: Those without constrictions and with an elaborate suture with a bifid, strongly asymmetrical L that undercuts E, and those with constrictions and with a simpler suture with a trifid, weakly asymmetrical L that does not undercut E. These forms are considered here as convergent with regard to shell shape and, in some cases, suture pattern. We regard the presence or absence of constrictions as an important and relatively common indicator of taxonomic affinity, whereas, gradumbilicate is a relatively rare condition in ammmonites. None of the constricted types has that kind of umbilicus. The first kind, exemplified by *B. beudanti*, ranges from early to late Upper Albian. The latter by "*Beudanticeras*" (of authors) ranges from just above the base of Lower Albian to early Middle Albian (Casey, 1961, Owen, 1988, Kennedy, 2000). As interpreted in the literature, the Upper Albian and the Lower-Middle Albian *Beudanticeras* are separated by a significant morphological and stratigraphical gap (Robert *et al.*, 2001, Robert, 2002, Bulot, 2010).

The Lower-basal Middle Albian morphologies with rounded umbilical shoulder, presence of constrictions at some stage in the ontogeny, a wider venter and a simpler suture, with no overlap, and with lower saddles that were previously assigned to the genus, are here placed within the new genus *Roberticeras*, type species *Ammonites dupinianus* d'Orbigny, 1841, p. 276, pl. 81, figs 6-8 (see Appendix 2). This genus is named after Emmanuel Robert (University of Lyon, France) who first adressed that issue.

The new genus *Roberticeras* is classified as a member of the new desmoceratid subfamily Uhligellinae (see Appendix 2), which includes ammonites with constrictions, and with a simpler suture line characterized by a symmetrical to feebly asymmetrical trifid L. This subfamily also includes the genera *Zuercherella* Casey, 1954; *Uhligella* Jacob, 1907; and *Pseudorbulites* Casey, 1961.

We assign to the new genus the following taxa:

Beudanticeras albense Breistroffer, 1947;
Beudanticeras ambajabense Collignon, 1963;
Beudanticeras ampanihense Collignon, 1963;
Beudanticeras arduennense Breistroffer, 1947;

Beudanticeras caseyi Collignon, 1963;
Ammonites cesticulatus d'Orbigny, 1841;
Ammonites dupinianus d'Orbigny, 1841, p. 276, pl. 81, figs 6, 8;
Desmoceras Dupinianum var. *Africana* – Pervinquière, 1907;
Beudanticeras (*Beudanticeras*) *dupinianum evolutum* Casey, 1961;
Beudanticeras dupinianum percostata Collignon, 1963;
Beudanticeras dupiniforme Collignon, 1963;
Beudanticeras hirtzi Collignon, 1950;
Beudanticeras hourcqi Collignon, 1949;
Beudanticeras komihevitraense Collignon, 1950;
Ammonites laevigatus J. de C. Sowerby, 1827;
Beudanticeras newtoni Casey, 1961;
Ammonites parandieri d'Orbigny, 1841;
Beudanticeras perchoisense Destombes, 1979;
Beudanticeras rectisulcatum Collignon, 1936;
Beudanticeras revoili Pervinquière, 1907;
Beudanticeras Sanctae-Crucis Bonarelli, 1921;
Beudanticeras subrotundum Collignon, 1963.

The synonymies given by Riccardi and Medina (2002), based on morphological resemblances between taxa that mostly come from condensed levels, are to be reconsidered. This stock is very probably polyphyletic and is needs further investigation and revision. The characteristics enumerated above separate *Beudanticeras* from all described taxa, for example *Brewericeras* Casey (Murphy and Rodda, 1960, p. 851). In particular, *Cleoniceras* is similar in gerontic shell shape, has an asymmetrically bifid suture, and smooth venter with ribs that do not cross the venter as in *Beudanticeras*. However, these differences are offset or insignificant when the details are reviewed. The ornamentation in *Cleoniceras* is weak on the middle flank and strong on the inner and outer flanks with well-developed bullae near the umbilical edge in the immature ontogenetic stages. The gerontic specimens of both taxa are smooth. The umbilicus meets the flank wall at an obtuse angle rather than a right angle as in *Beudanticeras.*

D'Orbigny's (1842, pl. 84) rendition of the suture line of *Cleoniceras cleon,* which was reproduced by Wright (1957, p. L393, fig. 2) has a narrow, symmetrically trifid L. However, Jacob (1908, p. 57, fig. 44, reproduced in Spath, 1923, p. 92, fig. 19) figures a different L for *C. cleon,* as does Casey (1966, p. 556, fig. 211). In both the latter cases, the L is broad, complexly incised, and markedly bifid. Spath (1923, p. 92) regards this type of suture as a convergent character that occurs in a number of unrelated genera. However, as mentioned above, this does not have to be the case and he gives no evidence for this interpretation. Although it can be described as bifid, it does not resemble the suture of *Beudanticeras beudanti* or *B. haydeni*.

The suture line in oxyconic ammonites that arise out of clades with more equant whorl shapes compensate for the loss of shell strength accompanying the change in several ways. Some have stretched the existing suture to cover a broader area, others have added lobes, and some have just developed more complex patterns in the existing elements. Because the problem is the same for this kind of change in shell shape, the solution may be similar in unrelated clades and the resulting characters are convergent. Convergence is an interpretation, which may be accurate in some clades, but inappropriate for others. It seems to us that when taxa show several similarities in the morphology of unrelated structures or parts, convergence is the less likely as the number of similarities increases.

In the present case, the differences between the genotypes of the two genera are 1) the depth of the E in *B. beudanti* is about equal to one half of the L, in *C. cleon* E is about equal L; 2) the L undercuts E in B. *beudanti,* but does not in *C. cleon*; 3) *B. beudanti* has no umbilical bullae, whereas *C. cleon* does; 4) *B. beudanti* is gradumbilicate, *C. cleon* umbilicus has a broadly rounded umbilical edge. Ribs when developed in *C. cleon* are sigmoidal, present on the inner flank and may be bullate and may bifurcate at the bullae. In *B. beudanti,* the ribs and are distinctively half-moon shaped and confined to the outer flank. The growth lines in both species are parallel to the margin of the aperture but is sigmoidal in *C. cleon* and falcoid in *B. beudanti*. Neither species consistently has constrictions, although one partial constriction has been observed on one specimen in over 60 of *B. beudanti* in the collection at the Museum of Natural History, Geneva from the type locality, Rochers de Fiz. We see no relation of *Beudanticeras* to other Albian taxa, and it is the sole genus of the Beudanticeratidae.

Alabushev (1988, p. 56) designates *Proplacenticeras sutherlandbrowni* McLearn as the type species of his new genus *Rapidoplacenticeras*. *Proplacenticeras sutherlandbrowni* McLearn is herein considered as a poorly known species of the genus *Beudanticeras* (see below) and consequently, *Rapidoplacenticeras* is a junior synonym of the genus *Beudanticeras*.

Beudanticeras flindersi (McCoy, 1865, p. 334), figured by Etheridge (1892, p. 494, pl. 30, fig. 2, and Whitehouse, 1928, pl. 25, figure 3), from Coolibah, Hughenden, Queensland, Autralia, ?Wallumbilla Formation, and *Beudanticeras mitchelli* (Etheridge, 1872, p. 345, pl. 3, fig. 1, lateral and aperture views) [refigured by Etheridge Jr., 1892, pl. 30, figs 1, 2 and by Whitehouse, 1928, pl. 25, fig. 2 (lectotype)], from Hughenden, Queensland, Autralia, ?Allaru Mudstone, respectively 150 and 128 mm in diameter, shows sigmoidal ribs that seem to be associated with shallow constrictions and low whorl section. Day (1968, unpublished) has claimed that both *Beudanticeras flindersi* and *Beudanticeras mitchelli* are contemporaneous with *Boliteceras daintreei,* which occurs in the Lower Albian, while McKenzie gives a middle Albian age. *B. mitchelli* is probably a junior synonym of *B. flindersi* and is very probably not related to the genus *Beudanticeras*. The holotype of

Beudanticeras flindersi (McCoy, 1865) (n° P.2185, Museums Victoria Collections, Australia), from the base of Walker's Table Mountain, West Bank, Flinders Range, Queensland, is a specimen about 145 mm in diameter, comprising the phragmocone and a 180° sector of body chamber (D: 108 – H: 54 (.50) – W: 36 (.33) – U: 23 (.21) – W/H: .66). The inner whorls almost smooth, with almost inconspicuous fine ribbing on the flanks when the shell is preserved. Constrictions may occur on the adult but are inconspicuous. Fine, almost inconspicuous biconcave ribs can be observed on the body chamber. This specimen seems to differ from *Boliteceras daintreei* only by its more compressed whorl section and by its feebler ornament. According to Day (1968, unpublished thesis), *Desmoceras* (?) sp. in Whitehouse (1928, p. 200, pl. 26, fig. l) is a juvenile of *B. flindersi*.

At present we assign only four species to the genus: *B. beudanti* Brongniart, *B. haydeni* Gabb and *B. sphaerotum* (Seeley 1866), and *B. sutherlandbrowni* (McLearn, 1972). *B. sphaerotum* we retain as a species provisionally on the basis of Spath's (1923, p. 54) statement that some consistent differences exist between the population from Hunstanton and those from Folkstone. Seitz (1932) also reached this conclusion, although he included much more in the genus than we would admit. Scholz (1979, p. 68) prefers to unite *B. beudanti* and *B. sphaerotum*.

Thus restricted the genus ranges through The *Dipoloceras cristatum* Zone to the *Mortoniceras* (*Mortoniceras*) *inflatum* Zone in western Europe. Scholz (1979) reports it also from the *Mortoniceras* (*Mortoniceras*) *fallax* Zone of Hungary.

In California, well-dated *B. haydeni* occur in the *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone and the *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone in the Dry Creek section (Murphy and Rodda, 1996; Amédro and Robaszinsky, 2005) and possibly in the *Mortoniceras* (*Mortoniceras*) *fallax* Zone, into the interval that also yields *Stoliczkaia dispar* var. *notha*.

Beudanticeras haydeni (Gabb, 1864)
Figures 2b, 3a-c, 4a-f, 5a-d, 6a-c, 7a-d, 8

Synonymy.

1864 *Ammonites haydeni* Gabb, p. 62, pl. 10, fig. 8.
1910 *Desmoceras haydeni* (Gabb); Grabau and Shimer, p. 171, fig. 1419.
1938 *Beudanticeras haydeni* (Gabb); Anderson, p. 190 (pars), non pl. 48, figs. 2, 3 (= *Brewericeras hulenense* Anderson 1938).
Non 1943 *Desmoceras haydeni* Gabb; Hanna and Hertlein, p. 168, fig. 61-8 (= *Brewericeras hulenense* Anderson, 1938).
1956 *Beudanticeras haydeni* (Gabb); Murphy, p. 2119, fig. 6.
1958 *Beudanticeras haydeni* (Gabb); Anderson, p. 212 (pars), non pl. 8, figs. 1 (= *Brewericeras hulenense* Anderson, 1938).
1960 *Beudanticeras haydeni* (Gabb); Murphy and Rodda, p. 851, pl. 104, fig. 4; pl. 105, figs. 1, 2.
1996 *Beudanticeras haydeni* (Gabb); Murphy and Rodda, p. 244-245, fig. 5 (A).

Holotype. UCMP 14973, *Ammonites haydeni* Gabb (1864, pl. 10, fig. 8), North Fork of Cottonwood Creek. This specimen was known only from the original drawing by Gabb and is herein figured for the first time (Figures 2b, 3a–c).

N°	D	H	W	U	W/H
UCMP14973	95.0	54.0 (.57)	24.0 (.25)	15.0 (.16)	0.44

The specimen has an estimated diameter of 105 mm, comprising the phragmocone and a 30° sector of body chamber. It is preserved as an internal mold retaining some parts of aragonitic shell. The coiling is involute (U/D = 0.16), the whorl section is compressed (W/H = 0.44), and sub-elliptical with of maximum of width at the inner third of the flanks. The flanks are slightly convex, converging to a narrowly convex venter. The umbilical wall is low, vertical and slightly concave. The umbilical shoulder is sharp to extremely narrowly rounded. There is no visible ornamentation. It can be seen that the suture figured by Gabb (1864, pl. 10, fig. 8c) and reproduced herein (Figure 2b), which has been drawn from a poorly preserved suture line with overlapping septa, is wrong. The external and lateral saddles are closer to each other and the first auxiliary lobe is not so deep.

Material examined. All California specimens recorded here are from the Upper-Chickabally Member of the Budden Canyon Formation of the Cottonwood District (Murphy *et al.*, 1969).

CASG60892, from NFV-M, is a fragment of a juvenile, about 18 mm in diameter, with parts of the shell preserved (Figure 4a, b). At this stage of growth, the whorl section is compressed (W/H = 0.6), subtriangular, with a maximum width just above the umbilical edge, flattened flanks converging to a narrow convex venter. The coiling is involute, the umbilicus comprises about 16% of the diameter. The umbilical wall is deep and vertical, the umbilical shoulder is narrowly rounded. The ornament, almost inconspicuous, is made of fine, straight, prorsiradiate striae arising on the umbilical shoulder, that are projected backward at mid-flank and then forward on the outer third of the flanks and across the venter.

CASG78582 (CS2001) (Figure 5a-d) is a very well preserved juvenile phragmocone preserved as an internal mold retaining very thin parts of shell. It shows the characteristic ribbing pattern of the species, with fine, growth striae and crescent-shaped riblets on the outer part of the flanks. The internal whorls of LACM IP 9859 are identical.

N°	D	H	W	U	W/H
CASG78582	55.0	29.0 (.53)	14.0 (.25)	8.0 (.15)	0.48

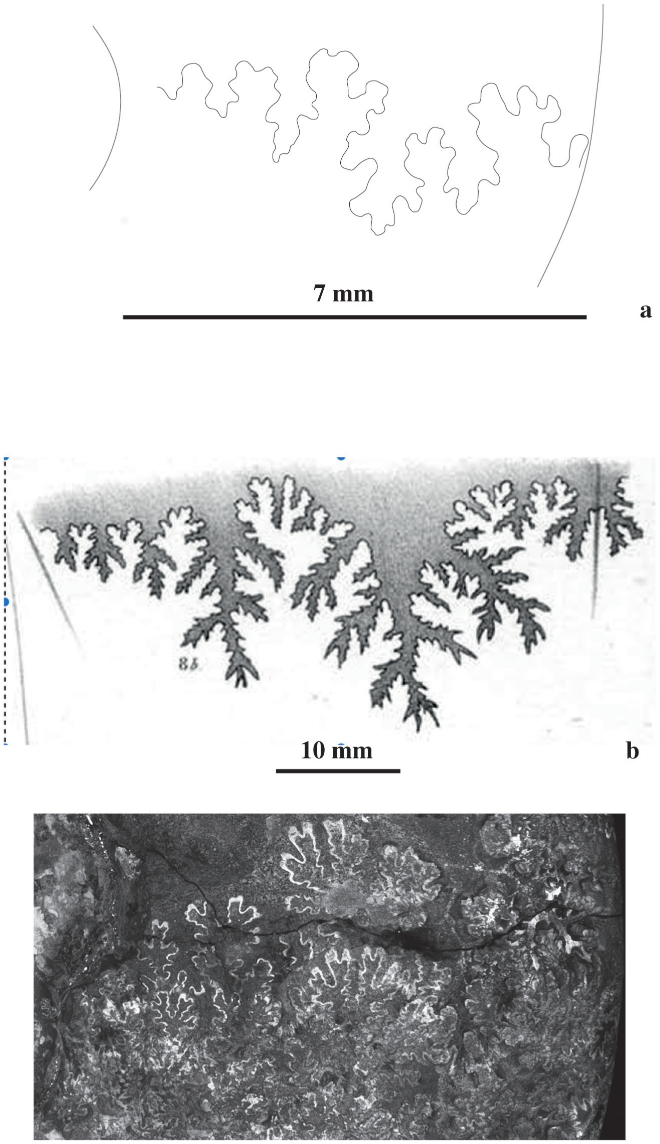

Figure 2. a, suture line of *Beudanticeras beudanti* (Brongniart, 1822), upper Albian of Entrèves-en-Bauges, Savoie, France. b, suture line of Beudanticeras haydeni (Gabb, 1864), uppermost Albian of California, the original drawing of Gabb (1964) and a photography of the same suture.

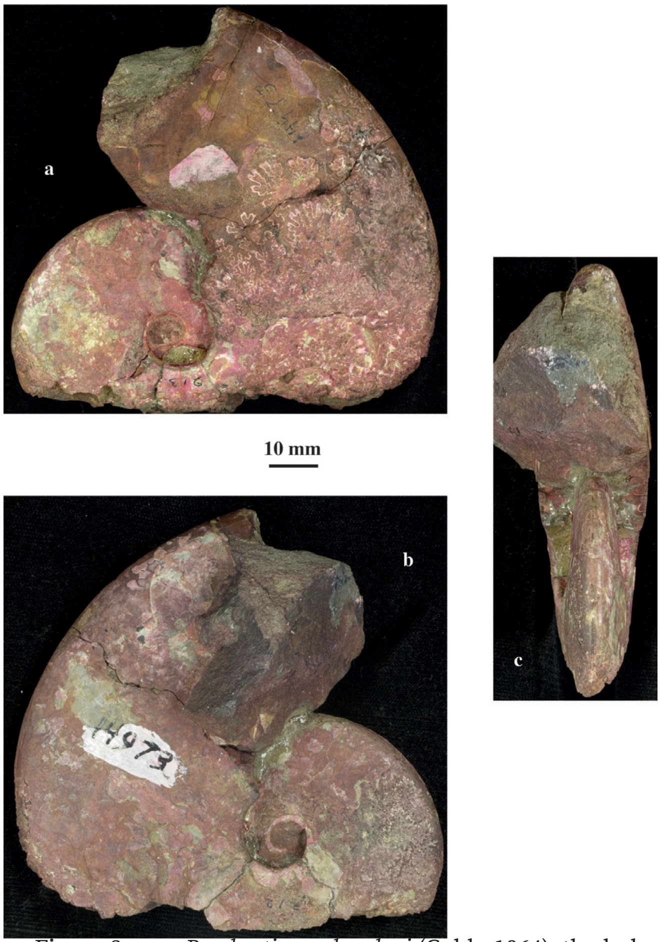

Figure 3. a–c, *Beudanticeras haydeni* (Gabb, 1864), the holotype, figured by Gabb (1864, pl. 10, fig. 8) as Ammonites haydeni, UCMP.14973, upper Albian of North Fork Cottonwood Creek, Shasta Co, California.

CASG78583 (CS1004 from NFV-K) (Figure 4f) is an incomplete juvenile phragmocone, about 65 mm in diameter, preserved as a slightly crushed internal mold with some remains of shell, showing vertical, slightly concave umbilical wall, sharp umbilical edge and flattened flanks. The ornamentation is of numerous, almost inconspicuous, fine striae.

CASG65042.01, from an unknown locality, is a fragment showing the whorl section with feebly convex flanks and narrow rounded venter (Figure 6a, b).

CASG78584 (NFV-K 86-2 below marker bed 3), (Figure 7a, b) is a distorted fragment of an internal mold, with an estimated diameter of 90 mm. There are also some large, poorly preserved fragments from NF V-K.86.2, with an estimated diameter of more than 200 mm seem to bear coarse, low sigmoidal ribs close to the aperture.

CASG78585 (CS1003) (Figure 8) is a well preserved phragmocone, about 100 mm in diameter, surrounded by a piece of crushed body chamber, for a total estimated diameter of 160 mm. The crescent-shaped ribs are well expressed on the outer part of the flanks of the phragmocone. We should note a spectacular broadening of the umbilicus on the last incomplete whorl and that in some specimens the umbilical spiral is distorted.

CASG78586 (CS 2006) (Figure 6c), from Huling Creek, 85 mm in diameter, clearly shows the angular umbilical edge.

CASG78587 (NFV I-3) is a well-preserved fragment showing the crescent shaped ribs on the upper half of the flanks rising from inconspicuous fine straight, prorsiradiate ribs on the inner half of the flanks. There are fine striae on the shell between ribs.

CASG78588 (NFVI 90-6 west chine) is a distorted fragment showing the narrow ventral area.

There are an additional ten poorly preserved fragments from the Schuchman collection at CASG.

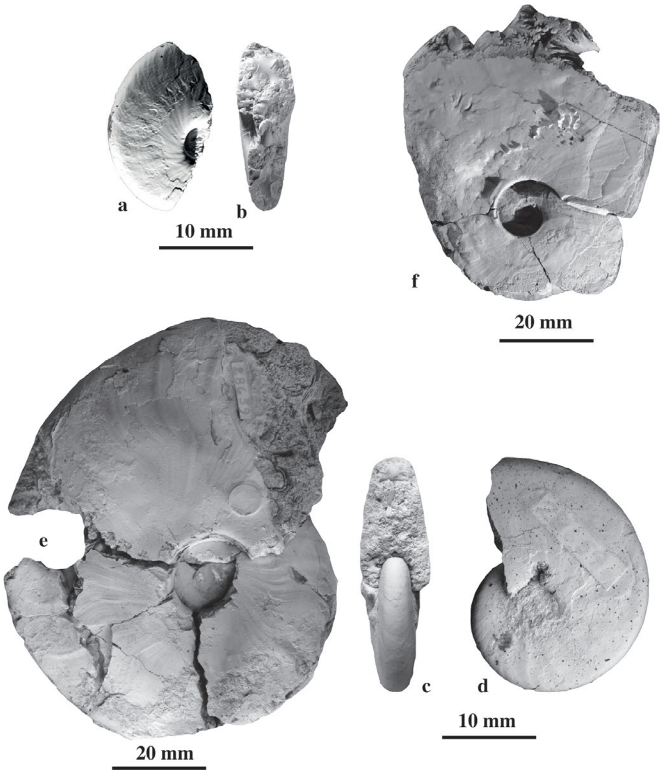

Figure 4. *Beudanticeras haydeni* (Gabb, 1864). a, b, CASG60892, NFV; c-e, LACMIP.9859; f, CASG78583.

LACMIP 9859, from loc. LACMIP 22901 (=UCLA 3467), in lowest conglomerate of the Bald Hills Member on the North Fork of Cottonwood Creek. The specimen, figured by Murphy and Rodda (1960, pl. 105, figs 1, 2), and refigured herein (Figure 4c–e), is a complete phragmocone, 82 mm in diameter, that shows the characteristic ribbing patterns and the extremely narrowly rounded umbilical shoulder on a piece of preserved body chamber.

N°	D	H	W	U	W/H
LACMIP9859	82.0	44.0 (.54)	21.0 (.26)	8.5 (.10)	0.48

LACMIP 9860, from locality LACMIP 22900 b (=UCLA 2900), Chickabally Member; Huling Creek. In conglomeratic sandstone, first sandstone downstream from junction with east fork of Huling Creek. (Murphy and Rodda, 1960, pl. 104, fig. 4) (herein refigured (Figure 7c, d), is a 90° sector of an adult phragmocone, with an estimated diameter of 105 mm that shows the suture line (Figure 7).

N°	D	H	W	U	W/H
LACMIP9860	25.0	14.0 (.56)	7.0 (.28)	? (?)	0.50

In summary, *B. haydeni* is characterized by juvenile stages with narrowly rounded umbilical shoulder and numerous prorsiradiate, falciform striae on the flanks and on the venter, by subadult stages with sharp, angular umbilical shoulder, vertical umbilical wall and sickle-shaped ribs on the outer flanks. The adult stages are not well-known but show a spectacular broadening of the umbilicus.

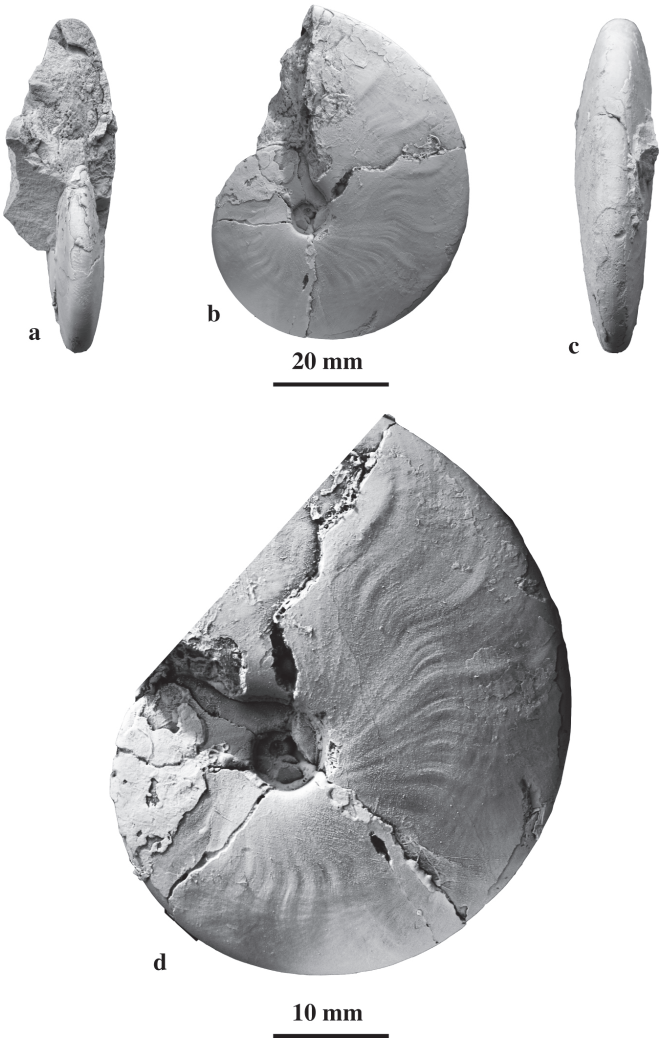

Figure 5. *Beudanticeras haydeni* (Gabb, 1864). a-d, CASG78582 (CS2001).

Discussion. *Beudanticeras* has been misinterpreted by Anderson (1938 and 1958). As pointed out by Murphy & Rodda (1960, p. 851), the specimens figured by Anderson (1938, pl. 8, figs. 3; 1958, pl. 8, fig.1) are small specimens of *Brewericeras hulenense* (Anderson).

Proplacenticeras sutherlandbrowni McLearn (1972, p. 56, pl. 8, figs. 3A, B) is poorly known. (This posthumous work was prepared for publication by J. A. Jeletzky from a nearly complete MS.) Only the Holotype is illustrated, and both its locality and age are in doubt. The figured specimen is a half whorl of an adult phragmocone with a compressed, high, oval, whorl section having maximum width at mid-flank. The slightly convex flanks converge to a narrowly rounded venter. The umbilical wall is high, steep, with a narrowly rounded, almost angular umbilical shoulder. No ornamentation is visible. The highly indented and interlocking suture line shown in the photograph is similar to the suture of *Beudanticeras beudanti* as figured by Spath (1923, p. 51, text-fig. 12c), with wide and deep asymmetrical lateral

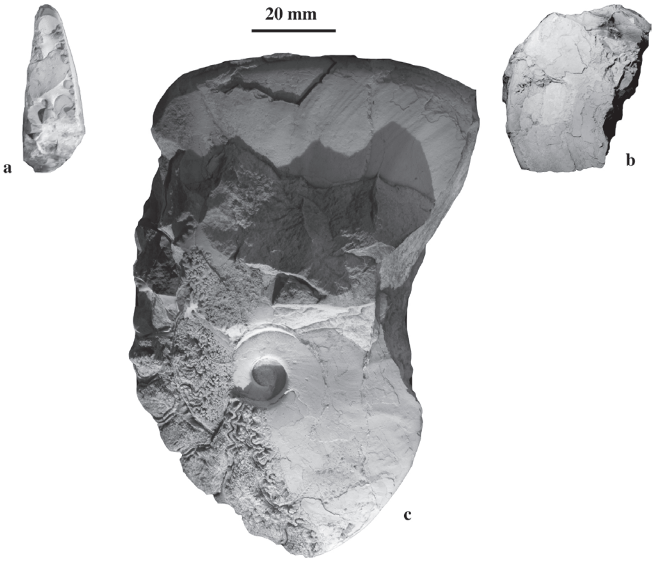

Figure 6. *Beudanticeras haydeni* (Gabb, 1864). a, b, CASG78582; c, CASG78586 (CS.2006), from Huling Creek.

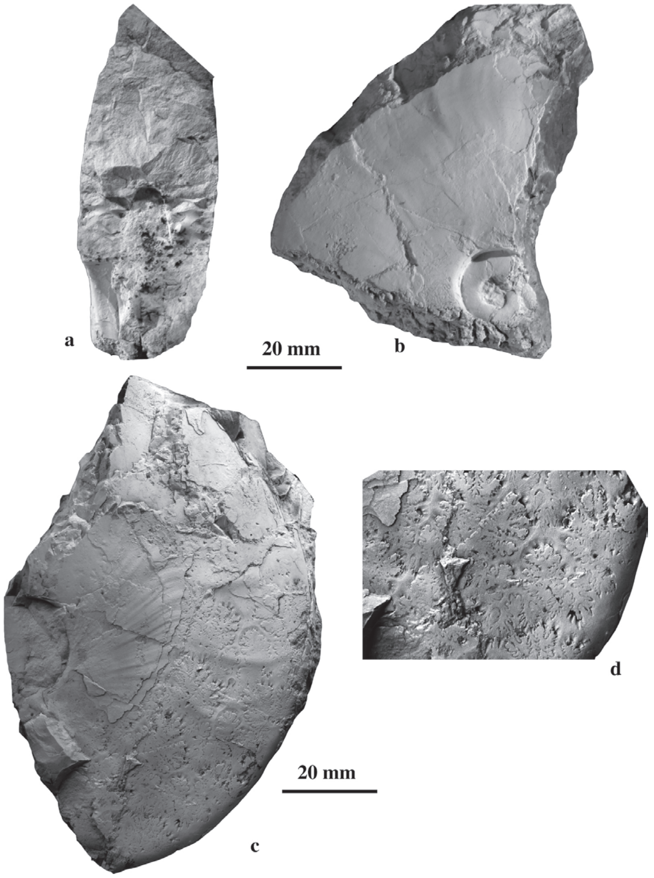

Figure 7. *Beudanticeras haydeni* (Gabb, 1864). a, b, CASG78584 from NFV-K.86-2; c, d, LACMIP.9860, from Huling Creek.

lobe, undercutting the external saddle. McLearn (1972, p.57) notes that 'this species is not a true *Proplacenticeras* and may be a new genus'. But, as Jeletzky notes on p. 56, "In the MS explanation of Pl. VIII, figs. 3a, b, McLearn has crossed out the generic name *Proplacenticeras* and replaced it by *Beudanticeras*." McLearn (1972, p. 56-57) notes that "most" specimens collected for this paper are from a high level in the Sandstone Member of the Haida Formation, at localities A11 and A15 (p. 7). These "Localities" includes several hundred feet of undescribed section for which a few ammonites are listed, including *P. sutherlandbrowni*, and two informal species of *Mortoniceras* similar to *M. pricei* (McLearn, 1972, p. 70-71, pls. 24-27). The age of the Haida specimens, and the Holotype is probably equivalent to the *Mortoniceras* (*M.*) *pricei* or *M.* (*M.*) *inflatum* Zone, the lower part of the Upper Albian, which would make *P. sutherlandbrowni* older than *B. haydeni*, though they are morphologically very close.

It should be noted that the material described as *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972) by Alabushev (1988, p. 56) from the Upper Albian-Lower Cenomanian of north-east Russia, comes from a higher stratigraphic level. It differs from the Canadian species by its narrower umbilicus, its more compressed and triangular whorl section, its flattened flanks and its more complex saddle L/E which is characteristic of the Placenticeratidae. The specimen described and figured as *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972) by Alabushev (1988, p. 56 pars, fig. 1, 2), Alabushev and Alabusheva (1988, p. 28, pl. 2, fig. 9); Alabushev and Wiedmann (1994, fig. 4H) and Alabushev (1995, p. 134, figs 11E-I) is placed within the genus *Proplacenticeras* Spath, 1926 (Jagt-Yazikova, 2011) and is renamed here *Proplacenticeras alabushevi nov. nom.* (holotype: specimen number.2060/4 in Alabushev (1988, fig. 1) (Zoobank Identification number: urn:lsid:zoobank.org:act:96B27619-6E26-4B89-8EFC-640EC229D19F).

Comparison of the Californian specimens with the holotype of *Beudanticeras beudanti* from Montagne de Fiz, France is difficult because of the distortion of the French specimen and its preservation as an internal mold. The specimen figured by Spath (1923, pl. 2, fig. 4), and the material from Entrèves-en Bauges herein figured (Figure 9a-h) are better standards for comparison. We earlier maintained the separation of *B. beudanti* and *B. haydeni* on the basis of a slightly more rounded venter and more numerous peripheral ribs in *B. haydeni*. With more material, it is evident that *B. beudanti* differs from *B. haydeni* in several respects:

The ribs that are less numerous in *B. beudanti* and not sickle-shaped as in *B. haydeni* and flexuous in *B. beudanti*;

The ornament that disappears earlier in the ontogeny in *B. beudanti*;

The sharp, angular, umbilical shoulder and the vertical wall in *B. haydeni* as opposed to the inclined umbilical wall and acutely rounded umbilical shoulder in *B. beudanti*, especially in the subadult stages;

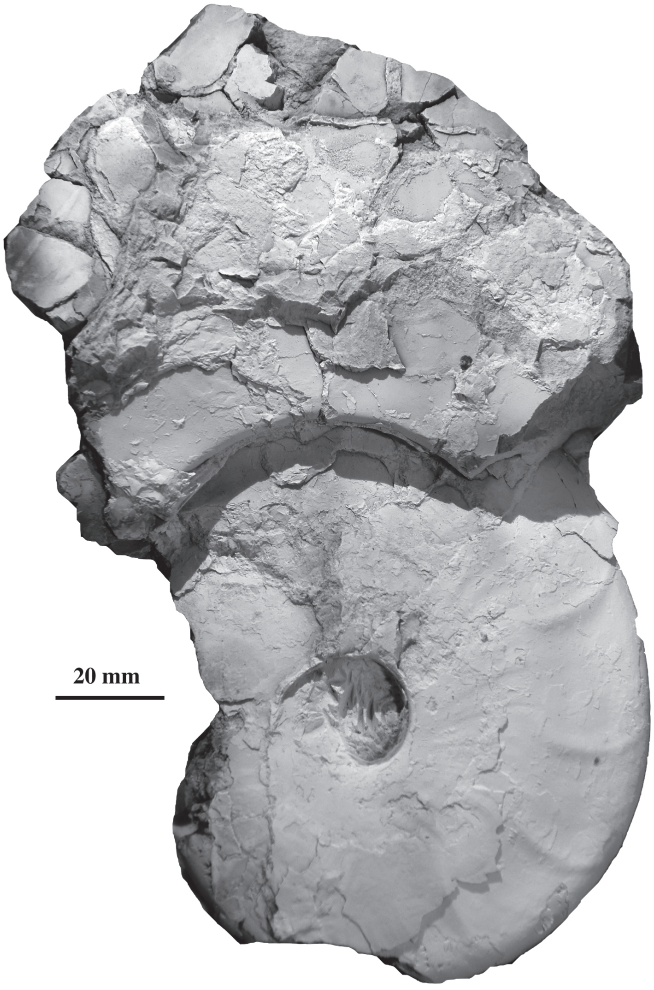

Figure 8. *Beudanticeras haydeni* (Gabb, 1864). CASG78585 (CS.1003)

These differences support the separation of the two species.

B. beudanti is known from the Upper Albian of Europe (*Dipoloceras cristatum*, *Mortoniceras pricei* and *Mortoniceras inflatum* zones). Kennedy and Hancock (1976, p. v-8, v-9) record it from the lower three subzones of the upper Albian (*cristatum, orbignyi,* and *varicosum* Subzones) in England and northern France. It has been reported with certainty from the Upper Albian of England and France by numerous authors, Hungary (Szives, 2007), Italy (Wiedmann and Dieni, 1968), Morocco (Robert and Latil personal data) and Iran (Seyed-Emami and Immel, 1995 and 1996). The presence of the species in Germany (Gümbel, 1888), Switzerland (Tajika *et al.*, 2017), and Crimea (Milaschevich, 1877) needs to be confirmed. The only one report of *B. beudanti* from the uppermost Albian (Scholz, 1979) needs confirmation. Breistroffer (1947, p. 54) remarks that *Beudanticeras* is one of the genera that completely disappears before the 'Vraconnian' [Post *Mortoniceras* (*Mortoniceras*) *inflatum* Zone], but he qualifies that statement paranthetically by saying "at least in Europe".

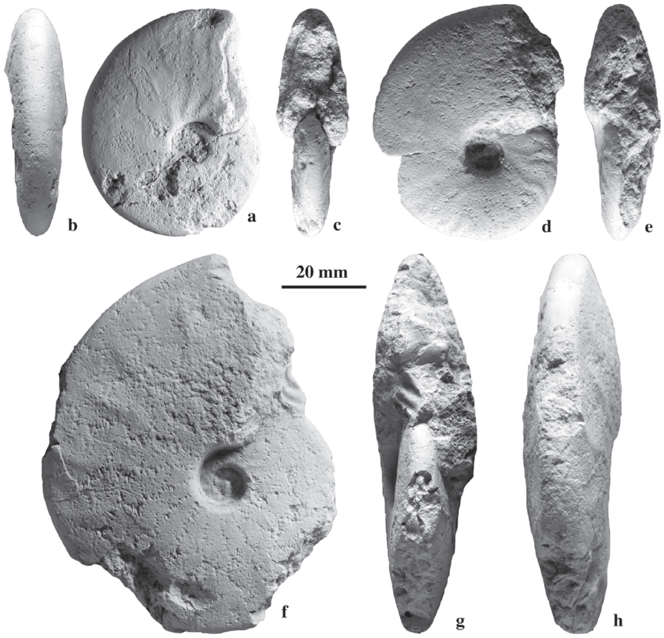

Figure 9. *Beudanticeras beudanti* (Brongniart, 1822). a-c, UJF-ID.15254. d, e, UJF-ID.15255. f-h, UJF-ID.15256. All from the upper Albian of Entrèves-en -Bauges, Savoie, France.

Distribution. *Beudanticeras haydeni* ranges through approximately the upper half of the Upper Albian (in the North Fork section from NF V-I through most of NFV-M), or from the *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone into the *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone. It should be noted that in Dry Creek section Amédro and Robaszynski (2005, Fig. 5) indicate that *B. haydeni* extends from well below Marker Bed 1, with no definite lowest occurrence indicated, up to a little below Marker Bed 6, definitely above *M. perinflatum*, but *B. haydeni* has never been reported below Marker Bed 1. Moreover, the presence in the *Mortoniceras* (*Mortoniceras*) *fallax* Zone, into the interval that also yields *Stoliczkaia dispar* var. *notha* is not fully documented.

The specimen figured by Murphy & Rodda (1960, pl. 10, fig. 4), and herein refigured (Figure 7c, d) was assigned to the Middle Albian by Murphy and Rodda (1960, p. 851), which is a mistake. This specimen comes from UCLA locality 2900: Chickabally Member; Huling Creek. In conglomeratic sandstone, first sandstone downstream from junction with east fork of Huling Creek. The age of this locality is without question uppermost Albian.

Appendix 1: Synonymy of other species assigned to the genus Beudanticeras.

Beudanticeras beudanti (Brongniart, 1822)
(Figures 2a, 9a–h)

We include here only the figured specimens in the literature that could be assigned to *Beudanticeras beudanti*.

The other citations have been removed (see Klein and Vašíček, 2011).

1822 *Ammonites Beudanti* Brongniart, p. 95, 99, 394, pl. 7, fig. 2.
1847 *Ammonites Beudanti* Brongniart Quenstedt, p. 222, pl. 17, fig. 10.
?1877 *Haploceras Beudanti* (Brongniart); Milaschevich, p. 116, pl. I, fig. 4, 5.
?1888 *Desmoceras Beudanti* (Brongniart); Gümbel, pl. 437, fig. 2.
1913 *Desmoceras Beudanti* Brong. var. *Jacobi* Heim, p. 286.
1923 *Beudanticeras beudanti* (Brongniart); Spath, p. 49, pl. 2, fig. 4a-d, text-fig. 12a-c.
?1923 *Beudanticeras beudanti* var. *ibiciformis* Spath, p. 51, pl. 2, fig. 4e, f
1932 *Beudanticeras beudanti* (Brongniart); Seitz, p. 409, 410, pl. 17, fig. 3 (=specimen Quenstedt, 1847, pl. 17, fig. 10)
1961 *Beudanticeras beudanti* (Brongniart); Casey, text-fig. 46a-c (=Spath, 1923, pl. II, fig. 4a, b, text-fig. 12c)
?1967 *Beudanticeras beudanti* (Brongniart); Collignon, p. 15, pl. 3, fig. 1.
1967 *Beudanticeras beudanti* (Brongniart); Cox *et al.*, pl. 63, fig. 4.
?1968 *Beudanticeras beudanti* (Brongn.); Wiedmann and Dieni, p. 128, pl. 11, fig. 10.
?1979 *Beudanticeras beudanti* (Brongniart); Scholz, p. 68, pl. 13, fig. 1, 6; text-fig. 21.
?1980 *Beudanticeras beudanti* (Brongniart); Thomel, p. 124, fig. 247
?1983 *Beudanticeras beudanti*; Van Diggelen, text-fig. 26
1988 *Beudanticeras beudanti* (Brongniart); Owen, fig. 43F (=Casey, 1961, text-fig. 46c)
1993 *Beaudanticeras beaudanti* (Brongniart)(sic); Kennedy, p. 233, text-figs. 1-2.
1995 *Beudanticeras beudanti* (Brongniart); Seyed-Emami and Immel, p. 388, fig. 30.
1996 *Beudanticeras* (*Beudanticeras*) *beudanti* (Brongniart); Wright *et al.*, p. 81, fig. 62: 1a, 1b, 1c (=Casey, 1961, text-fig. 46a-c).
1996 *Beudanticeras beudanti* (Brongniart); Seyed-Emami and Immel, p. 11, pl. 1, fig. 4-7; ?pl. 2, fig. 4; pl. 6, fig. 5, 6.
1997 *Beudanticeras beudanti* (Brongniart); Delamette *et al.*, pl. 14, fig. 8, pl. 18, fig. 3, pl. 38, fig. 4.
2007 *Beudanticeras* (*Beudanticeras*) *beudanti* (Brongniart); Szives, p. 54, 97, pl. 1, fig. 8; pl. 19, fig. 1; pl. 21, fig. 1; pl. 25, fig. 2, 6 only.
2008 *Beudanticeras beudanti* (Brongniart); Joly and Delamette, fig. 8A.
2010 *Beudanticeras* (*Beudanticeras*) *beudanti* (Brongniart); Matrion, p. 128, fig. 96B-E.
2011 *Beudanticeras beudanti* (Brongniart); Klein and Vašíček, p. 124.
?2017 *Beudanticeras* cf. *beudanti* (Brongniart); Tajika *et al.*, p. 32, figs X-AA, AL, AM.

Lectotype. MNHN-F-J07792, the specimen designated by Spath (1923, p.49), from Rochers des Fiz, Haute-Savoie, France, refigured by Kennedy (1993, fig. 2).

Beudanticeras sphaerotum (Seeley, 1866)

1866 *Ammonites sphaerotus* Seeley, p. 175.
1923 *Beudanticeras sphaerotum* (Seeley); Spath, p. 53, pl. 3, fig. 1.
1932 *Beudanticeras sphaerotum* (Seeley); Seitz, p. 409, 410, text-fig. 1b.

Holotype. The specimen figured by Spath (1923), pl. 3, fig. 1, from the Red Chalk of Hunstanton, England, Sedgwick Museum.

Beudanticeras sutherlandbrowni (McLearn, 1972)

1972 *Proplacenticeras sutherlandbrowni* McLearn; p. 56, pl. 8, fig. 3.
1988 *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972); Alabushev, p. 56 pars.
Not 1988 *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972); Alabushev, figs 1, 2.
Not 1988 *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972); Alabushev and Alabusheva, p. 28, pl. 2, fig. 9.
Not 1994. *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972), Alabushev and Wiedmann, fig. 4H.

Holotype. The specimen figured by McLearn (1972, pl. 8, fig. 3) from Fleury Island?, GSC 21227. The species very probably occurs in the Lower Sandstone Member of the Haida Formation in Bearskin Bay, Queen Charlotte Islands, Canada, above the base of the Upper Albian.

Appendix 2: Supraspecific classification of the new subfamily Uhligellinae.

Family Desmoceratidae Zittel, 1895
Subfamily Uhligellinae nov. subfamily

Zoobank identification number. urn:lsid:zoobank.org:act:748CA7CB-7B89-4358-8863-3E0DA5C7B315

Diagnosis. Desmoceratids with constrictions, and with a simple suture line characterized by a symmetrical to feebly asymmetrical trifid L. The subfamily Uhligellinae, as herein understood, is probably polyphyletic and brings together the genera *Zuercherella* Casey, 1954, *Uhligella* Jacob, 1907, *Pseudorbulites* Casey, 1961, *Grantziceras* Imlay, 1961, *Roberticeras* Latil, Murphy and Rodda, 2023, *Leconteites* Casey, 1954, *Brewericeras* Casey, 1954, and provisionally *Boliteceras* Whitehouse, 1928 and *Cophinoceras* Whitehouse, 1928 [see discussion above and Latil, Murphy and Rodda (this volume)].

Genus *Uhligella* Jacob, 1907

Type species. *Desmoceras clansayense* Jacob, 1905, p. 403, by the subsequent designation of Kilian, 1907, p. 63.

Diagnosis. Modified after Wright (1996): Whorl section broadest near umbilical edge; constrictions irregular and shallow; early whorls with sinuous, rounded main ribs distinctly raised into umbilical bullae, with several intercalated ribs; outer whorls smooth.

Genus *Zuercherella* Casey, 1954

(= *Corteziceras* Etayo Serna, 1979, p. 27; type species *C. cortezi* by original designation)

Type species. *Desmoceras zuercheri* Jacob, 1906, p. 9, by the original designation of Casey, 1954, p. 112.

Diagnosis. Medium-sized high-whorled shell with oval or subquadrate whorl-section, venter narrowly rounded; constrictions shallow, sinuous; between the constrictions are several ribs. Main ribs begin slightly above or at the umbilical rim; intercalatory ribs occur only in the upper half of the flanks. Outer whorls appear to be feebly ornamented based on a single specimen.

Genus *Pseudorbulites* Casey, 1961

Type species. *Uhligella convergens* Jacob, 1908, p. 29; pl. 2, figs. 24–26, by the original designation of Casey, 1961, p. 145.

Diagnosis. Stout section and funnel-shaped umbilicus; involute coiling; few, feeble constrictions; narrowly rounded venter.

Genus *Grantziceras* Imlay, 1961

Type species. *Beudanticeras* (*Grantziceras*) *multiconstrictum* Imlay, 1960, by the original designation of Imlay, 1961, p. 56.

Diagnosis. Large-sized ammonites with numerous, regularly spaced, falciform constrictions, broadly bunded striae on the flanks, and a scaphitoid body chamber.

Genus *Roberticeras* nov. gen.

Zoobank identification number. urn:lsid:zoobank.org:act:BB8E77ED-4AFA-4395-9BFD-CAFB453898F9

Type species. *Ammonites dupinianus* d'Orbigny, 1841, p. 276, pl. 81, figs 6–8.

Diagnosis. Rounded umbilical shoulder; presence of constrictions at some stage in the ontogeny, venter rounded; simple suture, with no overlap, and with lower saddles.

Genus *Leconteites* Casey, 1954

[= *Puzosigella* Casey, 1954; *Vnigriceras* Saveliev, 1973; *V.* (*Astrodiscus*) Saveliev, 1973]

Type species. *Desmoceras lecontei* Anderson, 1902, p. 95, by the original designation of Casey, 1954, p. 110.

Diagnosis. Modified after Wright (1996): Umbilical shoulder sharply rounded to angular; primary ribs sinuous, arising singly on umbilical wall or in twos or threes from umbilical bullae, projected towards venter, weakening or disappearing at venter; secondaries branching or intercalated at midflanks; constrictions, if present, with or without collars. Suture finely or coarsely frilled.

Genus *Brewericeras* Casey, 1954

Type species. *Ammonites breweri* Gabb, 1864, p. 62, by the original designation of Casey, 1954, p. 112.

Diagnosis. Modified after Wright (1996): whorl section compressed; coiling eccentric; lack of umbilical tubercles and paired ribs, rarity of constrictions; narrow stems to saddles of suture. A derivative of *Leconteites*.

? Genus *Boliteceras* Whitehouse, 1928

Type species. *Ammonites daintreei* R. Etheridge, 1872, p. 346, pl. 24 part., by the original designation.

Diagnosis. Involute, with funnel-shaped umbilicus; and inflated whorl section, with broad, shallow, sinuous constrictions, fine, feeble ribs and broadly rounded venter. The suture, not figured, is said to have wide-stemmed saddles and regularly trifid first lateral lobe.

? Genus *Cophinoceras* Whitehouse, 1928

(= *Beudantiella* Breistroffer, 1947, p. 99)

Type species. *Cophinoceras ogilviei* Whitehouse, 1928, p. 205, pl. 26, fig. 4, by the original designation.

Diagnosis. Elliptical whorl section, narrow funnel shape umbilicus, straight prorsiradiate primary ribs (constrictions covered by the test), each pair of such ribs being separated by 8-12 short straight intercalatories. The suture is said to have wide-stemmed saddles and regularly trifid first lateral lobe.

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Nuevo reporte de la langosta fósil *Atherfieldastacus magnus* (M´Coy, 1849) en la Formación San Juan Raya, Puebla, México

New report of the fossil lobster Atherfieldastacus magnus (M´Coy, 1849) in the San Juan Raya Formation, Puebla, Mexico

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Resumen

Se presenta una nueva localidad con el registro de la langosta fósil *Atherfieldastacus magnus* en los alrededores de San Martín Atexcal, dentro de la Formación San Juan Raya en el estado de Puebla. Dicho registro amplía la distribución espacial de la especie en la región. Adicionalmente, se reporta la probable asociación simbiótica entre este crustáceo con bivalvos, misma que ha sido confirmada para la misma especie en depósitos sedimentarios del Reino Unido.

Palabras clave: *Atherfieldastacus magnus*, Atexcal, Formación San Juan Raya, Cretácico Inferior, Puebla, México.

Abstract

A new locality with the record of the fossil lobster Atherfieldastacus magnus is presented in the surroundings of San Martín Atexcal within the San Juan Raya Formation in the state of Puebla. This record expands the spatial distribution of the species in the region. Additionally, the probable symbiotic association between this crustacean and bivalves is reported, which has been confirmed for the same species in sedimentary deposits in the United Kingdom.

Keywords: Atherfieldastacus magnus, Atexcal, San Juan Raya, Lower Cretaceous, Formation, Puebla, México.

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1. Introducción

Trece especímenes de la langosta mecoquiridae *Atherfieldastacus magnus* M´Coy, 1849 fueron colectados en un afloramiento del municipio de San Martín Atexcal, Puebla (Figura 1). A pesar de que el registro es fragmentario, fue posible determinar características morfológicas asociadas al caparazón como carinas rostrales, crestas branquiales y el surco cervical; forma y ornamentación de las pleuras abdominales; escasos apéndices locomotores; telson y diéreis en el exopodio. Adicionalmente, se reporta la interacción entre esta langosta fósil y bivalvos, aunque sin poder corroborar entre una relación simbiótica o una posterior a la muerte del crustáceo.

A. magnus (antes *Meyeria magna*) fue descrita originalmente para depósitos de la Isla de Wight al Sur del Reino Unido, en donde es muy abundante (González-León *et al.*, 2014). Esta especie representa un ejemplo de amplia distribución durante el Cretácico Temprano, con registros adicionales en España, Colombia, China y México (González-León *et al.*, 2019).

En México, esta langosta fósil ha sido reportada tanto en el norte del país perteneciente a la Formación La Peña en el estado de Chihuahua (González-León *et al.*, 2018a), como en la parte central (Formación San Juan Raya, estado de Puebla) (Figura 2) (Feldmann *et al.*, 1995; 2007 y González-León *et al.*, 2014; 2015; 2018b; 2019 y González-León, 2022). Particularmente, dentro la Formación San Juan Raya, su presencia es abundante, encontrándose en diversas localidades a partir de las cuales se han obtenido datos sobre su morfología, desarrollo ontogenético, dimorfismo sexual, así como información cronoestratigráfica (Feldmann *et al.*, 2007; González-León *et al.*, 2014; 2015; 2018b; 2019 y González-León, 2022). Sus fósiles han sido asociados a ambientes de laguna somera (Feldmann *et al.*, 1995), de mar abierto (González-León *et al.*, 2014, 2015) y de mar poco profundo (Vega *et al.*, 2006, 2019).

La Formación San Juan Raya, denominada así por Calderón García en 1956, es una unidad litoestratigráfica que aflora al Suroeste del estado de Puebla. Esta ha sido ampliamente estudiada desde finales de la primera mitad del siglo XIX debido a su gran contenido de invertebrados fósiles de origen marino, siendo los más abundantes los gasterópodos y los pelecípodos. De manera general, la Formación San Juan Raya presenta alternancias entre conglomerados, areniscas, limolitas, lutitas y calizas con estratificación que va de delgada a gruesa con bioturbación frecuentemente. Para más detalles sobre el marco geológico ver Mendoza-Rosales, 2010; González-León *et al.*, 2014; 2015 y Vega *et al.*, 2019.

La edad de esta unidad ha sido considerada por diversos autores como perteneciente al Aptiano (p. ej. Calderón-García, 1956; Barceló-Duarte, 1978; Feldmann *et al.*, 1995; 2007; Mendoza-Rosales, 2010; Quiroz-Barroso, 2012; Löser *et al.*, 2013; González-León

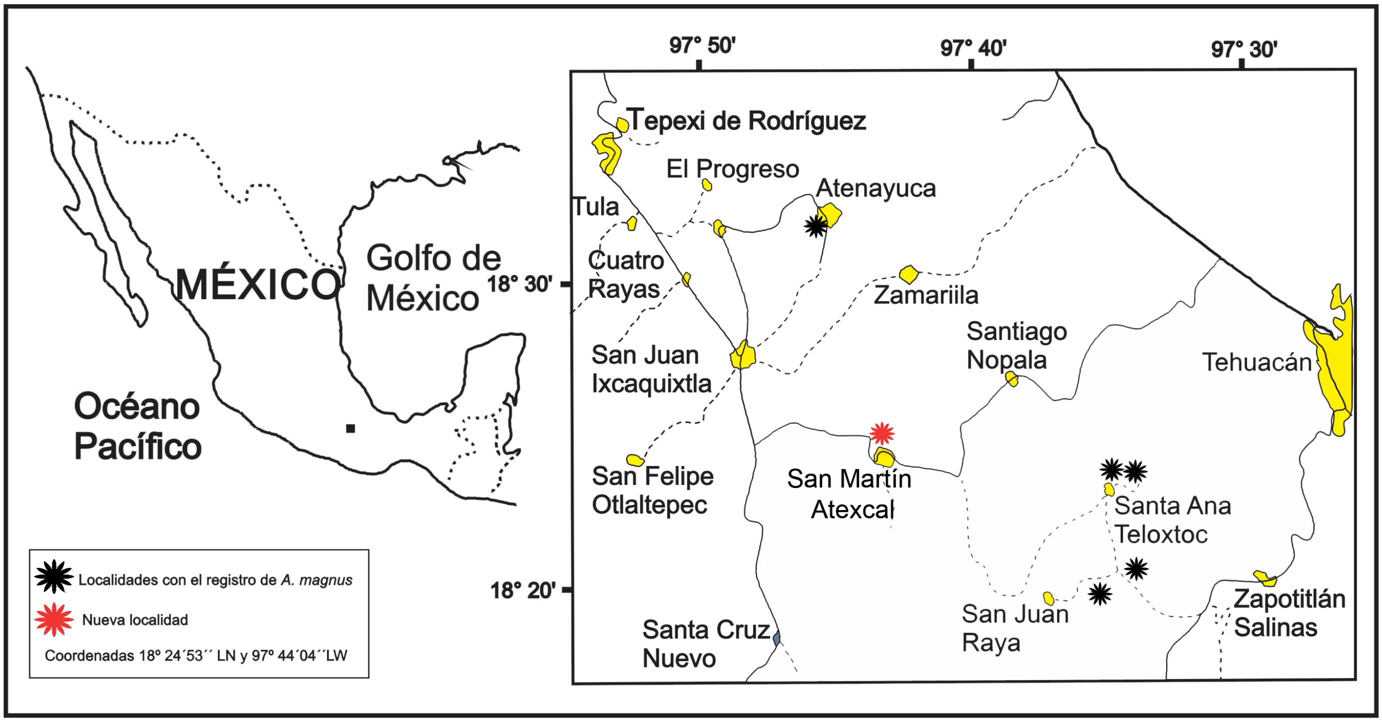

Figura 1. Área de estudio ubicada al noreste del municipio de San Martín Atexcal, al sureste de la Ciudad de Tehuacán, Puebla. Las estrellas negras indican las localidades reportadas previamente con el registro de la langosta fósil *A. magnus* (M´Coy, 1849). La estrella roja indica la nueva localidad Cerro de la Cruz, correspondiente a la Formación San Juan Raya, en donde fueron recolectados los ejemplares ilustrados en este trabajo (Modificado de González-León *et al.*, 2014).

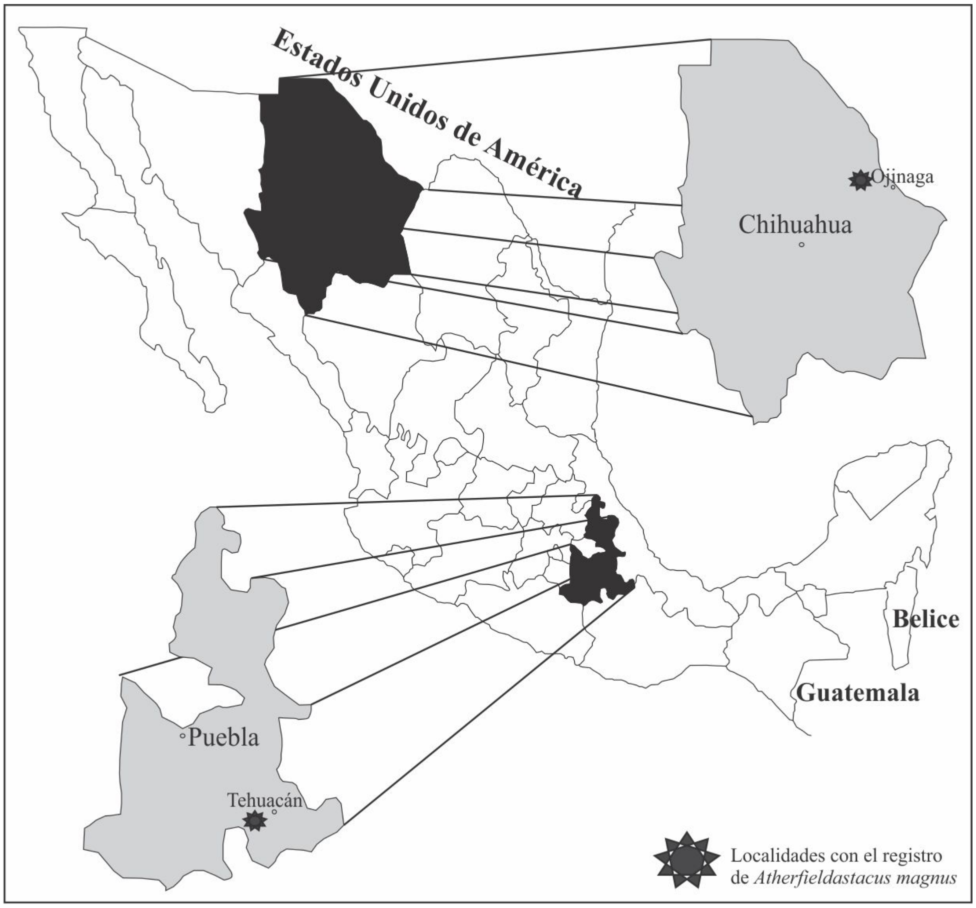

Figura 2. Mapa de la República Mexicana en el que se muestran los estados con el registro de la langosta fósil *Atherfieldastacus magnus* (M´Coy, 1849), al suroeste de la ciudad de Tehuacán en el estado de Puebla y al oeste de la ciudad fronteriza de Ojinaga en el estado de Chihuahua (Tomada de González-León *et al.*, 2018b).

et al., 2014; Serrano-Brañas y Centeno-García, 2014a y b; Hernández-Ocaña *et al.*, 2015; Martínez-Melo *et al.*, 2021). Sin embargo, esta edad ha sido objetada a partir del análisis de nanoplancton calcáreo asociado al registro de *A. magnus* para la parte inferior de la formación, en la que se ha propuesto una posible edad del Valanginiano tardío-Hauteriviano (González-León *et al.*, 2015 y Vega *et al.*, 2019).

Los ejemplares reportados aquí representan el segundo registro más occidental de la especie *A. magnus* para la Formación San Juan Raya, lo que aporta nueva información sobre la distribución paleogeográfica de esta especie a nivel regional durante el Cretácico Temprano.

2. Área de estudio

Los ejemplares fósiles fueron colectados en la Torrecilla-Cerro de la Cruces a 18˚24´53´´ de latitud norte y 97˚44´4´´de longitud oeste, en el municipio de San Martín Atexcal, aproximadamente a 49.7 kilómetros de la ciudad de Tehuacán en el estado de Puebla, México (Figura 1). Las rocas sedimentarias examinadas pertenecen a la Formación San Juan Raya y se componen de una secuencia de 5.7 metros de margas que van de colores grises, rojo vino y gris verdoso con intercalaciones de areniscas calcáreas. Asociado al registro de crustáceos fue posible encontrar abundantes gasterópodos, una cantidad moderada de bivalvos y escasos restos vegetales que no fueron identificados (Figura 3).

3. Paleontología sistemática

Orden Decapoda Latreille, 1802.
Suborden Pleocyemata Burkenroad, 1963.
Infraorden Glypheidae Zittel, 1885.
Superfamilia Glypheoidea Zittel, 1885.
Familia Mecochiridae Van Straelen, 1925.

Género *Atherfieldastacus* Simpson en Robin *et al.* (2016).

Especie Tipo. *Meyeria magna* M´Coy, 1849 por designación original de Robin *et al.* (2016).

Especies incluidas. *Atherfieldastacus magnus* (M´Coy, 1849), *Atherfieldastacus rapax* (Harbort, 1905) y *Atherfieldastacus schwartzi* (Kitchin, 1908).

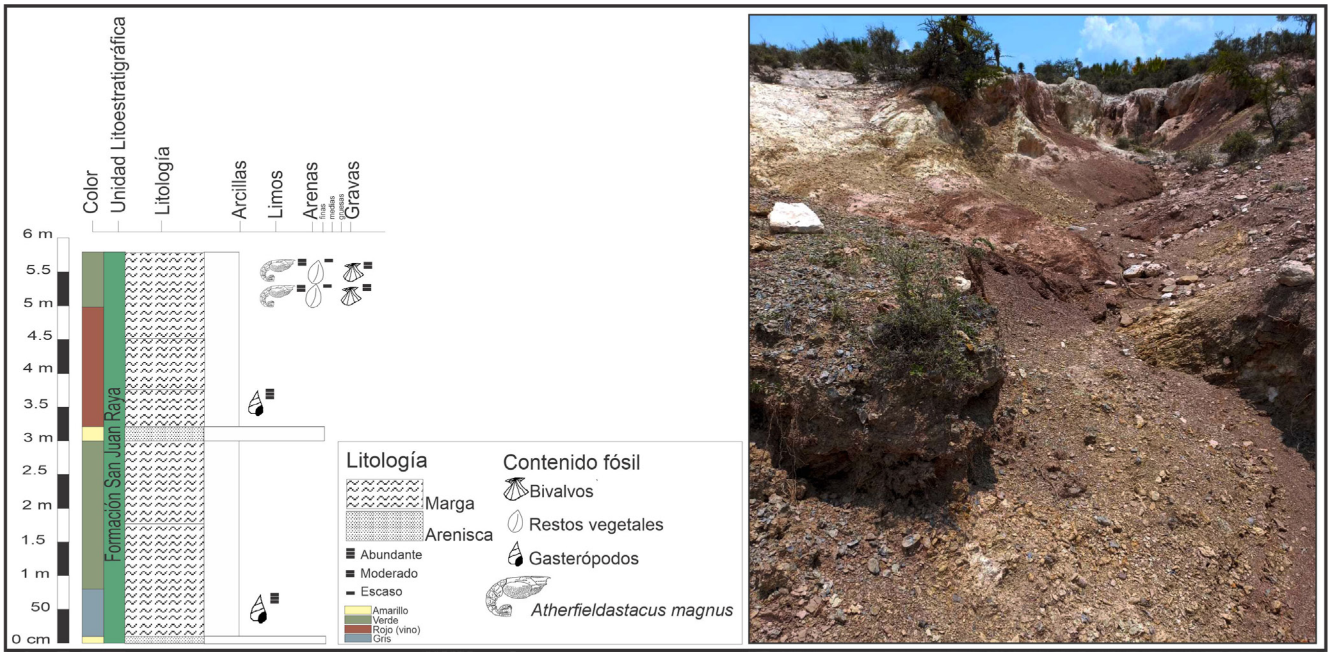

Figura 3. Columna estratigráfica y fotografía que muestra la secuencia de rocas de donde procede el registro de *Atherfieldastacus magnus* en el Cerro de la Cruz, Formación San Juan Raya, Puebla, México.

Diagnosis. Para consultar la diagnosis completa de *Atherfieldastacus magnus*, remitirse a los trabajos de Robin *et al.*, 2016 y González-León *et al.*, 2019.

(2023) *Atherfieldastacus magnus* (M´Coy, 1849). Figuras 4–5.

1849 *Meyeria magna* M'Coy, pág. 334, Figura 4; Woods, 1931, pág. 71, lám.19, Figuras 1–4; Vía Boada , 1975, pág. 33, Figuras 1.1–1.9, 2.1–2.6; Vega *et al.* (2008), pág. 5, Figuras 5.1–5.7; 6.1–6.7; 7.1, 7.6; López-Horgue (2009), pág. 27, Figura 2A–J; Astrop (2011), pág. 116, Figura 1B; Klompmaker (2013), apéndice. A-B; González-León *et al.* (2014), pág. 10 Figura 10A–Q; pág. 12, Figura 11A–M; pág. 14 Figura 12A–J; González-León *et al.* (2016), pág. 4 Figuras 3A–F, 4.

1863 *Meyeria vectensis* Bell, pág. 33, lam. 10, Figuras 1–5.

1863 *Oncopareia granulosa* Vilanova, pág. 98, lám. 3, Figura 2; Mallada (1892), pág. 157.

1881 *Meyeria pearcei* Spence-Bate in Lee, pág. 87, lam. 204, Figura 14.

1927 *Meyeria bolivari* Van Straelen, pág. 80, lám. 1, Figura 1–2; Glaessner (1929), pág. 254; Bataller (1937), pág. 617; Bataller (1945), págs. 48, 61; Bataller (1950), pág. 419, Figura 2; Förster (1971), págs. 408, 419.

1935 *Meyeria mexicana* Rathbun, pág. 30, lám. 9, Figura 3.

1951 *Hoploparia granulosa* Vía, pág. 154, Figura 10.

1985 *Meyerella magna* Simpson y Middleton, nomina nuda, págs. 203–215.

1995 *Meyeria pueblaensis* Feldmann *et al.* pág. 404, Figura 2.1–2.4; Feldmann *et al.* (2007), pág. 151, Figuras 6a–g, 7a-g, 8a-c.

2016 *Atherfieldastacus magnus* M'Coy, 1849; Robin *et al.* pág. 14, Figura 2 A–F. pág. 15, Figuras A–J, 4–5; López-Horgue y Bodego (2017), pág. 5, Figura 4F; pág. 8, Figura 7A–C; Ferratjes (2017), pág. 32, Figura 15; pág. 33, láminas 3A-B; González-León *et al.* (2018a), pág. 115, Figura 3A; pág. 116, Figura 4; pág. 118, Figura 5A–H; pág. 119, Figura 6A–F; pág. 120, Figura 7A–E; pág. 121, Figura 8A–D; pág. 122, Figura 9A–I; González-León *et al.*, 2018b, pág. 12, Figura 5; pág. 13, Figura 6; pág. 14, Figura 9; p. 15, Figuras 10–12; González-León *et al.*, 2019, pág. 6, Figura 6A-D; pág. 7, Figura 7A-E; pág. 8, Figura 8A–B; pág. 9, Figura 9A–C; pág. 10, Figura 10A–C; pág. 11, Figura 11A–C; pág. 12, Figura 12A–M; pág. 14, Figura 13A–J; pág. 15, Figura 14A–M; González-León *et al.*, 2020, pág. 57, Figura 3; pág. 58, Figura 4A–G; pág. 59A, C–L; González-León, 2022, pág. 14, Figura 1; pág. 16, Figura 4A y B; pág. 17, Figura 5A y B.

Material examinado. Los trece ejemplares estudiados en este trabajo fueron depositados en el Laboratorio de Ciencias de la Tierra, Biología Evolutiva y Paleontología de la Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México (UNAM), bajo los números de colección (CFESI-1-CFESI-13).

Descripción. Se analizaron trece especímenes aplastados y preservados en sedimentos de grano fino. La preservación del material estudiado incluye detalles moderadamente conservados de las carinas rostrales y crestas branquiales presentes en el caparazón, las pleuras abdominales, pereiópodos (apéndices locomotores) incompletos, así como detalles del endopodio y exopodio del telson.

Localidad. La Torrecilla, Cerro de la Cruz, San Martín Atexcal, estado de Puebla.

Caparazón. En la zona del *rostrum* se observan tres carinas longitudinales con una preservación moderada: 1) la carina ocular (oc), que se extiende hacia la parte frontal del *rostrum*, el cual no se encuentra preservado en ninguno de los ejemplares figurados, 2) la carina gástrica (cg) y 3) la carina antenal (ca), que están formadas por dos líneas dirigidas hacia la parte frontal del *rostrum* en los ejemplares CPFESI-1, CPFESI-2, (Figura 4 A y C), en el ejemplar CPFESI-5 (Figura 5 B) y en los ejemplares CPFESI-10, CPFESI-12 y CPFESI-13 (Figura 6B, D y E).

En la región branquial solo se observan dos de tres crestas branquiales que están moderadamente preservadas en los especímenes CPFESI -1, CPFESI-2, (Figura 4A y C), CPFESI-5 (Figura 5C) y en los ejemplares CPFESI-9, CPFESI-10, CPFESI-11 y CPFESI-13 (Figura 6A–C y E). El surco cervical presenta una inclinación aproximada de 48˚, esta característica esta preservada en los especímenes CPFESI-1, CPFESI-2 (Figura 4 A y C); CPFESI-5, CPFESI-6, CPFESI-8 (Figura 5B, C y E) y en los ejemplares CPFESI-9-CPFESI-13 (Figura 6A-E).

Abdomen. Los márgenes anterior e inferior son redondeados, el margen posterior es recto en CPFESI-2, CPFESI-3 (Figura 4C1, E y E1) CPFESI-4, CPFESI-5, CPFESI-7 y CPFESI-8 (Figura 5A, B, D y E). En el ejemplar CPFESI-3 (Figura 4E1) se aprecian los bordes aserrados de las pleuras abdominales. Los ejemplares CPFESI-9 y CPFESI-10 no muestran de manera clara la forma de estas estructuras morfológicas (Figura 6). El tamaño y forma de las pleuras es similar entre los segmentos del 2 al 5 en los especímenes.

Apéndices locomotores. Se preservan fragmentos de los diferentes apéndices CPFESI-1 y CPFESI-2 (Figura 4A y C) CPFESI-4, CPFESI-5 y CPFESI-6 (Figura 5A-C). Los segmentos (mero, carpo y propodio) en el primer apéndice se ilustran en el ejemplar CPFESI-1 (Figura 4A) y en el ejemplar CPFESI-4 (Figura 5A). Los mismos segmentos del segundo apéndice se observan en el ejemplar CPFESI-2 (Figura 4C).

Telson. El telson presenta una forma triangular, se distinguen los segmentos uropodiales: exopodio y endopodio. El primero presenta un borde aserrado hacia la porción distal, donde se observa claramente la presencia de diaeresis CPFESI-3 (Figura 4E2) y CPFESI-9 (Figura 6A).

4. Discusión

Atherfieldastacus es un género extinto con tres especies, de las cuales *A. magnus* (M´Coy, 1849) es la más representativa, con una amplia distribución geográfica y temporal. Ha sido reportada en localidades tanto del Viejo Mundo (Reino Unido, España, China), como del Nuevo Mundo (México, Colombia), esta distribución casi cosmopolita posiblemente está relacionada con la naturaleza planctónica de los estadios larvales asociados a sistemas de paleo corrientes durante el Cretácico Temprano, desde el Valanginiano hasta el Albiano (González-León *et al.*, 2019).

El registro de *A. magnus* en los alrededores de San Martín Atexcal se ubica entre las localidades previamente reportadas para Santa Ana Teloxtoc, San Juan Raya y Santa Isabel Atenayuca (Figura 1), lo cual indica una distribución ancestral y continua, inferido por la persistencia de la especie en la región, con un intervalo temporal que va del Valanginiano tardío al Barremiano Temprano (10.6 m.a. aprox.) en la Formación San Juan Raya (González-León *et al.*, 2014, 2015; Vega *et al.*, 2019).

A pesar de la pobre preservación de los ejemplares ilustrados en este trabajo, las características morfológicas corresponden con la diagnosis y descripción de la especie *A. magnus*. La presencia de estructuras como carinas rostrales, surco cervical, cresta hepática, surco antenal en el cefalotórax se observan en los ejemplares (Figuras 4A; y 5B, C y E) y en especímenes previamente publicados por González-León *et al.*, (2019, Figura 6A y B) (Figura 4B en este trabajo). Las pleuras abdominales presentan una forma redondeada en el margen anterior, y una forma recta en el margen posterior. Los tubérculos asociados se encuentran ligeramente marcados. La forma y tamaño de las pleuras abdominales son similares a partir de la segunda hasta la quinta pleura, y la sexta con una forma más triangular. Lo anterior se puede apreciar en los especímenes de las Figuras 4 (C1 y E) y 5 (A, B, D y E).

Las dimensiones de los ejemplares analizados en este trabajo oscilan entre los 0.8 mm (Figura 6A), hasta los 40.51 mm (Figura 6E) únicamente para el largo del cefalotórax. El ejemplar más grande fue inferido a partir de las dimensiones parciales del cefalotórax. De acuerdo con estas medidas se concluye que el material presentado en este trabajo incluye las tres etapas del desarrollo ontogenético sugeridas por González-León *et al.*, 2014 (tabla 1, página 67), y corresponden a los estadios: 1) juvenil de 10.7–17.4 mm, 2) juvenil-sub-adulto de 18–32.5 mm, y 3) Sub-adulto-adulto con rangos que van de 42.6–68.6 mm.

Por otra parte, las asociaciones intraespecíficas en fósiles son esporádicas y difíciles de documentar (Robin *et al.*, 2016), no obstante, en uno de los ejemplares analizados en este trabajo (Figura 4 C), así como en un estudio previo (González-León *et al.*, 2019, Figura 4D), es posible apreciar a *A. magnus* de México en asociación con bivalvos. Sin embargo, no existen criterios claros para inferir si la interacción ocurrió posterior a la muerte de los crustáceos o si representa un tipo de asociación simbiótica como la reportada por Robin *et al.* (2016), en donde, con base en estudios cualitativos y cuantitativos, los autores indican una asociación

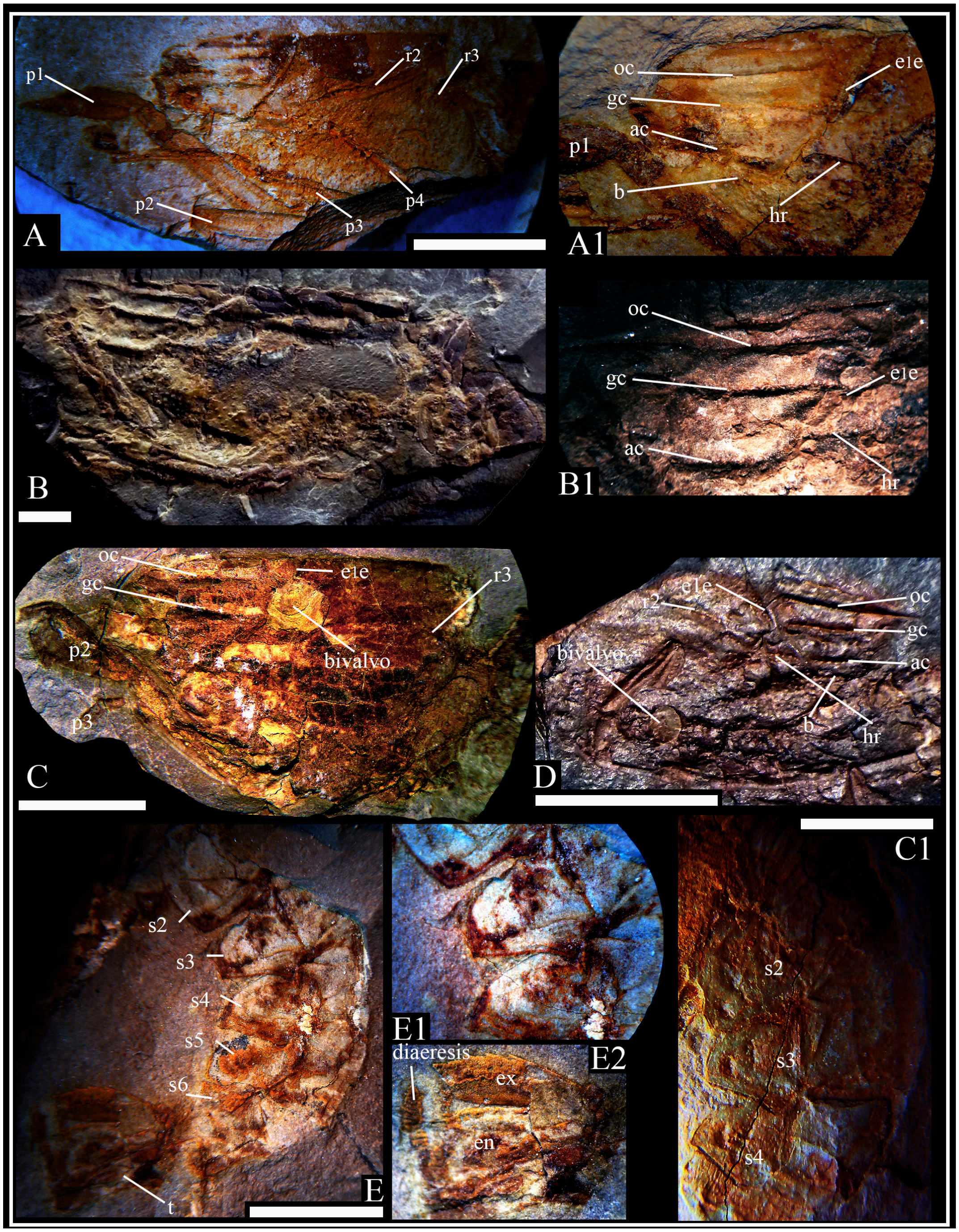

Figura 4. *Atherfieldastacus magnus* M´Coy, 1849, de la Torrecilla, Cerro de la Cruz en San Martín Atexcal, Puebla. A. Espécimen incompleto (CPFESI 01) en el que se aprecian detalles del cefalotórax como las crestas branquiales (r2 y r3), así como detalles incompletos de algunos apéndices locomotores (p1–p4). A1. Acercamiento de las regiones gástrica y antenal, en donde se indica la presencia de las carinas ocular, gástrica y antenal (oc, gc y ac); el surco cervical (e1e); surco antenal (b); la cresta hepática (hr) y parte del segundo pereiópodo (p2). B. Espécimen incompleto (IGM-11312) en donde se observan detalles del cefalotórax. B1. Acercamiento de este ejemplar en donde se observan las regiones gástrica y antenal en la que se indican casi los mismos detalles del ejemplar (CPFESI-1). C. Ejemplar con preservación pobre (CPFESI-2) en el que se pueden observar de talles de las carinas rostrales (oc, gc y ac); el surco cervical (e1e); la cresta branquial media (r3) y detalles del dáctilo, mero, carpo y propodio del segundo pereiópodo. C1. Abdomen del espécimen (CPFESI 01) se puede apreciar la forma y parte de la ornamentación de las pleuras (s2–s4). D. Ejemplar de comparación (IGM-11313) con detalles de las carinas rostrales (oc, gc y ac); surco cervical (e1e); surco antenal (b) y cresta hepática (hr). Los ejemplares C y D presentan bivalvos sobre el caparazón y pereiópodos. E. Ejemplar incompleto en el que se aprecian las pleuras abdominales y el telson (CPFESI-3). E1. Acercamiento de este ejemplar en el que se observa la forma de las pleuras abdominales (s2–s4). E2. Detalle en el que se observan el exopodio (ex) con diaeresis el borde aserrado y en endopodio del telson. Especímenes B y D para comparación tomados de González-León *et al.* (2019, Figura 6. A y B), reproducidos con permiso. Barra de escala A, C y E = 5mm.

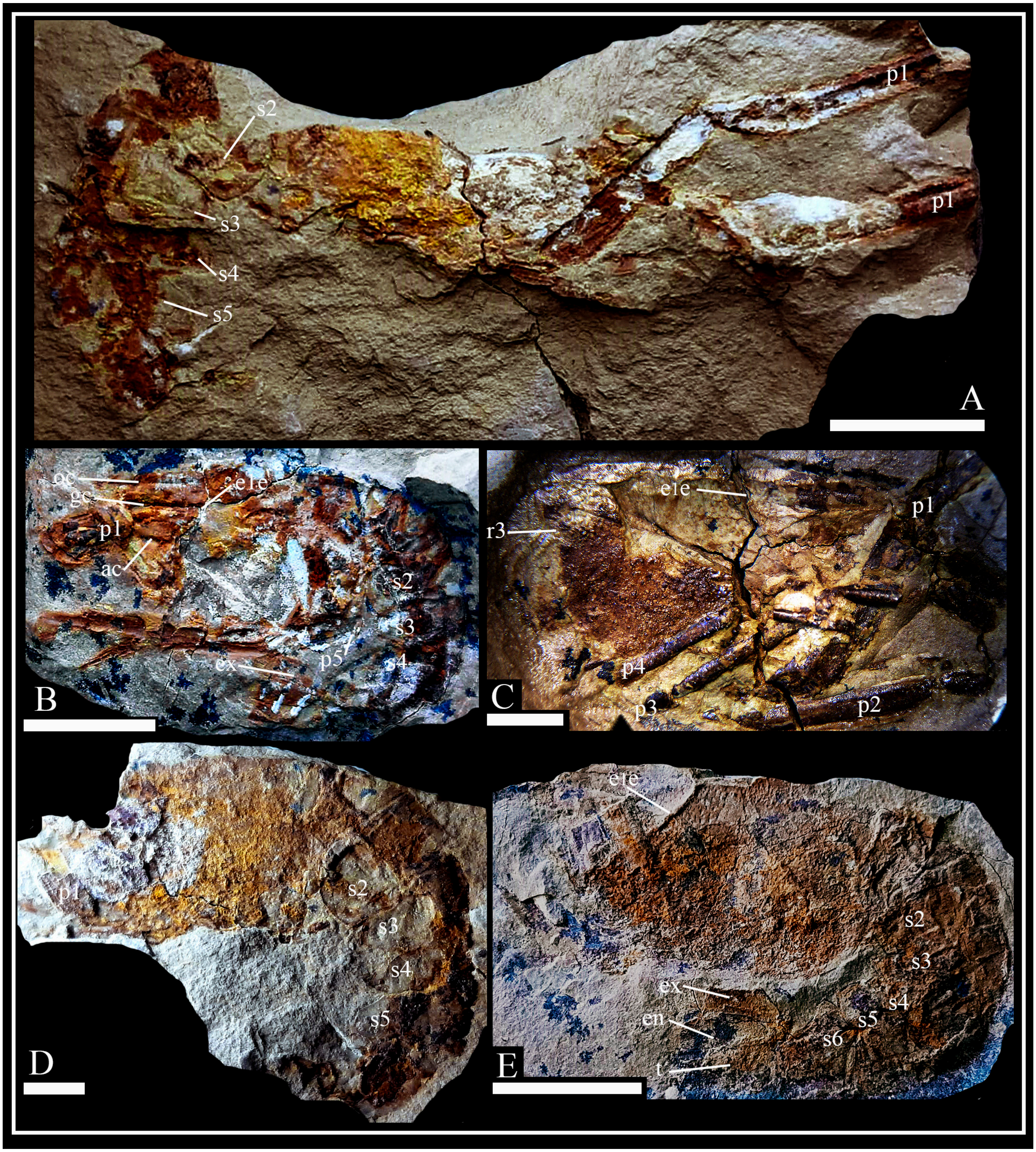

Figura 5. *Atherfieldastacus magnus* M´Coy, 1849, la Torrecilla, Cerro de la Cruz en San Martín Atexcal, Puebla. A. Ejemplar incompleto (CPFESI-4) en donde únicamente se aprecian detalles de las pleuras abdominales (s2–s5) y detalles incompletos del primer par de apéndices locomotores (p1). B. Ejemplar (CPFESI-5) con detalles de las carinas rostrales (oc, gc y ac); surco cervical (e1e); pleuras abdominales (s2–s4) y parte de los apéndices (p1 y p5). C. Fragmento (CPFESI-6) que muestra escasos detalles del cefalotórax como el surco cervical (e1e) y la cresta branquial media (r1), así como la preservación parcial de los apéndices locomotores (p1-p4). D. Ejemplar con clave (CPFESI-7) que presenta pobremente preservados detalles del cefalotórax, pero se distinguen ligeramente la forma de las pleuras abdominales (s2–s5). Pocos detalles de los apéndices locomotores se parecían (p1). E. Ejemplar (CPFESI-8) en el que únicamente se observa la forma de parte del cefalotórax con el surco cervical bien marcado (e1e); ligeros detalles de algunos apéndices (pereiópodos); se observan las pleuras abdominales (s2–s6) aunque, no son claros los detalles sobre la ornamentación de estas estructuras. Del mismo modo se observan ligeramente preservados el telson, así como el exopodio y el endopodio. Barra de escala A, B y E = 1cm; C y D = 5mm.

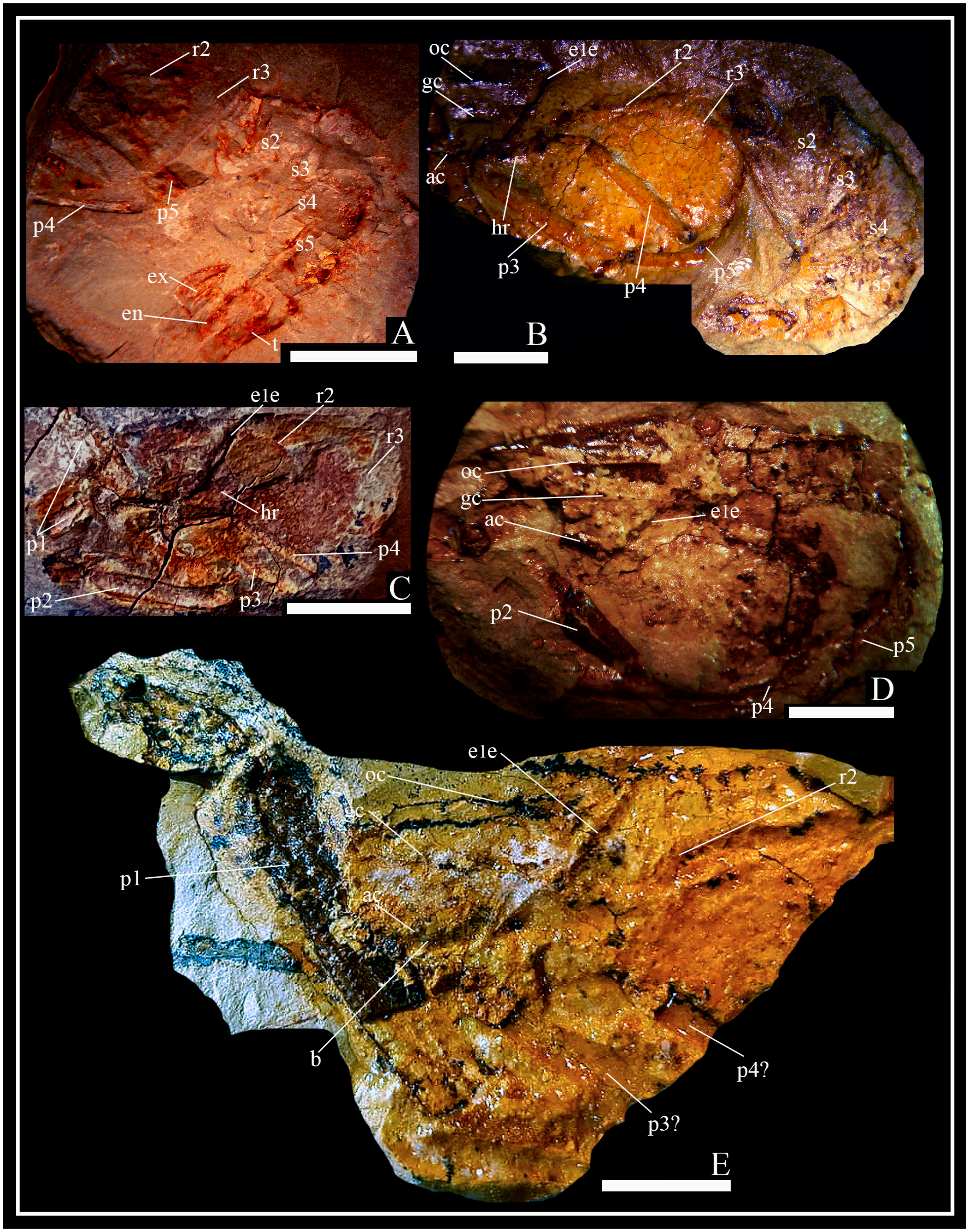

Figura 6. Atherfieldastacus magnus (M´Coy, 1849), la Torrecilla, Cerro de la Cruz en San Martín Atexcal, Puebla. A. Espécimen CPFESI-9 en el que se observan caracteres morfológicos como las crestas branquiales (r2 y r3), pleuras abdominales (s2–s5), exopodio y endopodio del telson (ex, en, t) y fragmentos de los pereiópodos 4 y 5 (p4–p5). B. Ejemplar (CPFESI-10) con un grado de preservación mayor a otros ejemplares y que muestra detalles más claros del cefalotórax (oc, gc, ac, e1e, r2 y r3) y abdomen (s2–s5), así como de los apéndices locomotores (p3–p5). C. Fragmento del cefalotórax (CPFESI-11) en el que se pueden observar segmentos de los pereiópodos (p1–p4); en el cefalotórax se distinguen características asociadas al surco cervical (e1e); cresta hepática (hr) y crestas branquiales (r2 y r3). D. Fragmento del cefalotórax (CPFESI-12) con una costra de sedimento calcáreo que solo permite observar en parte las carinas rostrales (oc, gc y ac) y el surco cervical (e1e). Fragmentos de los apéndices (p2, p4 y p5) son visibles. E. Ejemplar incompleto y pobremente preservado (CPFESI-13) que muestra preservados partes del cefalotórax en el que se aprecian detalles de las carinas rostrales (oc, gc y ac); surco cervical (e1e) y la cresta branquial (r2). Se observa parte del primer par de pereiópodos y de manera menos clara la impresión de los pereiópodos (p3? y p4?). Barra de escala A, B y D = 5mm; C y E = 1cm.

paleosimbiótica entre la langosta *A. magnus* y el bivalvo *Annomia laevigata*. Así mismo, en referencia al bivalvo, sugieren un comportamiento asociado a posturas de enterramiento medio, con base en la diferencia porcentual de bivalvos epibiontes, que es mayor en el caparazón en comparación con otras partes anatómicas como el abdomen y el telson (Robin *et al.*, 2016, Figura 5).

En el presente estudio, el ejemplar CPFESI-02 (Figura 4C) presenta un bivalvo en la región gástrica, el cual aparentemente se encuentra fijado sobre la cutícula del caparazón, debido a que no existen sedimentos intermedios que sugieran el establecimiento posterior del posible epibionte. De igual manera, en el ejemplar IGM-11313 (Figura 4D) previamente publicado por González-León *et al.*, 2019, es posible apreciar un organismo en posición de muerte con el bivalvo ubicado entre uno de los apéndices locomotores y la parte inferior del cefalotórax. Lo anterior podría sugerir que la presencia del bivalvo sobre el crustáceo se dio después de la muerte del organismo. Para ambos casos no existe un muestreo significativo de ejemplares en el que se presenten esta interacción que permita avalar algunas de las hipótesis planteadas sobre la naturaleza de la interacción crustáceo-bivalvo.

La colecta y examinación de especímenes mejor preservados en esta localidad permitirá a futuro describir de mejor manera los detalles anatómicos de estas comunidades y sus posibles relaciones interespecíficas y geocronológicas con otras localidades de la región y su comparación con faunas de otras partes del mundo.

5. Conclusiones

La revisión taxonómica de trece ejemplares de la langosta fósil *Atherfieldastacus magnus*, procedentes de una nueva localidad dentro de la Formación San Juan Raya, permiten inferir una distribución regional amplia a lo largo de esta unidad litoestratigráfica.

Las diferencias morfométricas asociadas al caparazón de los ejemplares analizados permitieron asignarlos a tres estadios ontogenéticos (juvenil; juvenil-sub-adulto y adulto) previamente reconocidos en la literatura.

El análisis de dos ejemplares que presentan incrustaciones de bivalvos en el cuerpo sugiere posibles relaciones simbióticas reconocidas previamente en el registro de esta especie. Sin embargo, no es posible verificar si el registro refleja algún tipo de simbiosis o representan algún evento de colonización *post-mortem*.

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Los autores agradecemos a los revisores anónimos que gracias a sus acertadas observaciones y comentarios enriquecieron el contenido del presente manuscrito. A la Dra. Ninon Robin de la Royal Belgian Institute of Natural Sciences por sus amables comentarios sobre la presencia de bivalvos en el registro de *A. magnus*. Agradecemos también a los pobladores de San Martín Atexcal, en especial a las familias Velasco-Olmedo y Gil-Cortés por su apoyo en el trabajo de campo, así como a Rosa Elena Luciano Pioquinto, por compartir el descubrimiento de esta nueva localidad. Por último, agradecemos al comité editorial de la Revista Paleontología Mexicana, así como a su editor en jefe, el Dr. Josep Anton Moreno Bedmar por su apoyo y comentarios sobre la presente contribución.

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A Troodontid (Theropoda: Troodontidae) Neurocranium from the Cerro del Pueblo Formation (Late Campanian) of Coahuila, Mexico

Un neurocráneo de troodontido (Theropoda: Troodontidae) de la Formación Cerro del Pueblo (Campaniano superior) de Coahuila, México

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Abstract

The fossil record of Troodontidae from Mexico's Late Cretaceous is scarce since the majority of theropod specimens have not been identified beyond their family. In Coahuila's locality La Parrita, a neurocranium that contributes to our understanding of Late Campanian troodontids in the Cerro del Pueblo Formation has been found. It is the first non-dental material described in Mexico for the family.

Keywords: Troodontidae, neurocranium, Coahuila, Mexico.

Resumen

El registro fósil de Troodontidae del Cretácico Tardío de México es escaso, pues la mayoría de los especímenes de terópodo no han sido identificados más allá de su familia. En la localidad de La Parrita en Coahuila, se ha encontrado un neurocráneo que contribuye a nuestra comprensión de los troodóntidos en la Formación Cerro del Pueblo en Coahuila durante el Campaniano Tardío. Siendo el primer material no dental descrito en México de la familia.

Palabras clave: *Troodontidae, neurocráneo, Coahuila, México.*

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1. Introduction

Troodontids are a group of lightly built feathered maniraptoran dinosaurs, with unusually elongated legs, a large curved claw on their second toe, and the largest relative brain sizes within Dinosauria (Currie, 2005). They also had large orbits, a broad postorbital region, and a narrow snout, which helped their eyes face forward and attain overlapping fields of view (Currie, 2005). It has been proposed that the long legs and small sickle-shaped claws indicate an adaptation for capturing small prey while having a cursorial lifestyle, suggesting an ecological separation from dromaeosaurids (Fowler *et al.*, 2011).

They have elongated middle ear cavities that help them in the detection of low-frequency sounds (Currie, 1985). The extreme specialization of the ears may indicate that troodontids hunted in a similar manner to owls, in that they used their hearing to locate small prey (Castanhinha and Mateus, 2006).

The group is best known from Upper Cretaceous deposits of Asia and North America (Makovicky & Norell, 2004). Although, it was established in Asia since the Early Cretaceous (Barsbold *et al.*, 1987; Russell and Dong, 1993; Xu *et al.*, 2002).

The fossil record of troodontids from southern Laramidia is scarce (Zanno *et al.*, 2011; Zanno *et al.*, 2013) and mainly based on isolated teeth from microvertebrate localities within Upper Cretaceous beds of northern Mexico. The only referenced teeth of this family are from the Campanian of Coahuila from the Cerro del Pueblo Formation (Aguillón-Martínez, 2010) and the Aguja Formation (Torres-Rodríguez *et al.*, 2010). In addition, Troodontidae from El Gallo Formation (Campanian) of Baja California (Romo de Vivar, 2011) have been identified due to their teeth. Material referred to as a troodontid phalanx from the Cerro del Pueblo Formation by Rodríguez de la Rosa and Cevallos-Ferríz (1998) was later reassigned as a turtle (Evans *et al.*, 2014). Below, we describe the first cranial material of a troodontid from southern Laramidia. The specimen was collected from the Cerro del Pueblo Formation in the La Parrita locality, Coahuila, Mexico (Figure 1a).

1.1. Abbreviations

AMNH = American Museum of Natural History, New York, U.S.A.; **CPC** = Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo, Mexico; **MPC** = Mongolian Paleontological Center, Ulaanbaatar, Mongolia; **MUDE** = Museo del Desierto, Saltillo, Mexico; **TMP** = Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **UALVP** = University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Canada.

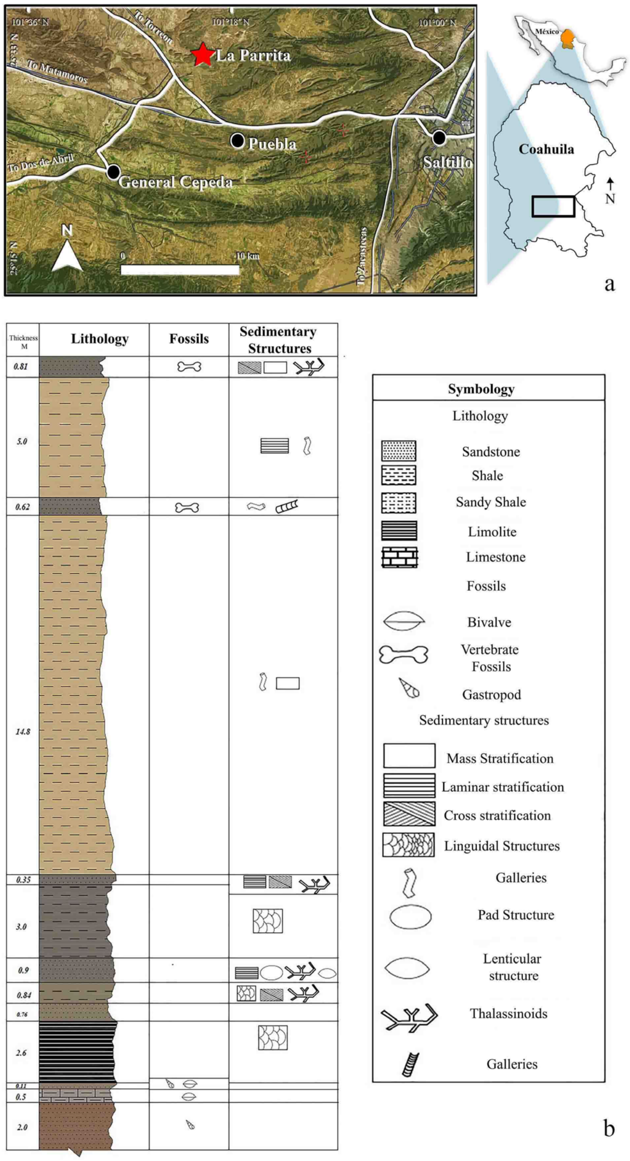

Figure 1. a) Map of La Parrita locality; b) Stratigraphic column of the Cerro del Pueblo Formation in southern Coahuila, Mexico (Illustration by Jorge Ortiz-Mendieta, 2023).

2. Geology

The Difunta Group is located in the northeastern Mexican states of Chihuahua, Coahuila, and northeastern Nuevo León. The sediment sequence is Late Campanian to Eocene in age (Soegaard *et al.*, 2003) and was deposited under deltaic conditions, representing marsh, lagoonal, and eulittoral to shallow marine environments (Eberth *et al.*, 2004). The delta drained into the ancient Gulf of Mexico to the East.

The Cerro del Pueblo Formation (Late Campanian) represents the basal unit of this sequence, and it appears as an outcrop in the southeast region of

Coahuila, northeast Mexico. It has a thickness of 162m, becoming thicker to the west, reaching 445m from Saltillo to Rincon Colorado (Eberth *et al.*, 2004). The Cerro del Pueblo Formation was dated with strontium isotope with an absolute age of 73+1 Ma (Vogt *et al.*, 2016), corresponding to the uppermost part of the Campanian. The Cerro del Pueblo Formation consists of shales, sandstones, and limestones deposited in a low gradient homogeneous coastal plain (Eberth *et al.*, 2004).

The stratigraphic sequence outcropping at La Parrita locality is composed of alternating layers of sandstone, siltstone and shale (Vivas-González, 2013; Figure 1b). At the base, Bed 1 consists of 0.20 m of ochre-gray shales with greenish tones. Marine taxa, such as the ammonite *Sphenodiscus* and some isolated weathered dinosaur bones, are associated with this layer. According to Eberth *et al.* (2004), *Sphenodiscus* is present in facies 1 corresponding to the Parras Shale, which is the base of the Cerro del Pueblo Formation (Vivas-González, 2013). Above the base is Bed 2, a 0.30m layer consisting of exfoliated siltstones with a high concentration of oysters of diverse size, which indicate a brackish environment. The Cerro del Pueblo Formation sandstone and siltstone deposits are characteristic of brackish conditions, indicated by oyster banks and abundant non-ostrean bivalves and gastropods (Stinnesbeck and Frey, 2014). Above the siltstone lies Bed 3, a 0.90m thick hard, massive, coarse-grained sandstone bed with high concentrations of gastropods at the top, which indicates marine coastal environments (Vivas-González, 2013). Bed 4 is a grit layer 1m thick, with a 0.40m thick concentration of gastropods. Bed 5 consists of 10m of ochre-gray shale characterized by a diverse fossil assemblage; here, the marine gastropods *Cerithium nodosa* and *Lissapiopsis* sp. are common, as well as oysters (*Flamingostrea* sp.), representing the most common invertebrates in this shale layer; wood fragments are also present, along with vertebrate fossils (Vivas-González, 2013). Eberth *et al.*, (2004) placed this fossil assemblage between facies 10-12. The assemblage is suggestive of overflooded coastal plains, and the marine and limnic faunal assemblages that coexist in this layer indicate an estuarine environment (Vivas-González, 2013; Stinnesbeck and Frey, 2014 ; Vogt *et al.*, 2016).

The next layer, Bed 6 consists of 0.40m of massive, gray, fine-grained sandstones, followed above by Bed 7, with 0.50m of dark-gray shale, and Bed 8, composed of 0.35m of fine-grained sandstones (Vivas-González, 2013). The Bed 9 is composed of 0.60m shale while Bed 10, has 0.20m of fractured sandstones. Above the fractured sandstone layer lies Bed 11, with 32m of shale, which is devoid of fossils. Above this shale layer, Bed 12, is a 3m layer of massive medium-grained sandstones with high concentrations of bivalves, referred to as *Inoceramus vamuxemi* in the top of the layer. No other fossils are reported in this layer. Bed 13 consists of 18m of shales, and the Bed 14 consists of 3m of medium-grained sandstones. No fossils were observed or reported in both top layers (Vivas-González, 2013).

The depositional setting at La Parrita locality was influenced by cyclically fluctuating paleoenvironments of intermittent shallow-marine, brackish to fresh water or even subaerial conditions. The abundance of oysters throughout the Formation displays the permanent mixing of salt and freshwater, generating intermittent brackish environmental conditions with changing salinities (Vogt *et al.*, 2016).

This alternating sediment suggests the La Parrita locality underwent a series of events related to marine regressions and transgressions during deposition, which is consistent with other localities associated with the Cerro del Pueblo Formation (Eberth *et al.*, 2004).

3. Material and methods

The material described herein was discovered by the first author during surface collecting in the field season of March 2007, and it is curated in the Museo del Desierto (MUDE). The specimen was mechanically prepared using pneumatic hand tools of various sizes, with the final preparation completed using dental picks and pin vises.

For anatomical comparisons, *Saurornithoides mongoliensis* (AMNH 6516), *Latenivenatrix mcmasterae* (TMP 1982.019.0023), *Gobivenator mongoliensis* (MPC-D 100/86), and *Stenonychosaurus inequalis* (UALVP 52611), were compared with CPC 2973. The specimen was measured using a digital caliper, to the nearest millimeter or 0.1 mm, and photographed using a Canon EOS Rebel T2i with a Canon Zoom Lens EF 35-80mm 1:4–5.6 III with filters close ups 1-3 and a Nikon COOLPIX P610 with a lens NIKKOR 60X Wide Optical Zoom ED VR (4.3–258mm 1:3.3–6.5).

4. Systematic paleontology

Theropoda Marsh, 1881
Deinonychosauria Colbert and Russell, 1969
Troodontidae Gilmore, 1924

Troodontidae indet.
Fig. 2 a–f

Material. Frontoparietal (CPC 2973).

Horizon and Locality. Cerro del Pueblo Formation (Upper Campanian), La Parrita locality, 54 km west of Saltillo; municipality of General Cepeda, Coahuila, Mexico.

Description. *Frontoparietal.* The fragment is the posterior portion of the frontal and the anteriormost section of the parietal. The frontal is strongly convex dorsally, with a bulbous appearance reflecting an expansion of the brain cavity accommodating the cerebrum.

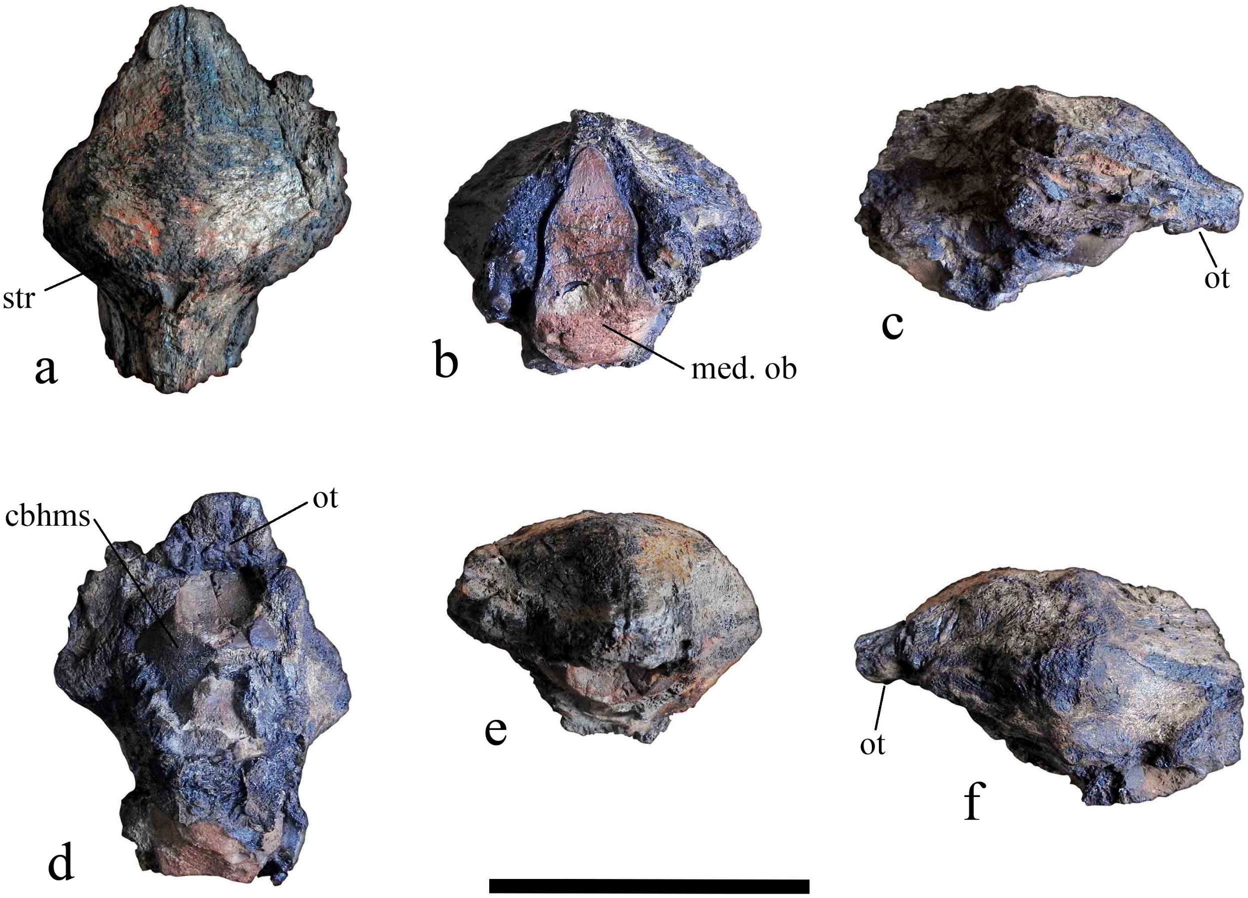

Figure 2. CPC 2973 neurocranium in: a) dorsal, b) caudal; c) right lateral; d) ventral; e) frontal; and f) left lateral views. Abbreviations: cbhms- cerebral hemispheres; ot- olfactory tract; med. ob.- medulla oblongata; str- supratemporal ridge. Scale = 10 cm.

The midline interfrontal contact has an interdigitated morphology, and posteriorly, it forms a 90° angle with a sigmoidal transverse suture to the parietal. The supratemporal fosses are delimited by a transversely oriented ridge. In ventral view, the parietal is broken away. On the anteriormost section, impressions of the olfactory tract are visible, as well as the ventral section of the cerebral hemispheres.

The cranial portion of the parietals is preserved; they are fused, and in the anteriormost section, the joint between the two forms an isosceles triangle shaped foramen. In the posterior section, there is a sagittal crest. In ventral and posterior views, the infilling of the medulla oblongata is visible.

Measurements are given in Table 1.

Discussion. Frontal morphology within Troodontidae is variable and preserves features considered diagnostic at relatively lower taxonomic levels (Currie, 1987; Evans *et al.*, 2014). The frontals in CPC 2973 (Fig 3a) are massive like those of *Latenivenatrix mcmasterae* (Fig. 3b, TMP 1982.019.0023). In troodontids, the supratemporal fossa does not extend onto the dorsal surface of the frontal, and the anterior margin of the supratemporal fenestra is defined by a prominent transverse ridge along with the posterodorsal margin of the frontal adjacent to the parietal (Evans *et al.*, 2014) as seen in CPC 2973, where the supratemporal fossa emargination is identical to the condition of other troodontids (Fig. 3b-e) (AMNH 6516; TMP 1982.019.0023; MPC-D 100/86). In CPC 2973 there is an interfrontal suture with an interdigitated morphology throughout its entire length, as observed in Troodontidae (Evans *et al.*, 2014), differing from the tongue and groove morphology seen in dromaeosaurids (Evans *et al.*, 2014). The frontal can be differentiated from ornithomimid frontals by the angle formed between the midline interfrontal contact and the transverse parietal contact: in CPC 2973, it is a right angle, while in ornithomimids it is obtuse (Currie, 1987). In CPC 2973 the olfactory tract is not well preserved, but the proximal portion to it is preserved (Currie, 1985). It is more

Table 1. Select neurocranium measurements (mm) for CPC 2973.

Dimension	CPC 2973
Length	92.3
Max. width	73
Max. height	56.3
Max. width cerebral hemisphere	53.3
Width from midline to postorbital process	41.8

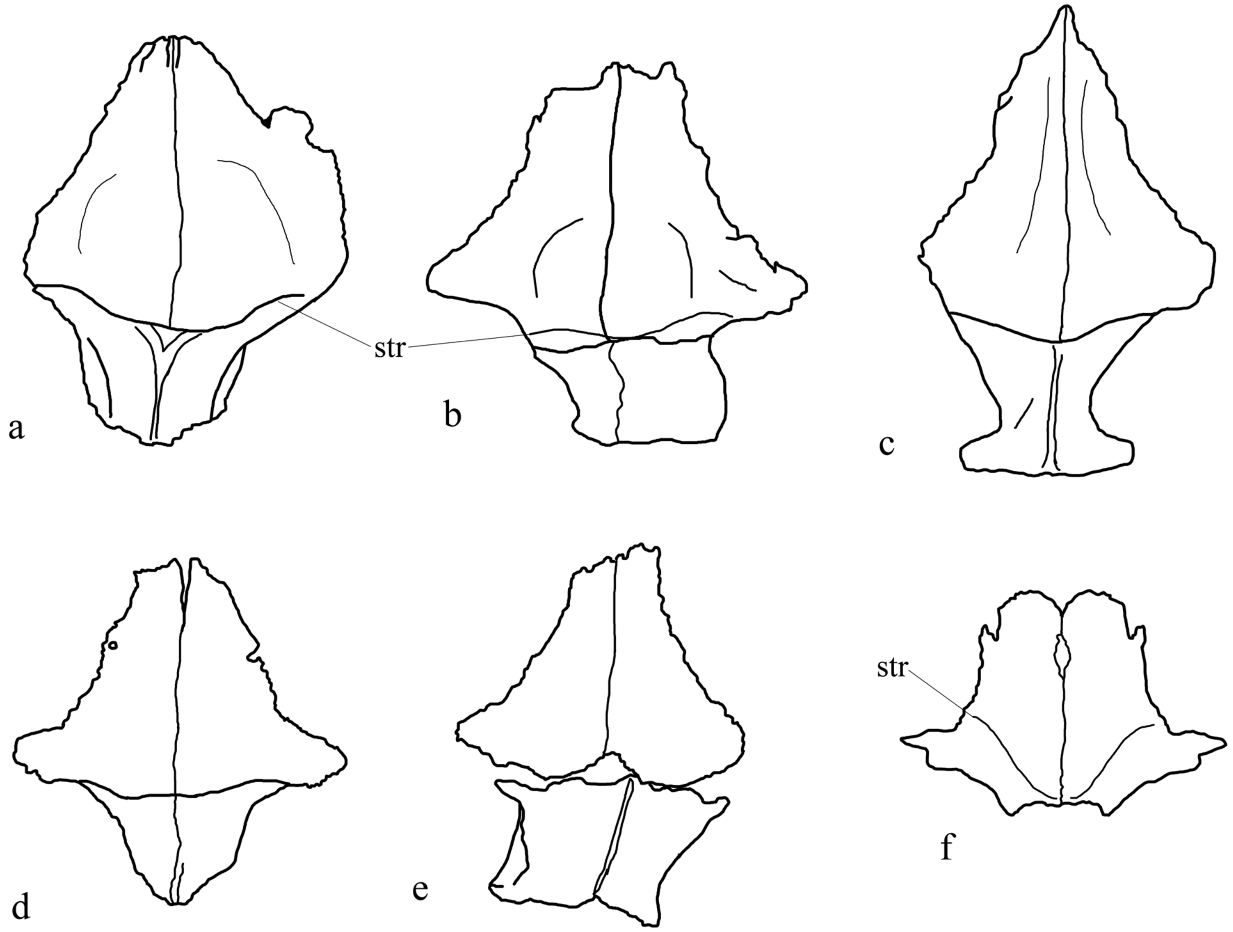

Figure 3. Comparative line drawings of a) CPC 2973; b) *Latenivenatrix mcmasterae* (TMP 1982.019.0023); c) *Saurornithoides mongoliensis* (AMNH 6516); d) *Stenonychosaurus inequalis* (UALVP 52611); e) *Gobivenator mongoliensis* (MPC-D 100/86); f) *Dromaeosaurus albertensis* (TMP 2009.003.0062). Abbreviations: str- supratemporal ridge. Not to scale.

elongated than those of dromaeosaurids, where the olfactory tract is short, *e.g. Saurornitholestes langstoni* and *Bambiraptor feinbergi* (Sues, 1978; Burnham, 2004). This condition is opposite in troodontids, where the olfactory bulbs and olfactory tract are longer.

The parietal shows a sagittal crest, although eroded, which is present in *Stenonychosaurus inequalis*, *Gobivenator mongoliensis*, and *Latenivenatrix mcmasterae* (Sternberg, 1932; Tsuihiji *et al.*, 2014; van der Reest and Currie, 2017).

The frontal has no diagnostic dromaeosaurid characters, but has several features of troodontids, such as the exclusion of the supratemporal fossa from the dorsal surface of the frontal (Fig. 3f). Because of the weathered condition of CPC 2973, it represents an indeterminate troodontid, matching in size and thickness with the range variation seen in troodontids.

When comparing CPC 2973 to more complete troodontid specimens such as *Saurornithoides mongoliensis*, *Gobivenator mongoliensis* and *Zanabazar junior*, the skull has a total length of 344 millimeters. This measurement, in turn, provides an estimate for a total body length of the animal, of about 2.6 meters.

5. Discussion

The discovery of troodontids in southern Laramidia represents a significant advance in our understanding of the biogeography and evolution of these theropod dinosaurs, for it provides new insights into their biogeography during the Late Cretaceous.

Latenivenatrix mcmasterae (van der Reest and Currie, 2017) and *Stenonychosaurus inequalis* (Sternberg, 1932) are from time-equivalent beds of the Dinosaur Park Formation of Alberta, as is *Stenonychosaurus inequalis* (Sternberg, 1932), and *Talos sampsoni* from the Kaiparowits Formation of Utah (Zanno *et al.*, 2011). The specimen CPC 2973 could belong to a different taxon with phylogenetic affinity with *Latenivenatrix mcmasterae* based on the morphology of the frontal.

The Coahuila specimen comes from rocks containing a large diversity of dinosaurs, crocodiles, and freshwater turtles (Brinkman *et al.*, 2016; Rivera-Sylva *et al.*, 2019). Furthermore, this is the first time that non-dental material of a troodontid from Mexico has been described.

Furthermore, the discovery of a new species of troodontid in southern Laramidia highlights the potential for future discoveries in this region. As more fossil localities are discovered and studied, we may gain a more complete understanding of the evolution and biogeography of troodontids during the Late Cretaceous.

6. Conclusions

Dinosaur diversity from the Cerro del Pueblo Formation in southern Coahuila is predominantly limited to microvertebrate samples. Our increased understanding of the Cerro del Pueblo theropod fauna based on the new material, allows broad paleogeographical comparisons with other coeval Campanian formations in Laramidia, including the Dinosaur Park Formation in southern Alberta, Canada and the Kaiparowits Formation of southern Utah, USA.

To date the specimens recovered so far indicate that troodontids lived in this part of Mexico during the Campanian. Determination of the exact number of troodontid species in the Cerro del Pueblo Formation will presumably require the recovery of a much larger sample of well-preserved specimens. The occurrence of troodontids remains from the Cerro del Pueblo Formation extends the distribution of those theropods during the Cretaceous to the southernmost part of North America and supports the claim that Late Cretaceous dinosaur faunas were dominated by these highly specialized forms.

The potential of new discoveries of troodontids from Coahuila is very high, and it is likely that many more findings will become available as researchers concentrate on the already known localities.

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Primer registro de una inclusión de planta hepática del género *Frullania* (Frullaniaceae, Porellales) en el ámbar miocénico de Chiapas, México

First record of a liverwort inclusion of the genus Frullania *(Frullaniaceae, Porellales) in the Miocene amber of Chiapas, Mexico*

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Resumen

En México la diversidad de hepáticas es muy importante en zonas tropicales y subtropicales, desafortunadamente es poco lo que se ha descrito formalmente con base en material fósil. En este estudio se documenta por primera vez el género *Frullania* en el ámbar miocénico de Chiapas, sur de México. Esta planta se caracteriza por una ramificación irregular, terminal del tipo *Frullania*. Tiene hojas con inserción íncuba, alternas, distantes a contiguas, ovadas a orbiculares, con margen entero y liso, y sus ápices redondeados. Posee lóbulos alargados con forma de saco, dos veces más largos que anchos y anfigastrios bífidos y obovados con rizoides dispuestos en mechones en su base. Este registro de *Frullania* indica que la flora fósil de Chiapas también estaba integrada por hepáticas y que este género formó parte de la diversidad tropical y subtropical del sur de México desde el Mioceno Temprano.

Palabras clave: Ámbar, Briofitas, Chiapas, *Frullania*, Mioceno.

Abstract

In Mexico, the diversity of liverworts is very important in tropical and subtropical zones, unfortunately, based on fossil material, little has been formally described. For the first time is documented the genus Frullania *is for the Miocene amber from Chiapas, southern Mexico. This plant is characterized by an irregular, terminal branching of the* Frullania *type. Leaves with incubate insertion, alternate, distant to contiguous, ovate to orbicular, with entire and smooth margins, and rounded apices. Lobes elongate, twice as long as wide. Bifid and obovate amphigastria. Rhizoids are present in tufts at the base of the amphigastria. This record of the genus* Frullania *indicates that the fossil flora of Chiapas was also made up of liverworts and that it was part of this tropical and subtropical flora of southern Mexico since the Early Miocene.*

Keywords: *Amber, Bryophytes, Chiapas,* Frullania*, Miocene.*

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1. Introducción

Los depósitos de ámbar de Chiapas son una de las zonas ambaríferas más importantes a nivel mundial con inclusiones de hongos, plantas, artrópodos y vertebrados (Riquelme *et al.*, 2014; Estrada-Ruiz, 2023). El origen botánico de la resina fósil se ha asociado con dos especies fósiles del género *Hymenaea* L. (Fabaceae), *H. mexicana* Poinar *et* Brown y *H. allendis* Calvillo-Canadell, Cevallos-Ferriz *et* Rico-Arce, basado en estructuras vegetativas y reproductivas (Poinar Jr. y Brown, 2002; Calvillo-Canadell *et al.*, 2010). Estos depósitos con ámbar corresponden a las rocas sedimentarias de la Formación Simojovel, que presenta extensas áreas ambaríferas , entre las que destacan las comunidades de Totolapa, Estrella de Belén en Palenque y Simojovel de Allende, siendo esta última la localidad mejor conocida y estudiada actualmente.

En los últimos 10 años se ha descrito gran diversidad de organismos vegetales, con base en flores y frutos principalmente (*e.g.* Miranda, 1963; Castañeda-Posadas y Cevallos-Ferriz, 2007; Estrada-Ruiz *et al.*, 2023; Estrada-Ruiz, 2023). Por el contrario, para las briofitas solo se han reportado y descrito cuatro ejemplares fosilizados en ámbar, un ejemplar de musgo del género *Hypnodontopsis* (Rhachitheciaceae) (Estrada-Ruiz y Riquelme, 2017) y tres ejemplares de hepáticas, pertenecientes a *Ceratolejeunea* (Spruce) Schiffn., y *Mastigolejeunea* (Spruce) Schiffn. Los dos géneros de las hepáticas pertenecen a la familia Lejeuneaceae (Grolle, 1984a; Scheben, *et al.*, 2014; Heinrichs *et al.*, 2015).

Con base en el registro fósil de hepáticas, los estratos paleontológicos más notables provienen de depósitos de ámbar del Cenozoico. Entre los más importantes están los yacimientos de ámbar del Báltico, los depósitos miocénicos de Zhangpu, China y el ámbar de República Dominicana. Referente a este último yacimiento los registros incluyen más de 20 hepáticas fósiles relacionadas con las familias Lejeuneaceae, Frullaniaceae, Lepidoziaceae y Radulaceae (p. ej., Grolle, 1984b, c; Grolle y Braune, 1988; Gradstein, 1993; Frahm y Newton, 2005). Dos nuevos yacimientos de ámbar muestran una diversidad importante de briofitas; el primero proviene del Grupo Fotan del ámbar Zhangpu del Mioceno medio, China, y del ámbar etíope del Mioceno, África (Bouju *et al.*, 2022).

En este trabajo se registra y describe el primer fósil para México del género *Frullania* (Frullaniaceae), del Mioceno de la Formación Simojovel, en Simojovel de Allende, Chiapas, México. Sumando a los registros previos de hepáticas, es evidente que este grupo de plantas formó parte de la flora tropical y subtropical del sur de México desde el Mioceno Temprano.

2. Marco geológico

Las muestras de ámbar para el presente estudio fueron recolectadas en minas que se encuentran alrededor del poblado de Simojovel de Allende. Estas minas se encuentran ubicadas en el municipio de Simojovel de Allende, Chiapas, México, latitud: 17º08´40.7´´N y longitud: 92º43´36.7´´O (Figura 1). La pieza objeto de

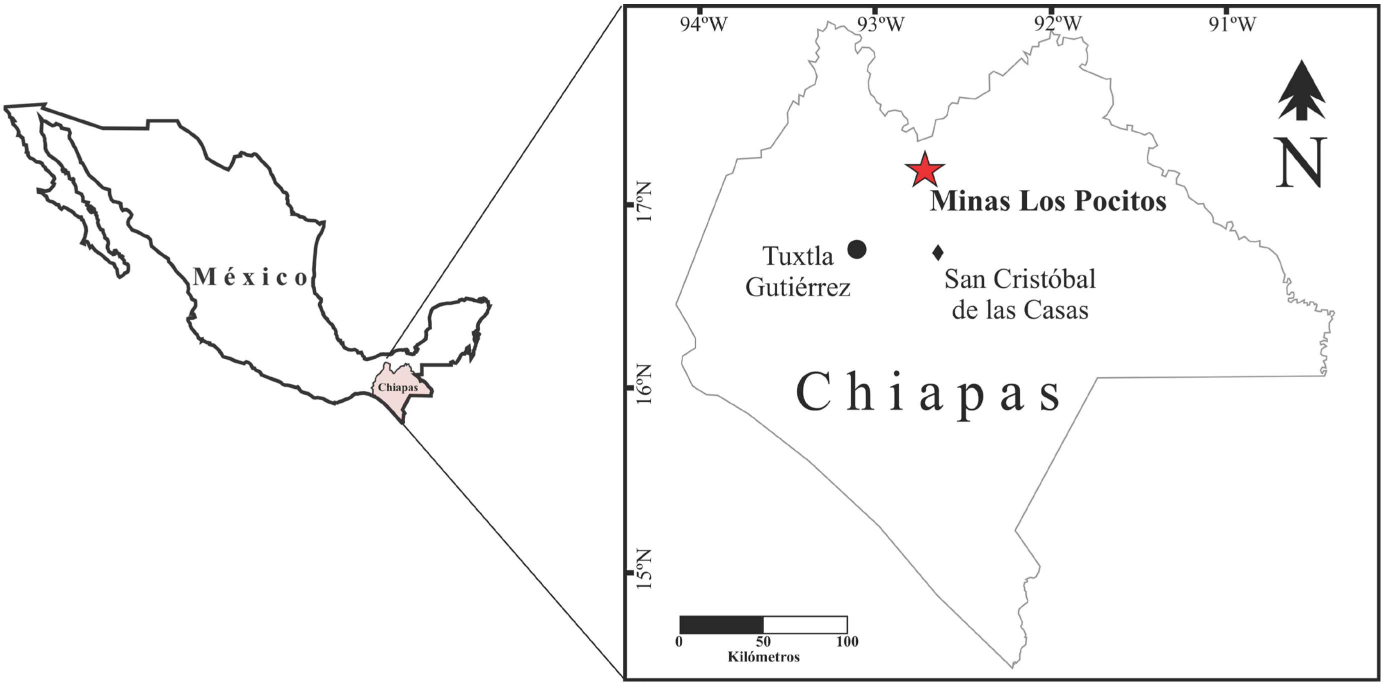

Figura 1. Mapa de la ubicación de la localidad de las minas de Los Pocitos, Municipio de Simojovel de Allende, Chiapas, México.

estudio fue obtenida por los recolectores de ámbar de las minas de Los Pocitos en el año 2021. Los depósitos de ámbar corresponden a rocas sedimentarias de la Formación Simojovel con un rango de edad que va del Oligoceno medio al Mioceno temprano (De la Rosa *et al.*, 1989; Estrada-Ruiz *et al.*, 2023). Los estratos que contienen ámbar en las minas de Los Pocitos consisten principalmente en lignito y areniscas fosilíferas de grano muy fino con abundantes óxidos de hierro y nódulos de pirita. Estos sedimentos fueron depositados en facies que oscilan desde una plataforma somera hasta condiciones litorales, donde prevalecen ambientes lagunares o estuarinos (Frost y Langenheim, 1974; Quezada-Muñetón, 1987; Perrilliat *et al.*, 2010).

3. Materiales y métodos

La muestra de ámbar en estudio presenta un color amarillo, donde el ejemplar de la hepática se encuentra en sin inclusión con dos termitas aladas de la familia Mastotermitidae. Para la observación con mayor detalle, la pieza de ámbar se lijó en húmedo con diferentes tamaños de grano abrasivo. Se comenzó con el de mayor tamaño (macrograno 80 a 220) y se terminó con granos de menor proporción (micrograno 600–1500), con la finalidad de eliminar cualquier rayadura y permitir el paso de luz al momento de observar y tomar fotografías. Una vez que toda la superficie fue lijada (con grano de 1500) se usó una pasta con pulimento y un paño de microfibra y se frotó con movimientos circulares hasta que la superficie del ejemplar quedó pulida. El fósil de la planta representa a una hepática estéril, donde se observaron y describieron las características morfológicas más importantes. Se utilizaron dos microscopios estereoscópicos. Para la toma de fotografías se usó un Zeiss AXIO Zoom V16, con una cámara AxioCam MRc5 (Instituto de Biología, UNAM) y para la obtención de las medidas se usó un Olympus SZX10, con una cámara digital SC100 de 10.5 Mpix (Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (ENCB, IPN)). Para analizar la afinidad taxonómica se consultó literatura especializada en el tema (p. ej., Gradstein, *et al.*, 2001; Hentschel, *et al.*, 2009). El ejemplar utilizado para este trabajo se encuentra depositado en la Colección de Paleontología (IPN-PAL) de la Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, ubicado en la Ciudad de México.

4. Resultados

4.1. Sistemática paleobotánica

Clase Jungermanniopsida Stotler y Crandall-Stotler, 1977
Orden Porellales Schljakov, 1972
Familia Frullaniaceae Lorch, 1914
Género *Frullania* Raddi, 1818

Espécimen. IPN-PAL 21

Repositorio. Colección de Paleontología de la Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Ciudad de México, México (Espécimen, IPN-PAL).

Localidad. Mina Los Pocitos, Oligoceno medio– Mioceno Temprano, Formación Simojovel, Simojovel de Allende, Chiapas, México.

Descripción. Planta sin estructuras reproductoras visibles. Tallo de 8 mm de largo de color pardo o rojizo (Figura 2A, B). Ramificación irregular, terminal del tipo *Frullania* (Figura 2B, C). Largo de las ramas entre 366–555 (1,381) µm. Hojas con inserción íncuba, alternas, distantes a contiguas, ovadas a orbiculares, diferenciadas en un lobo dorsal y un lóbulo ventral (Figura 3A–C). Lobos planos, ligeramente más largos que anchos, 139–184 µm × 153–186 µm, respectivamente (Figura 3D). Margen del lobo entero y liso, ápice redondeado y ligeramente recurvado (Figura 3D). Células medias del lobo hexagonales, 8–11.7 µm de largo. Lóbulos cercanos al tallo, en forma de saco, inflados a lo largo de toda su longitud. El largo del lóbulo es dos veces su ancho: 100–108 µm × 34–60 µm. Abertura del lóbulo dirigida hacia la base del tallo. Anfigastrios bífidos y obovados (Figura 3D). Rizoides presentes en mechones en la base de los anfigastrios (Figura 3D).

4.2. Afinidad taxonómica

La muestra representa un solo ejemplar fósil que fue asignado al género *Frullania* de la familia Frullaniaceae. Su asignación a uno de los doce subgéneros dentro de *Frullania* (Mamontov *et al.*, 2021) se dificultó debido a que la morfología del estilo y de los anfigastrios no se aprecian claramente y a que no posee los caracteres taxonómicos primarios (p. ej. morfología del perianto y de las brácteas femeninas). Por lo tanto, su clasificación a uno de los subgéneros deberá esperar hasta obtener más ejemplares de este grupo.

5. Discusión

La diversidad actual de hepáticas en México se estima en ~592 especies y variedades. Alrededor de 53 especies pertenecen al género *Frullania* (Delgadillo-Moya y Juárez-Martínez, 2014), morfológicamente bien delimitado, pero con una taxonomía subgenérica muy compleja. La diversidad pasada de hepáticas en México es pobremente conocida debido a la escasez del registro fósil (Heinrichs *et al.*, 2015), lo que dificulta las interpretaciones sobre la historia evolutiva de las primeras plantas terrestres para nuestro país. Por esta razón, se debe poner especial atención en la recuperación, exploración y estudio de los fósiles de plantas, especialmente de briofitas, que pueden ser indicadores de la aparición

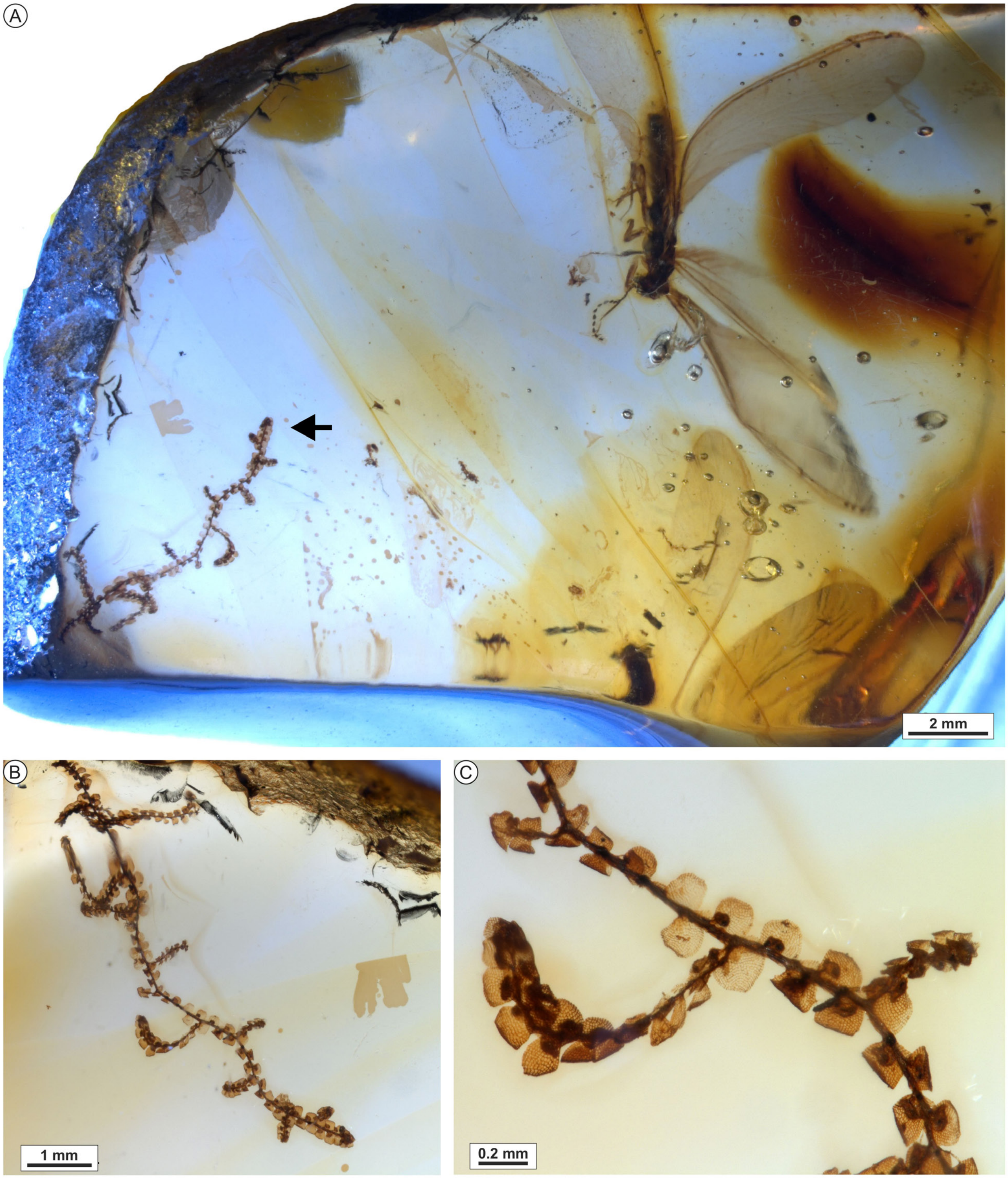

Figura 2. Vista del ejemplar *Frullania*, IPN-PAL 21. A. Vista general mostrando el ápice del tallo (flecha). B. Tallo con hojas distantes a contiguas. C. Porción del tallo mostrando la ramificación terminal del tipo *Frullania*.

y evolución de caracteres morfológicos fundamentales para la colonización del ambiente terrestre.

A nivel mundial, se han descrito alrededor de 16 especies fósiles relacionadas con *Frullania*. Su registro se remonta desde el Cretácico medio hasta el Mioceno temprano (Bouju *et al.*, 2022). Con base en el registro del Mioceno, se han descrito solamente tres especies fósiles del ámbar de República Dominicana y de Etiopía. Heinrichs y Schmidt (2010) describen a *Frullania* subgénero *Diastaloba*. Este fósilitaxon tiene algunas características que no se encuentran en el fósil de Chiapas, como las células de la hoja de tipo isodiamétricas a poco rectangulares y los rizoides en forma de haces, por lo que se descarta alguna afinidad

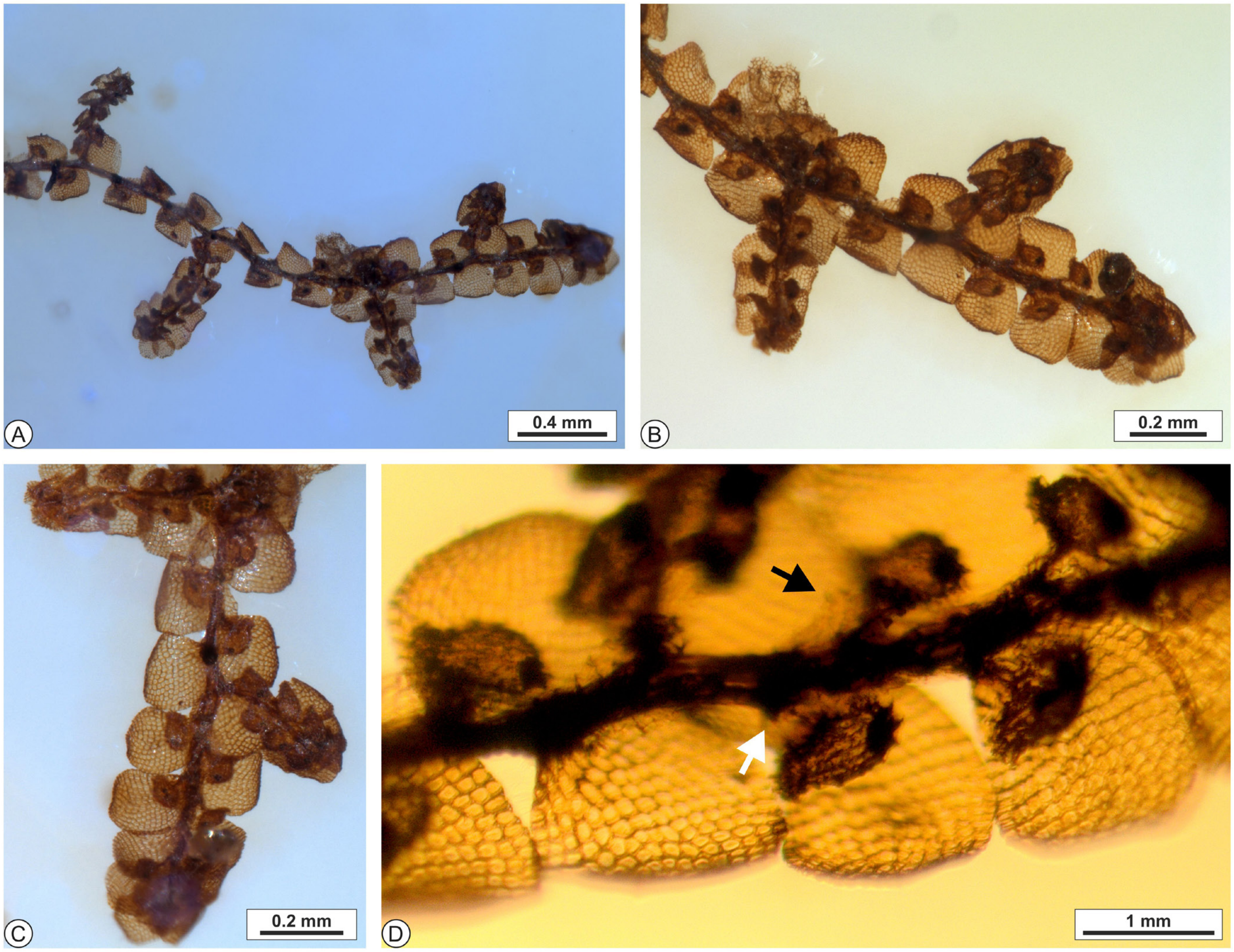

Figura 3. Acercamientos del ejemplar *Frullania*, IPN-PAL 21. A. Porción del tallo mostrando las hojas diferenciadas en lobo y lóbulo. B. Superficie dorsal mostrando los lóbulos en forma de saco. C. Márgenes de las hojas enteros. D. Superficie ventral mostrando los anfigastrios (flecha negra) y la forma de las células de la hoja, así como posibles rizoides (flecha blanca).

taxonómica. Recientemente, en el ámbar miocénico de Etiopía, se describieron dos nuevas especies fósiles de *Frullania* (Bouju *et al.*, 2022). La primera de ellas descrita como *F. shewanensis*, con características que no están presentes en el fósil de Chiapas, como las hojas con ápice subagudo a acuminado, lóbulos más grandes y anfigastrios ovalados, además de no visualizarse el tipo de rizoides. La segunda especie descrita fue *F. palaeoafricana*, con caracteres no observados en el ejemplar de Chiapas, como hojas ovadas con células en la parte media de forma isodiamétricas a elongadas y lóbulos más grandes. Tampoco se visualizaron los rizoides. Por lo tanto, se concluye que el ejemplar fósil de Chiapas es diferente de las dos especies encontradas en el ámbar de Etiopía (Bouju *et al.*, 2022).

En esta contribución, se describe el primer fósil del género *Frullania* reportado para México. Este nuevo registro respalda aún más la hipótesis que propone que la mayoría de los fósiles en ámbar miocénico pertenecen a familias y géneros existentes en la actualidad, y que pueden ser considerados fuentes de información significativas para las estimaciones de tiempos de divergencia con base en datos moleculares para diferentes grupos de plantas (Cevallos-Ferriz *et al.*, 2022; Heinrichs *et al.*, 2018; Estrada-Ruiz *et al.*, 2023).

6. Conclusiones

1. Se reporta y describe el primer registro del género *Frullania* para México, evidenciando que desde el Mioceno temprano el género ya se distribuía en el territorio nacional.

2. La presencia del género *Frullania* indica que formó parte del grupo de las hepáticas en la selva miocénica de Chiapas.

3. Debido a las condiciones tafonómicas del fósil no fue posible la asignación subgenérica de la hepática,

por lo que es necesaria la recolección de más ejemplares que permitan precisar su taxonomía.

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