This article was downloaded by: [UNAM Ciudad Universitaria]
On: 16 May 2014, At: 08:02
Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tjsp20

A new genus and four new species of cladid crinoids from the Carboniferous of Oaxaca State, Mexico

Rafael Villanueva-Olea[a] & Francisco Sour-Tovar[b]

[a] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510 México D. F., Mexico

[b] Museo de Paleontología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510 México D. F., Mexico

Published online: 16 May 2014.

To cite this article: Rafael Villanueva-Olea & Francisco Sour-Tovar (2014): A new genus and four new species of cladid crinoids from the Carboniferous of Oaxaca State, Mexico, Journal of Systematic Palaeontology, DOI: 10.1080/14772019.2014.913719

To link to this article: http://dx.doi.org/10.1080/14772019.2014.913719

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions

Journal of Systematic Palaeontology, 2014
http://dx.doi.org/10.1080/14772019.2014.913719

Taylor & Francis
Taylor & Francis Group

A new genus and four new species of cladid crinoids from the Carboniferous of Oaxaca State, Mexico

Rafael Villanueva-Olea[a] and Francisco Sour-Tovar[b]*

[a]*Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510 México D. F., Mexico;*
[b]*Museo de Paleontología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510 México D. F., Mexico*

(Received 15 November 2013; accepted 25 March 2014)

Eight cladid (Subclass Cladida) crinoids are described from the Carboniferous Ixtaltepec Formation of Oaxaca State, southern Mexico. Most of the material consists of external and internal moulds of cups, arms and the proximal parts of the stem. *Ekteinocrinus mixteca* sp. nov. is assigned to the Order Dendrocrinida; newly recognized taxa in the Order Poteriocrinida include *Stipecrinus splendidus* gen. et sp. nov., *Hydriocrinus amplus* sp. nov. and *Aesiocrinus profundus* sp. nov. *Cosmetocrinus* sp., *Contocrinus* cf. *kingi*, an indeterminate Scytalocrinidae and a cup probably belonging to the Family Stellarocrinidae are also described. *Stipecrinus splendidus* sp. nov. and *Cosmetocrinus* sp. are Middle–Upper Mississippian (Visean–Serpukhovian), the other crinoids being Lower-Middle Pennsylvanian (Bashkirian–Moscovian). The present study reveals a strong similarity, expressed in terms of palaeobiodiversity, between the Oaxaca crinoids and those reported from Mississippian–Pennsylvanian faunas from the central-east region of North America. This similarity is also evident in the composition of the associated non-echinoderm fauna.

http://zoobank.org/urn:lsid:zoobank.org:pub:347E74B9-82EB-49B8-BA16-61A65835CA5E

Keywords: Echinodermata; Crinoidea; Cladida; Carboniferous; Mexico

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Introduction

The crinoid record from the Upper Palaeozoic of Mexico is abundant but, with the exception of a cup of the species *Parspaniocrinus beinerti* from the Permian of Coahuila (Strimple 1971a), consists mainly of disarticulated columnals reported from the states of Sonora, Coahuila, Tamaulipas, Hidalgo, Guerrero, Puebla, Chiapas and Oaxaca (Buitrón-Sánchez 1977; Buitrón-Sánchez *et al*. 1987, 1998, 2007a, 2007b; Villaseñor-Martínez *et al*. 1987; Velasco de León & Buitrón 1992; Esquivel-Macías 1996; Esquivel-Macías *et al*. 2000, 2004; Villanueva-Olea *et al*. 2011). All of this material has been classified using the parataxonomic approach of Moore & Jeffords (1968) and the abundance and diversity of crinoid plate morphotypes indicate that these organisms were an important constituent group of marine communities during the Late Palaeozoic.

Amongst the fossil invertebrates discovered in Palaeozoic rocks from the Santiago Ixtaltepec region (Municipality of Nochixtlan, Oaxaca State), Carboniferous crinoids represent one of the most abundant and diverse components. In this region, the fossil record of crinoids is generally represented by columnals (Villanueva-Olea *et al*. 2011) preserved generally as moulds within shales and sandstones; mineralized plates, pluricolumnals and cups associated with arms and plates are comparatively rare. The present study describes specimens that correspond to the latter, less common types of preservation. The material is mostly disarticulated and relatively poorly preserved due to the formation of external and internal moulds associated with dissolution of the original plates.

Geological setting

Several outcrops of Carboniferous rocks are found in the towns of La Cumbre and Santiago Ixtaltepec, approximately 16 km north of the city of Nochixtlán, Oaxaca (17° 31′–17° 33′ N; 97° 06′–97° 07′ W). The crinoids described herein were collected from the type section of the Ixtaltepec Formation, located on Arroyo de las Pulgas, 500 m north of the town of Santiago Ixtaltepec (Fig. 1). The oldest rocks exposed in the area belong to the so-called Complejo Oaxaqueño, and consist of gneiss, schist and pegmatite with ages ranging from 990 to 1100 million years (Fries *et al*. 1962; Solari *et al*. 2003). The Tiñú Formation (Fig. 2) overlies this Precambrian basement, and consists of a succession of limestones and shales. This formation preserves a diverse fauna including brachiopods (Streng *et al*. 2011), gastropods (Yochelson 1968), cephalopods (Flower 1968), trilobites (Robison & Pantoja-Alor

*Corresponding author. Email: fcosour@ciencias.unam.mx

© The Trustees of the Natural History Museum, London 2014. All Rights Reserved.

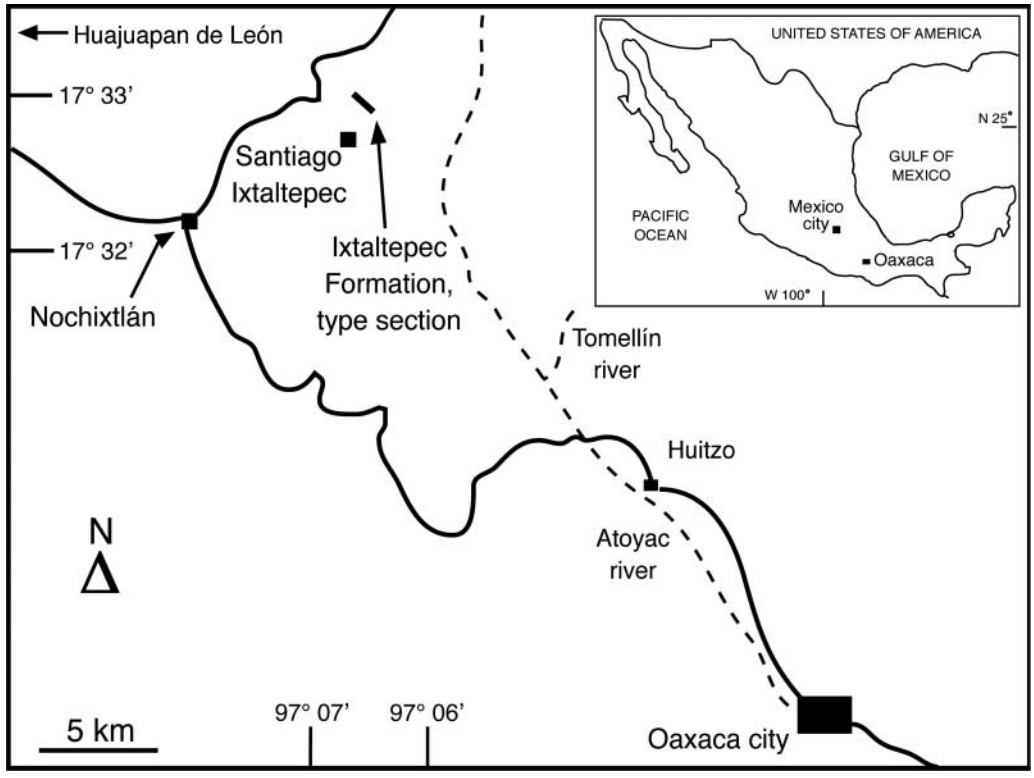

Figure 1. Map showing the location of the type section of the Ixtaltepec Formation at Arroyo de Las Pulgas, Oaxaca, Mexico.

1968) and graptolites (Sour-Tovar & Buitrón-Sánchez 1987). The Tiñú Formation is subdivided into a lower calcareous member of Late Cambrian (Furongian) age, and an upper shale member that is Early Ordovician (Tremadocian) (Pantoja-Alor 1970; Sour-Tovar 1990; Sour-Tovar & Buitrón-Sánchez 1987).

The Carboniferous rocks belong to the informal 'Santiago formation' and the Ixtaltepec Formation, previously assigned to the Late Mississippian and Middle Pennsylvanian (Pantoja-Alor 1970). Both units contain abundant sponges, tabulate corals, brachiopods, bryozoans, gastropods, conulariids, bivalve molluscs, cephalopods and crinoids; the preserved fauna likely formed part of a community in a neritic environment and was buried *in situ*, or in some cases transported into deeper water. According to Pantoja-Alor (1970), the type section of the Santiago formation at Arroyo de las Pulgas comprises 192 m of limestones, sandstones, mudstones and shales resting with an angular discordance on the Tiñú Formation (Fig. 2). The basal part of the Santiago formation includes deposits of sandy limestone with abundant invertebrate fossils that have an Osagean age (Tournaisian) (Quiroz-Barroso *et al*. 2000; Navarro-Santillán *et al*. 2002). Diverse invertebrates, including cephalopods that indicate a Meramecian–Chesterian age (Visean) (Castillo-Espinoza 2008; Castillo-Espinoza *et al*. 2010), have been found in concretions at several argillaceous levels in the upper member.

The Santiago formation is transitionally overlain by clastic deposits of the Ixtaltepec Formation, which at Arroyo de Las Pulgas has a thickness of 600 m (Fig. 2). This formation begins with siltstone, fine-grained calcareous sandstone and thin layers of slightly clayey calcarenite. Above these, thick banks of slightly sandy shale are interbedded with fine-grained sand, followed by siltstone and fine-grained micaceous sand. The upper part of the formation consists of thick banks of sandy shale intercalated with fine-grained shale.

For palaeontological study, the Ixtaltepec Formation has been subdivided into eight fossiliferous units, distinguished by the abbreviation API (Arroyo de Las Pulgas, Ixtaltepec). These subdivisions preserve an abundant invertebrate fauna that is mainly composed of rugose corals, bryozoans, brachiopods, gastropods, bivalved molluscs, trilobites and crinoids. In the middle part of the formation, at the API-4 level, there are remains of terrestrial plants. The studied material comes from four different stratigraphical levels of the Ixtaltepec Formation – API-2, API-6, API-7 and API-8 – all composed by shale, and whose location is marked on Figure 2.

The Palaeozoic sequence is completed by a conglomerate dominated by calcareous clasts, some containing Permian fusulinid foraminifera. This conglomerate is known as the Yododeñe Formation and its age is likely constrained between Late Permian and Jurassic. Lower

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

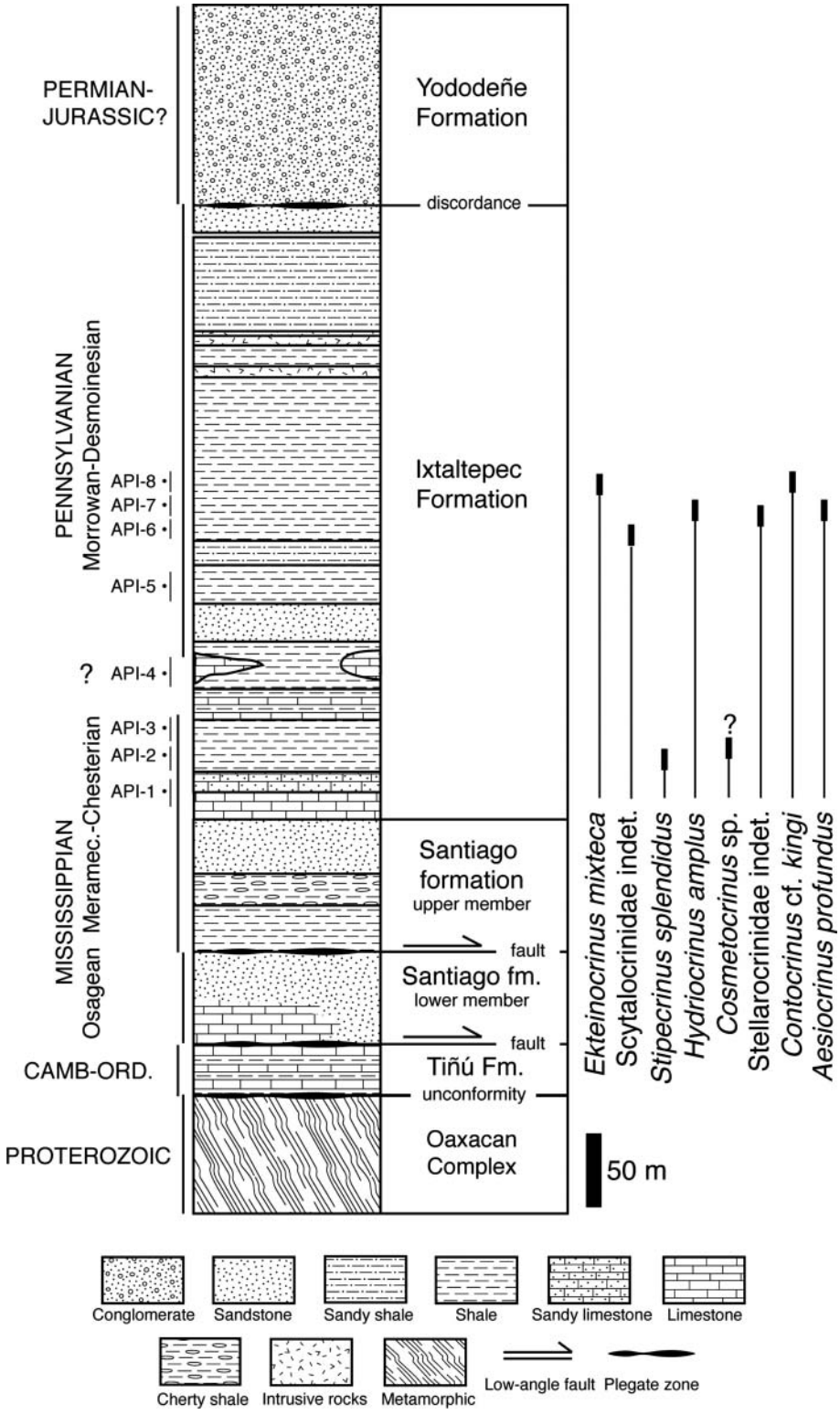

Figure 2. Stratigraphical column at Arroyo de Las Pulgas, showing the distribution of crinoid taxa in the Ixtaltepec Formation. Abbreviation: API: Arroyo de Las Pulgas Ixtaltepec Formation.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Cretaceous calcareous rocks cap the Palaeozoic succession (Pantoja-Alor 1970).

Material and methods

The material from the Ixtaltepec Formation includes 15 specimens, mostly disarticulated and relatively poorly preserved as external and internal moulds following dissolution of the original plates. Silicon casts were prepared to enhance study of the crinoids.

The terminology used in this work follows that of Ubaghs (1978). Classification is in accordance with the *Treatise on Invertebrate Palaeontology* (Moore & Teichert 1978), with modifications by Simms & Sevastopulo (1993) to subclass and order levels. For the genus *Ekteinocrinus*, we followed the taxonomy of Webster & Lane (2007).

All specimens are deposited in the collection of the Museo de Paleontología at the Faculty of Sciences (FCMP), Universidad Nacional Autónoma de México.

Anatomical abbreviations

S, stem; **IB**, infrabasals; **B**, basals; **R**, radials; **IBr**, primibrachials; **IIBr**, secundibrachials; **IIIBr**, tertibrachials; **IVBr**, tetrabrachials; **A**, anal plate.

Systematic palaeontology

Subclass **Cladida** Moore & Laudon, 1943
Order **Dendrocrinida** Bather, 1899
Family **Bridgerocrinidae** Webster & Lane, 2007
Genus ***Ekteinocrinus*** Webster & Lane, 2007

Type species. *Ekteinocrinus battleshipensis* Webster & Lane, 2007; Permian, Nevada.

Diagnosis. Crown cylindrical and elongate; cup medium bowl-shaped with a planate base; 10 arms; isotomous branching; brachials slightly cuneate with an angular median ridge proximally, becoming rounded distally; only one axillary elongate primibrachial; stem rounded and heteromorphic.

Ekteinocrinus mixteca sp. nov.
(Fig. 3A–G)

Material. Holotype: crown, FCMP 959. Paratypes: FCMP 958 and FCMP 960, found in the same sample as the holotype.

Occurrence. The specimens described here come from the API-8 level, corresponding to Lower–Middle Pennsylvanian (Morrowan–Desmoinesian) in the type section Arroyo de Las Pulgas, Ixtaltepec Formation.

Diagnosis. An ekteinocrinid exhibiting a menoplax 4 subcondition with the radianal in contact both with CD and BC basals supporting anal X and right tube plate above, and the suture between radials and brachials very prominent.

Derivation of name. The specific name ‘mixteca’ refers to the name of the local culture of the northern part of Oaxaca State.

Description. Crown cylindrical and elongate; cup cone-shaped with a truncate base. Isotomous branching with arms bifurcating once on primibrachial 1. Five preserved arms on one side. Radials and basals prominent, with sutures distinct and impressed. Infrabasal circlet only visible in one specimen, in which the distal tips of infrabasal plates are visible. Basal circlet does not show the proximal parts of basals in side view; the shape of basals is difficult to determine but, presumably, could be hexagonal; basals smaller than radials, convex transversally and longitudinally, in apparent contact with column or with the distal tips of infrabasal plates. Radials large, wider than high, convex transversally and slightly concave longitudinally. Radial articular facets plenary; sutures gaping that separate the radials from the primibrachials. Three anal plates in cup; radianal largest, resting upon right side of CD basal and, in its most proximally end, upon BC basal; anal X located above and to the left of radianal in contact with CD basal in a small area; more than a half of right tube plate above cup summit resting just above the radianal. Brachials elongate, rectangular to slightly cuneate, convex transversally and slightly concave longitudinally with a median straight ridge that runs longitudinally; one primibrachial per ray, axillary and sandglass-shaped; primibrachial A the longest with a wide base equal to width of subjacent radial, becoming narrow to mid-length and widening slightly in the distal part to form the shoulders where the secundibrachials are located, primibrachial B the smallest, with a height a little more than a half the height of primibrachial A. Secundibrachials are elongated, some with a pinnule that originates in the distal part of the plate. Stem poorly preserved, but apparently heteromorphic and slender.

Measurements. Specimen FCMP 959, corresponding to a mould and counter-mould (asterisk indicates a measurement taken from incomplete or poorly preserved plates): crown height*, 20 mm; crown width, 9.04 mm; cup height, 2.67 mm; cup width, 7.16 mm; basal AB height*, 1.27 mm; basal AB width, 2.32 mm; radial A height, 1.72 mm; radial A width, 3.00 mm; primibrachial A height, 4.02 mm; primibrachial A width, 2.67 mm; primibrachial B height, 2.3 mm; primibrachial B width, 2.97 mm; primibrachial C height*, 3.3 mm; primibrachial D height*, 3.24 mm; primibrachial D width, 3.08 mm; primibrachial E height*, 2.84 mm; radianal height, 1.56 mm; radianal width, 1.33 mm; anal X height, 1.27 mm; anal X width, 1.16 mm; right tube plate height, 1.18 mm; right tube plate width, 1.2 mm.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

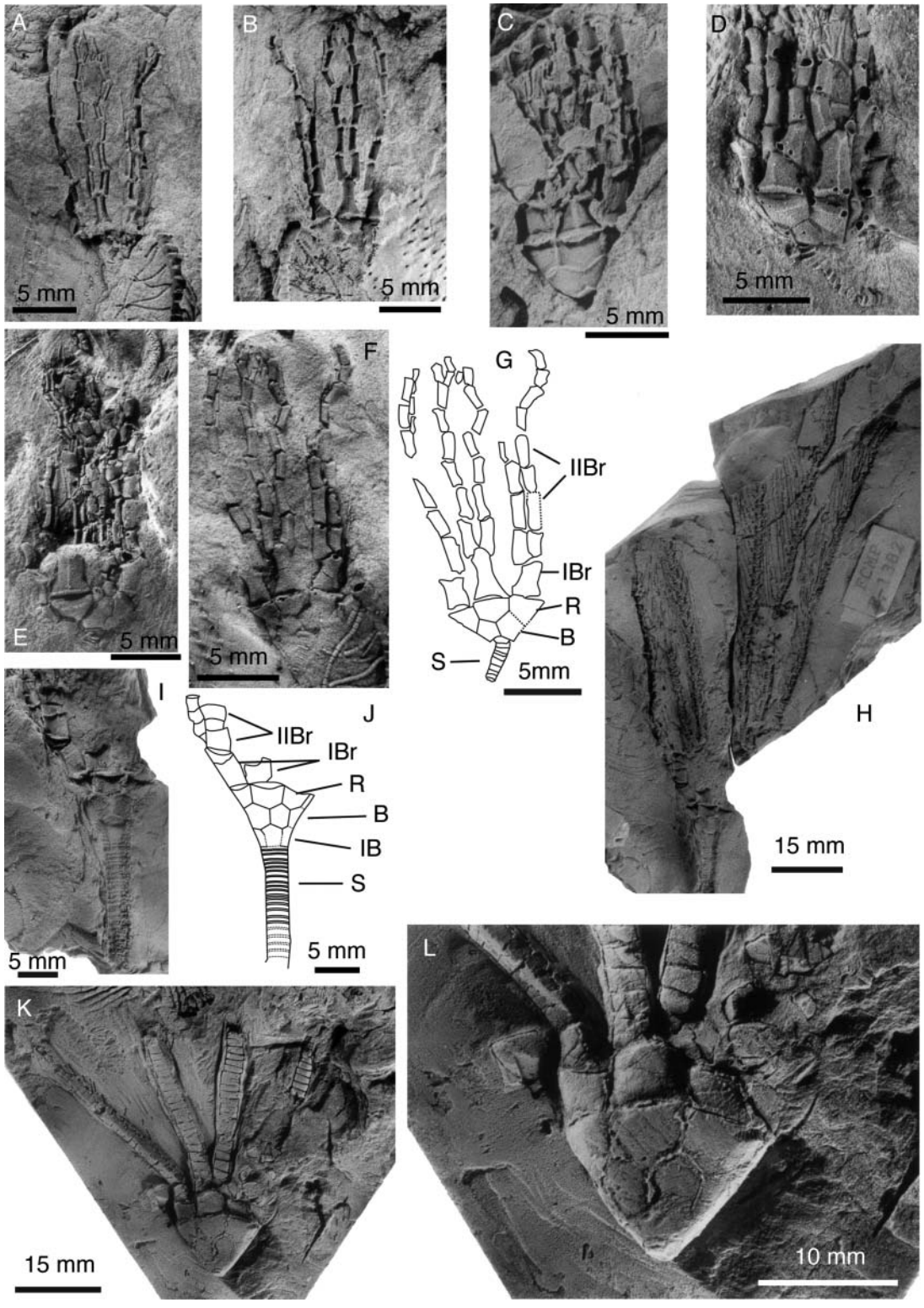

Figure 3. **A**–**G,** *Ekteinocrinus mixteca* sp. nov. in lateral view; **A, B,** FCMP 958, mould and counter-mould; **C,** FCMP 960; **D, E,** silicone casts of the holotype, FCMP 959; **F,** silicone cast of FCMP 958; **G,** interpretative drawing of F. **H**–**J,** Scytalocrinidae indet., FCMP 961, in lateral view; **H,** entire specimen; **I,** close-up, showing details of the cup and stem; **J,** interpretative drawing of I. **K**–**L,** *Stipecrinus splendidus* gen. et sp. nov., FCMP 962, in lateral view at different scales. **A, B, D, F** and **G** are A-ray views; **E** is a CD interray view; it is not possible to determine the orientations of **C, H, J, K** and **L**.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Remarks. The Mexican species differs from *Lanecrinus* from the Carboniferous of the USA (Kammer & Ausich 1993; Ausich *et al*. 2000) in its brachials of rectangular shape and equal size; in *Lanecrinus* the brachials are strongly cuneate, giving a zigzag shape to the arms. A greater similarity is found with *Bridgerocrinus* from the Upper Devonian–Lower Mississippian of the USA (Moore & Teichert 1978). The most notable differences between *Ekteinocrinus mixteca* and *Bridgerocrinus* are that in the latter it is possible to observe the infrabasal circlet in side view and, consequently, the contact between the column and the infrabasal circlet; in addition, *Bridgerocrinus* has brachials with longer pinnules and some branchings occur on primibrachials 2 or 3.

The Oaxaca species differs from other genera of Bridgerocrinidae by having the cup medium bowl-shaped, whereas in *Ekteinocrinus mixteca* it is of short length. The main difference found between *Ekteinocrinus mixteca* and the type species of *Ekteinocrinus*, *E. battleshipensis* from the Bird Spring Formation (Wolfcampian) of Nevada, is the arrangement of the anal plates, as the latter species appears to have the menoplax 5 subcondition according to Webster & Lane (2007), characterized by the occurrence of three anal plates in the cup, with the radianal in contact with CD basal (Webster & Maples 2006), whereas the Ixtaltepec species deploys a menoplax 4 subcondition with the radianal in contact both with CD and BC basals. Moreover, the suture between radials and brachials is more prominent in the Oaxaca species.

Order **Poteriocrinida** Jaekel, 1918
Superfamily **Scytalocrinoidea** Moore & Laudon, 1943
Family **Scytalocrinidae** Moore & Laudon, 1943
Scytalocrinidae indet.
(Fig. 3H–J)

Material. Two complementary specimens, FCMP 961.

Occurrence. The described specimens come from level API-6, corresponding to Lower–Middle Pennsylvanian (Morrowan–Desmoinesian) in the type section of the Ixtaltepec Formation, Arroyo de Las Pulgas.

Description. Crown very large and expanded. Cup low cone-shaped. Arms observed six, long, slender and uniserial, which open above cup. Branching apparently isotomous. Infrabasals short; proximal parts of these plates are apparently hidden by the proximal columnal. Basals hexagonal, medium sized, higher than wide and convex transversely and longitudinally. Radials are medium sized, pentagonal, and wider than long. Sutures between radials and primibrachials, gaping. Primibrachials are poorly preserved, but two in a ray: primibrachial 1, quadrangular in shape and primibrachial 2 pentagonal, axillary, and almost triangular with upper sides sloping for the reception of two arms. Secundibrachials cuneate with long, slender pinnules, which arise from the wider side of plates in their distal part, on both sides of the arms, although this pattern is not evident in all rays. Column heteromorphic, with noditaxis of 4 columnals, wider than arms with strong tendency to be wider in proximal part to cover the base of infrabasals.

Measurements. Specimen FCMP 961: crown width, 66 mm; crown height, 99.21 mm; cup width, 10.06 mm; cup height, 6.33 mm; basal height, 3.2 mm; radial width, 4.2 mm; radial height, 3.2 mm.

Remarks. This specimen is assigned to the family Scytalocrinidae on account of the general cup shape and respective plates, the presence of only one branching close to the cup and the lack of further bifurcations above the primibrachials. Although branching in all rays is not evident in the specimen, the number of conserved arms and their closeness in pairs indicate that they bifurcate only once, probably in the first or second primibrachial; this means that the specimen would be composed of 10 arms. This material presents similarities with families Aphelecrinidae and Blothrocrinidae but is different because, in these families, there is more than one division of the arms. A generic attribution is not given here because there is no preservation of the posterior side, anal sac, radial articular facets, or all of the primibrachials. Primibrachials observed on the anterior side are poorly conserved and in only one ray is it clear that primibrachial 2 is axillar; in the remaining rays it is not possible to see in which primibrachial the branching starts.

Genus ***Stipecrinus*** gen. nov.

Type species. *Stipecrinus splendidus* sp. nov.

Diagnosis. Crown expanded; cup low, cone-shaped; arms stout, uniseriate; isotomous branching; brachials wide, short, rectangular to slightly cuneate; primibrachials large, pentagonal with no gaping sutures.

Derivation of name. The genus name comes from the Latin *stipes*, meaning ‘stem’, referring to the arms that resemble a homeomorphic crinoid column.

Stipecrinus splendidus sp. nov.
(Fig. 3K, L)

Diagnosis. As for genus.

Derivation of name. From the Latin *splendidus*, meaning ‘gorgeous’.

Material. Holotype: FCMP 962, a partly complete crown.

Occurrence. Dark grey shale of stratigraphical level API-2, Ixtaltepec Formation, corresponding to

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Middle–Upper Mississippian (Meramecian–Chesterian), Arroyo de Las Pulgas, Oaxaca.

Description. Scytalocrinid with a crown expanded upward; cup conical, low, with convex base, slightly wider than high, with a ratio width/height of 1.38. Four visible arms, stout, rounded like a heteromorphic column. Five pentagonal infrabasals visible in side view, sloping upward, that occupy less than 25% the height; of the cup, slightly higher than wide. Radial articular facets not visible. Sutures not gaping. Primibrachials large and pentagonal, with a width and height similar to the subjacent radial; apparently each ray with only one primibrachial, axillary, although because of the poor preservation of some arms and one primibrachial, it is difficult to affirm this condition in all rays. Secundibrachials wider than high and proximal brachials higher than distals. Pinnules only preserved in the side of one arm, slender and short. Stem not preserved.

Measurements. Crown height (from crown base to tip of longest arm), 53.68 mm; crown width, 49.84 mm; cup height, 10.25 mm; cup width, 14.2 mm; infrabasal height, 2.7 mm; infrabasal width, 2.39 mm; basal height, 4.66 mm; basal width, 3.83 mm; radial height, 5 mm; radial width, 5.42 mm; primibrachial height, 4.06 mm; primibrachial width, 5.57 mm; secundibrachial 2 height, 1.7 mm; secundibrachial 2 width, 2.8 mm.

Remarks. *Stipecrinus splendidus* gen. et sp. nov. is assigned to the family Scytalocrinidae as it has a cup and cup plates like those of scytalocrinids and only isotomous branching. There are similarities with cups of Blothrocrinidae but this family is distinguished by having arms with numerous bifurcations. Although the preservation of the cup is good, the poor preservation or total absence of some arms makes the recognition of primibrachials per ray and the branchings difficult. Other genera of Scytalocrinidae lack branching above the primibrachials. The Oaxaca material is distinguished from *Phacelocrinus* from the Lower Carboniferous of the USA (Kirk 1940; Moore & Teichert 1978) because the brachials are not cuneate and the cup is cone-shaped. It differs from *Morrowcrinus* from the Morrowan of the USA (Moore & Teichert 1978), which does not have a crown with opened arms and has shorter primibrachials. *Hypselocrinus* is different in having strongly cuneate brachials and slenderer arms. *Ophiurocrinus* from the Carboniferous of Russia and England (Moore & Teichert 1978) has very short brachials of variable length; in the Mexican material the brachials are relatively short and have an almost uniform length. The general shape of the arms and the brachial size prompt comparison with some species of *Scytalocrinus*; however, this genus is characterized by having a bowl-shaped or a truncate cone-shaped cup, as well as arms arranged in a more enclosed position.

Genus ***Hydriocrinus*** Trautschold, 1867

Type species. *Hydriocrinus pusillus* Trautschold, 1867; Moscovian, Russia.

Diagnosis. A scytalocrinid with a cone-shaped cup, infrabasals prominently visible in side view, with brachials strongly cuneate and 10 arms that bifurcate on first primibrachial, column transversely pentagonal.

Hydriocrinus amplus sp. nov.
(Fig. 4)

Diagnosis. A species of *Hydriocrinus* which has a medium-sized cup, with a width/length ratio of 1.5, as well as sutures gaping between radials and primibrachials, except in D ray.

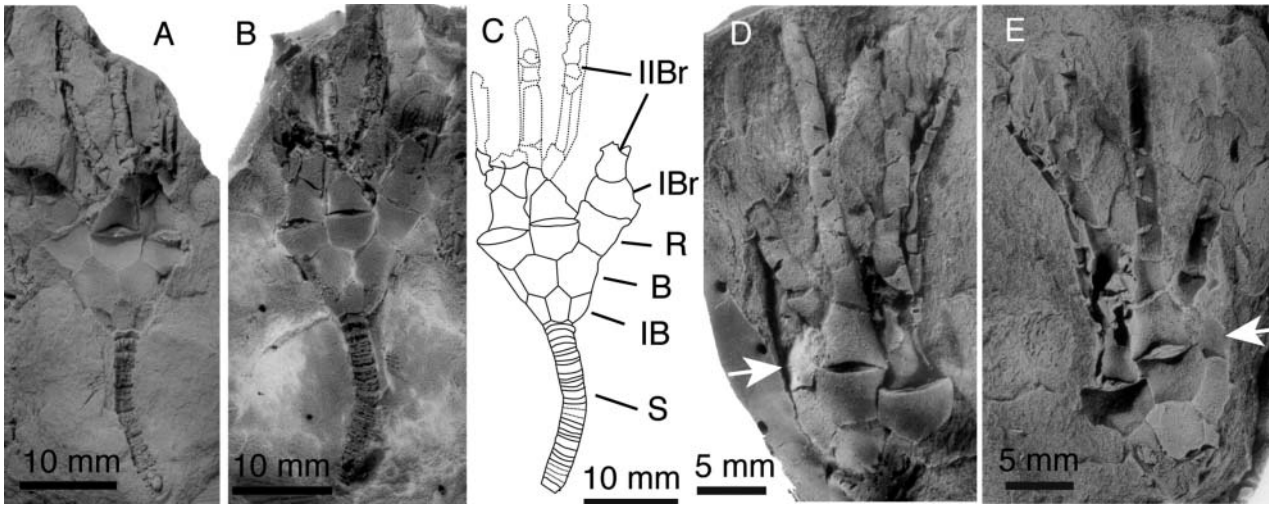

Figure 4. *Hydriocrinus amplus* sp. nov. in lateral view. **A,** FCMP 963; **B,** silicone cast of A; **C,** interpretative drawing of B; **D,** silicone cast of E; **E,** counter-mould of A. **A, B** and **C** are E-ray views; **D** and **E** are C-ray views. Arrows point to the anal plate.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Derivation of name. From the Latin *amplus*, meaning wide, referring to the very wide cup.

Material. Holotype: FCMP 963, a relatively complete crown preserved as mould and counter-mould.

Occurrence. The exact stratigraphical level in the Arroyo de Las Pulgas section could not be determined during collection but is presumed to be level API-7, Lower–Middle Pennsylvanian (Morrowan–Desmoinesian), because of matrix lithology.

Description. Crown large, cylindrical, and narrow. Cup conical of medium size; the cup ratio width/length is 1.5. Arms slender with branching on primibrachial 1; above primibrachials there is no evidence of new bifurcations. Five prominent infrabasals, pentagonal, visible in side view, almost as high as the radials, higher than wide, straight longitudinally and slightly convex transversely, with the bases flat delimiting the stem outline. Basals large, hexagonal, higher than radials, higher than wide, straight longitudinally, and slightly convex transversely. Radials large, wider than high, convex longitudinally and transversely. Radial articular facets plenary with a very narrow outer margin. Suture gaping between radial and primibrachial, except in D ray. Only a small fragment of anal X conserved, with distal half extending above radial summit. Primibrachial 1 pentagonal and axillary. Secundibrachials narrow, cuneate, higher than wide and the highest located in the proximal portion, being smaller in the distal part. Pinnules not preserved. Column heteromorphic, pentagonal transversely.

Measurements. Crown height, 33.91 mm; crown width, 19.4 mm; cup height, 10.45 mm; cup width, 16.05 mm; infrabasal E height, 3.49 mm; infrabasal E width, 2.8 mm; basal DE height, 6.26 mm; basal DE width, 5.42 mm; radial E height, 4.03 mm; radial E width, 5.84 mm; primibrachial E height (approximate value due to poor preservation), 4.28 mm; primibrachial E width, 5.07 mm; secundibrachial 2 height (D ray), 2.74 mm; secundibrachial 2 width (D ray), 2.19 mm.

Remarks. Primibrachial preservation is good except in for the B and D rays in which it is difficult to determine a pentagonal shape. Primibrachial D has an apparently quadrangular shape; this could be confused with an atomous ray, nevertheless, it is considered that the left side of primibrachial D, as well as the left arm that originates from this plate, are not preserved. The observed fragment of anal X exhibits an elevated position with regard to radial C, but this same radial is found in an elevated position with respect to radial B as well; in the same way, radial D is found out of its original position, which indicates the calyx was strongly deformed post mortem. This observation is an indicator that the anal X in the specimen was perhaps dislocated.

Hydriocrinus amplus from Oaxaca can be compared with the genus *Cosmetocrinus* from the Mississippian of the USA (Moore & Teichert 1978) because of similarities such as cup shape and the fact that the primibrachial 1 is axillary in both cases. However, *Cosmetocrinus* has one or two additional branchings. In addition, some differences between the Oaxaca specimen and the genus *Hypselocrinus* have been found, such as gaping sutures between the radials and brachials, a wider cup and a pentagonal column in the former.

The type species of *Hydriocrinus*, *H. pusillus* Trautschold, 1867 from the Moscovian of Russia, has a much more elongate cup. *Hydriocrinus amplus* has a similar cup to that of *Hydriocrinus turbinatus* from the Wann Formation, Missourian (Pennsylvanian) of Oklahoma (Strimple 1971b); however, the new species has low primibrachials, while *H. turbinatus* has elongate primibrachials. *H. lorraineae* from the Desmoinesian of Texas (Strimple & Watkins 1969) has primibrachials of similar height to *H. amplus*, but cup shape resembles that of *H. pusillus*. *H.? rosei* from the Brentwood Limestone (Morrowan) of Oklahoma (Moore & Plummer 1938) has a cup similar to that of the studied specimen, but the finely ornamented surface distinguishes it from *H. amplus*.

The differences found between the described material and species previously reported indicate that the specimen studied represents a new species of the genus *Hydriocrinus*. This genus is distributed in many localities of the Pennsylvanian of Oklahoma, Texas and Nebraska in the USA (Moore & Plummer 1938; Strimple & Watkins 1969; Strimple 1971b; Pabian & Strimple 1985), and in the Moscovian of Russia (Trautschold 1867).

Family **Aphelecrinidae** Strimple, 1967
Genus ***Cosmetocrinus*** Kirk, 1941

Type species. *Cosmetocrinus gracilis* Kirk, 1941; Mississippian, Indiana.

Diagnosis. Cladid with large and narrow crown, with the cup cone-shaped; 2–3 bifurcations per ray; infrabasals visible in side view; brachials cuneate to subcuneate; primibrachial 1 axillary.

***Cosmetocrinus* sp.**
(Fig. 5A–D)

Material. FCMP 964.

Occurrence. API-2? level of Ixtaltepec Formation, Arroyo de Las Pulgas. The exact horizon was not established during collection but is tentatively assigned to the API-2 level (Meramecian–Chesterian) on lithological grounds.

Description. Crown cylindrical, high, and narrow; cup medium, cone-shaped. Arms branching isotomously with 3 bifurcations: the first occurs on primibrachial 1; the

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

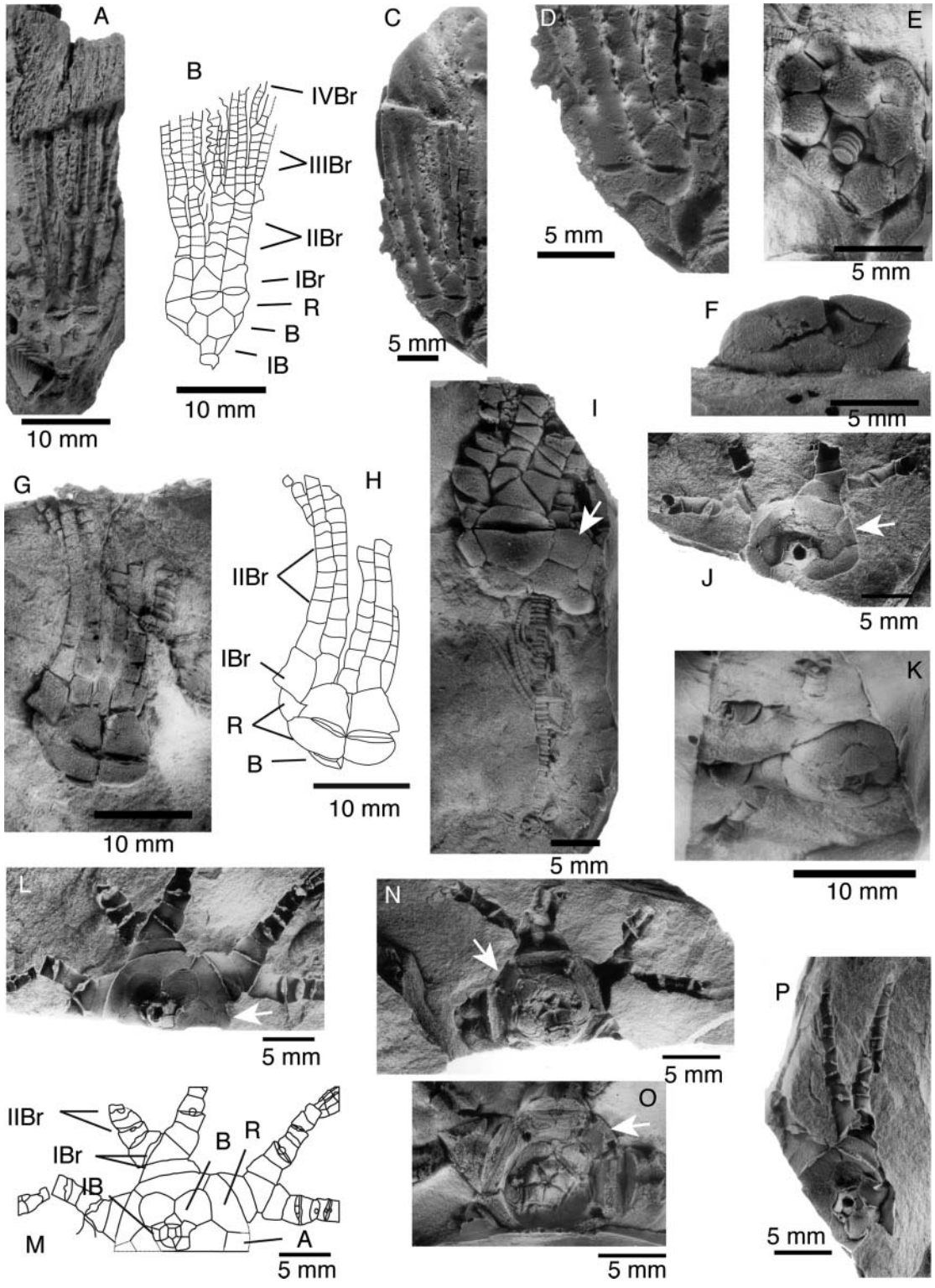

Figure 5. **A**–**D,** *Cosmetocrinus* sp. in lateral view, FCMP 964; **A,** specimen in the rock; **B,** interpretative drawing of A; **C, D,** silicone cast at different scales. **E,** Stellarocrinidae? indet. in basal view, FCMP 965. **F**–**H,** *Contocrinus* cf. *kingi*, silicone cast, FCMP 966; **F,** basal view; **G,** lateral view; **H,** interpretative drawing of G. **I**–**P,** *Aesiocrinus profundus* sp. nov.; **I,** silicone cast of FCMP 967; **J, K,** holotype FMCP 968 and corresponding silicone cast; **L,** FCMP 969; **M,** interpretative drawing of L; **N, O,** counter-mould of holotype FCMP 968, showing details of the radial articular facets and the axial canal of the arms, and its corresponding silicone cast, showing more details of the inside of the cup; **P,** FCMP 970 in lateral view. For **A**–**H** and **P** it is not possible to determine the orientation; **I,** D-ray view; **J,** aboral view, B and C rays with proximal arms; **K, L, M,** B ray in first plane; **N,** B and C rays with proximal arms, CD interray at left; **O,** B and C rays at left and CD interray at right. Arrows point to the anal plate.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

second on secundibrachials 7 or 8; and the third on tertibrachials 8 or 9. Ten preserved arms, uniserial, in enclosed position and quite close to each other; judging by the number of divisions per ray, it can be inferred that the total number of arms is approximately 40. Infrabasal circlet visible in side view, occupying less than a quarter of the cup height; two visible infrabasals, as wide as high. Basal circlet having a little less than a half of the cup height; basals are hexagonal, higher than wide. Radial plates are pentagonal, wider than high and shorter than basals. Sutures gaping between radials and primibrachials. Brachial plates short; primibrachials pentagonal, as wide as high and as large as radials; secundibrachials short, most are rectangular, although some are slightly cuneate, with a pinnule on the distal end; tertibrachials small, quadrangular to slightly subcuneate. Column poorly conserved but probably transversely pentagonal.

Measurements. Crown height, 44.6 mm; crown width, 13.84 mm; cup height, 7.2 mm; cup width, 9.08 mm; infrabasal height, 2.25 mm; infrabasal width, 2.08 mm; basal height, 3.73 mm; basal width, 2.85 mm; radial height, 2.53 mm; radial width, 3.48 mm; primibrachial height, 3.2 mm; primibrachial width, 3.49 mm; secundibrachial 5 max height, 1.15 mm; secundibrachial 5 max width, 1.68 mm.

Remarks. We have only a calyx impression. Details of the arrangement of the anal plates, anal tube or branching pattern in every ray are lacking. This makes it impossible to know the specimen orientation. Nevertheless, the preserved features allow assignment to the genus *Cosmetocrinus*.

Cosmetocrinus includes species with rectangular to slightly cuneate brachials, as in the Ixtaltepec specimen. Some morphological features are shared with *Aphelecrinus* from the Mississippian of the USA and England (Kirk 1944; Moore & Teichert 1978) and *Ulrichicrinus* from the Mississippian–Lower Pennsylvanian of the USA (Moore & Teichert 1978); however, *Cosmetocrinus* sp. differs by having three arm divisions. In *Paracosmetocrinus* from the Mississippian of the USA (Moore & Teichert 1978), the first division occurs above primibrachial 1 on the A ray; however, in *Cosmetocrinus* sp. all preserved arms, including those of the A ray, bifurcate on primibrachial 1.

Finally, this material is similar to that of *Cosmetocrinus* sp. from the Banff Formation, Alberta (Kinderhookian) reported by Laudon *et al.* (1952). In their specimen, the brachials are more rectangular than in other species belonging to this genus. They highlight this difference and indicate that their specimen is perhaps an ancestral species of the stock belonging to *Cosmetocrinus*, a genus mainly characterized by having strongly cuneate brachials. Therefore, our specimen and the specimen of Laudon *et al.* (1952) are similar, although in the latter the brachials are more elongate and the arms bifurcate once more above the primibrachials instead of twice.

The typical features of the Ixtaltepec specimen indicate the possibility that it is a new species not previously described. However, because we only have one incomplete specimen, it is left in open nomenclature. *Cosmetocrinus* has been found in Late Devonian rocks of China (Lane *et al.* 1997) and in the Lower Carboniferous (Mississippian) of several localities in Ohio, Iowa and Indiana, USA (e.g. Hall 1863; Meek & Worthen 1869; Worthen 1883; Wachsmuth & Springer 1890; Kirk 1941).

Superfamily **Lophocrinoidea** Bather, 1899
Family **Stellarocrinidae** Strimple, 1961
Stellarocrinidae? indet.
(Fig. 5E)

Material. FCMP 965.

Occurrence. API-7 level, Ixtaltepec Formation, Arroyo de Las Pulgas.

Description. Cup low, bowl-shaped; cup plates are ornamented with granulations. Only radial proximal parts, basals and infrabasals are preserved. Infrabasal circlet stellate, confined inside a shallow concavity; infrabasals are small, pentagonal, wider than high, and in almost horizontal attitude, sloping slightly downward without reaching the basal plane of the cup. Basals are recurved, larger than infrabasals, slightly wider than high and form the basal plane of cup; proximal ends of these plates are part of the basal concavity, the middle part forming the basal plane, and the distal ends sloping strongly upward, producing a very angular and bulbous shape for these plates; at the centre of each basal some ridges or keels arise that join with the keels of adjacent basal and radial plates; the distal tips of basals are interrupted and have an abrupt sloping inward the cup; in the same way, the proximal portions of radials, at suture height, are invaginated; because of this, the joint between two radial plates and subjacent basal forms a prominent apical pit; in the specimen it is not possible to observe a complete radial plate but the proximal parts are evident and indicate that they are wider than the basals, that the horizontal proximal part of the radial plates is above the sides of the basals forming part, together with the basals, of the basal plane, and that the distal ends of the radials arise vertically, forming a 90° angle with respect to the proximal end that is found in horizontal position. Between two basals is a plate, presumably an anal plate, with a pentagonal shape, and keel-like projections that attach it to the basals, and present granulations. The column is subpentagonal, heteromorphic, with strong tendency to be circular in the distal part.

Measurements. Cup width (approximate), 10.36 mm; infrabasal height, 1.2 mm; infrabasal width, 1.83 mm; basal height, 3.6 mm; basal width, 3.84 mm; column diameter, 1.66 mm.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Remarks. We only have one incomplete cup that includes the infrabasal and basal circlets and the proximal parts of some radials. It is tentatively assigned to the family Stellarocrinidae on account of the low, bowl-shaped cup, large basals, and keels that originate in a radial pattern from the centre of the basal plate outward. The lack of information about the radial plates, arms and total number of anal plates precludes a more confident determination.

Superfamily **Erisocrinoidea** Wachsmuth & Springer, 1886

Family **Graphiocrinidae** Wachsmuth & Springer, 1886

Genus ***Contocrinus*** Knapp, 1969

Type species. *Graphiocrinus stantonensis* Strimple, 1939; Pennsylvanian, Kansas.

Diagnosis. Crown cylindrical and slender with a bowl-shaped cup; 10 arms; basals relatively large; radial facets plenary; single slender anal plate.

Contocrinus* cf. *kingi (Moore & Plummer, 1940) (Fig. 5F–H)

Material. FCMP 966.

Occurrence. Level API-8, corresponding to the Lower–Middle Pennsylvanian (Morrowan–Desmoinesian), Ixtaltepec Formation, Arroyo de Las Pulgas.

Description. Crown cylindrical and elongate. Cup low, bowl-shaped, base concave. Arms slender, nearly in contact with each other. One isotomous branching on primibrachial 1. The cup impression on the rock is poor. Infrabasal circlet not visible in side view, confined to the basal concavity. Five basal plates, not visible on one side, but visible on the opposite side, poorly preserved, some pentagonal but some probably hexagonal, with proximal tips sloping inward into the concave base and forming the flat base of the cup. Radial plates large, wider than high; in the face where the basals are not clearly visible, the radials are observed with proximal tips sloping to the concavity; on the opposite side, the radials are seen in a much more elevated position without sloping; radials swollen or bulbous in appearance, strongly convex longitudinally or slightly convex transversely. Radial articular facets plenary. Suture between primibrachs and radials gaping. Primibrachial 1 axillary, varying slightly in size, according to the ray, but wide on base, narrowing at mid-height and widening slightly distally at the shoulders on which the secundibrachials rest; primibrachials ornamented with some irregular lines on surface. Secundibrachials quadrangular, being higher proximally and shorter distally. Pinnules, anal sac and column not preserved. Poor preservation of some basals, radials and primibrachials.

Measurements. Crown height (incomplete), 27.46 mm; crown width, 11.81 mm; cup height, 3.12 mm; cup width, 11.29 mm; basal height, 3.3 mm (maximum observed value but probably slightly higher); basal width, 3 mm; radial height, 2.78 mm; radial width, 5.35 mm; primibrachial height, 3.61 mm; primibrachial width, 4.65 mm; secundibrachial height, 1.62 mm; secundibrachial width, 2.26 mm.

Remarks. The specimen can be compared with *Trautscholdicrinus* from the Upper Carboniferous of Moscow (Moore & Teichert 1978) with which it shares the cylindrical shape of the crown and an extended cup, but the Ixtaltepec material differs by having brachials that are slightly quadrangular. It is also similar to *Apographiocrinus* from the Lower Pennsylvanian–Lower Permian of the USA and from the Upper Permian of Russia and Indonesia (Moore & Teichert 1978) but the subcylindrical shape of the crown, the occurrence of projections on the radial outer surface in the interbrachial area, as well as primibrachials that are less wide than the radials in *Apographiocrinus*, allow differentiation between the two genera. The greatest similarity was found with *Graphiocrinus* from the Lower Carboniferous of Europe (Moore & Teichert 1978) but this differs by having primibrachials much higher than radial height, whereas in the specimen from Oaxaca the primibrachials are shorter than radial height.

Strong compaction during fossilization explains the difference in this specimen between one surface and the opposite. Presumably, cup height is underestimated because of this deformation; possibly it is higher, similar to the heights of congeneric species. Not all of the arm height is preserved, but there is no evidence of branching above primibrachial 1.

The basals in *Contocrinus andamanensis* from the Early Permian of Thailand (Webster & Jell 1993) are clearly larger, being slightly wider than high; in our specimen the basals are higher than wide. In *C. andamanensis*, the primibrachials are higher and more slender at mid-height than those in our specimen. In *C. delicatulus* from the Brownsville Limestone (Virgilian) of Oklahoma (Moore 1939), cup height is similar to that of the Oaxaca species (3.1 mm in *G. delicatulus* versus 3.12 mm in *Contocrinus* cf. *kingi*), but width is only 7.5 mm, much less than that of the Oaxaca species (11.3 mm). The Oaxaca species is most similar to *C. kingi* (Moore & Plummer, 1940) from the Middle Pennsylvanian of Texas, in the bulged shape of the radials, basals that are barely visible in side view, and infrabasals completely hidden in the basal concavity. The arms are in near lateral contact, bifurcating on primibrachial 1. However, in the Oaxaca species, secundibrachials are more slender than in any other species of *Contocrinus*, but the non-preservation of the posterior side where the anal plate and the subjacent

basal are found precludes species-level determination. *Contocrinus kingi* is found in Middle Pennsylvanian rocks of Texas (Moore & Plummer 1940). The genus occurs in the Pennsylvanian (Desmoinesian–Virgilian) of the USA (Pabian & Rushlau 2002) and Permian (Wolfcampian) of Thailand (Webster & Jell 1993).

Superfamily **Texacrinoidea** Strimple, 1961
Family **Cymbiocrinidae** Strimple & Watkins, 1969
Genus ***Aesiocrinus*** Miller & Gurley, 1890

Type species. *Aesiocrinus magnificus* Miller & Gurley, 1890; Pennsylvanian, Kansas.

Diagnosis. A cymbiocrinid with a low, bowl-shaped calyx, single anal plate, pentagonal stem, and with 10 arms bifurcating on primibrachial 2. Plates smooth or finely granulous. The arms are slender, long, and transversely round with slender pinnules. Anal sac long and stout. Radial articular facets plenary, inclinate. The anal plate is normally quadrangular, projecting slightly above radial summit and has facets for reception of two tube plates. Infrabasals might or might not form a concavity, but never can be observed in side view.

Aesiocrinus profundus sp. nov.
(Fig. 5I–P)

Material. Holotype: FCMP 968**,** crown with cup and proximal parts of arms (mould and counter-mould). Paratypes*:* FCMP 967, FCMP 969 (mould and counter-mould), FCMP 970. Other material: FCMP 971, FCMP 972.

Diagnosis. An aesiocrinid that has a deeper basal concavity, as well as an unornamented and strongly asymmetrical cup.

Derivation of name. From the Latin *profundus*, meaning deep, in reference to the deep basal concavity.

Occurrence. Level API-7, corresponding to the Lower-Middle Pennsylvanian (Morrowan–Desmoinesian), of the Ixtaltepec Formation, Arroyo de Las Pulgas.

Description. Cup low, pentagonal outline in basal view; asymmetrical in lateral view, with the anterior side sloping more steeply than the posterior; base concave; isotomous branching. Arms slender, uniserial, widely separated and extended outward of the cup. Two arms originate from each ray; this pattern, if maintained, would result in 10 arms. Infrabasal circlet forms a stellate disc; infrabasals pentagonal, slightly higher than wide, confined to the concavity and sloping downward, with the distal tips sloping outward; the base of each infrabasal delineates the stem outline; inside the cup the infrabasal circlet is cone-shaped, lower than cup summit. Basals hexagonal, except for heptagonal CD basal, truncated distally for reception of the anal plate; basals form the base of the cup, however their distal tips slope upwards and are visible in side view; basals slightly convex transversely and strongly convex longitudinally, marked by the tendency of being more bulbous on the anterior side; CD basal straight transversely and longitudinally. Radials large, pentagonal, larger than basals, wider than high; positioned subhorizontally, sloping slightly upwards and extending outwards. Radial articular facets plenary; the outer marginal area is short, slightly excavated and with a deep ligament pit and conspicuous; between the fossa and outer margin runs an outer short marginal ridge barely conspicuous and parallel to the transverse ridge; length of transverse ridge is almost equal to width of the radials; the inner ligament area is short, flat to subhorizontal, sloping inwards and downwards and with a well-defined central muscular groove that separates two muscular elongate fossae. Anal plate quadrangular in some specimens and truncated on distal part at the cup summit level; in other cases, this plate is completely preserved and the distal quarter of it is above cup summit, the distal side is irregular. Two primibrachials per ray; suture between primibrachials rigid; primibrachial 1 trapezoidal, narrower than subjacent radial; primibrachial 2 axillary, triangular or pentagonal in shape. Proximal secundibrachials are wider than distal secundibrachials, slightly to strongly cuneate; in proximal parts of the arms, the secundibrachials organized in zyzygial pairs, with smooth articular surfaces between each member of a pair; the joint between a pair and other is marked with articular facets which contain a distinct transverse ridge and a prominent ligamentary fossa, representing articulation areas of ligaments and muscles. Column heteromorphic, pentagonal transversely.

Measurements. FCMP 968 (mould and counter-mould): cup height, approx. 3.02 mm; cup width, 10.45 mm; infrabasal height from inside the cup, 1.36 mm; infrabasal width from inside the cup, 1.6 mm; BC basal height, 3.07 mm; BC basal width, 3.63 mm; CD basal height, 2.78 mm; CD basal width, 3.36 mm; C radial height, 3.04 mm; C radial width, 5.03 mm; column diameter, 1.52 mm. FCMP 969 (mould and counter-mould): cup width, 11.73 mm; cup height, 3 mm; B radial height, 3.02 mm; B radial width, 6.8 mm; BC basal height, 3.4 mm; BC basal width, 3.57 mm; infrabasal height, 1.41 mm; infrabasal width, 1.76 mm; primibrachial 1 height, 1.44 mm; primibrachial 1 width, 5.79 mm; primibrachial 2 height, 2.47 mm; primibrachial 2 width, 4.34 mm; secundibrachial 1 height (highest side), 2.3 mm; secundibrachial 1 width, 3.16 mm; column diameter, 1.81 mm.

Remarks. The Oaxaquian specimens are assigned to *Aesiocrinus* because of the low cup and wide anal plate; these features distinguish them from *Oklahomacrinus*, which has a flat cup and a relatively slender anal plate.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Aesiocrinus profundus sp. nov. differs from *A. dilatus* from the Virgilian of Oklahoma (Moore 1939) in the presence of an infrabasal disc that forms a deep basal concavity; it is also distinguished by the unornamented cup surface, whereas in *A. dilatus* the cup surface is finely granulose. *A. luxuris*, from the Missourian of Oklahoma (Strimple 1951a), whose cup has a slightly asymmetrical bowl-shape, differs from *A. profundus* sp. nov., which has a more elongated and more asymmetrical cup, and larger outer ligament area. Some traits are shared with *A. erectus* from the Desmoinesian of Tulsa, Oklahoma (Strimple 1951b), but in this species the radial and basal tips have depressions not observed in *A. profundus*, and the cup is relatively larger. *A. typus* from the Pennsylvanian of Oklahoma (Strimple 1939) has a more symmetrical cup, with a more elongate posterior side and a basal posterior with wider, lower lateral sides. The genus *Aesiocrinus* occurs in several Pennsylvanian and Permian localities in the USA (e.g. Miller & Gurley 1890; Strimple 1951a, b; Webster & Lane 1967; Washburn 1968; Strimple & Watkins 1969). It is also found in the Middle Carboniferous of Russia (Trautschold 1879), and at Penton Linns, Liddesdale, Scotland (Wright 1937).

Discussion

Taphonomic implications

It is notable that the crinoid fauna in the region of Santiago Ixtaltepec is exclusively composed of species belonging to the Subclass Cladida. It is possible that this is the result of collector bias, which would imply that further collections would be necessary to recover specimens from other crinoid groups. However, it is also possible that different crinoid groups show different preservational potentials, with the local environment only allowing the preservation of cladids. In this context, species belonging to the Subclass Camerata, which have cups with firmly articulated plates, are very resistant to disarticulation and have the highest preservational potentials within crinoids. In contrast, representatives of the subclass Cladida are characterized by cups with weak articulations, and therefore disarticulate more easily (Meyer *et al*. 1989; Ausich 2001). The crinoids from Oaxaca show poorer preservation than other localities in North America; reports of specimens from the USA indicate a very complete preservation, including the stem and arms. Ausich & Sevastopulo (1994) demonstrated that camerates preserve better in shallower facies with high energy than cladids, as this type of environment is often associated with the exhumation of buried remains; consequently, the more tightly articulated camerates are more resistant to post-mortem disarticulation. This observation suggests that the deposition of the Ixtaltepec Formation included periods of low energy with relatively low sedimentation rates, which favoured colonization of the area by cladids, and also hindered the establishment of members of other crinoid groups. Alternating with this regime, there were sporadic increments of sedimentation that allowed the preservation of some complete individuals.

Biostratigraphical implications

The Ixtaltepec Formation was originally assigned to the Lower–Middle Pennsylvanian based on the presence of the brachiopod *Anthracospirifer occiduus*. However, recent studies have reported the presence of this species also in the Mississippian (Butts 2007), arguing against its utility as an index fossil. Sour-Tovar & Martínez-Chacón (2004) and Torres-Martínez *et al*. (2008) reported several genera of exclusively Pennsylvanian (Morrowan–Desmoinesian) brachiopods in the upper units of the Ixtaltepec Formation (API-5–API-8). Recently Torres-Martínez & Sour-Tovar (2012) reported in the lower levels of the formation, particularly API-2 and API-4, brachiopods of the genera *Inflatia*, *Echinoconchus*, *Ovatia* and *Sinuatella* that indicate a Lower–Middle Mississippian age (Meramecian–Chesterian). These data indicate these levels to be Mississippian (possibly Meramecian–Chesterian), while levels API-5 to API-8 correspond to the Pennsylvanian.

Based on this stratigraphical context, the presence of the genus *Ekteinocrinus*, previously reported from the Permian (Wolfcampian) of Nevada (Webster & Lane 2007), correlating with level API-8, allows extension of its stratigraphical range down to the Pennsylvanian. The genus *Hydriocrinus* has been reported only from the Pennsylvanian of the USA, while *Contocrinus* and *Aesiocrinus* have been found at both Pennsylvanian and Permian localities in North America. Their presence at levels API-7 and API-8 in the Ixtaltepec Formation is consistent with a Pennsylvanian age. The current study records the occurrence of *Cosmetocrinus* in unit API-2 of the Ixtaltepec Formation, considered of Middle–Upper Mississippian age (Meramecian–Chesterian); this information is consistent with previous reports of the genus that indicate a Mississippian age based on deposits in the USA (e.g. Hall 1863; Meek & Worthen 1869; Worthen 1883; Wachsmuth & Springer 1890; Kirk 1941).

Palaeobiogeographical implications

The crinoids found in the Ixtaltepec Formation are similar to faunas from Mississippian and Pennsylvanian localities in the mid-continent of the USA. This palaeobiogeographical affinity is consistent with observations of other invertebrate groups, especially brachiopods and molluscs, from the region of Santiago Ixtaltepec (Quiroz-Barroso & Perrilliat 1997, 1998; Quiroz-Barroso *et al*. 2000; Navarro-Santillán *et al*. 2002; Sour-Tovar & Martínez-Chacón 2004; Torres-Martínez *et al*. 2008), thus

supporting the idea that southern Mexico was part of an epicontinental sea that extended from what is currently the US mid-continent into the north-eastern and south-eastern parts of Mexico.

Acknowledgements

An anonymous reviewer, Thomas Guensburg and G. D. Edgecombe (Associate Editor) are thanked for their effort, comments and suggestions. Daniel Navarro-Santillán and Leonora Martín-Medrano provided field and laboratory assistance. Héctor Hernández-Campos helped with photography. We would like to thank to Sara A. Quiroz-Barroso, Javier Ortega-Hernández, Omar R. Regalado and Gary D. Webster for their constructive reviews of the first version of this paper. This work was supported by the Dirección General de Asuntos del Personal Académico de la Universidad Nacional Autónoma de México [PAPIIT IN213710], [IN215013-2].

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

References

Ausich, W. I. 2001. Echinoderm Taphonomy. Pp. 171–227 in M. Jangoux & J. M. Lawrence (eds) *Echinoderm studies*. *Volume 6*. Balkema, Lisse.

Ausich, W. I. & **Sevastopulo, G. D.** 1994. Taphonomy of Lower Carboniferous crinoids from the Hook Head Formation, Ireland. *Lethaia*, **27**, 245–256.

Ausich, W. I., **Goldstein, A.** & **Yates, R.** 2000. Crinoids from the Muldraugh Member of the Borden Formation in north-central Kentucky (Echinodermata, Lower Mississippian). *Journal of Paleontology*, **74**, 1072–1082.

Bather, F. A. 1899. A phylogenetic classification of the Pelmatozoa. *British Association for the Advancement of Science*, **1898**, 916–923.

Buitrón-Sánchez, B. E. 1977. Invertebrados (Crinoidea y Bivalvia) del Pensilvánico de Chiapas. *Revista del Instituto de Geología, Universidad Nacional Autónoma de México*, **1**(2), 144–150.

Buitrón-Sánchez, B. E., **Patiño, J.** & **Moreno, A.** 1987. Crinoideos del Paleozoico Tardío de Calnali, Hidalgo. *Revista de la Sociedad Mexicana de Paleontología*, **1**, 125–136.

Buitrón-Sánchez, B. E., **Arellano-Gil, J.** & **Flores de Dios, L. A.** 1998. Crinoideos del Pensilvánico del Cañón de la Peregrina, estado de Tamaulipas, México. Pp. 1–55 in S. Alanis, L. Ferrari & A. F. Nieto (eds) *Memorias de la Primera Reunión Nacional de Ciencias de la Tierra*, Facultad de Ciencias UNAM, México D. F., México.

Buitrón-Sánchez, B. E., **Almazán-Vázquez, E.** & **Vachard, D.** 2007a. Middle Permian crinoids (Echinodermata, Crinoidea) from Cerros Los Monos, Caborca, Sonora, Mexico and paleogeographic considerations. *Revista Mexicana de Ciencias Geológicas*, **24**(3), 344–353.

Buitrón-Sánchez, B. E., **Gómez-Espinosa, C.**, **Almazán-Vázquez, E.** & **Vachard, D.** 2007b. A late Atokan regional encrinite (early late Moscovian, Middle Pennsylvanian) in the Sierra Agua Verde, Sonora State, NW Mexico. *Geological Society of London Special Publication*, **275**, 201–209.

Butts, S. H. 2007. Silicified Carboniferous (Chesterian) Brachiopoda of the Arco Hills Formation, Idaho. *Journal of Paleontology*, **81**, 48–63.

Castillo-Espinoza, K. M. 2008. *Cefalópodos de la Formación Santiago, Misisípico de la Región de Nochixtlán, Oaxaca*. Unpublished thesis, Universidad Nacional Autónoma de México, 52 pp.

Castillo-Espinoza, K. M., **Escalante-Ruiz, A. R.**, **Quiroz-Barroso, S. A.**, **Sour-Tovar, F.** & **Navarro-Santillán, D.** 2010. Nuevos invertebrados del Viseano (Mississippiano), Formación Santiago, Oaxaca, sudeste de México. *X Congreso Argentino de Paleontología y Bioestratigrafía and VII Congreso Latinoamericano de Paleontología, La Plata, Argentina, Universidad Nacional de La Plata, Museo de La Plata*, 145.

Esquivel-Macías, C. 1996. *Invertebrados del Paleozoico Tardío de las regiones de Olinalá, Gro. y Patlanoaya, Pue*. Unpublished MSc thesis, Universidad Nacional Autónoma de México, 82 pp.

Esquivel-Macías, C., **Ausich, W. I.**, **Buitrón-Sánchez, B. E.** & **Flores de Dios, A.** 2000. Pennsylvanian and Mississippian pluricolumnal assemblages (Class Crinoidea) from southern Mexico and a new occurrence of a column with a tetralobate lumen. *Journal of Paleontology*, **74**, 1187–1190.

Esquivel-Macías, C., **Solís-Marín, F.** & **Buitrón-Sánchez, B. E.** 2004. Nuevos registros de placas columnares de crinoideos (Echinodermata, Crinoidea) del Paleozoico Superior de México, algunas implicaciones paleobiogeográficas y paleoambientales. *Coloquios de Paleontología*, **54**, 15–23.

Flower, R. H. 1968. Cephalopods from the Tiñú Formation, Oaxaca State, Mexico. *Journal of Paleontology*, **43**, 804–809.

Fries, C., **Schmitter, E.**, **Damony, P. E.** & **Livingstone, D. E.** 1962. Rocas Precámbicas de edad Grenvilliana de la parte central de Oaxaca en el Sur de México. *Boletín del Instituto de Geología, Universidad Nacional Autónoma de México*, **64**, 45–53.

Hall, J. 1863. *Preliminary notice, of some species of Crinoidea from the Waverly Sandstone series of Summit Co., Ohio, supposed to be of the age of the Chemung Group of New York*. Preprint of Seventeenth Annual Report of the Regents of the University of the state of New-York, on the Condition of the State Cabinet of Natural History, and the Historical and Antiquarian Collection annexed thereto, State of New York in Senate Document 189, Comstock and Cassiday Printers, Albany, 50–60 pp.

Jaekel, O. 1918. Phylogenie und System der Pelmatozoen. *Palaeontologische Zeitschrift*, **3**, 1–128.

Kammer, T. W. & **Ausich, W. I.** 1993. Advanced cladid crinoids from the Middle Mississippian of the east-central United States: intermediate-grade calyces. *Journal of Paleontology*, **67**, 614–639.

Kirk, E. 1940. Seven new genera of Carboniferous Crinoidea Inadunata. *Journal of the Washington Academy of Sciences*, **30**(8), 321–334.

Kirk, E. 1941. Four new genera of Mississippian Crinoidea Inadunata. *Journal of Paleontology*, **15**, 82–88.

Kirk, E. 1944. *Aphelecrinus*, a new inadunate crinoid genus from the Upper Mississippian. *American Journal of Science*, **242**, 190–203.

Knapp, W. D. 1969. Declinida, a new order of Late Paleozoic inadunate crinoids. *Journal of Paleontology*, **43**, 340–391.

Lane, N. G., **Waters, J. A.** & **Maples, C. G.** 1997. Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian), Xinjiang-Uygur Autonomous Region, People's

Republic of China. *Paleontological Society, Memoir*, **47**, 1–43.

Laudon, L. R., **Parks, J. M.** & **Spreng, A. C.** 1952. Mississippian crinoid fauna from the Banff Formation, Sunwapta Pass, Alberta. *Journal of Paleontology*, **26**, 544–575.

Meek, F. B. & **Worthen, A. H.** 1869. Descriptions of new Carboniferous fossils from the western States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1869**, 137–172.

Meyer, D. L., **Ausich, W. I.** & **Terry, R. E.** 1989. Comparative taphonomy of echinoderms in carbonate facies: Fort Payne Formation (Lower Mississippian) of Kentucky and Tennessee. *Palaios*, **4**, 533–552.

Miller, S. A. & **Gurley, W. F. E.** 1890. Description of some new genera and species of Echinodermata from the Coal Measures and Subcarboniferous rocks of Indiana, Missouri and Iowa. *Journal of the Cincinnati Society of Natural History*, **13**, 3–25.

Moore, R. C. 1939. New crinoids from Upper Pennsylvanian and Lower Permian rocks of Oklahoma, Kansas, and Nebraska. *Journal of the Scientific Laboratories of Denison University*, **34**, 171–279.

Moore, R. C. & **Plummer, F. B.** 1938. Upper Carboniferous crinoids from the Morrow subseries of Arkansas, Oklahoma, and Texas. *Bulletin of the Scientific Laboratories of Denison University*, **32**, 209–313.

Moore, R. C. & **Plummer, F. B.** 1940. Crinoids from the Upper Carboniferous and Permian strata in Texas. *University of Texas Publication*, **3945**, 1–468.

Moore, R. C. & **Laudon, L. R.** 1943. Evolution and classification of Paleozoic crinoids. *Geological Society of America*, *Special Paper*, **46**, 1–153.

Moore, R. C. & **Jeffords, R. M.** 1968. Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. *University of Kansas Paleontological Contributions, Echinodermata, Article*, **9**, 1–86.

Moore, R. C. & **Teichert, C.** (eds). 1978. *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea*. *Volumes 2 and 3*. Geological Society of America and University of Kansas Press, Boulder and Lawrence, 622 pp.

Navarro-Santillán, D., **Sour-Tovar, F.** & **Centeno-García, E.** 2002. Lower Mississippian (Osagean) brachiopods from the Santiago Formation, Oaxaca, Mexico: stratigraphic and tectonic implications. *Journal of South American Earth Sciences*, **15**, 327–336.

Pabian, R. K. & **Strimple, H. L.** 1985. Classification, paleoecology, and biostratigraphy of crinoids from the Stull Shale (Late Pennsylvanian) of Nebraska, Kansas, and Iowa. *Bulletin of the University of Nebraska State Museum*, **11**(1), 1–81.

Pabian, R. K. & **Rushlau, W. J.** 2002. Taphonomic analysis and systematic descriptions of some Late Pennsylvanian and Early Permian crinoids from Southeastern Nebraska, Eastern Kansas and Southwestern Iowa. *Conservation and Survey Division, Institute of Agriculture and Natural Resources, University of Nebraska-Lincoln, Geological Survey Paper*, **20**, 1–45.

Pantoja-Alor, J. 1970. Rocas sedimentarias paleozoicas de la region centro-septentrional de Oaxaca. Sociedad Geológica Mexicana. *Libro Guía de la Excursión México, Oaxaca*, 67–84.

Quiroz-Barroso, S. A. & **Perrilliat, M. C.** 1997. Pennsylvanian nuculoids (Bivalvia) from the Ixtaltepec Formation, Oaxaca, Mexico. *Journal of Paleontology*, **71**, 400–407.

Quiroz-Barroso, S. A. & **Perrilliat, M. C.** 1998. Pennsylvanian bivalves from the Ixtaltepec Formation, Mexico. *Journal of Paleontology*, **72**, 1011–1024.

Quiroz-Barroso, S. A., **Pojeta, J. Jr.**, **Sour-Tovar, F.** & **Morales-Soto, S.** 2000. *Pseudomulceodens*: a Mississippian rostroconch from Mexico. *Journal of Paleontology*, **74**, 1184–1186.

Robison, R. A. & **Pantoja-Alor, J.** 1968. Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *Journal of Paleontology*, **42**, 767–800.

Simms, M. J. & **Sevastopulo, G. D.** 1993. The origin of articulate crinoids. *Palaeontology*, **36**, 91–109.

Solari, L. A., **Keppie, J. D.**, **Ortega-Gutiérrez, F.**, **Cameron, K. L.**, **López, R.** & **Hames, W. E.** 2003. 990 and 1100 Ma Grenvillian tectonothermal events in the northern Oaxacan Complex, southern Mexico: roots of an orogeny. *Tectonophysics*, **365**, 257–282.

Sour-Tovar, F. 1990. Comunidades Cámbrico-Ordovícicas de la Formación Tiñú, en el área de Santiago Ixtaltepec, Oaxaca. Implicaciones paleoambientales y paleogeográficas. *Revista de la Sociedad Mexicana de Paleontología*, **3**(1), 7–23.

Sour-Tovar, F. & **Buitrón-Sánchez, B. E.** 1987. Los graptolitos del Tremadociano de Ixtaltepec, Oaxaca. Consideraciones sobre el limite Cambrico- Ordovícico de la región. *Revista de la Sociedad Mexicana de Paleontología*, **1**, 380–395.

Sour-Tovar, F. & **Martínez-Chacón, M. L.** 2004. Braquiópodos chonetoideos del Carbonífero de México. *Revista Española de Paleontología*, **19**, 125–138.

Streng, M., **Mellbin, B.**, **Landing, E.** & **Keppie, J. D.** 2011. Linguliform brachiopods from the terminal Cambrian and Lowest Ordovician of the Oaxaquia Microcontinent (Southern Mexico). *Journal of Paleontology*, **85**, 122–155.

Strimple, H. L. 1939. A group of Pennsylvanian crinoids from the vicinity of Bartlesville, Oklahoma. *Bulletins of American Paleontology*, **24**(87), 1–26.

Strimple, H. L. 1951a. Some new species of Carboniferous crinoids. *Bulletins of American Paleontology*, **33**(137), 5–40.

Strimple, H. L. 1951b. New Desmoinesian crinoids. *Journal of the Washington Academy of Sciences*, **41**(6), 191–194.

Strimple, H. L. 1961. Late Desmoinesian crinoids faunule from Oklahoma. *Oklahoma Geological Survey*, *Bulletin*, **93**, 6–189.

Strimple, H. L. 1967. Aphelecrinidae, a new family of inadunate crinoids. *Oklahoma Geology Notes*, **27**(4), 81–85.

Strimple, H. L. 1971a. A Permian crinoid from Coahuila, Mexico. *Journal of Paleontology*, **45**, 1040–1042.

Strimple, H. L. 1971b. The occurrence of *Hydriocrinus* in Oklahoma and Russia. *University of Kansas Paleontological Contributions*, *Paper*, **56**(3), 16–18.

Strimple, H. L. & **Watkins, W. T.** 1969. Carboniferous crinoids of Texas with stratigraphic implications. *Paleontographica Americana*, **6**(40), 141–275.

Torres-Martínez, M. A. & **Sour-Tovar, F.** 2012. Nuevos braquiópodos prodúctidos (Rhynchonelliformea, Strophomenata) del Carbonífero de la región de Nochixtlán, Oaxaca. *Revista Mexicana de Ciencias Geológicas*, **29**, 696–712.

Torres-Martínez, M. A., **Sour-Tovar, F.** & **Pérez-Huerta, A.** 2008. Neospiriferinid brachiopods (Spiriferida, Trigonotretidae) from Ixtaltepec Formation, Pennsylvanian of Oaxaca State, Southern Mexico. *Fossils and Strata*, **54**, 157–166.

Trautschold, H. 1867. Einige Crinoideen des jüngeren Berkalks von Moskau. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **40**(3), 1–49.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014

Trautschold, H. 1879. Die Kalkbrüche von Mjatschkowa. Eine Monographie des Oberen Bergkalks. *Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou*, **14**, 3−82.

Ubaghs, G. 1978. Skeletal morphology of fossil crinoids. Pp. T58−T216 in R. C. Moore & C. Teichert (eds) *Treatise on Invertebrate Paleontology. Volume 1, Part T, Echinodermata 2, Crinoidea*. Geological Society of America and University of Kansas Press, Boulder and Lawrence.

Velasco de León, P. & **Buitrón-Sánchez, B. E.** 1992. Algunos crinoideos (Echinodermata-Crinoidea) del Misisípico-Pensilvánico de San Salvador Patlanoaya, estado de Puebla. *Revista de la Sociedad Mexicana de Paleontología*, **5**, 71−81.

Villaseñor-Martínez, A. B., **Martínez-Cortés, A. M.** & **Contreras y Montero, B.** 1987. Bioestratigrafía del Paleozoico Superior de San Salvador Patlanoaya, Puebla, México. *Revista de la Sociedad Mexicana de Paleontología*, **1**, 396−417.

Villanueva-Olea, R., **Castillo-Espinoza, K. M.**, **Sour-Tovar, F.**, **Quiroz-Barroso, S. A.** & **Buitrón-Sánchez, B. E.** 2011. Placas columnares de crinoides del Carbonífero de la Región de Santiago Ixtaltepec, Municipio de Nochixtlán, Oaxaca; consideraciones estratigráficas y paleobiogeográficas. *Boletín de la Sociedad Geológica Mexicana*, **64**(3), 429−443.

Wachsmuth, C. & **Springer, F.** 1886. Revision of the Palaeocrinoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **3**(2), 64−226.

Wachsmuth, C. & **Springer, F.** 1890. New species of crinoids and blastoids from the Kinderhook Group of the Lower Carboniferous rocks at Le Grand, Iowa; and a new genus from the Niagara Group of Western Tennessee. *Geological Survey of Illinois*, **8** (Part 2, Section 2), 155−208.

Washburn, A. T. 1968. Early Pennsylvanian crinoids from the south-central Wasatch Mountains of central Utah. *Brigham Young University. Geology Studies*, **15**(1), 115−132.

Webster, G. D. & **Lane, N. G.** 1967. Additional Permian crinoids from southern Nevada. *University of Kansas Paleontological Contributions*, *Paper*, **27**, 1−32.

Webster, G. D. & **Jell, P. A.** 1993. Early Permian inadunate crinoids from Thailand. *Memoirs of the Queensland Museum*, **33**(1), 349−359.

Webster, G. D. & **Maples, C. G.** 2006. Cladid crinoid (Echinodermata) anal conditions: A terminology problem and proposed solution. *Palaeontology*, **49**, 187−212.

Webster, G. D. & **Lane, N. G.** 2007. New Permian crinoids from the Battleship Wash Patch Reef in southern Nevada. *Journal of Paleontology*, **81**, 951−965.

Worthen, A. H. 1883. Description of fossil invertebrates. *Illinois Geological Survey*, **7** (Part 2, Section 2), 265−338.

Wright, J. 1937. Scottish Carboniferous crinoids. *Geological Magazine*, **74**, 385−411.

Yochelson, E. L. 1968. Tremadocian mollusk from the Nochixtlan region, Oaxaca, Mexico. *Journal of Paleontology*, **42**, 801−803.

Downloaded by [UNAM Ciudad Universitaria] at 08:02 16 May 2014