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Columnar ossicles of Permian crinoids, including two new genera, from the Gruper Formation (Asselian–Sakmarian) of Chiapas, Mexico

Osículos columnares de crinoideos pérmicos, incluidos dos géneros nuevos, de la Formación Gruper (Asseliano–Sakmariano) de Chiapas, México

Miguel A. Torres-Martínez^{1,*}, Rafael Villanueva-Olea², Francisco Sour-Tovar³

¹ Departamento de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica, Avenida Universidad 3000, Coyoacán, 04510, Mexico City, Mexico.

² Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Interior, Avenida Universidad 3000, Coyoacán, 04510, Mexico City, Mexico.

³ Museo de Paleontología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Interior, Avenida Universidad 3000, Coyoacán, 04510, Mexico City, Mexico.

* Corresponding author: (M.A. Torres-Martínez) miguelatm@geologia.unam.mx

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ABSTRACT

Eleven morphotypes of columnar ossicles of Permian crinoids collected from the Gruper Formation (Asselian–Sakmarian) are described. *Floricycloclon heteromorpha* and *Cyclogruper minor* are proposed as new morphogenera and morphospecies. Preserved elements allow relating the depositional paleoenvironment to restricted waters of the inner ramp. The stratigraphical range of *Cyclocaudiculus regularis*, *Heterostelechus keithi*, *Lamprosterigma erathense* and *Cyclocaudex insaturatus* is extended from the Pennsylvanian (Upper Carboniferous) to the lower Cisuralian (lower Permian). The record of all parataxa studied is the first in Chiapas, Mexico, and the first formal work on Permian crinoids from the Chicomuselo region. Because the specimens were found in a Permian unit that had been related to the Grandian Province of North America (Texas and New Mexico in USA; Coahuila, Sonora and Chiapas in Mexico; and Palmarito in Venezuela), it is suggested that crinoids should be part of the same paleoprovince.

Keywords: Parataxa, *Floricycloclon*, *Cyclogruper*, Asselian–Sakmarian, Grandian Province.

RESUMEN

Se describen 11 morfotipos de osículos columnares de crinoideos pérmicos de la Formación Gruper (Asseliano–Sakmariano). *Floricycloclon heteromorpha* y *Cyclogruper minor* se proponen como nuevos morfógenos y morfoespecies. Los elementos conservados permitieron relacionar el paleoambiente de depósito con aguas restringidas de la rampa interna. El alcance estratigráfico de *Cyclocaudiculus regularis*, *Heterostelechus keithi*, *Lamprosterigma erathense* y *Cyclocaudex insaturatus* se extiende del Pensilvaniano (Carbonífero Superior) al Cisuraliano inferior (Pérmico inferior). Todos los parataxones se registran por primera vez para Chiapas, México, además de que éste es el primer trabajo formal sobre crinoideos pérmicos de la región de Chicomuselo. Debido a que los ejemplares fueron encontrados en una unidad pérmica que ha sido relacionada con la Provincia Grandiana de Norteamérica (Texas y Nuevo México en EUA; Coahuila, Sonora y Chiapas en México; y Palmarito en Venezuela), se sugiere que los crinoideos formarían parte de esta misma paleoprovincia.

Palabras clave: Parataxones, *Floricycloclon*, *Cyclogruper*, Asseliano–Sakmariano, Provincia Grandiana.

1. Introduction

Crinoids have been considered one of the most important group of invertebrates of shallow marine environments, especially during the Paleozoic. Although the fossil record of crinoids is common and diverse in Phanerozoic rocks, the abundance of disarticulated ossicles that make up their skeletons is greater than the reports of articulated specimens. In particular, assemblages of articulated crinoids are exceptional, and they are typically confined to particular bedding planes or localized lenses (Hess *et al.*, 2002). The scarcity of complete specimens is the result of the way in which the peduncle, calyx and crown that compose the body are articulated. These parts are composed of a series of plates or ossicles of calcitic-magnesian composition adjoined by means of ligamentary connective tissue, either rigid or flexible. Upon death these connective tissues quickly decay, and the great majority of fossil crinoidal remains are disarticulated by various processes (Hess *et al.*, 2002). This causes the post-mortem disjoining of crinoids to occur quickly, resulting in the common finding of isolated ossicles. This process makes it difficult to accurately identify these elements to low taxonomic levels whereby they are essentially ignored (Thomka *et al.*, 2012; Donovan and Doyle, 2019).

Considering this problem, several researchers (*e.g.*, Moore and Jeffords, 1968; Fearnhead and Donovan, 2015; Donovan and Doyle, 2019) have proposed a classification system based on the morphology of the ossicles, working mainly on Paleozoic records. Such a scheme is based on the temporal and spatial distribution of each morph, suggesting the possibility that these fossils could be biostratigraphic or paleobiogeographic useful. In this context, all works about isolated or disarticulated ossicles are essential tasks in crinoid paleontology (Hess *et al.*, 2002), because the value of such incomplete material has been recognized as an important, but neglected, area of research (Thomka *et al.*, 2012). According to the classification of Moore and Jeffords (1968) and given that

there are no previous studies on Permian crinoids from Chiapas, this paper aims to describe a series of columnar ossicles from the Gruperá Formation, a unit of early Cisuralian age (Asselian–Sakmarian). This information expands the current data on the distribution of isolated elements of Paleozoic crinoids. A second aim is to discuss the possible biostratigraphic and paleogeographic implications of the material studied in the Permian of Chiapas.

2. Geological setting

The locality, where the material studied was sampled, is about 15° 43' 14.2" N – 92° 26' 46" W, in the Chicomuselo municipality, Chiapas, Mexico (Figure 1). The specimens were deposited in calcareous sandstones of fine grain in the Gruperá Formation, considered the oldest Permian lithostratigraphic unit from the Chicomuselo region. This formation is well-exposed in southeastern Chiapas extending from Loma Alta and La Pinta to the Guatemala frontier (Gutiérrez-Gil, 1956).

The Paleozoic succession begins with the Santa Rosa Formation (Upper Mississippian–Middle Pennsylvanian). This unit is mainly composed of shale, phyllite and slate (Gutiérrez-Gil, 1956). Overlaying the Santa Rosa Formation is the Gruperá Formation from the Asselian–Sakmarian (Cisuralian), age assigned by Thompson and Miller (1944) by means of the foraminifera *Schwagerina gruperensis* and *Schwagerina chiapasensis*. Its base is made up of 300 m of silicified shale intercalated with dark gray limestone; above, there are 117 m of gray shale and sandstone strata, followed by 110 m of alternations of dark gray limestone and shale (Gutiérrez-Gil, 1956). The succession continues with La Vainilla Limestone, composed of limestone and argillaceous limestone.

This unit apparently overlays the Gruperá Formation; however, its actual stratigraphic position remains unclear and has been suggested that the La Vainilla Limestone could be the base of the Paso Hondo Formation (Gutiérrez-Gil, 1956; López-Ramos, 1979). The Paleozoic succession

ends with the Paso Hondo Formation (upper Cisuralian–lower Guadalupian) mainly composed of 600 m of light to dark gray limestones of Artinskian–Roadian age (Gutiérrez-Gil, 1956; Hernández-García, 1973; Torres-Martínez *et al.*, 2019) (Figure 2).

3. Systematic paleontology

The material described is deposited at Museo de Paleontología of the Facultad de Ciencias, Universidad Nacional Autónoma de México. Figured and type specimens are designated in the descriptions by the prefix FCMP. The specimens are preserved in calcareous sandstone as authigenic molds. In all cases rubber casts were made.

Class Crinoidea Miller, 1821
Subclass and Order Uncertain Moore and

Jeffords, 1968

[Group Pentameri] Moore and Jeffords, 1968

Family Pentacauliscidae Moore and Jeffords, 1968

Genus *Pentagonopternix* Moore and Jeffords, 1968

Type species. *Pentagonopternix insculptus* Moore and Jeffords, 1968.

Diagnosis. Heteromorphic and transversely pentastellate stem; nodals with 5 elliptical cirrus scars; internodals with 14 columnals, alternating in size; sutures indented forming pits wider than high with no development of radial pores; articular facets having a star-shaped belt of medium-length straight crenulae, their outer ends aligned in inwardly bent curve, the inner ends abutting stellate areola with a slightly concave floor; lumen moderately large and circular.

Pentagonopternix? sp.
Figure 3A and 3B

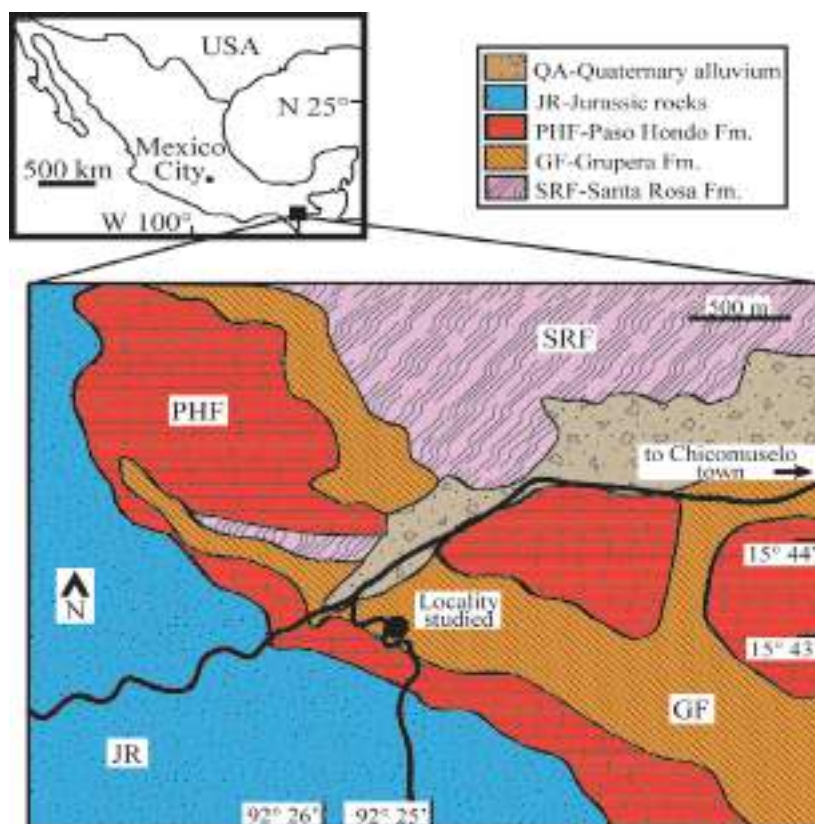


Figure 1 Geological position of the locality, where crinoids occur, in the Grupera Formation. Map modified from Jiménez-Hernández *et al.* (2005).

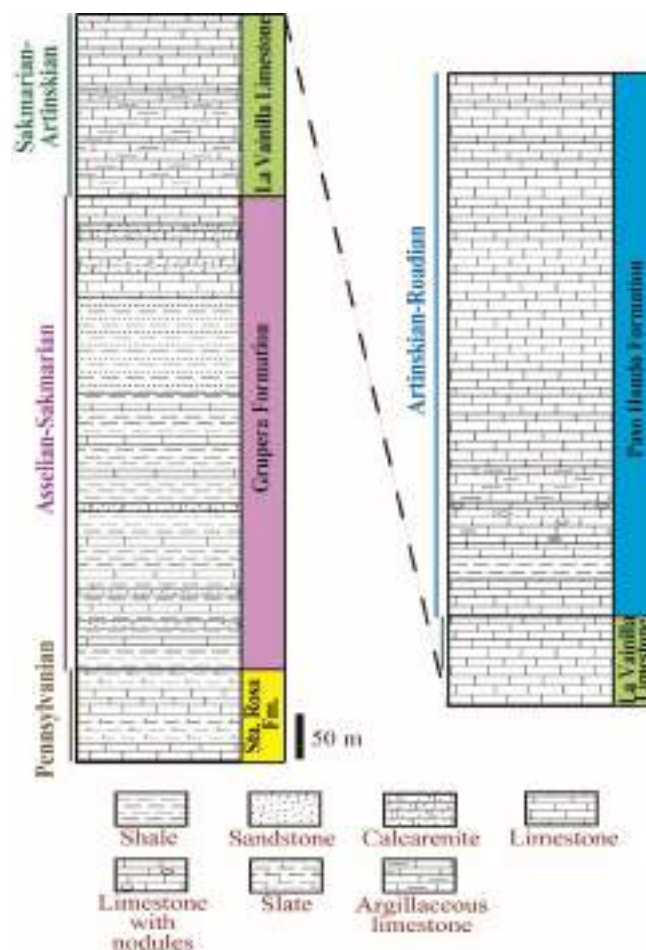


Figure 2 Paleozoic stratigraphy of the Chicomuselo region.

Description. Columnals with a pentastellate shape; crenularium poorly preserved; small, sub-pentagonal lumen.

Material. FCMP 1349, 1350.

Occurrence. Fine-grained calcareous sandstones, Gruper Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The specimens are questionably assigned to the morphogenus *Pentagonopternix* mainly due to the stellate shape of the ossicle. The poor conservation of several features of the articular facet, as well as the lack of a noditaxis, does not allow making a reliable assignment.

This morphogenus has been found in the Chaffin Limestone from Gzhelian (Upper Pennsylvanian) age of Texas (Moore and Jeffords, 1968), in the Antiinskiy Horizon from the middle Permian (Roadian–Wordian) of the Transbaikal

region of Russia (Kotlyar *et al.*, 2006), and in the Imtchan Formation from the upper Permian (Lopingian) of Verkhoyansk, Russia (Biakov *et al.*, 2016). In Mexico, it had only been recorded in the Middle Pennsylvanian of Sierra Agua Verde, Sonora (Buitrón-Sánchez *et al.*, 2015).

[Group Cyclici] Moore and Jeffords, 1968
Family Cyclomischidae Moore and Jeffords, 1968
Genus *Cyclogruper* n. gen.

Type species. *Cyclogruper minor* n. sp.

Etymology. Refers to the circular shape of the articular facet, as well as to the lithostratigraphic unit where the specimens were collected.

Diagnosis. Homeomorphic stem of small diameter, gently rounded in longitudinal profile; granulose walls; articular facet circular; crenularium

large, reaching the outline of perilumen; crenulae coarse, with crenellae and culmina of the same size; without areola; perilumen gently marked, delineating the lumen outline; lumen small, circular.

Cyclogruperia minor n. sp.

Figure 3C and 3D

Etymology. Refers to the tiny size of the specimens.

Diagnosis. As the genus.

Description. With traits of the genus; besides this displays 13 crenulae, lumen 0.5 mm diameter and crenularium 0.7 mm width.

Material. FCMP 1351.

Occurrence. Fine-grained calcareous sandstones, Gruperia Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The Chiapas material was assigned to the family Leptocarphiidae due to the slender stem, broad crenularium and presence of a perilumen surrounding the circular lumen. *Cyclocaudex* differs from *Cyclogruperia* by the lack of areola; *Nothrosterigma* differs by its coarser, convex and ring-shaped perilumen surrounding the lumen, and *Heterostelechus* displays an elevated perilumen from the surface of the articular facet.

Genus *Cyclocaudex* Moore and Jeffords, 1968

Type species. *Cyclocaudex typicus* Moore and Jeffords, 1968.

Diagnosis. Stem heteromorphic; straight-sided to gently convex longitudinal profile; nodals bearing cirrus scars, not wider than internodals and slightly taller; crenularium wide with long and straight crenulae; areola small, lacking or becoming a perilumen; lumen small to medium in size, and circular, subpentagonal or quinquelobate in outline.

Cyclocaudex typicus Moore and Jeffords, 1968

Figure 3E to 3N

Description. Column with straight to slightly rounded longitudinal profile, with granulose walls; heteromorphic stem; sutures gently crenulate; articular facet subcircular; crenularium broad, with slender crenulae, many bifurcated; areola is not conspicuous, reduced in size, granulose and flat, which surrounds a large, circular lumen; inside of the lumen, a circular and minute jugula is observed.

Material. FCMP 1352-1357.

Occurrence. Fine-grained calcareous sandstones, Gruperia Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The specimens of the Gruperia Formation resemble *Lomalegnum hormidium*. However, *C. typicus* has neither the sutures strongly crenulate nor the peripheral ends of culmina typical of *Lomalegnum*.

The material can also be distinguished from *Cyclocaudex jucundus* by the lack of a broad areola with a depressed surface. *Cyclocaudex typicus* has been reported in the Upper Pennsylvanian of Texas in the United States (Moore and Jeffords, 1968), as well as in the Carboniferous of Oaxaca (Villanueva-Olea *et al.*, 2011), Upper Pennsylvanian of Puebla (Esquivel-Macías, 1996) and middle Permian of Oaxaca in Mexico (Vachard *et al.*, 1997). This is the first record of the taxon in the lower Permian of North America.

Cyclocaudex plenus Moore and Jeffords, 1968

Figure 3O to 3S

Description. Ossicles of circular shape in outline; conspicuous cirrus, which endow a greater size to the nodals; sutures slightly crenulate; ossicles of at least three different heights, which suggests a minimum noditaxis of four columnals; crenularium very wide with narrow crenulae; culmina wider than crenellae, bifurcating near margins; areola narrow and flat; lumen of reduced size, irregular to circular in outline.

Material. FCMP 1358-1360.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The material of Chiapas is distinguished from *Mooreanteris waylandensis* from the Graham Formation of Texas (Moore and Jeffords, 1968) by its symmetric articular facet and suture strongly crenulate. *Cyclocaudex plenus* is dissimilar to *Cyclocaudex typicus* from the Thrifty Formation of the Upper Pennsylvanian of Texas (Moore and Jeffords, 1968) by its poorly defined boundary between the reduced areola and the crenularium, and the crenulae bifurcated near the edge of the areola. *Cyclocaudex plenus* has been reported in the Upper Pennsylvanian of Texas (Moore and Jeffords, 1968) and in the lower Permian of Calnali (Moreno and Patiño 1981) and Pemuxco, Hidalgo (Arellano *et al.*, 1998; Buitrón-Sánchez *et al.*, 2017).

Cyclocaudex jucundus Moore and Jeffords, 1968
Figure 3T and 3U

Description. Latex of columnals slightly rounded and convex; columnals with slight differences in height; sutures crenulate; articular facet circular; crenularium of medium size, with some bifurcations at the outer half; crenulae narrow with culmina wider than crenellae; lumen large and circular; areola broad, depressed, which deepens towards the interior of the lumen.

Material. FCMP 1361.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. *Cyclocaudex jucundus* occurs in the Upper Pennsylvanian of Texas (Moore and Jeffords, 1968), in addition to the Pennsylvanian of Calnali, Hidalgo (Buitrón *et al.*, 1987), the Upper Pennsylvanian (Velasco de León and Buitrón, 1992) and Permian (Esquivel *et al.*, 2000) of San Salvador Patlanoaya, Puebla, the lower Permian of Pemuxco, Hidalgo (Arellano *et al.*, 1998), Middle–Upper Pennsylvanian of Sonora (Buitrón-Sánchez *et al.*, 2012; Villanueva-Olea *et al.*, 2016) and in the middle Permian of Sonora (Buitrón *et al.*, 2007a).

Cyclocaudex insaturatus Moore and Jeffords, 1968
Figure 3V

Description. Articular facet circular; crenularium very wide, reaching the rim of the lumen; crenulae very narrow, with culmina wider than crenellae, some bifurcating in the medium part; lumen of medium size and circular.

Material. FCMP 1362.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The specimen of Chiapas differs from *Cyclocaudex plenus* by its larger lumen and crenulae reaching the rim of the lumen. *Cyclocaudex insaturatus* is dissimilar to *Cyclocaudex aptus* from the Lower Mississippian of Kentucky (Moore and Jeffords, 1968) by its coarser and less abundant crenulae and a larger lumen. The species differs from *Cyclocaudex congregalis* of the Lower Mississippian of Kentucky (Moore and Jeffords, 1968) by its flat crenularium, without inner rounded edges. *Cyclocaudex insaturatus* occurs in the Middle Pennsylvanian of Kansas (Moore and Jeffords, 1968), as well as in the Pennsylvanian of Calnali, Hidalgo (Buitrón-Sánchez *et al.*, 1987) and the Middle Mississippian and Lower–Middle Pennsylvanian of Santiago Ixtaltepec, Oaxaca (Villanueva-Olea *et al.*, 2011). This is the first record of *C. insaturatus* from the Permian.

Family Floricyclidae Moore and Jeffords, 1968
Genus *Floricyclacion* n. gen.

Type species. *Floricyclacion heteromorpha* n. sp.

Etymology. Refers to the floriform lumen.

Diagnosis. Floricyclidae characterized by a straight and heteromorphic stem columnals with median length crenulae, flat areola and medium sized stellate lumen.

Floricyclacion heteromorpha n. sp.
Figure 4A and 4B

Etymology. Refers to the heteromorph stem.

Diagnosis. As the genus.

Description. Column straight in lateral view, heteromorphic, with columnals of different length; articular facet circular; crenularium of medium size, with straight and coarse crenulae; culmina slightly coarser than crenellae; areola flat and granulose; lumen medium sized and stellate.

Material. FCMP 1363.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The morphogenus *Cyclocion* is distinguished from *Floricyclon* by its very short crenulae and larger lumen; sutures strongly crenulate and nodals strongly keeled. On the other hand, the genus *Lamprosterigma* displays a depression in the areola, in addition to very slender and numerous crenulae. Likewise, the *Floricyclus* differs from the new morphogenus by its very marked and granulose perilumen, with division of some crenulae. *Floricyclon* is assigned to the family Floricyclidae by its floriform lumen and the presence of a straight longitudinal profile of the stem.

Genus *Lamprosterigma* Moore and Jeffords, 1968

Type species. *Lamprosterigma mirificum* Moore and Jeffords, 1968.

Diagnosis. Homeomorphic stem; low-height columnals; longitudinal profile straight or a little convex; sutures noncrenulate, not indented; articular facet with moderately broad crenularium; crenulae straight, set off from the areola by a sharp edge; areola bowl-shaped with smooth surface, extending to the edge of the pentalobate broad lumen, or separated from it by a narrow perilumen.

Lamprosterigma erathense Moore and Jeffords, 1968
Figure 4C

Description. Articular facet circular; crenularium wide with slender crenulae, some bifurcating close to the periphery; culmina wider than crenellae; areola granulose, set off from the crenularium

by a depression and grades into a discrete perilumen; lumen wide, floriform, with poorly developed petals.

Material. FCMP 1364.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The specimen was compared with *Lamprosterigma mirificum* (Middle Pennsylvanian) of Kansas (Moore and Jeffords, 1968) however *L. mirificum* does not display a developed perilumen. *Plummeranteris* from the Pennsylvanian of Texas (Moore and Jeffords, 1968) is dissimilar to the morphogenus *Lamprosterigma* by its coarse and straight crenulae, and strongly floriform perilumen, with well-developed petals. *Lamprosterigma erathense* is reported from the Middle Pennsylvanian of Texas (Moore and Jeffords, 1968) and the Middle Pennsylvanian (Atokan) of Sonora (Buitrón-Sánchez *et al.*, 2007b). This is the first occurrence of *L. erathense* in Permian rocks.

Family Leptocarphiidae Moore and Jeffords, 1968
Genus *Preptopremnum* Moore and Jeffords, 1968

Type species. *Preptopremnum rugosum* Moore and Jeffords, 1968

Diagnosis. Medium-sized column; articular facets slightly narrower than the largest column width; rounded longitudinal profile; crenularium narrow; medium to coarse crenulae set off from a broad and flat areola, slightly concave or convex, with marks of vermiculate or granulose irregularities; large and circular lumen, bordered by a narrow perilumen or an accentuated edge of the areola; lumen with claustra at mid-height of columnal plates, jugulum and jugular ramparts in the center of claustra.

Preptopremnum cf. *laeve* Moore and Jeffords, 1968
Figure 4D to 4H

Description. Column with a slightly rounded longitudinal profile; articular facet circular with a very slender crenularium and coarse crenulae; culmina wider than crenellae; areola wide and granulose

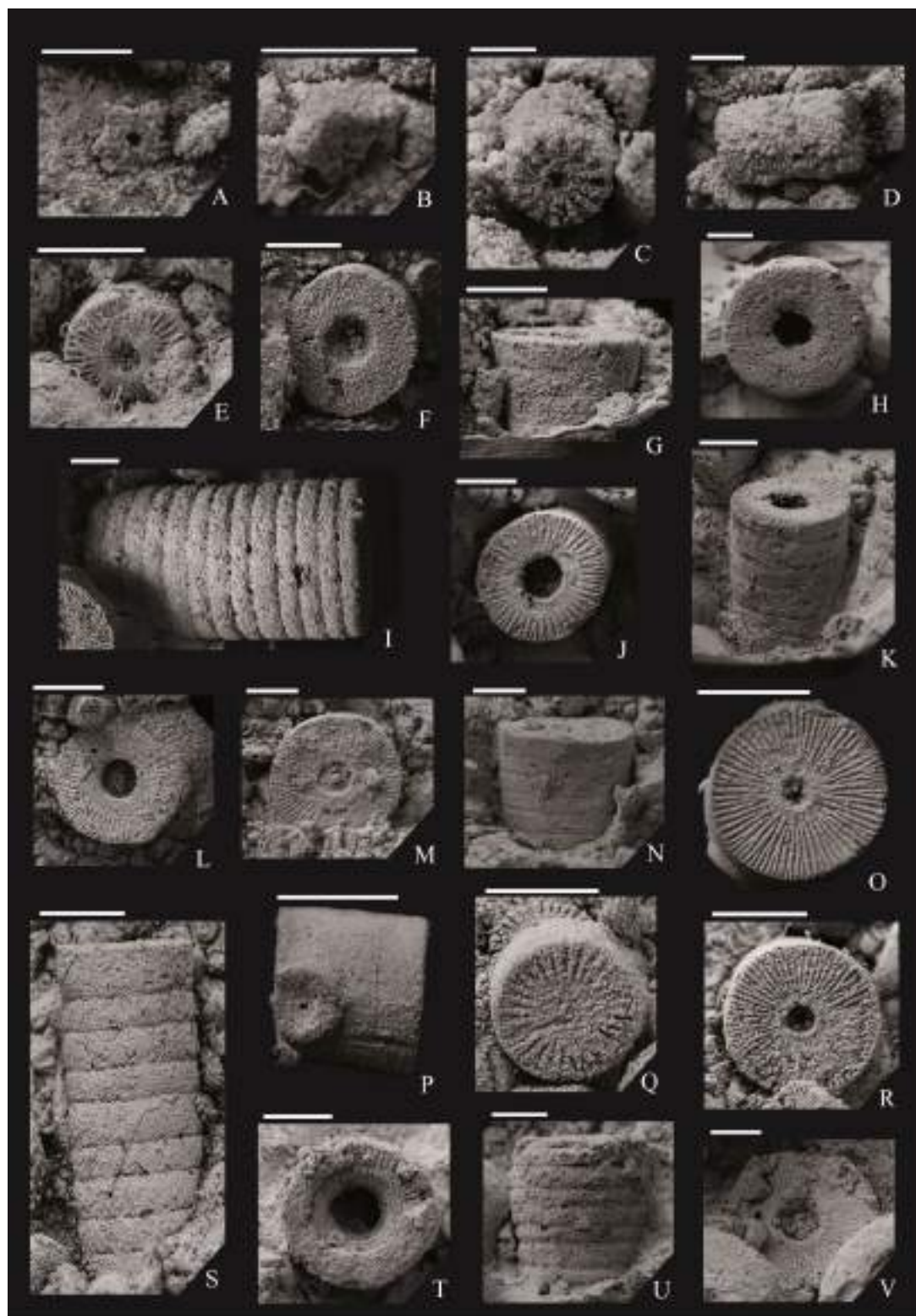


Figure 3 (A, B) *Pentagonopternix?* sp., samples A) FCMP 1350; B) FCMP 1349. (C, D) *Cyclogruperia minor* n. gen and n. sp., sample FCMP 1351. (E-N) *Cyclocaudex typicus*, samples E) FCMP 1354; F, G) FCMP 1357; H, I) FCMP 1352; J, K) FCMP 1355; L) FCMP 1356; M, N) FCMP 1353. (O-S) *Cyclocaudex plenus*, samples O, P) FCMP 1359; Q) FCMP 1360; R, S) FCMP 1358. (T, U) *Cyclocaudex jucundus*, sample FCMP 1361. (V) *Cyclocaudex insaturatus*, sample FCMP 1362. All specimens illustrated are rubber casts. Scale bars = 5 mm, except A, B, L = 2 mm; C, D = 1 mm.

in the area surrounding lumen, slightly elevated, resembling a broad perilumen; lumen circular.

Material. FCMP 1365-1368.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. *Preptopremnum rugosum* is distinguished from *P. laeve* by the longer crenulae, a granulose and rounded medium-sized areola, and a circular large lumen. Nevertheless, the Chiapas specimens are slightly different to those described by Moore and Jeffords (1968) because of the occurrence of great quantity of granules on the latus of the columnals. *Preptopremnum laeve* occurs in the Middle Pennsylvanian of Texas in the United States (Moore and Jeffords, 1968), as well as in the Pennsylvanian of Sonora (Buitrón-Sánchez *et al.*, 2005, 2007b, 2012; 2015) and in the Middle Pennsylvanian–lower Permian of Sierra Las Pintas, Baja California, Mexico (Navas-Parejo *et al.*, 2018).

Genus *Heterostelechus* Moore and Jeffords, 1968

Diagnosis. Stem heteromorphic; columnals rounded in longitudinal profile; indented and crenulate sutures; one or more cirrus scars in nodals, which are taller than internodals, but not much wider; coarse straight crenulae of medium length; areola concave, elevated tract around circular lumen, also classifiable as a perilumen.

Heterostelechus jeffordsi Miller, 1968 (in Moore and Jeffords, 1968)
Figure 4I to 4N

Description. Column with a straight profile; noditaxis of three different sizes in the height of columnals (nodals and internodals 1IN and 2IN); sutures crenulate; articular facet circular; medium-sized crenularium with coarse crenulae; culmina and crenella of the same size; areola elevated and granulose; medium-sized subpentagonal lumen.

Material. FCMP 1369-1373.

Occurrence. Fine-grained calcareous sandstones,

Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The material of Chiapas was assigned to the morphospecies by the articular facet features. *Heterostelechus jeffordsi* is distinguished from the rest of the morphospecies mainly by its column profile slightly rounded. This taxon has been recorded in the Late Pennsylvanian of Texas (Moore and Jeffords, 1968) and Guerrero, Mexico (Flores de Dios and Buitrón-Sánchez, 1982; Esquivel-Macías *et al.*, 2004). This is the first report of the morphospecies in the early Permian.

Heterostelechus cf. *keithi* Miller, 1968 (in Moore and Jeffords, 1968)
Figure 4O and 4P

Description. Plate with a smooth and straight latus; articular facet circular; crenularium of medium size; coarse and straight crenulae, with crenellae and culmina of the same width; areola slightly concave, forming a pentagonal outline in the inner edge of the crenularium; lumen small and circular.

Material. FCMP 1374, 1375.

Occurrence. Fine-grained calcareous sandstones, Grupera Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. The material resembles *Heterostelechus keithi* but its straight longitudinal profile and smaller lumen does not allow making a reliable assignment. *Heterostelechus keithi* has been recorded in the Pennsylvanian of Texas (Moore and Jeffords, 1968), in addition to Hidalgo (Buitrón-Sánchez *et al.*, 1987), Puebla (Velasco de León and Buitrón-Sánchez, 1992) and Sonora in Mexico (Buitrón-Sánchez *et al.*, 2007b, 2008, 2015). This is the first report in the Permian of North America.

Genus *Cyclocaudiculus* Moore and Jeffords, 1968

Type species. *Cyclocaudiculus regularis* Moore and Jeffords, 1968.

Diagnosis. Stem with a straight longitudinal profile; nodals bearing one single scar; crenularium

with coarse and straight crenulae; lumen circular, small or medium.

Cyclocaudiculus regularis Moore and Jeffords, 1968
Figure 4Q to 4V

Description. Stem heteromorphic, straight in longitudinal profile; articular facet circular which occupies the width of the columnal; crenularium with coarse crenulae; culmina wider than crenulae; areola flat with perilumen; crenularium small and subcircular.

Material. FCMP 1376-1379.

Occurrence. Fine-grained calcareous sandstones, Gruper Formation (Asselian–Sakmarian), Chiapas, Mexico.

Remarks. *Cyclocaudiculus regularis* is reported in the Gzhelian (Upper Pennsylvanian) of Texas in the United States (Moore and Jeffords, 1968) and in the Pennsylvanian of Sierra Las Mestañas, Sonora, Mexico (Villanueva-Olea *et al.*, 2016). This is the first record of the taxon in the lower Permian.

4. Discussion

4.1. DEPOSITIONAL PALEOENVIRONMENT

The study of Paleozoic environments of the Chicomuselo region has been, in general, very scarce, especially for the Gruper Formation. Previously, only the study of one carbonate succession from the Paso Hondo Formation (Artinskian–Roadian) was included in which the features of a carbonated homoclinal ramp were described (Torres-Martínez *et al.*, 2017). Nonetheless, the Gruper Formation underlays the Paso Hondo Formation, having clear lithological differences. The only previous interpretation of an environment of the Gruper Formation is that done by Hernández-García (1973), who described the paleoenvironment of the Gruper unit as shallow waters of low energy, well-illuminated and oxygenated, protected from the waves. This interpretation is extremely shallow because the author focused on a group of sedimentary

features without considering the lithological changes through the unit.

In this context, the parataxa studied are embedded in calcareous sandstone of fine grain, which is characterized by clay-rich matrix and calcareous cement. The skeletal grains are mainly represented by abundant ossicles and pleuricolumnals articulated of crinoids whereas phylloid algae and benthic foraminifera of the genera *Geinitzina* and *Nodosinelloides* are rare. Scattered microbial components are observed. Euhedral dolomite crystals and pyrite as well as iron oxides are dispersed in the fine-grained matrix.

The presence of benthic foraminifera and phylloid algae suggests nearness with open waters; on the contrary, the occurrence of microbial growth, clay and sands indicates a proximity with the intertidal zone. The abundance of crinoids suggests high productivity in the euphotic zone, relating the environment to restricted waters of the inner ramp. Although crinoid ossicles studied are mostly disarticulated, the poor sorting of crinoid fragments associated with well-preserved crinoid pleuricolumnals indicates burial in quiet-water settings without longer transport (Flügel, 2010). Nonetheless, there is a chance that the association was produced by possible scavenging dispersion of crinoid remains.

4.2. PALEOBIOGEOGRAPHY AND IMPLICATIONS IN AGE

In previous studies (Müllerried *et al.*, 1941; Thompson and Miller, 1944; Torres-Martínez *et al.*, 2016, 2019), it has been pointed out that the early–middle Permian faunas of southern Chiapas have a great resemblance with those described in different localities from Texas and New Mexico. The similarity of faunas has established that, during this period, there was a marine connection through an epicontinental sea which linked the south-central United States and the south of Mexico (Torres-Martínez *et al.*, 2016). This connection occurred in the Grandian Province, characterized by numerous taxa of fusulinids, cephalopods and brachiopods of tropical and subtropical environments (Yancey, 1975; Shen and Shi, 2004; Shen *et al.*, 2013).

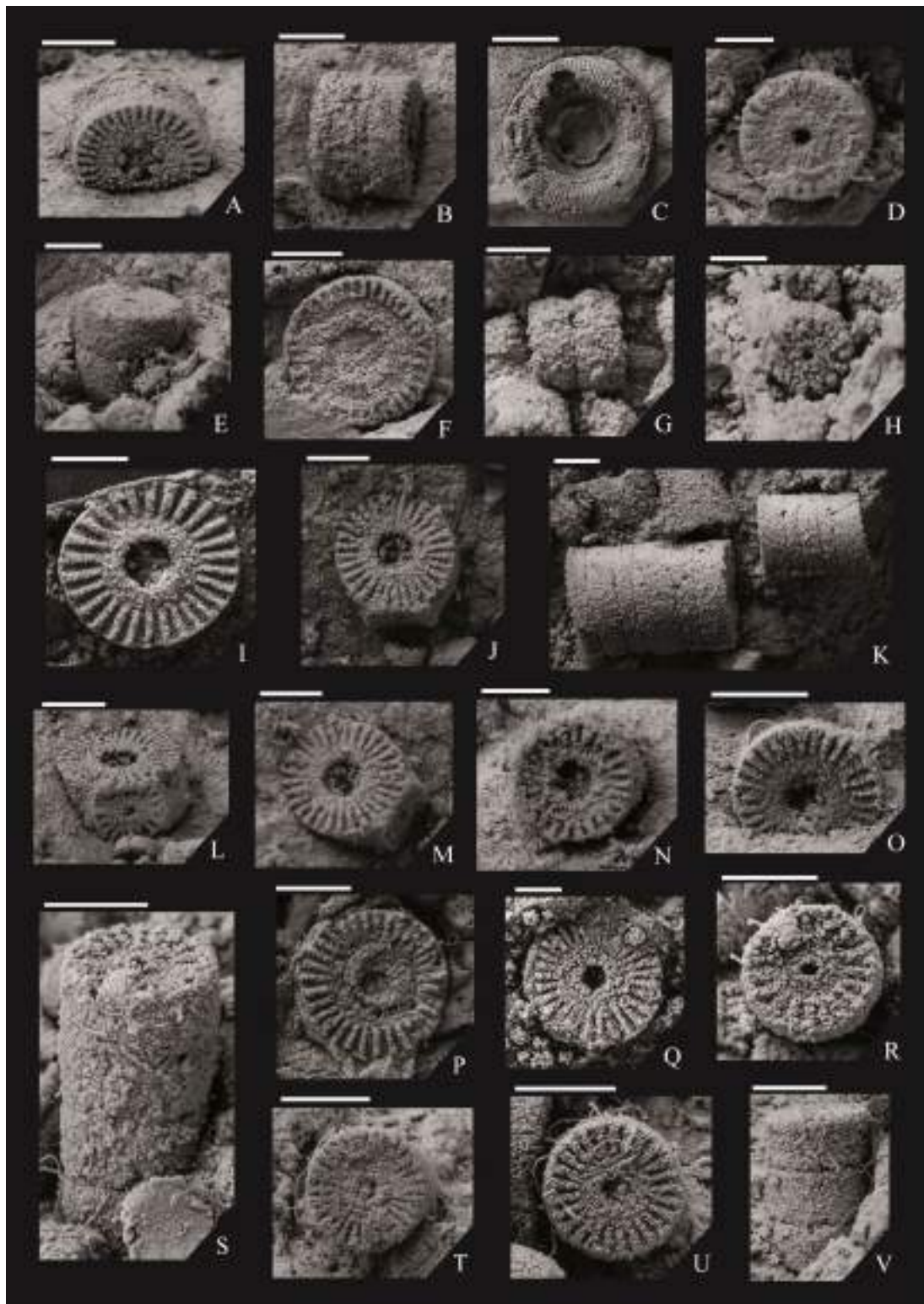


Figure 4 (A, B) *Floricycloclion heteromorpha* n. gen and n. sp., sample FCMP 1363. (C) *Lamprosterigma erathense*, sample FCMP 1364. (D-H) *Preptopremnum* cf. *laeve*, samples D, E FCMP 1365; F FCMP 1368; G, H FCMP 1366. (I-N) *Heterostelechus jeffordsi*, samples I) FCMP 1369; J) FCMP 1370; K) FCMP 1373; L, M) FCMP 1370; N) FCMP 1372. (O, P) *Heterostelechus* cf. *keithi*, samples O) FCMP 1371; P) FCMP 1375. (Q-V) *Cyclocaudiculus regularis*, samples Q) FCMP 1377; R, S) FCMP 1376; T) FCMP 1378; U, V) FCMP 1379. Scale bars = 2 mm, except C = 5 mm; G, H = 1 mm.

Regarding columnar ossicles herein described and highlighting that all known taxa had been reported in Moscovian or Gzhelian (Middle–Late Pennsylvanian) localities of the United States, Mexico is the only country with previous Permian records of some taxa. Nonetheless, Russian work groups have also published descriptions of Permian material (Kotlyar *et al.*, 2006; Biakov *et al.*, 2016).

Except for the genus *Pentagonopternix*, they have not recorded any taxa from the late Paleozoic of Mexico or the south-central United States. With the current data, it can be stated that the columnar ossicles of Mexican localities, from Mississippian and Pennsylvanian ages, have high similarities with those recorded in localities of the Mid-Continent region (Villanueva-Olea *et al.*, 2011; Villanueva-Olea and Sour-Tovar, 2015). Nonetheless, the lack of reports in the Permian of North America does not allow comparisons or correlations. Concerning the columnar ossicles described from the Gruper Formation, it can be noted that there are no coeval associations allowing comparative analysis outside Mexico, except Texas. However, considering the composition of the associated fauna, such as brachiopods or fusulinids, it can be hypothesized that common forms of crinoids might be found in Permian localities related to the Grandian Paleoprovince, located in Coahuila, Sonora and Chiapas from Mexico, New Mexico and Texas from the United States and Palmarito from Venezuela.

As mentioned above, the columnar ossicles of crinoids that are described in this work have already been referred to diverse localities of the Carboniferous or Permian of Mexico and all of them have records in localities of the Pennsylvanian of Texas. In Table 1, the occurrences and their bibliographic reference have been detailed. In this manner, it is observed that, some taxa have a very broad temporal distribution.

For example, *Cyclocaudex typicus* has a stratigraphic range from the Lower Mississippian to the Permian of Oaxaca. *Cyclocaudex insaturatus* was known from the Lower Mississippian of Oaxaca to the Pennsylvanian of Oaxaca and

Hidalgo, extending in the present work its temporal distribution to the lower Permian. Something similar is established for *Lamprosterigma erathense*, *Heterostelechus keithi* and *Cyclocaudex regularis* whose previous records were limited to Pennsylvanian localities. *Cyclocaudex plenus*, *Preptopremnum leave* and *Heterostelechus jeffordsi* have been previously reported in other Mexican localities of Permian age, including Baja California, Hidalgo and Guerrero. Hence, the record of all parataxa represents the first for the Permian (early Cisuralian) of Chiapas, Mexico, since the only previous reports of crinoids in the region were *Cylindrocauliscus fiski*? and *Lamprosterigma mirificum*, both from the Santa Rosa Formation (Carboniferous) of Chicomuselo (Buitrón-Sánchez, 1977). Because these parataxa have long temporal ranges, their biostratigraphic utility is still under discussion, yet, they are very useful to establish environmental features.

5. Conclusions

The report of eleven morphospecies of crinoid ossicles has allowed recognizing part of the marine invertebrates that inhabited the Chicomuselo region during the early Permian (Asselian–Sakmarian). The record of these taxa is the first made in Chiapas, Mexico, highlighting the occurrence of two new morphogenera: *Floricyclacion* and *Cyclogruper*. These crinoids were deposited in a restricted marine environment of the inner ramp, characterized by well-oxygenated conditions, high productivity and good illumination. Previously, the taxa *Cyclocaudex regularis*, *Heterostelechus keithi*, *Lamprosterigma erathense* and *Cyclocaudex insaturatus* had only been recorded in different localities from the Pennsylvanian of North America but their occurrence in rocks from the Gruper Formation allows extending their stratigraphical range at least until the lower Cisuralian. The crinoid ossicles were deposited in a geographic region associated with the biotic Grandian Province of North America which groups different Permian localities of Mexico, Venezuela and the United States.

Table 1. Occurrences and stratigraphic range of crinoid ossicles herein studied.

Morphotype	Mississippian	Pennsylvanian	Permian
<i>Pentagonopternix</i> Moore and Jeffords, 1968		- Sierra Agua Verde, Moscovian, Sonora, Mexico (Buitrón-Sánchez <i>et al.</i> , 2015). - Chaffin Limestone, Gzhelian, Texas, USA (Moore and Jeffords, 1968).	- Antiinskiy Horizon (Roadian-Wordian), Transbaikal, Russia (Kotlyar <i>et al.</i> , 2006). - Imtachan Fm. (Lopingian), Verkhoyansk, Rusia (Biakov <i>et al.</i> , 2016).
<i>Cyclocaudex typicus</i> Moore and Jeffords, 1968	- Santiago Fm., Visean, Oaxaca, Mexico (Villanueva-Olea <i>et al.</i> , 2011).	- Ixtaltepec Fm., Bashkirian-Moscovian, Oaxaca, Mexico (Villanueva-Olea <i>et al.</i> , 2011). - Patlanoaya Fm., Gzhelian, Puebla, Mexico (Villaseñor-Martínez <i>et al.</i> , 1987; Esquivel-Macías, 1996). - Thrifty Fm., Gzhelian, Texas, USA (Moore and Jeffords, 1968).	- La Cruz Fm., Wordian, Ihuatpec, Oaxaca (Vachard <i>et al.</i> , 1997).
<i>Cyclocaudex plenus</i> Moore and Jeffords, 1968		- Calnali, Hidalgo (Moreno-Cano and Patiño-Ruiz, 1981). - Graham and Thrifty fm., Gzhelian, Texas, USA (Moore and Jeffords, 1968).	- Tuzancoa Fm., Sakmarian-Artinskian, Pemuxco, Hidalgo (Arellano-Gil <i>et al.</i> , 1998; Buitrón-Sánchez <i>et al.</i> , 2017).
<i>Cyclocaudex jucundus</i> Moore and Jeffords, 1968		- Del Monte Fm., Pennsylvanian, Calnali, Hidalgo, Mexico (Buitrón-Sánchez <i>et al.</i> , 1987). - Sierra Las Mesteñas, Pennsylvanian, Sonora, Mexico (Villanueva-Olea <i>et al.</i> , 2016). - Cerros El Tule, Moscovian-Kasimovian, Sonora, Mexico (Buitrón-Sánchez <i>et al.</i> , 2012). - Patlanoaya Fm, Gzhelian, Puebla, Mexico (Velasco de León and Buitrón-Sánchez, 1992). - Thrifty Fm, Gzhelian, Texas, USA (Moore and Jeffords, 1968).	- Patlanoaya Fm, lower Permian, Puebla, Mexico (Esquivel-Macías <i>et al.</i> , 2000). - Guacamaya Fm., Sakmarian-Artinskian, Pemuxco, Hidalgo, Mexico (Arellano-Gil <i>et al.</i> , 1998). - Tuzancoa Fm., Sakmarian-Artinskian, Hidalgo, Mexico (Buitrón-Sánchez <i>et al.</i> , 1987). - Cerros Los Monos, Wordian, Sonora, Mexico (Buitrón-Sánchez <i>et al.</i> , 2007a).
<i>Cyclocaudex insaturatus</i> Moore and Jeffords, 1968	- Santiago Fm., Visean, Oaxaca, Mexico (Villanueva-Olea <i>et al.</i> , 2011).	- Del Monte Fm., Pennsylvanian, Calnali, Hidalgo, Mexico (Buitrón-Sánchez <i>et al.</i> , 1987). - Ixtaltepec Fm., Bashkirian-Moscovian, Oaxaca, Mexico (Buitrón-Sánchez <i>et al.</i> , 2000). - Canabiss Fm., Moscovian, Kansas, USA (Moore and Jeffords, 1968).	
<i>Lamprosterigma erathense</i> Moore and Jeffords, 1968		- Sierra Agua Verde, Atokan, Sonora, Mexico (Buitrón-Sánchez <i>et al.</i> , 2007b). - Mingus Shale, Moscovian, Texas, USA (Moore and Jeffords, 1968).	

Table 1. (Continuation) Occurrences and stratigraphic range of crinoid ossicles herein studied.

Morphotype	Mississippian	Pennsylvanian	Permian
<i>Preptopremnum laeve</i> Moore and Jeffords, 1968		<ul style="list-style-type: none"> - Sierra Agua Verde, Pennsylvanian, Sonora, Mexico (Buitrón-Sánchez et al., 2005, 2007b, 2015). - Cerros El Tule, Bashkirian, Sonora, Mexico (Buitrón-Sánchez et al., 2012). - Sierra Las Pintas, upper Pennsylvanian – lower Permian Baja California (Navas-Parejo et al., 2018). - Mingus Shale, Moscovian, Texas, USA (Moore and Jeffords, 1968). 	<ul style="list-style-type: none"> - Sierra Las Pintas, upper Pennsylvanian – lower Permian Baja California (Navas-Parejo et al., 2018).
<i>Heterostelechus jeffordsi</i> Miller, 1968 (in Moore and Jeffords, 1968).		<ul style="list-style-type: none"> - Graham Fm., Gzhelian, Texas, USA (Moore and Jeffords, 1968). 	<ul style="list-style-type: none"> - Olinalá/Los Arcos, Wordian-Capitanian, Guerrero, Mexico (Flores de Dios and Buitrón-Sánchez, 1982; Esquivel-Macías et al., 2004).
<i>Heterostelechus keithi</i> Miller, 1968 (in Moore and Jeffords, 1968).		<ul style="list-style-type: none"> - Del Monte Fm., Pennsylvanian, Calnali, Hidalgo, Mexico (Buitrón-Sánchez et al., 1987). - Patlanoaya Fm, Gzhelian, Puebla, Mexico (Velasco de León and Buitrón-Sánchez, 1992). - La Joya Fm., Pennsylvanian, Sonora, Mexico (Buitrón-Sánchez et al., 2007b, 2015). - Cerros El Tule, Moscovian-Kasimovian, Sonora, Mexico (Buitrón-Sánchez et al., 2008). - Graham Fm., Gzhelian, Texas, USA (Moore and Jeffords, 1968). 	
<i>Cyclocaudiculus regularis</i> Moore and Jeffords, 1968		<ul style="list-style-type: none"> - Sierra Las Mesteñas, Pennsylvanian, Sonora, Mexico (Villanueva-Olea et al., 2016). - Thrifty Fm., Gzhelian, Texas, USA (Moore and Jeffords, 1968). 	

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