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First record of caenagnathid dinosaurs (Theropoda, Oviraptorosauria) from the Cerro del Pueblo Formation (Campanian, Upper Cretaceous), Coahuila, Mexico

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ABSTRACT

Herein we report the first caenagnathid dinosaur (Theropoda, Oviraptorosauria) material from the Upper Cretaceous Cerro del Pueblo (CdP) Formation of Coahuila, Mexico, comprising three partial tibiae. Caenagnathids are an unusual group of oviraptorosaur theropod dinosaurs mostly known by way of their toothless, beak-like jaws. Fossils ascribed to Caenagnathidae are well-known from many Late Cretaceous localities in Asia and North America, with a high number of specimens found in the mid-latitudes of North America. The postcranial material described in this study represents the southernmost Laramidian locality in which caenagnathids have been found to date and adds to the scant number of caenagnathid fossils found in southern North America. Overall, these discoveries underscore the high diversity of the dinosaurian fauna found in the CdP Formation.

1. Introduction

Oviraptorosaurs are a clade of unusual theropod dinosaurs that are mostly characterized by the presence of deep, short skulls with variable bony crests and toothless jaws, with rare exceptions (Wang et al., 2018). Body size in this group ranges from small forms, such as the turkey-sized *Caudipteryx*, to the 8-m-long Gigantoraptor (Sues and Averianov, 2015; Funston et al., 2015; Lü et al., 2015). Currently, oviraptorosaurs are known from many Cretaceous geological formations of North America and Asia and have been classified into two families, Oviraptoridae and Caenagnathidae, from which more than 30 genera have been currently described (Osmólska et al., 2004; Funston et al., 2015; Lü et al., 2015; Funston et al., 2020). Most Asian oviraptorosaurs belong to Oviraptoridae, although some caenagnathid specimens are also represented (Xu et al., 2007; Funston, 2020). In contrast, North American oviraptorosaurs are only represented by Late Cretaceous caenagnathids, which were relatively diverse during the Campanian and Maastrichtian Ages (e.g. Currie and Russell, 1998; Osmólska et al., 2004; Longrich et al., 2013, 2015; Funston et al., 2015; Funston, 2020). The majority of North American caenagnathid discoveries have been made in southern Canada and northern USA, with few reports from southern USA (Zanno and Sampson, 2005; Longrich et al., 2010; Sullivan et al., 2011; Longrich et al., 2013; Funston, 2020). Notably, no caenagnathid remains have been reported previously from the southernmost parts of North America, such as Mexico, until now.

The Cerro del Pueblo Formation (CdP) located in the southeast of the state of Coahuila, corresponds to one of the richest and most important dinosaur-bearing formations from the Upper Cretaceous of Mexico (Janensch, 1926; McBride et al., 1974; Kirkland et al., 2000; Eberth et al., 2004; Serrano-Brañas et al., 2006). The most important discoveries of dinosaur fauna in the CdP Formation have been made relatively recently, resulting in multiple descriptions of new genera and species within the past two decades (e.g. Gates et al., 2007; Loewen et al., 2010; Prieto-Márquez and Serrano-Brañas, 2012; Serrano-Brañas et al., 2020; Ramírez-Velasco et al., 2021). Compared to some groups of herbivorous dinosaurs (hadrosaurs and ceratopsians), discoveries of theropod remains in the CdP are relatively rare. However, a recent reexamination of the paleontological collection of the Benemérita Escuela Normal de

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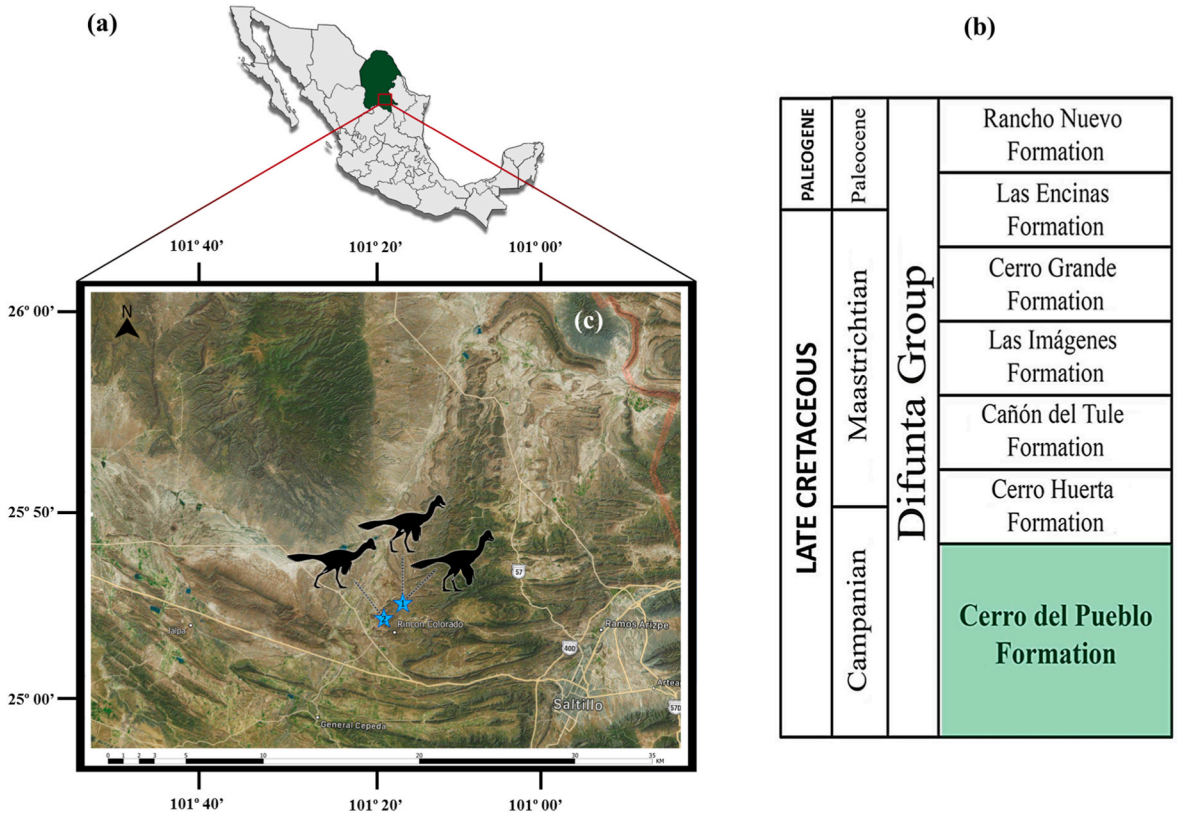

Fig. 1. Geological setting. Location of the Parras Basin (red square) at the south of the state of Coahuila (a); Difunta Group outline indicating the position of the Cerro del Pueblo Formation (in green) (b); Location of the El Palmar [sites A (BENC $^{1}/_{2}$) and B (BENC $^{1}/_{1}$), marked with a blue star with a 1] and the USB (BENC $^{18}/_{1}$, marked with a blue star with a 2) collecting sites (c). Satelital map modified from https://satellites.pro/mapa de Mexico #25.653,906,-101.550751, 10.

Coahuila (BENC) revealed the presence of caenagnathid remains that were previously collected in the CdP during the early 1990's. Herein, we describe this fossil material and compare it to other caenagnathids previously known from other contemporaneous Upper Cretaceous localities of North America and Asia. In addition, we discuss the implications of this finding for the dinosaur faunas of the CdP and their paleogeographical distribution in the southern coastal subtropics of North America.

1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA, BENC, Benemérita Escuela Normal de Coahuila, Mexico, CEU, College of Eastern Utah Prehistoric Museum, Utah, USA, CM, Carnegie Museum of Natural History, Pennsylvania, USA, CMN, Canadian Museum of Nature, Ottawa, Canada, DNHM, Dalian Natural History Museum, Dalian Liaoning, China, FRDC, Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo-Exploration and Mineral Development, Lanzhou, China, FMNH, Field Museum of Natural History, Illinois, USA, GI; Geological Institute of the Mongolian Academy of Sciences, Ulaan Bataar, Mongolia, IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, MOR, Museum of the Rockies, Montana, USA, MPC-D, Mongolian Paleontological Center (Dinosaur Collection), Mongolian Academy of Sciences, Ulaan Baatar, Mongolia, TMP, Royal Tyrrell Museum of Palaeontology; Alberta, Canada, UALVP, University of Alberta Laboratory of Vertebrate Palaeontology, Alberta, Canada, YPM; Yale Peabody Museum of Natural History, Connecticut, USA, ZCDM, Zhucheng Dinosaur Museum, Zhucheng, Shandong, China, ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

2. Geographic and stratigraphic setting

The Difunta Group is part of the east-west-trending Parras Basin, which extends over 27,000 km^2 and is located in the southern region of the state of Coahuila, Mexico (Fig. 1a). This geological group overlays the thick marine strata of the Parras Shale Formation and is estimated uppermost Campanian to Paleocene in age (McBride et al., 1974; Eberth et al., 2004). The Cerro del Pueblo Formation (CdP) is the basal-most formation of the Difunta Group (Fig. 1b), and consists of interdigitating mudstones (50%), sandstones (45%), siltstones (4%), and minor conglomerate and limestone facies (1%) (Eberth et al., 2004; Murray et al., 1962). The upper-most deposits of the CdP correspond to cyclic mudstone, siltstone, and fine-grained sandstone sequences; whereas sandstone packages predominate throughout the first 15–30 m (McBride et al., 1974; Eberth et al., 2004). Interpretation of sedimentological data from the CdP suggest that this formation was a homogeneous coastal plain, with shallow-marine, brackish and terrestrial environments that were developed along the eastern shore of Laramidia at a palaeolatitude of 33.9° N, and dated to ca. 72.5 Ma (Late Campanian) (McBride et al., 1974; Rodríguez de la Rosa and Cevallos-Ferriz, 1998; Kirkland et al., 2000; Eberth et al., 2004).

The fossiliferous strata of the CdP are well-known for the presence of both marine and non-marine fossils that include bivalves and gastropods (Vega et al., 2019), arthropods (Cifuentes-Ruiz et al., 2006; Maccracken com. pers.), distinct groups of plants (Calvillo-Canadell and Cevallos-Ferriz, 2007; Estrada-Ruiz and Cevallos-Ferriz, 2007; Maccracken com. pers.), several dinosaur taxa (Murray et al., 1962; McBride et al., 1974; Rodríguez de la Rosa and Cevallos-Ferriz, 1998; Serrano-Brañas et al., 2006; Gates et al., 2007; Loewen et al., 2010; Aguillón-Martinez, 2010; Prieto-Márquez and Serrano-Brañas, 2012; Serrano-Brañas and Espinosa-Chávez, 2017; Serrano-Brañas et al., 2020), other types of vertebrates (Rodríguez de la Rosa and

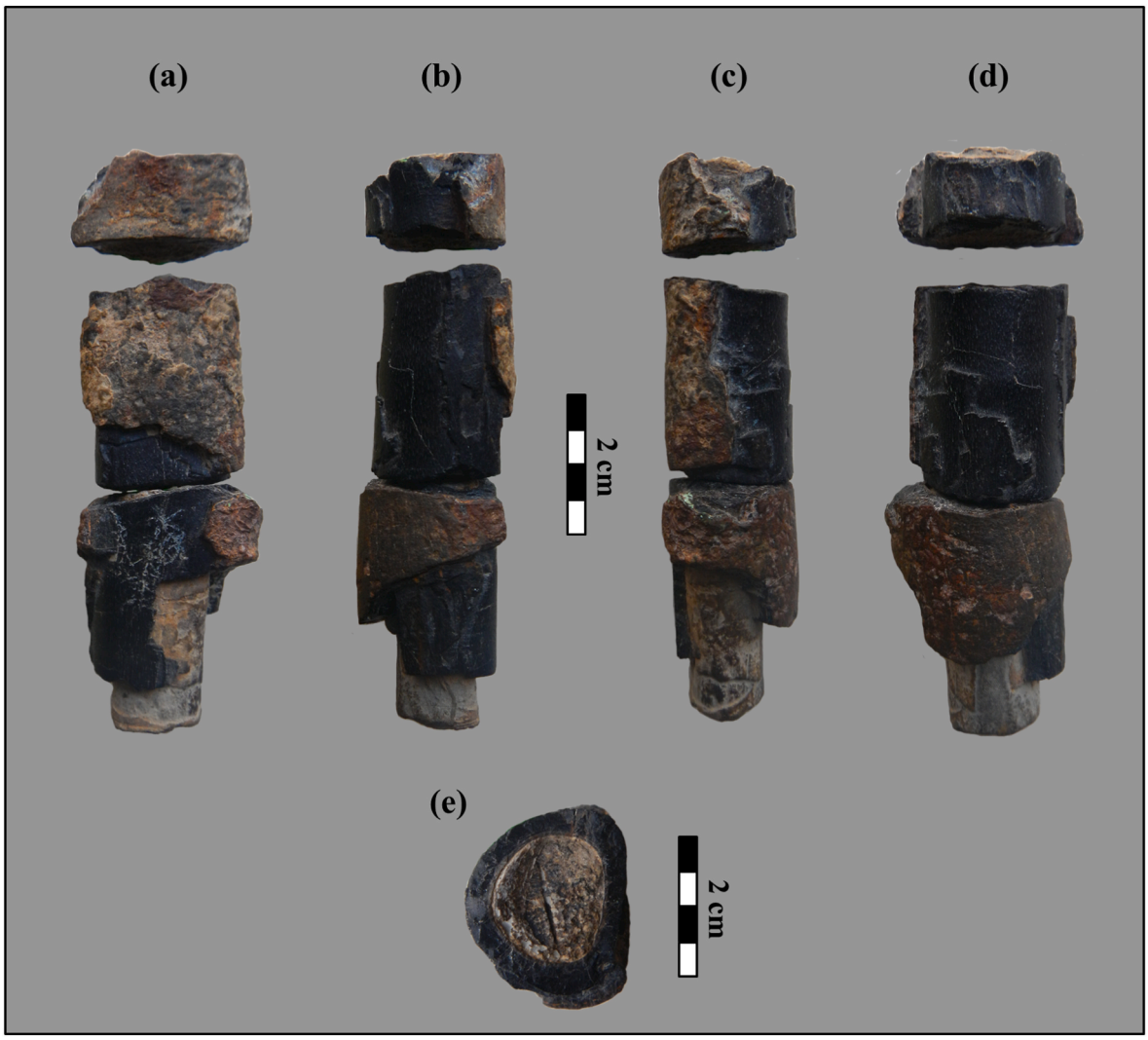

Fig. 2. Partially preserved midshaft of BENC $^{18}/_{1}$-0004 in anterior (a), medial (b), lateral (c), posterior (d), cross-section (e).

Cevallos-Ferriz, 1998; Brinkman and Rodríguez-de la Rosa, 2006), and ichnofossils (Rodríguez de la Rosa, 2003; Serrano-Brañas et al., 2018a; Serrano-Brañas et al., 2018b; Serrano-Brañas et al., 2019). Terrestrial and marine fossils are commonly found in close association due to interdigitated marine and terrestrial facies coupled with erosional forces (McBride et al., 1974; Eberth et al., 2004).

The specimens described in this study were collected from two localities within the CdP. The first collecting locality El Palmar [sites A (BENC $^{1}/_{2}$) and B (BENC $^{1}/_{1}$)] is located 10 km northwest of the Rincón Colorado Town; whereas the second site, UBS (BENC $^{18}/_{1}$) is located 3 km northeast of the La Rosa town, both in the municipality of General Cepeda (Fig. 1c). The predominant lithology in the El Palmar locality (sites A and B) corresponds to tabular beds of massive to laminate, gray clayey-siltstones and mudstones up to 3 m thick. Sedimentary structures include ripple marks. Associated to articulated skeletons of dinosaurs, other types of vertebrates such as fresh-water fishes, turtles and crocodiles are also locally common. Non-vertebrate fossils found at these sites include fresh-water bivalves and gastropods, vertical trace fossils, Fe-stained wood, seeds and vertical to horizontal root traces. According to Eberth et al. (2004), the lithology of the El Palmar locality (sites A and B) is representative of coastal flood basin settings (i.e. Facies 7) (e.g. wetlands, ponds, lakes or bayfill deposits); whereas the fossil content can be assigned to the fresh-water assemblage of Kirkland et al. (2000). On the other hand, the predominant lithology in the UBS site corresponds to tabular beds of black-grayish mudstones intercalated with siltstones and fine-grained sandstones up to ~50 cm thick. Sedimentary structures include symmetrical ripple marks and parallel laminations. Coquinas of *Flemingostrea subspatulata* oysters and brackish-water corbulids are common, as well as, disarticulated dinosaur bones, coprolites, invertebrate feeding/dwelling traces and rare wood fragments. According to Eberth et al. (2004), the lithology of the UBS site is

Table 1
Tibiae measurements of the caenagnathid (oviraptorosaur) specimens from the Cerro del Pueblo Formation described in this paper (in mm). Abbreviations: **E**, estimated measurement for incomplete element; **L**, left element; **NA**, measurement not available; **R**, right element; *, incomplete element, measurement as preserved.

MEASUREMENTS	BENC$^{18}/_{1}$-0004	BENC$^{1}/_{2}$-0002	BENC$^{1}/_{1}$-0086
Length, proximodistal	270^{E}	220^{LE}	410^{RE}
Length, shaft	70*	NA	NA
Length, proximal end	NA	43^{L}	NA
Width of proximal end, mediolateral	NA	29^{L}	NA
Depth of proximal end, anteroposterior	NA	36^{L}	NA
Length, distal end	NA	37^{L}	87^{R}
Width of distal end, mediolateral	NA	32^{L}	63^{R}
Depth of distal end, anteroposterior	NA	11^{L}	22^{R}

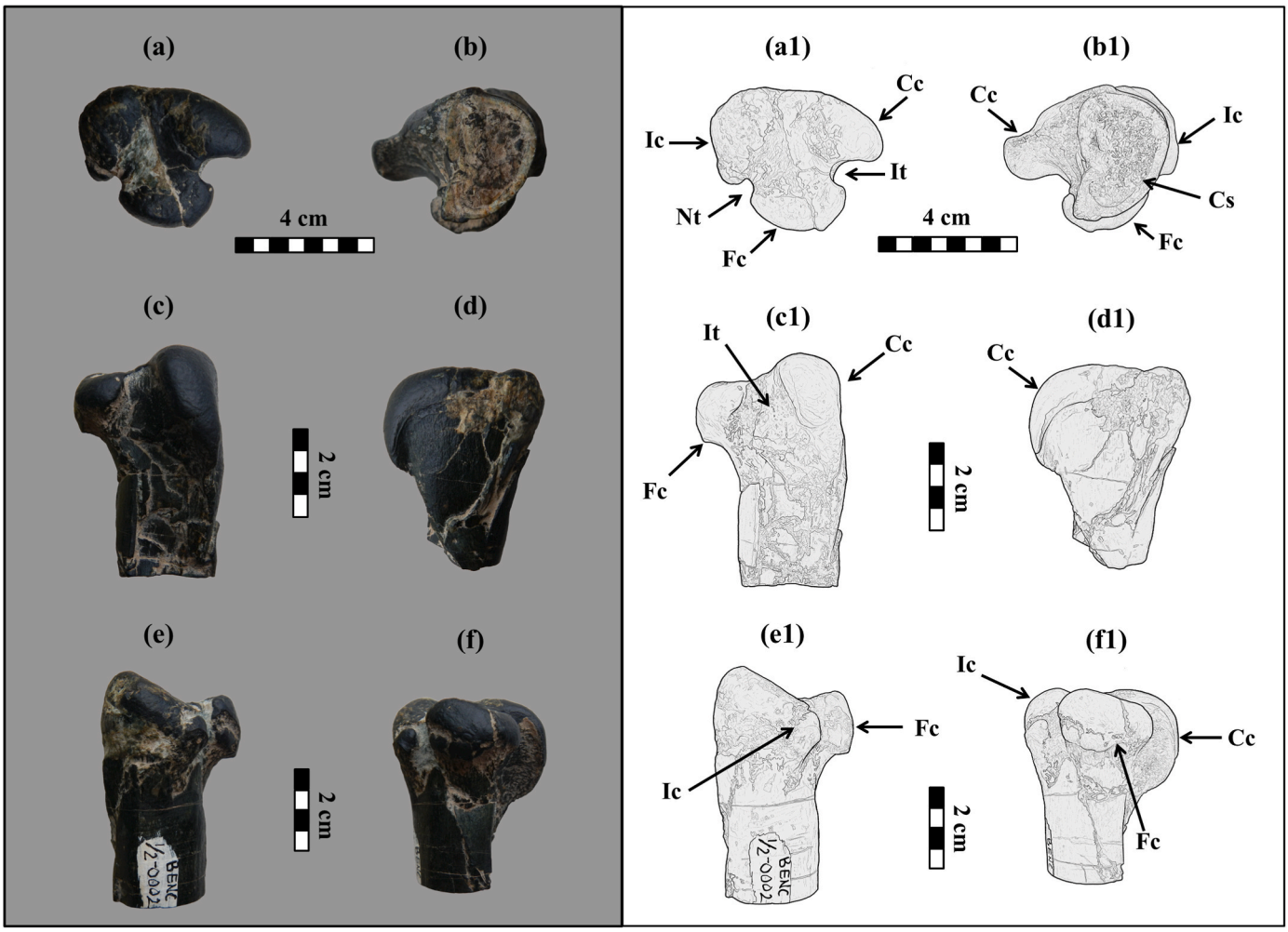

Fig. 3. Proximal end of the right tibia of BENC $^{1}/_{2}$-0002 in proximal (a), distal (b), anterior (c), medial (d), posterior (e) and lateral (f) views. Schematic illustrations of the proximal end of the right tibia of BENC $^{1}/_{2}$-0002 in proximal (a1), distal (b1), anterior (c1), medial (d1), posterior (e1) and lateral (f1) views. Abbreviations: **Cc,** cnemial crest; **Fc**, fibular condyle; **Ic**, inner condyle; **It**, Incisura tibialis; **Nt**, notch.

representative of a lower coastal plain lagoon (i.e. Facies 4); whereas the fossil content can be assigned to the brackish-water assemblage of Kirkland et al. (2000).

3. Systematic paleontology

Theropoda Marsh, 1881, Coelurosauria von Huene, 1914, Maniraptora Gauthier, 1986, Oviraptorosauria Barsbold, 1976.

Material: BENC $^{18}/_{1}$-0004 is represented by three midshaft fragments from a tibia (Fig. 2). Measurements of this specimen are shown in Table 1.

Stratigraphic horizon and locality: BENC $^{18}/_{1}$-0004 was collected in the Upper Cretaceous Cerro del Pueblo Formation (Campanian) of the Difunta Group at the UBS site (BENC $^{18}/_{1}$), located 3 km northeast of the La Rosa Town in the municipality of General Cepeda (25° 54′77″N, 101° 36′ 0.8″W).

3.1. Description

BENC $^{18}/_{1}$-0004 is a partially fragmented tibia shaft that corresponds to the mid-region located below the fibular crest (Fig. 2). Anteriorly, the midshaft is flat (Fig. 2a–c), whereas posteriorly it is rounded (Fig. 2b–d), giving the bone a semicircular cross-section (Fig. 2e). The midshaft has a circumference of 72.2 mm at its widest portion and 59.6 mm at its thinnest. None of the bone surfaces show significant morphological structure, such as ridges or grooves; instead they are entirely smooth. There are some reddish-areas located particularly on the anterior side, which have some fossilized encrusting bryozoans.

Caenagnathidae Sternberg, 1940.

Material: BENC $^{1}/_{2}$-0002 is represented by the proximal and distal ends of a right tibia (Figs. 3, 4 and 5a). Measurements of the described material are shown in Table 1.

Stratigraphic horizon and locality: This specimen was collected in the Upper Cretaceous Cerro del Pueblo Formation (Campanian) of the Difunta Group at the El Palmar site A (BENC ½), located 10 km northwest of the Rincón Colorado Town in the municipality of General Cepeda (25° 34′8.16″N, 101° 20′ 4.6″ W).

3.2. Description

BENC $^{1}/_{2}$-0002 is represented also by a partially fragmented tibia, which consists of only the proximal and distal ends (Figs. 3 and 4). The proximal end of BENC $^{1}/_{2}$-0002 is anteroposteriorly expanded, whereas proximally is slightly concave (Fig. 3a and a1). Distally, the partially preserved shaft has a semicircular cross-section (Fig. 3b and b1). The cnemial crest is separated from the fibular condyle by a deep incisura tibialis, which in turn, extends along the partially preserved shaft towards its distal end and possesses a semicircular profile (Fig. 3c and c1). The cnemial crest is prominent, slopes anteroventrally and does not extend far distally, occupying approximately 18.71% of the estimated

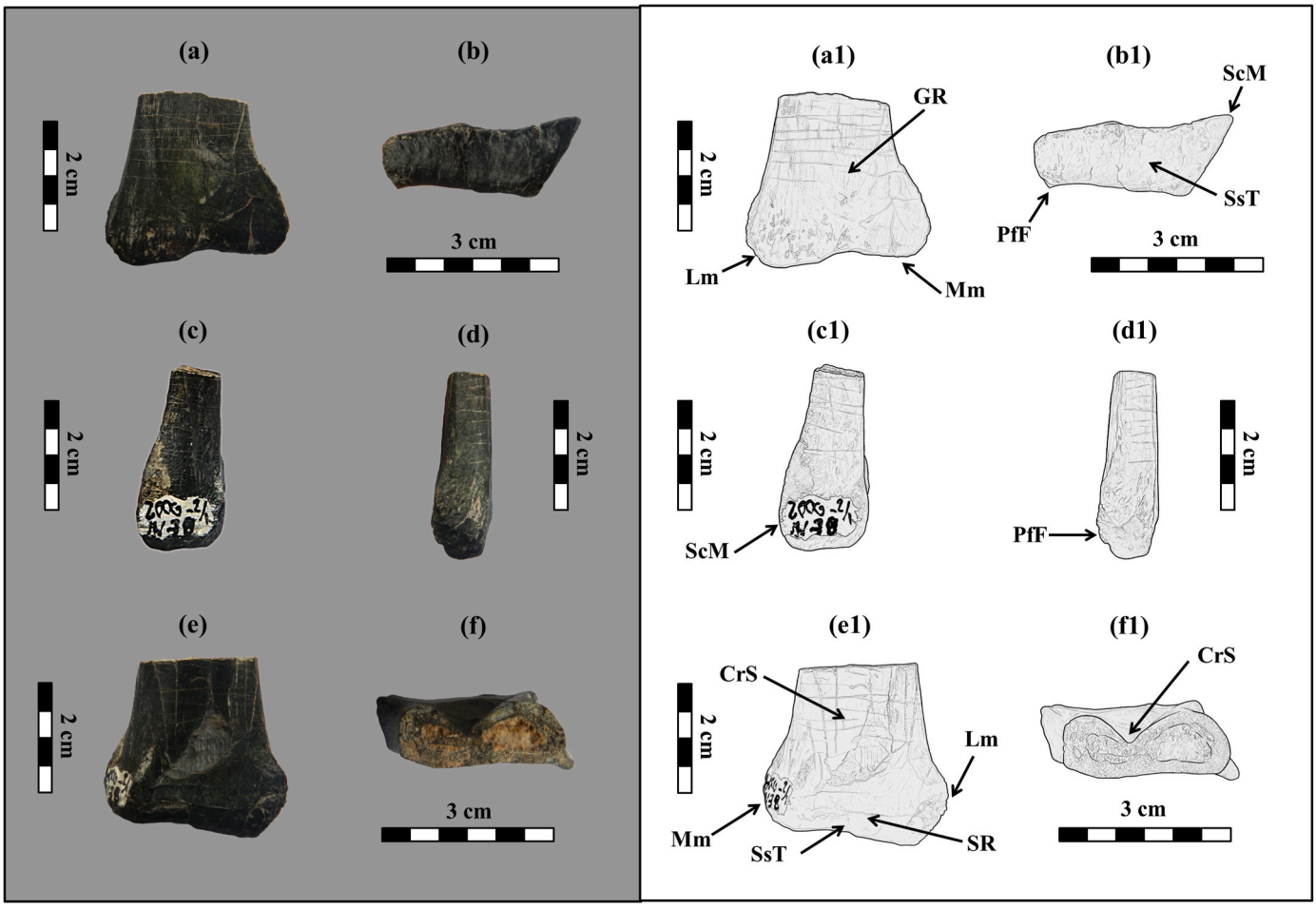

Fig. 4. Distal end of the right tibia of BENC $^{1}/_{2}$-0002 in anterior (a), distal (b), medial (c), lateral (d), posterior (e) and proximal (f) views. Schematic illustrations of the distal end of the right tibia of BENC $^{1}/_{2}$-0002 in anterior (a1), distal (b1), medial (c1), lateral (d1), posterior (e1) and proximal (f1) views. Abbreviations: **CrS**, crushed surface**; GR**, green colored region; **Lm**, lateral malleolus; **Mm,** medial malleolus; **PfF**, postfibular flange; **ScM**, sharp crest of the medial malleolus; **SR**, shallow ridge; **SsT**, semi-striated texture.

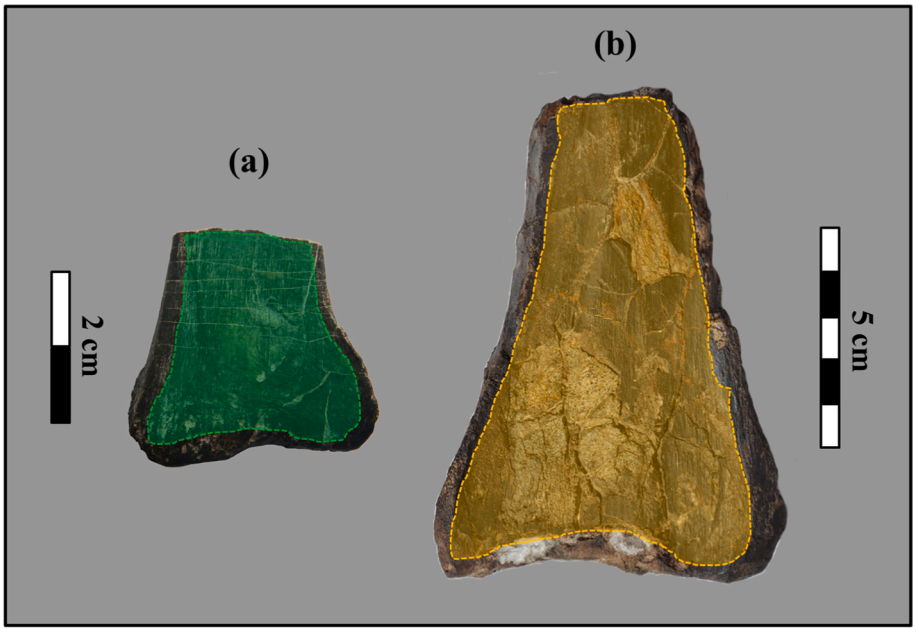

Fig. 5. Comparison of the distal ends of BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 in anterior view, showing the contact surface for the ascending process of the astragalus: (a) Contact surface of BENC $^{1}/_{2}$-0002 in green; (b) contact surface of BENC $^{1}/_{1}$-0086 in yellow.

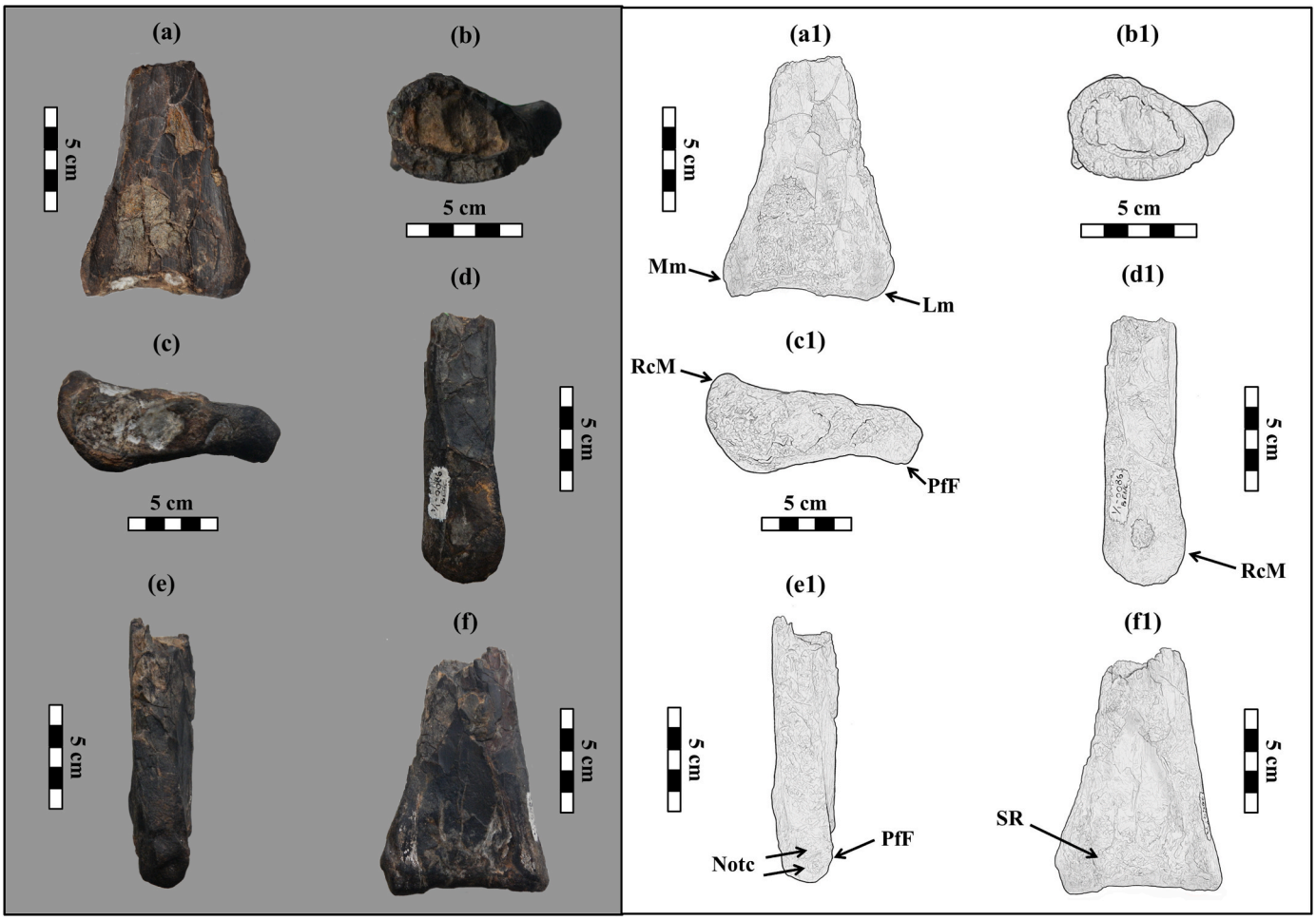

Fig. 6. Distal end of the left tibia of BENC $^{1}/_{1}$-0086 in anterior (a), proximal (b), distal (c), medial (d), lateral (e) and posterior (f) views. Schematic illustrations of the distal end of the left tibia of BENC $^{1}/_{1}$-0086 in anterior (a1), proximal (b1), distal (c1), medial (d1), lateral (e1) and posterior (f1) views. Abbreviations: **Lm**, lateral malleolus; **Mm,** medial malleolus; **PfF**, postfibular flange; **RcM**, rounded crest of the medial malleolus; **Notc**, notch; **SR**, shallow ridge.

tibia length (Fig. 3c, c1, 3 d and 3d1). The fibular condyle is well-developed and has a subovoid shape (Fig. 3a, a1, 3c, 3c1, 3e and 3e1); its lateral surface for the articulation with the fibula has a posterolateral orientation (Fig. 3f and f1). This condyle is separated from the inner condyle by a small and shallow notch, which in turn causes the posterolateral surface for the femoral condyle to have a small projection (Fig. 3a and a1).

The distal end of BENC $^{1}/_{2}$-0002 has a subtriangular shape that flares mediolaterally into sharply define ridges; whereas it is compressed anteroposteriorly. Anteriorly, the distal end is flat and lacks an anterior crest. The contact with the ascending process of the astragalus is marked by the presence of a slightly greenish area on the bone surface (Fig. 4a–a1 and 5a); which in turn is bisected by a shallow, longitudinal ridge. The medial malleolus is anteriorly flat and extends laterally into a sharp crest (Fig. 4b, b1, 4c and 4c1); posteriorly, it adopts a concave shape (Fig. 4b, b1). The lateral malleolus is slightly worn, but a small portion of the postfibular flange can still be observed (Fig. 4b, b1, 4 d and 4d1). Both malleoli have a similar anteroposterior thickness (Fig. 4b, b1) and extend distally to almost the same level; however, the lateral malleolus is slightly larger (Fig. 4a, a1, 4e and 4e1). The lateral surface of the distal end is completely flat, showing no evidence of the presence of a groove or facet for the reception of the fibula (Fig. 4d and d1). The distal articular surface of BENC ½-0002 has a semi-striated texture throughout its entire transverse width (Fig. 4b, b1); which also extends onto the posterior side, where it is delimited by a shallow ridge (Fig. 4b, b1, 4e and 4e1). This semi-striated area appears to indicate that the astragalus covered the entire tranverse width of the tibia and wrapped completely around during articulation. Finally, the posterior side of the upper portion of the distal end in BENC ½-0002 is crushed, causing this area to cave in (Fig. 4e, e1, 4f and 4f1).

Caenagnathidae Sternberg, 1940.

Material: BENC $^{1}/_{1}$-0086 is represented by the distal end of a left tibia (Figs. 5b and 6). Measurements of the described element are shown in Table 1.

Stratigraphic horizon and locality: This specimen was collected in the Upper Cretaceous Cerro del Pueblo Formation (Campanian) of the Difunta Group, at the El Palmar site B (BENC $^{1}/_{1}$, only a few meters away from site A), located 10 km northwest of the Rincón Colorado Town in the municipality of General Cepeda (25° 34′8.16″N, 101° 20′ 4.6″W).

3.3. Description

BENC $^{1}/_{1}$-0086 is represented by the distal end of a left tibia that belonged to a large individual (Fig. 6). This element also has a sub-triangular shape that flares mediolaterally into sharply defined ridges (Fig. 6a and a1) and is anteroposteriorly compressed. A small portion of the tibial shaft is still preserved and has a semicircular cross-section (Fig. 6b and b1), with a circumference of 97.4 mm. Anteriorly, BENC $^{1}/_{1}$-0086 possesses a flat surface that has degradation (cracking and loss of the external bone layer) in certain areas and also lacks any evidence of the presence of an anterior crest (Fig. 6a and a1). In addition, the preserved contact surface for the ascending process of the astragalus

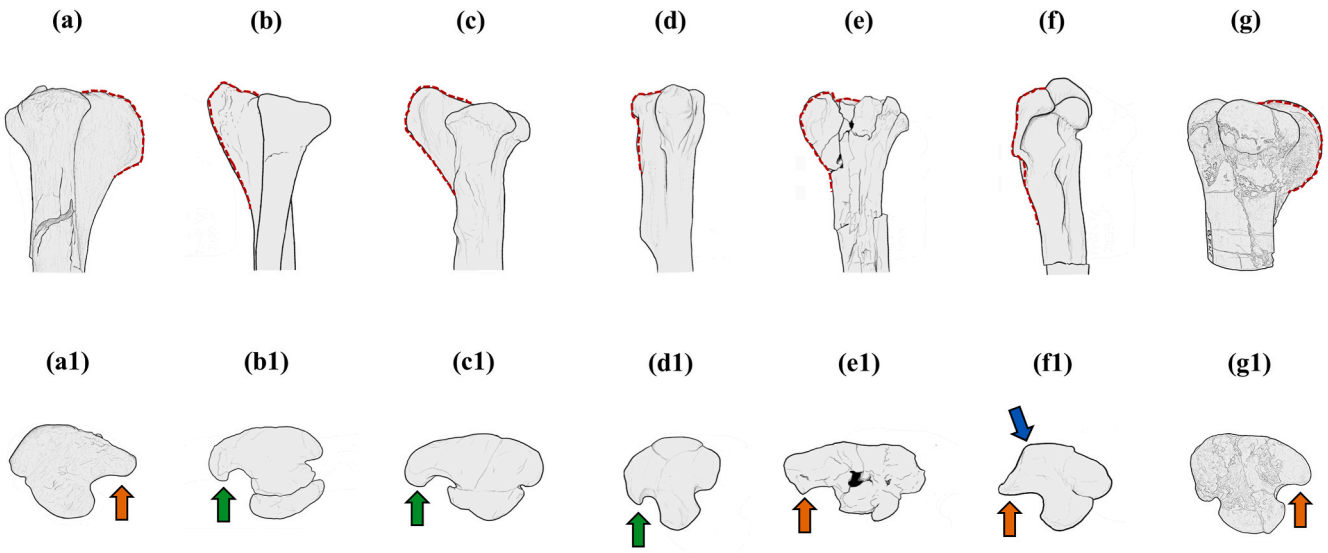

Fig. 7. Schematic comparison of the proximal ends of tibiae from different groups of Late Cretaceous coelurosaur theropods in lateral (a–g) and proximal (a1-g1) views: (a–a1) Oviraptorosaurs [*Elmisaurus rarus* right tibia (MPC-D 102/007; Funston and Currie, 2018)]; (b) Ornithomimosaurs [*Garudimimus brevipes* left tibia (GIN 100/13; Kobayashi and Barsbold, 2005)]; (b1) Ornithomimosaurs [*Sinornithomimus dongi* left tibia (IVPP–V11797-23; Kobayashi and Lü, 2003)]; (c–c1) Tyrannosaurids [*Tyrannosaurus rex* left tibia (FMNH PR 2081; Brochu, 2003)]; (d–d1) Troodontids [*Sinovenator changii* left tibia (IVPP V12583; Xu et al., 2002)]; (e–e1) Dromaeosaurids [*Velociraptor mongoliensis* left tibia (IGM 100/986; Norell and Makovicky, 1999)]; (f–f1) Alvarezsaurids [*Mononykus olecranus* left tibia (GI N107/6; Perle et al., 1994)]; (g–g1) BENC $^{1}/_{2}$-0002 right tibia. Red dotted lines indicate the contour and extension of the cnemial crest. Orange arrows show straight cnemial crests that do not curve laterally. Green arrows show cnemial crests that curve laterally. Blue arrow shows the presence of a second smooth crest on the medial face of the tibia in alvarezsaurids. Schematic figures not to scale.

extends up to ~65 mm, forming a tall triangle that covers the entire transverse width of the tibia (Fig. 5b). This contact surface is not bisected by a shallow longitudinal ridge. The medial malleolus is anteriorly flat and extends laterally into a prominent crest (Fig. 6c, c1, d and d1); whereas posteriorly, it adopts a concave shape (Fig. 6c and c1). Particularly, the lateral crest of the medial malleolus has a rounded shape. The lateral malleolus is complete, posteriorly deflected and has a well-developed postfibular flange (Fig. 6c, c1, 6e and 6e1). In general, both malleoli have similar anteroposteriorly thicknesses (Fig. 6d, d1, 6e and 6e1) and extend distally to the same level (Fig. 6a, a1, 6f and 6f1). The lateral surface of BENC $^{1}/_{1}$-0086 is flat and lacks a groove or facet for the reception of the fibula (Fig. 6e and e1). Finally, the distal articular surface of the tibia is mostly flat, becoming slightly concave on the region of the medial malleolus (Fig. 6a and a1). Distolaterally, this articular surface possesses two small, shallow notches (Fig. 6e and e1); whereas posteriorly, a shallow horizontal ridge is present, suggesting that the astragalus covered the entire transverse width and wrapped completely around the tibia (Fig. 6f and f1).

4. Discussion

4.1. Oviraptorosaur features of specimens BENC $^{18}/_{1}$-0004, BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086

The specimens described in this study possess a series of morphological characteristics that confirm their taxonomic assignation to oviraptorosaur dinosaurs. While the fragmentary nature of these specimens precludes their taxonomic identification below family level, the diagnostic characteristics are as follows:

4.1.1. Cross-section of the tibia shaft

As previously stated by Funston and Currie (2018), the cross-sectional shape of the mid-point of the tibia shaft can be useful to distinguish between coelurosaur taxa, since this area shows considerable variation among these theropod groups (see Funston and Currie, 2018; Fig. 5A). For example, the anterior and posterior surfaces of the tibia are rounded in most Late Cretaceous theropods, such as ornithomimids [e.g. *Ornithomimus edmontonicus* (CMN 12070; Cullen et al., 2014); *Gallimimus bullatus* (Z.Pal.No.Mg. D-I/94; Osmólska et al., 1972)], tyrannosaurids [e.g. *Tyrannosaurus rex* (MOR 009, Horner and Padian, 2004; FMNH PR 2081; Brochu, 2003)] and alvarezsaurs [e.g. *Albertonykus borealis* (TMP, 2000.045.0098; Funston and Currie, 2018); *Linhenykus monodactylus* (IVPP V17608; Xu et al., 2013); *Mononykus olecranus* (GI N107/6; Perle et al., 1994)], conferring it an elliptical or circular cross-section. On the other hand, the midshaft cross-sectional shape of the tibia in troodontids can vary from oval to circular in most specimens (e.g. *Troodon formosus*, MOR 748; Varricchio et al., 2009); although in *Daliansaurus liaoningensis* (DNHM D2885), it adopts a squared-like shape (Shen et al., 2017). Most dromaeosaurids possess tibiae with rectangular cross-sections, since the anterior and posterior surfaces of the shaft are flattened (e.g. *Saurornitholestes* sp., UALVP 55700; Funston and Currie, 2018); however in some specimens, the shaft has an oval or subtriangular shape [e.g. *Utahraptor ostrommaysi* (CEU 84v.260; Kirkland et al., 1993); *Deinonychus antirrhopus* (AMNH 3015; Ostrom, 1969)]. In the case of oviraptorosaurs, these differ from other theropod groups in that only the anterior surface of the tibia is flat, resulting in a characteristic semicircular cross-section [e.g. *Elmisaurus rarus* (MPC-D 102/07; Funston and Currie, 2018), *Citipes elegans* (TMP, 1994.012.0880; Parks, 1933; Funston et al., 2016; Funston, 2020) and *Anomalipes zhaoi* (ZCDM V0020; Yu et al., 2018)]. It is important to note that in juvenile tyrannosaurs the tibia midshaft can also be semicircular in cross-section similar to that of oviraptorosaurs (Funston and Currie, 2018); however, the lateral surface of the shaft, distal to the fibular crest in the former, possesses a series of striations or grooves that run distolaterally along the posterior surface of this element. These striations are absent in oviraptorosaur tibiae. Although BENC $^{18}/_{1}$-0004 is fragmented and partially preserved, the mid-shaft cross-section of this element is semicircular and the lateral and posterior surfaces are not striated or grooved (Fig. 2e), supporting previous observations of tibia morphology in oviraptorosaur dinosaurs.

4.1.2. Shape of the cnemial crest and other morphological characteristics of the proximal end

As in the case of the cross-section of the tibial shaft, there is

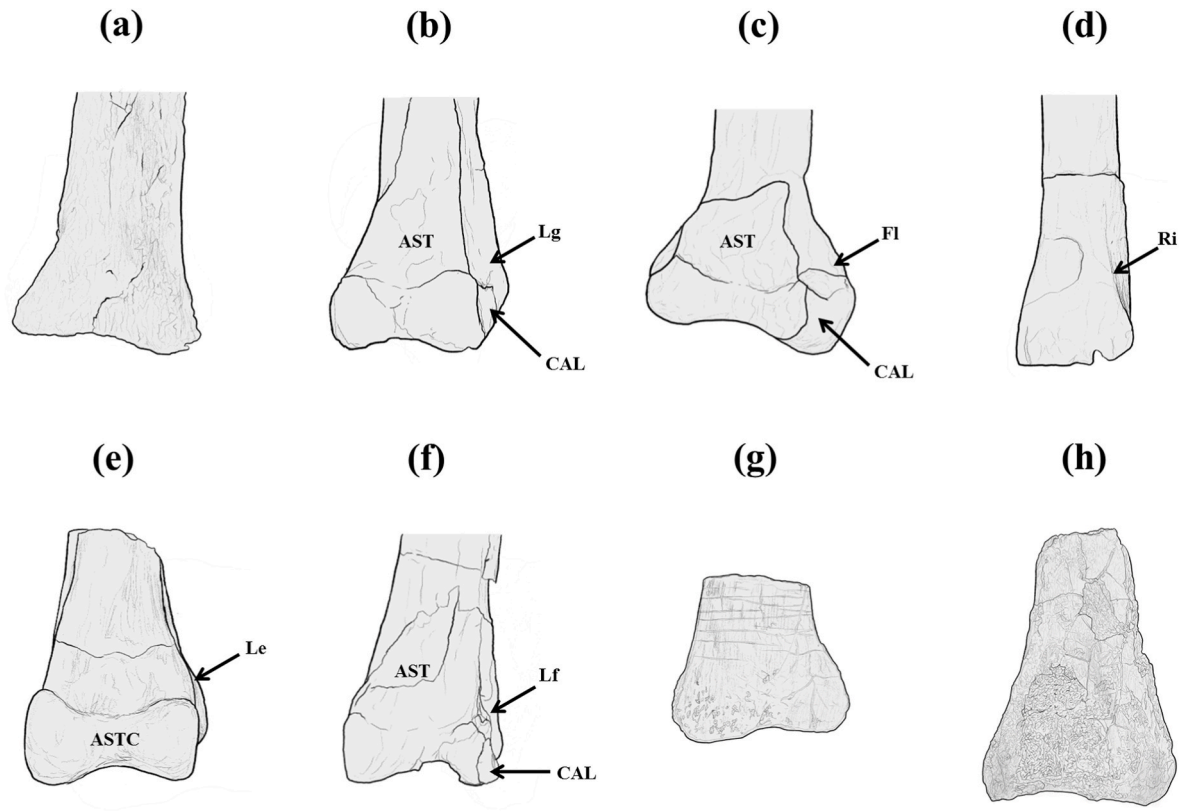

Fig. 8. Schematic comparison of the distal ends of tibiae from different groups of Late Cretaceous coelurosaur theropods in anterior view: (a) Oviraptorosaurs [*Elmisaurus rarus* left tibia (MPC-D 102/007; Funston and Currie, 2018)]; (b) Ornithomimosaurs [*Garudimimus brevipes* left tibia (GIN 100/13; Kobayashi and Barsbold, 2005)]; (c) Tyrannosaurids [*Tyrannosaurus rex* left tibia (FMNH PR 2081; Brochu, 2003)]; (d) Alvarezsaurids [*Linhenykus monodactylus* left tibia (IVPP V17608; Xu et al., 2013)]; (e) Troodontids [*Zanabazar junior* left tibia (IGM 100/1; Norell et al., 2009)]; (f) Dromaeosaurids [*Velociraptor mongoliensis* left tibia (IGM 100/986; Norell and Makovicky, 1999)]; (g) BENC $^{1}/_{2}$-0002 right tibia; (h) BENC $^{1}/_{1}$-0086 left tibia. Abbreviations: **AST**, astragalus; **ASTC**, classified astragalus-calcaneum; **CAL**, calcaneum; **Fl**, flange; **Le,** lateral excavation; **Lf**, lateral facet; **Lg**, lateral groove; **Ri**, ridge. Schematic figures not to scale.

considerable variation in the development of the cnemial crest for various coelurosaur groups. For example, oviraptorosaurs possesses a short but pronounced single cnemial crest that slopes anteroventrally and does not hook towards the fibula [e.g. *E. rarus* (MPC-D 102/007 and MPC-D 102/010) (Fig. 7a – 7a1), *Apatoraptor pennatus* (TMP, 1993.051.0001; Funston and Currie et al., 2016), *Anzu wyliei* (CM 78000; Lamanna et al., 2014) and *C. elegans* (TMP, 1994.012.0880)]. In contrast, ornithomimosaur dinosaurs possess a single and strong cnemial crest with a dorsal apex that projects above the level of the articular surface, particularly in members of the Deinocheiridae family [e.g. *Beishanlong grandis* (FRDC-GS GJ (06) 01–18; Makovicky et al., 2010), *Deinocheirus mirificus* (MPC-D 100/127; Lee et al., 2014) and *Garudimimus brevipes* (GIN 100/13; Kobayashi and Barsbold, 2005) (Fig. 7b)]; also, the cnemial crest curves outwards towards the fibula [e.g. *Sinornithomimus dongi* (IVPP–V11797-23, Kobayashi and Lü, 2003) (Fig. 7b1), *G. brevipes* (GIN 100/13) and *G. bullatus* (Z.Pal.No.Mg. D-I/94)]. As in ornithomimosaurs, tyrannosaurids also have a single cnemial crest that broadly curves laterally and projects above the level of the articular surface (Fig. 7c–c1); however, the tyrannosaurid cnemial crest bears a broad shallow notch on its lateral tip [e.g. *T. rex* (FMNH PR 2081)]. Most troodontids have a single, moderately developed cnemial crest that raises anteromedially and slopes anteroventrally at its proximal edge [e.g. *D. liaoningensis, Sinornithoides youngi* (IVPP V9612; Currie and Zhiming, 2001) and *Sinovenator changii* (IVPP V12583; Xu et al., 2002) (Fig. 7d–d1)]. In contrast, the single cnemial crest in most dromaeosaurs is well-developed and has an anterior edge that hooks laterally, as in other theropod groups (e.g. *D. antirrhopus* and *U. ostrommaysi*). Only velociraptorines have an unhooked and well-expanded cnemial crest, which possesses a large rugose boss [e.g. *Velociraptor mongoliensis* (IGM 100/986, Norell and Makovicky, 1999) (Fig. 7e–e1) and *Rahonavis ostromi* (UA 8656, Turner et al., 2012)]. Finally, the cnemial crest in alvarezsaurids is robust, extends distally along the tibial shaft and a second smooth crest is developed on its medial face [e.g. *L. monodactylus* and *M. olecranus* (Fig. 7f–f1)]. In the case of BENC $^{1}/_{2}$-0002, the proximal end of the tibia bears an unhooked, short, prominent cnemial crest that slopes anteroventrally, as in oviraptorosaurs (Fig. 3c, c1, 3 d, 3d1 and 7 g–7g1).

4.1.3. Articular relationship between the tibia and fibula at their distal ends

As pointed out by Funston and Currie (2018), the articulation of the tibia and fibula in oviraptorosaurs is unique, since the anterolateral surface of the distal end of the tibia lacks any distinctive grooves, crests or facets for the articulation with the fibula. This suggests that the fibula ran laterally to the tibial shaft along its entire length, rather than being anterior to the tibial shaft [e.g. *E. rarus* (MPC-D 102/007; Fig. 8a)]. Unlike oviraptorosaurs, the tibia in ornithomimids distally bears an anterior crest and a shallow or deep lateral groove for the articulation with the fibula [e.g. *G. bullatus* (Z.Pal.No.Mg. D-I/94), *S. dongi* (IVPP–V11797-23), *O. edmontonicus* (CMN 12070), *Ornithomimus velox* (YPM 542; Claessens and Lowell, 2015) and *G. brevipes* (GIN 100/13)] (Fig. 8b). In tyrannosaurids, the lateral margin of the distal end of the tibia has a thin flange that extends into the anterior side of the bone, contributing to the articular surface for the fibula [e.g. *T. rex* (FMNH PR 2081; Fig. 8c)]. The distal end of the tibia in alvarezsaurids has a long, sharp ridge that separates the anterior and lateral surfaces [e.g. *L. monodactylus* (IVPP V17608; Fig. 8d)]. In contrast, most troodontids have tibiae with a lateral excavation for the reception of the fibula [e.g. *Zanabazar junior* (IGM 100/1; Norell et al., 2009) (Fig. 8e)]; whereas in

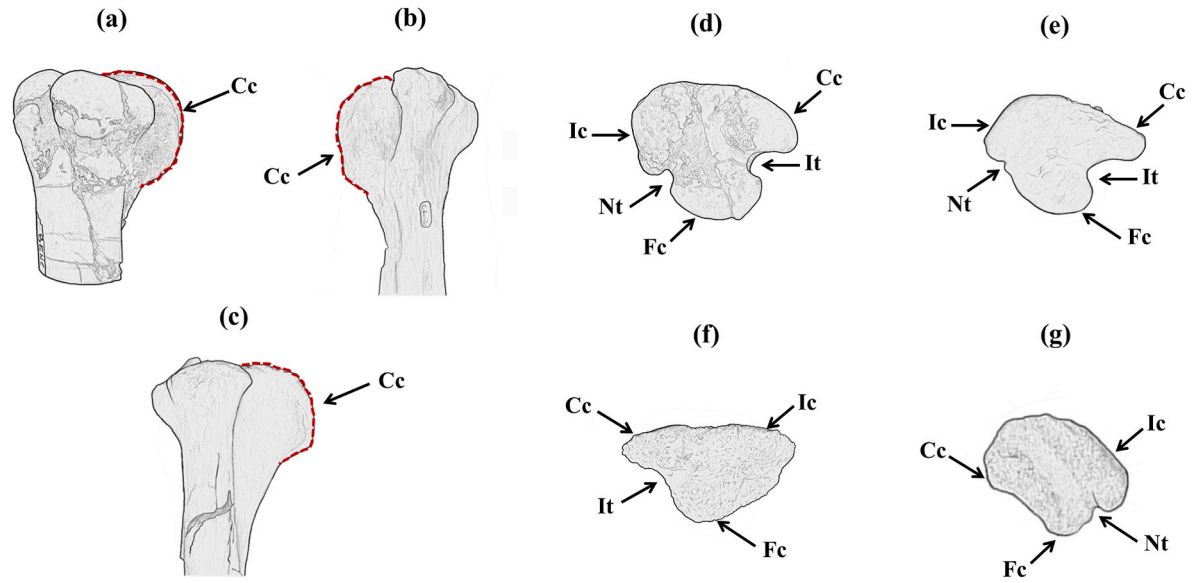

Fig. 9. Schematic comparison of the proximal ends of tibiae from different caenagnathids in lateral (a, c), medial (b) and proximal (d–g) views: (a, d) Right tibia of BENC $^{1}/_{2}$-0002; (b) right tibia of *Anzu wyliei* (CM 78000; Lamanna et al., 2014); (c, e) right tibia of *Elmisaurus rarus* (MPC-D 102/007; Funston and Currie, 2018); (f) left tibia of *Citipes elegans* (TMP, 1994.012.0880; Parks, 1933; Funston et al., 2016; Funston, 2020); (g) left tibia of UALVP 57349 (Funston and Currie, 2018). Abbreviations: **Cc,** cnemial crest; **Fc**, fibular condyle; **Ic**, inner condyle; **It**, Incisura tibialis; **Nt**, notch. Red dotted lines indicate the contour and extension of the cnemial crest. Schematic figures not to scale.

dromaeosaurids, the tibia has an anterior crest and/or lateral facet in its distal end for the articulation with the fibula [e.g. *V. mongoliensis* (IGM 100/986; Fig. 8f)]. In the case of BENC $^{1}/_{2}$-0002 (Fig. 8g) and BENC $^{1}/_{1}$-0086 (Fig. 8h), the anterolateral surfaces of both distal ends, show no evidence of the presence of a shallow or deep lateral groove, facet or an anterior crest for the articulation of the fibula, supporting their referral to Oviraptorosauria.

4.2. Caenagnathid features of specimens BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 and morphological comparisons to other caenagnathids from North America and Asia

Specimens BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 possess several characteristics that verify their identities as caenagnathids. These morphological characteristics are as follows:

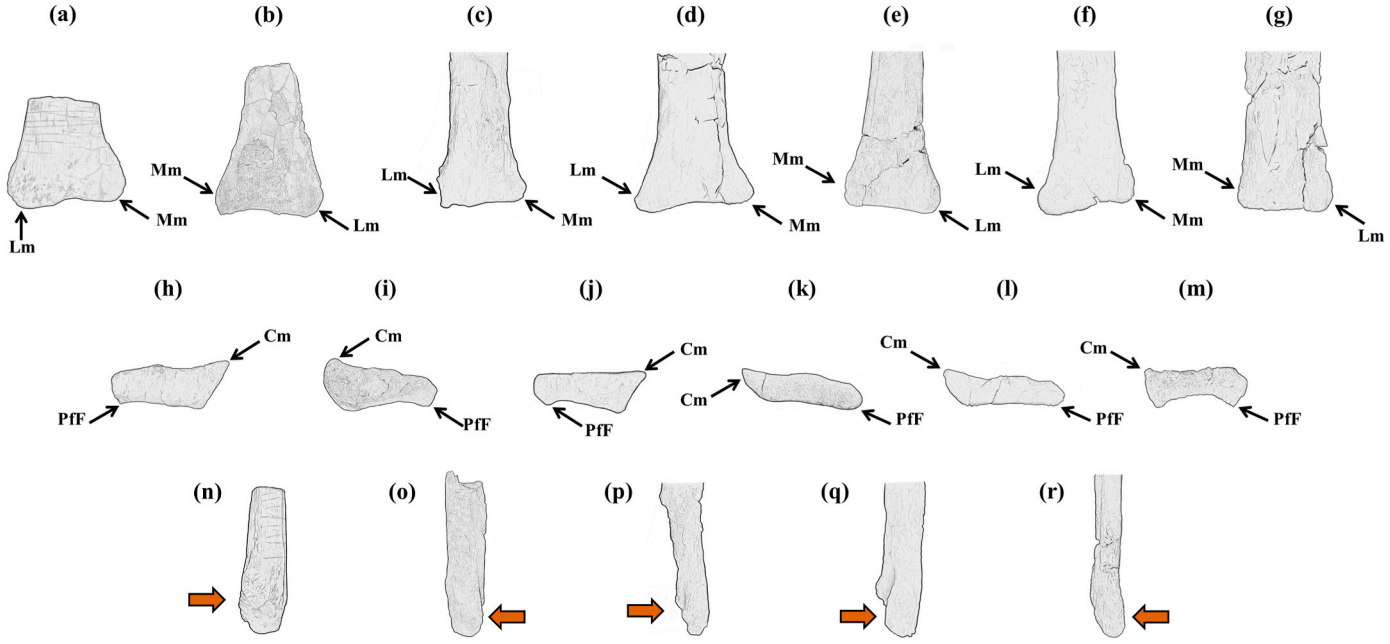

Fig. 10. Schematic comparison of the distal ends of tibiae from different caenagnathids in anterior (a-e, g), posterior (f), distal (h–m) and lateral (n–r) views: (a, h, n) Right tibia of BENC $^{1}/_{2}$-0002; (b, i, o) left tibia of BENC $^{1}/_{1}$-0086; (c, p) right tibia of *Chirostenotes pergracilis* (TMP, 1979.020.0001; Currie and Russell, 1988); (d, j, q) right tibia of *Elmisaurus rarus* (MPC-D 102/007; Funston and Currie, 2018); (e, k, r) left tibia of UALVP 57349 (Funston and Currie, 2018); (f, l) left tibia of *Anomalipes zhaoi* (ZCDM V0020; Yu et al., 2018)]; (g, m) left tibia of *Citipes elegans* (TMP, 1994.012.0880; Parks, 1933; Funston et al., 2016; Funston, 2020). Abbreviations: **Cm**, crest of medial malleolus; **Lm**, lateral malleolus; **Mm**, medial malleolus; **PfF**, postfibular flange. Orange arrows show the posteriorly deflected position of the lateral malleolus. Schematic figures not to scale.

4.2.1. Proximal end of the tibia

The recovered proximal end of BENC $^{1}/_{2}$-0002 has a prominent cnemial crest that slopes anteroventrally and does not extend far distally (Figs. 3 and 9a). Comparing this structure with other previously described oviraptorosaurs, we can observe that it is similar to the one present in *Chirostenotes pergracilis* (TMP, 1979.020.0001; Currie and Russell, 1988), *A. wyliei* (CM 78000) (Fig. 9b), *E. rarus* (MPC-D 102/07) (Fig. 9c), *C. elegans* (TMP, 1994.012.0880), and other previously described caenagnathids (Funston and Currie et al., 2016; Funston and Currie, 2018; Funston, 2020). In addition, the cnemial crest in BENC $^{1}/_{2}$-0002 (Fig. 9d) is separated from the fibular condyle by a deep incisura tibialis as in *E. rarus* (MPC-D 102/07) (Fig. 9e) and *C. elegans* (TMP, 1994.012.0880) (Fig. 9f). Finally, the fibular condyle in BENC $^{1}/_{2}$-0002 is separated from the inner condyle by a small notch (Fig. 9d), as in other caenagnathids, producing a small projection of the posterolateral surface of the femoral condyle, similar to the condition observed in *E. rarus* (MPC-D 102/07) (Fig. 9e), *C. pergracilis* (TMP, 1979.020.0001) and a small, isolated caenagnathid tibia from the Horseshoe Canyon Formation (UALVP 57349, Funston and Currie, 2018) (Fig. 9g).

4.2.2. Distal end of the tibia

The distal ends of BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 are transversely wide, occupying 14.97% and 12.1% (respectively; Fig. 10a and b) of the estimated length of the tibia; these percentages are similar to the ones seen in *C. pergracilis* (13%) (Fig. 10c), *E. rarus* (14%) (Fig. 10d) and UALVP 57349 (~16%) (Fig. 10e). Conversely, the medial malleoli of BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 have flat anterior surfaces and convex posterior surfaces, which extend laterally into a sharp crest (Fig. 10h and i, respectively), as in *A. wyliei* (CM 78000), *C. pergracilis* (TMP, 1979.020.0001), *E. rarus* (MPC-D 102/07) (Fig. 10j), UALVP 57349 (Fig. 10k) and *C. elegans* (TMP, 1994.012.0880) (Fig. 10m). Particularly, this crest in BENC $^{1}/_{1}$-0086 has a more rounded shape as in *A. zhaoi* (ZCDM V0020) (Fig. 10L). The lateral malleoli in BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 (Fig. 10n and °, respectively) are posteriorly deflected as is the case for all known caenagnathids [e.g. *C. pergracilis* (Fig. 10p), *E. rarus* (Fig. 10q) and UALVP 57349 (Fig. 10r)], and in BENC $^{1}/_{1}$-0086, the lateral malleolus possesses a well-developed post-fibular flange (Fig. 10i), as in *E. rarus* (MPC-D 102/07) (Fig. 10j) and *C. elegans* (TMP, 1994.012.0880) (Fig. 10m). Finally, the medial and lateral malleoli in BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 are equal in anteroposterior thickness and extend distally to nearly the same level (Fig. 10a and b, respectively), as in *A. wyliei* (CM 78000) and *C. pergracilis* (TMP, 1979.020.0001) (Fig. 10c).

The contact surface for the ascending process of the astragalus in BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 appear to be tall and cover the entire transverse width of the tibia (Fig. 5), as is the case for most oviraptorosaurs. Particularly in BENC $^{1}/_{2}$-0002, this surface is bisected by a shallow longitudinal ridge as in *A. wyliei* (CM 78000) and *C. pergracilis* (TMP, 1979.020.0001); whereas in BENC $^{1}/_{1}$-0086, this surface is flat and triangular, similar to the condition observed in *Microvenator celer* (AMNH 3041; Makovicky and Sues, 1998). In addition, the astragalar articulation in BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 seem to wrap completely around onto the posterior surface of the tibia, as in all known caenagnathids (e.g. Currie and Russell, 1988; Lamanna et al., 2014; Funston et al., 2015; Currie et al., 2016; Funston, 2020); this is indicated by the presence of a shallow horizontal ridge on the posterodistal surface of the tibia in both BENC specimens (Fig. 4e, e1, 6f and 6f1) and the distal striated surface in BENC ½-0002 (Fig. 4b and b1).

4.3. Dinosaur diversity in the Cerro del Pueblo Formation

As previously mentioned, the Cerro del Pueblo Formation (CdP) has become one of the most productive fossil-bearing formations in northern Mexico during the last two decades, gaining international visibility mainly due to discoveries of unique dinosaur remains. Notably, the dinosaur discoveries of greatest scientific importance have been made relatively recently, resulting in multiple descriptions of new genera and species. Among these discoveries are the hadrosaurs *Velafrons coahuilensis* (Gates et al., 2007), *Latirhinus uitstlani* (Prieto-Márquez and Serrano-Brañas, 2012; Serrano-Brañas and Prieto-Márquez, 2022) and *Tlatolophus galorum* (Ramírez-Velasco et al., 2021), the ceratopsian *Coahuilaceratops magnacuerna* (Loewen et al., 2010), and the deinocheirid ornithomimosaur *Paraxenisaurus normalensis* (Serrano-Brañas et al., 2020). Other dinosaur groups have also been reported so far from the CdP, such as ankylosaurids (Rivera-Sylva and Espinosa-Chávez, 2006), thescelosaurs (Parkosauridae, Rivera-Sylva et al., 2018), dromaeosaurids (Aguillón-Martinez, 2010), troodontids (Rodríguez de la Rosa and Cevallos-Ferriz, 1998), ornithomimids (Aguillón-Martinez, 2010; Rivera-Sylva et al., 2019) and tyrannosaurids (Torres-Rodríguez et al., 2010; Rivera-Sylva et al., 2019). However, their fragmentary remains have not been diagnostic, precluding their taxonomic identification below family level.

As for abundance, the most abundant dinosaurs in the CdP are represented by saurolophine and lambeosaurine hadrosaurs, followed by ceratopsians and then ankylosaurs. In contrast, the fossil record of theropods is relatively scarce and their remains are among the rarest dinosaur discoveries in the CdP (e.g. Aguillón-Martinez, 2010; Torres--Rodríguez et al., 2010; Rivera-Sylva and Carpenter, 2014). Therefore, any new theropod material greatly adds to our knowledge of the diversity and evolution of theropods within the dinosaur faunas of the Campanian aged CdP. In particular, the discovery of the BENC remains described in this study reveals the presence of a new group of theropods in the CdP, representing not only the first record of caenagnathid oviraptorosaurs for the state of Coahuila, but also for the entirety of the Late Cretaceous of Mexico.

4.4. Caenagnathid diversity during Late Cretaceous and paleobiogeographic distribution

Caenagnathids were relatively diverse during the Campanian and Maastrichtian. At least four genera from Asia and seven genera from North America are reported in the scientific literature (Longrich et al., 2013; Funston et al., 2015; Funston et al., 2018). In particular, North American caenagnathids are known from over a dozen geological formations in Canada and the USA (e.g. Funston et al., 2015; Funston et al., 2016; Funston, 2020). Interestingly, two to three genera of caenagnathids are known to coexist within single formations, such as Citipes elegans, Chirostenotes pergracilis and Caenagnathus collinsi, which coexisted in the Dinosaur Park Formation of Alberta, Canada (Funston, 2020). However, the diversity of caenagnathids is likely underrepresented in Upper Cretaceous formations because these theropods lack teeth and therefore are not common components of microvertebrate sites (Funston et al., 2015).

In general, the majority of reported North American caenagnathids are found in northern latitudes (e.g. Funston, 2020), whereas very few are known from southern USA (Zanno and Sampson, 2005; Sullivan et al., 2011; Longrich et al., 2011, 2013). Thus, the remains of BENC $^{18}/_{1}$-0004, BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 described in this study represent the southernmost record of caenagnathids in Laramidia during the Late Cretaceous. Although caenagnathid diversity in the CdP is difficult to quantify given the fragmentary and disarticulated nature of BENC specimens, differences in morphology and body size, particularly between BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086, may suggest the presence of two different morphotypes of caenagnathids in the CdP. Regarding morphology, current evidence indicates that BENC $^{1}/_{2}$-0002 and BENC $^{1}/_{1}$-0086 are distinct from each other in several features, such as (Aguillón-Martinez, 2010): the presence of a shallow longitudinal ridge that bisects the anterior contact surface for the ascending process of the astragalus in BENC $^{1}/_{2}$-0002, which is absent in BENC $^{1}/_{1}$-0086 (Barsbold, 1976); the medial and lateral malleoli in BENC $^{1}/_{1}$-0086 are relatively equal, while in BENC $^{1}/_{2}$-0002 the lateral malleolus is slightly

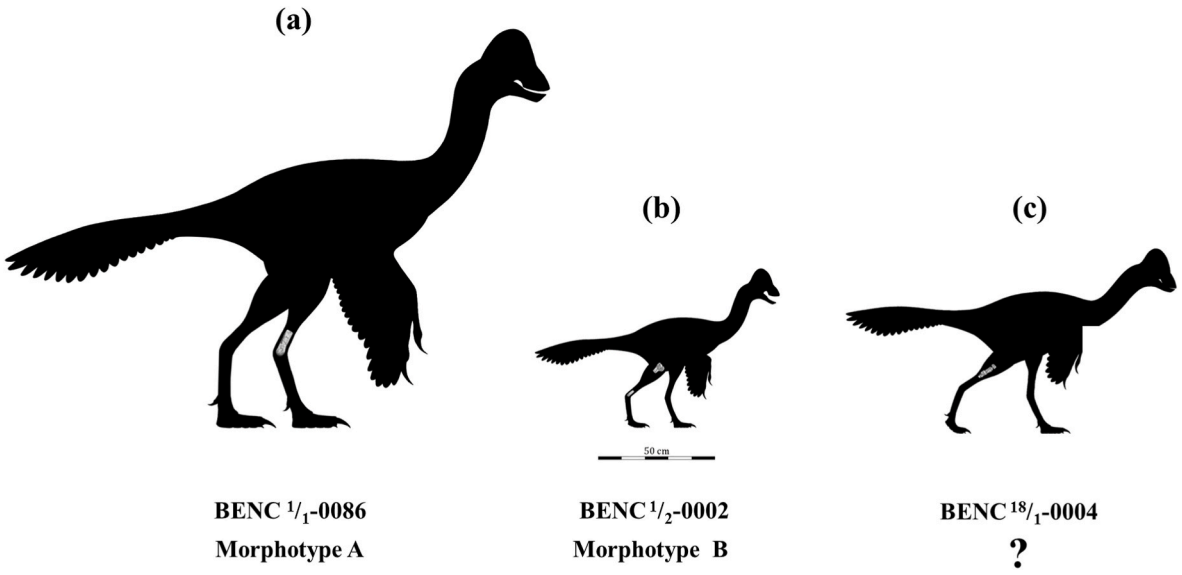

Fig. 11. Schematic figure showing the estimated body size and different morphotypes of the caenagnathid (oviraptorosaur) specimens found in the Cerro del Pueblo Formation (CdP): (a) BENC $^{1}/_{1}$-0086, morphotype A; (b) BENC $^{1}/_{2}$-0002, morphotype B; and (c) BENC $^{18}/_{1}$-0004. Scale in cm.

larger (Brinkman and Rodríguez-de la Rosa, 2006); the lateral crest of the medial malleolus in BENC $^{1}/_{1}$-0086 is wider and has a more rounded shape, whereas in BENC $^{1}/_{2}$-0002 this crest is narrower and sharper (Brochu, 2003); the distal contact surface of the tibia in BENC $^{1}/_{2}$-0002 is completely striated, while in BENC $^{1}/_{1}$-0086 it is smooth and has a slight concavity on the region of the medial malleolus; and (Calvillo--Canadell and Cevallos-Ferriz, 2007) the presence of two small, shallow notches on the distolateral surface of BENC $^{1}/_{1}$-0086, which are absent in BENC $^{1}/_{2}$-0002.

On the other hand, BENC specimens also vary in size. Measurements of the distal end of BENC $^{1}/_{1}$-0086 show that this specimen is substantially larger than BENC $^{1}/_{2}$-0002 (see Table 1), again allowing us to hypothesize the presence of at least two different morphotypes based on body size: a large morphotype represented by BENC $^{1}/_{1}$-0086 (Fig. 11a) and a smaller size morphotype represented by BENC $^{1}/_{2}$-0002 (Fig. 11b). In the case of BENC $^{18}/_{1}$-0004, it appears that it may correspond to an intermediate size morphotype between BENC $^{1}/_{1}$-0086 and BENC $^{1}/_{2}$-0002 (see Table 1; Fig. 11c). However, due to its fragmentary condition and the lack of the distal end in this specimen, at present BENC $^{18}/_{1}$-0004 cannot be directly compared to BENC $^{1}/_{1}$-0086 and BENC $^{1}/_{2}$-0002; therefore, only two morphotypes are currently being recognized for the CdP. Future discoveries, particularly skull material, will hopefully reveal the diversity of these extraordinary theropods in southernmost Laramidia.

5. Conclusions

Three specimens of caenagnathid dinosaurs are reported from two localities within the Upper Cretaceous Cerro del Pueblo Formation of Coahuila, Mexico. These postcranial specimens are the southernmost evidence of the oviraptorosaur family Caenagnathidae in the ancient subcontinent of Laramidia and are among the few specimens reported from southern North America. Based on morphology and size variation among these specimens, we hypothesize the presence of two caenagnathid morphotypes in the CdP. The discovery of caenagnathids herein highlights the high diversity of dinosaurs in the CdP Formation and the need to continue to explore the fauna of this Campanian aged formation.

CRediT authorship contribution statement

Claudia Inés Serrano-Brañas: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Belinda Espinosa-Chávez:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation, Conceptualization. **S. Augusta Maccracken:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Daniela Barrera Guevara:** Writing – review & editing, Visualization, Investigation. **Esperanza Torres-Rodríguez:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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