



CARBONIFEROUS BRACHIOPODS (PRODUCTIDA AND ORTHOTETIDA) FROM SANTIAGO IXTALTEPEC, OAXACA, SOUTHERN MEXICO

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ABSTRACT – Ten species of Carboniferous brachiopods of the orders Productida and Orthotetida are described. The material occurs in Santiago Ixtaltepec, considered as one of the most important regions where Paleozoic rocks of Mexico are exposed. *Ozora* sp., *Tolmatchoffia keokuk* and *Marginatia* sp. were found in rocks from the Santiago Formation (APS-1), meanwhile the other taxa were collected in different strata from the Ixtaltepec Formation (API-2, API-5, API-6 and API-7). The record of the genera *Ozora* and *Marginatia* and the species *Tolmatchoffia keokuk* corroborate the Tournaisian–Visean age for the Lower Member of the Santiago Formation. The presence of *Productus concinnus* at API-2 level of the Ixtaltepec Formation places it in at least Visean age. *Antiquatonia* sp., *Orthotetes mixteca*, *Derbyia* sp. and *Schuchertella* sp. were found in previously dated Pennsylvanian strata. The fossil associations and the lithology allowed to relate each level where brachiopods were found with an intertidal, subtidal or peri-reef paleoenvironment. The presence of typical taxa from the Tournaisian of the Mid-Continent (United States) in the Santiago Ixtaltepec region suggests that there was a marine connection that joined both areas at least since the Early Mississippian. The occurrence of *Productus concinnus* in the Ixtaltepec Formation (API-2) confirms that Europe and Santiago Ixtaltepec region were linked during the Middle Mississippian. *Antiquatonia*, *Orthotetes*, *Derbyia* and *Schuchertella* are considered as cosmopolite genera whose presence in localities from the Mid-Continent is very common.

Keywords: Productida, Orthotetida, Carboniferous, Santiago Ixtaltepec, Oaxaca, Mexico.

RESUMO – O presente estudo descreve dez espécies de braquiópodes das ordens Productida e Orthotetida do Carbonífero. O material ocorre em Santiago Ixtaltepec, considerada uma das mais importantes regiões do México com exposição de rochas do Paleozoico. *Ozora* sp., *Tolmatchoffia keokuk* e *Marginatia* sp. foram encontrados em rochas da Formação Santiago (APS-1), enquanto os outros táxons foram coletados em diferentes extratos da Formação Ixtaltepec (API-2, API-5, API-6 e API-7). O registro dos gêneros *Ozora* e *Marginatia* e da espécie *Tolmatchoffia keokuk* corroboraram uma idade Tournaisiano–Viseano para o Membro Inferior da Formação Santiago. A presença de *Productus concinnus* no nível API-2 da Formação Ixtaltepec indica pelo menos idade Viseano. *Antiquatonia* sp., *Orthotetes mixteca*, *Derbyia* sp. e *Schuchertella* sp. foram encontrados nos extratos previamente datados como Pennsylvânico. As associações fossilíferas e a litologia permitiram relacionar os níveis onde os braquiópodes foram encontrados como de paleoambiente perirrecifal, subtidal ou intertidal. A presença de táxons típicos do Tournaisiano dos Estados Unidos na região de Santiago Ixtaltepec sugere que houve uma conexão marinha que uniu ambas as áreas pelo menos desde o Eomississipiano. A ocorrência de *Productus concinnus* na Formação Ixtaltepec (API-2) confirma que a Europa e a região de Santiago Ixtaltepec estavam interligadas durante o Mesomississipiano. *Antiquatonia*, *Orthotetes*, *Derbyia* e *Schuchertella* são considerados como gêneros cosmopolitas, cuja presença nas localidades dos Estados Unidos é muito comum.

Palavras-chave: Productida, Orthotetida, Carbonífero, Santiago Ixtaltepec, Oaxaca, México.

INTRODUCTION

Santiago Ixtaltepec has been considered one of the most important regions in Mexico where Paleozoic rocks are exposed. In particular, the Carboniferous is well represented by two lithostratigraphic units, the Santiago Formation of Tournaisian–Viséan age (Early Mississippian) and the Ixtaltepec Formation of Viséan–Moscovian age (Late Mississippian–Middle Pennsylvanian). Both are characterized by their diverse fossil record of marine invertebrates, such as conularids, corals, bivalves, gastropods, cephalopods, trilobites, bryozoans, brachiopods, and crinoids (Quiroz-Barroso & Perrilliat, 1997, 1998; Torres-Martínez & Sour-Tovar, 2012, 2016a,b, 2018; González-Mora & Sour-Tovar, 2014; Villanueva-Olea & Sour-Tovar, 2015). Brachiopods is the best represented group, being productidines the most diverse and abundant Order. In case of orthotetoids, they are not so varied but are very abundant in the upper levels of the Ixtaltepec Formation. The finding of index brachiopods from the Mississippian in the Santiago Formation and at the base of the Ixtaltepec Formation has allowed to date the strata as Tournaisian–Serpukhovian, confirming the age of the bearing rocks. In the same way, numerous brachiopods have been related with those recorded in different localities from the Mid-Continent in the United States, suggesting that during the Carboniferous there was a marine connection that related both regions (Quiroz-Barroso & Perrilliat, 1997; Torres-Martínez & Sour-Tovar, 2012, 2016a, b; Villanueva-Olea & Sour-Tovar, 2015). Nonetheless, this relation is not clear for the Mississippian due to the regionalization of North American taxa, which presumably occurred until the Pennsylvanian (Pérez-Huerta, 2007; Qiao & Shen, 2014). The aim of this work is to report several brachiopods for the first time in Mexico, which in turn allow defining the age of the bearing strata.

GEOLOGICAL SETTING

In the region of Santiago Ixtaltepec, near Nochixtlán municipality (Oaxaca State, Mexico, Figure 1), there are several Paleozoic outcrops in which Cambrian–Ordovician, Mississippian, and Pennsylvanian rocks have been identified (Pantoja-Alor, 1970). Paleozoic sedimentary rocks overly the Oaxacan Complex (Figure 2), composed of Proterozoic pegmatites, schists, paragneiss, and orthogneiss, with ages ranging from 900 to 1100 million years (Fries *et al.*, 1962; Solari *et al.*, 2003). The earliest sedimentary Paleozoic unit is the Tiñú Formation, composed of limestone and shale strata. This unit is divided in a Lower Member of limestone with abundant trilobites, linguliform brachiopods and other invertebrates from the Furongian (late Cambrian) (Robison & Pantoja-Alor, 1968; Landing *et al.*, 2007; Streng *et al.*, 2011), and an Upper Member of shale that records graptolites from the Lower Ordovician (Tremadocian) (Pantoja-Alor, 1970; Sour-Tovar & Buitrón-Sánchez, 1987; Sour-Tovar, 1990).

The Carboniferous succession comprises the Santiago Formation, informal unit by homonymy, and the Ixtaltepec

Formation, originally assigned to the Late Mississippian and Middle Pennsylvanian respectively (Pantoja-Alor, 1970). The Santiago Formation overlaps the Tiñú Formation in angular unconformity. This unit is 165 m thick, and is composed of limestone, sandstone and shale in its type section. It is divided in two members: the Lower Member, composed by sandstone and limestone with invertebrate fossils of Tournaisian age (Early Mississippian) (Quiroz-Barroso *et al.*, 2000; Navarro-Santillán *et al.*, 2002), and the Upper Member, composed of shale and sandstone with cephalopods indicating a Viséan age (Castillo-Espinoza, 2008, 2013; Castillo-Espinoza *et al.*, 2010). The Ixtaltepec Formation is transitionally placed on top of the Santiago Formation, which at its type section (Arroyo de las Pulgas) presents a thickness of 430 m, and exposes strata of siltstone, followed by intercalations of shale, fine-grained calcareous sandstone, and thin layers of slightly clayish calcarenite. Over these beds, there are banks of slightly sandy shale with fine-grained sand beds, followed by shale and fine-grained micaceous strata. In the upper levels there are thick layers of sandy shale interbedded with fine-grained shale. The Ixtaltepec Formation has been divided into eight informal levels, which are characterized by different fossiliferous associations. These subdivisions are named with the prefix API (Arroyo de las Pulgas Ixtaltepec) and their corresponding number. Rocks from units API-1 to API-4 bear several invertebrates of Mississippian age (Viséan–Serpukhovian), and units API-5 to API-8 are characterized by typical Pennsylvanian fauna (Bashkirian–Moscovian) (Torres-Martínez & Sour-Tovar, 2012, 2016a, 2016b; Villanueva-Olea & Sour-Tovar, 2015). Above the Ixtaltepec Formation is the Yododeñe Formation, composed of conglomerate, whose calcareous clasts have been assigned to the upper Permian–Lower Jurassic by the presence of fusulinid foraminifera. The Paleozoic sequence is covered by Cretaceous calcareous rocks (Pantoja-Alor, 1970).

SYSTEMATIC PALEONTOLOGY

All studied specimens are deposited in the collections of the Museo de Paleontología, Facultad de Ciencias, Universidad Nacional Autónoma de México. Type and figured specimens are designated in the descriptions by the prefix FCMP. The material is preserved as internal and external molds of both valves. In many cases, the internal molds of ventral valves are composite molds where is just possible to see the external morphology. The classification and terminology are based on Brunton *et al.* (2000) and Williams *et al.* (2000).

Class STROPHOMENATA Williams *et al.*, 1996
 Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959
 Suborder PRODUCTIDINA Waagen, 1883
 Superfamily PRODUCTOIDEA Gray, 1840
 Family PRODUCTELLIDAE Schuchert, 1929
 Subfamily MARGINIFERINAE Stehli, 1954
 Tribe BREILEENIINI Brunton & Lazarev, 1997

Desmoinesia Hoare, 1960

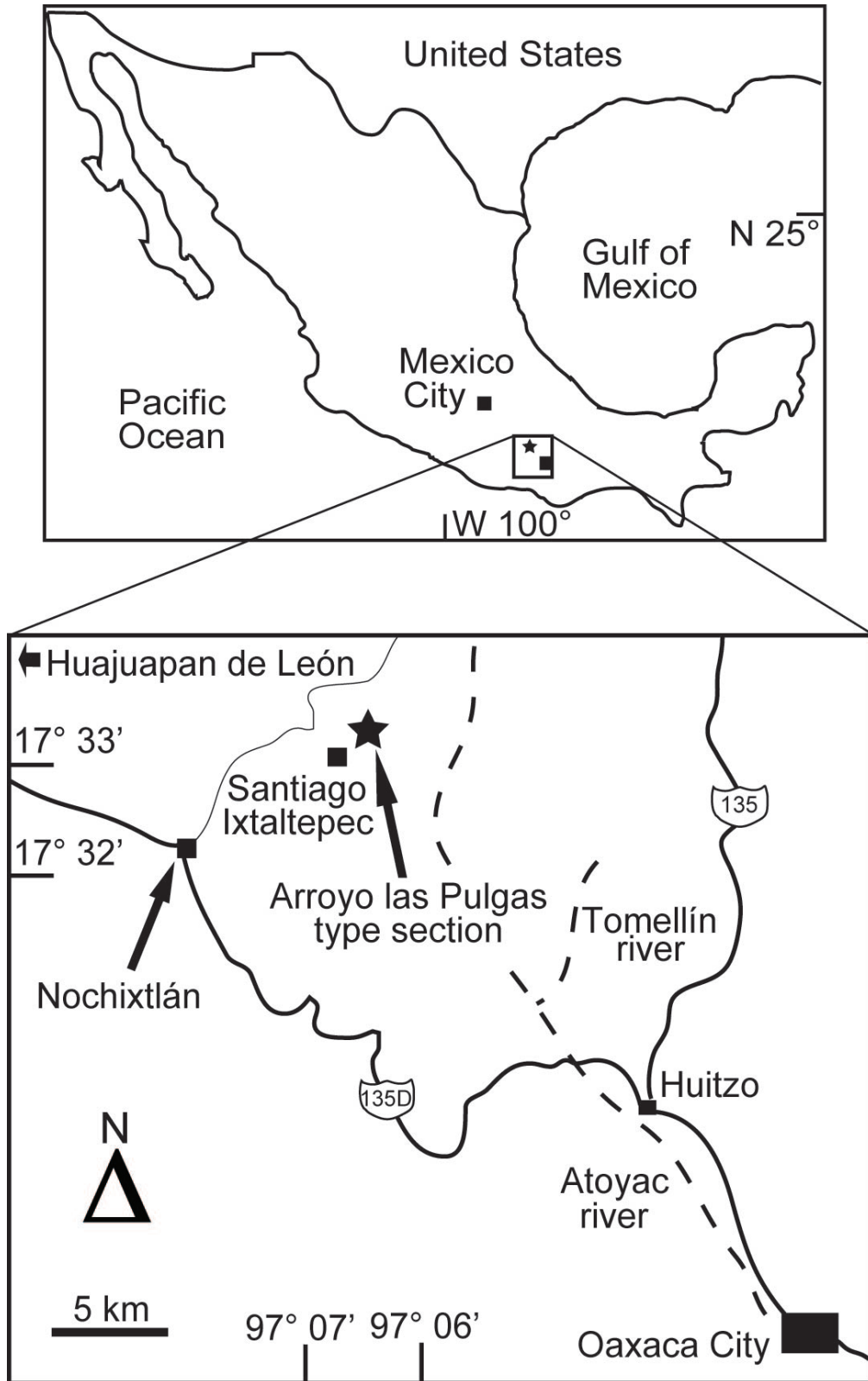


Figure 1. Geographic location of Santiago and Ixtaltepec formations in their type section (Arroyo de las Pulgas), where brachiopods herein studied were collected. Dashed lines represent rivers and solid lines roads.

Type species. *Productus muricatus* Norwood & Pratten, 1855. Pennsylvania, United States. Moscovian/Kasimovian (Middle Pennsylvanian).

Desmoinesia aff. *D. muricatina* (Dunbar & Condra, 1932)
(Figures 3A–D)

1855 *Productus muricatus* Norwood & Pratten, p. 14, pl. 1, figs. 8a–e.

1903 *Marginifera muricata* Girty, p. 373, pl. 5, figs. 5–5b, 6–6b, 7.

1932 *Marginifera muricatina* Dunbar & Condra, p. 222–224, pl. 35, figs. 1–10.

1960 *Desmoinesia muricatina* (Dunbar & Condra); Hoare, p. 226, 227, pl. 33, figs. 8–13.

1960 *Rudinia muricatina* (Dunbar & Condra); Muir-Wood & Cooper, p. 229, pl. 64, figs. 11–25.

1961 *Desmoinesia muricatina* (Dunbar & Condra); Hoare, p. 61–63, pl. 4, figs. 17–22.

Material. Two ventral internal molds (FCMP 1211, 1212) and two ventral external molds (FCMP 1212, 1213).

Description. Small-sized ventral valve, subrectangular, slightly convex, with its greatest width at mid-length. Short ears, slightly convex. Small up to 11 mm in length and 18 mm in width. Geniculated, especially in anterior region. Narrow sulcus, slightly deep. The beak is small and protrudes five millimeters beyond hinge. Ornamentation consists of irregular costae, bifurcating randomly on the valve, eight to nine occurring in space of 5 mm over anterior margin. Strong concentric rugae, numerous, closely spaced, crossing costae along the valve. Small spines are on the costae, occurring (1) scattered over valve, and (2) two in single row parallel to hinge. Interior not observed.

Occurrence. Ixtaltepec Formation, level API-7, Arroyo de las Pulgas type section. Bashkirian–Moscovian (Lower–Middle Pennsylvanian).

Remarks. The specimens of *Desmoinesia* from Santiago Ixtaltepec display features that resemble *Desmoinesia muricatina* of the Cherokee Group from Desmoinesian of Missouri (Hoare, 1960, p. 61), such as its small size, subrectangular shape, short and slightly convex ears, greatest width at mid-length, valve convex, more so in the posterior region, geniculated at anterior region, beak small which protrudes beyond hinge, number and shape of costae, and scattered spines on the valve as well. Nonetheless, our material differs from that species by the presence of two spines parallel to the hinge, and prominent rugae over the anterior two-thirds of the valve, features that have never been described for *Desmoinesia muricatina*. These traits suggest that Oaxacan material could be a new species, but the lack of dorsal valves and internal features prevents us to do a new specific assignment. Nevertheless, this is the first occurrence of the genus in Mexico.

Family PRODUCTIDAE Gray, 1840
Subfamily PRODUCTINAE Gray, 1840

Tribe PRODUCTINI Nalivkin, 1979

Productus Sowerby, 1814

Type species. *Anomites productus* Martin, 1809. Derbyshire, England. Visean (Middle Mississippian).

Productus concinnus Sowerby, 1821

(Figures 3E–G)

1821 *Productus concinnus* Sowerby, p. 16, pl. 318, fig. 1.

1928 *Productus concinnus* Sowerby; Muir-Wood, p. 49, pl. 1, figs. 7–10.

1943 *Proboscidella fasciculate* Delépine, p. 71, pl. 3, figs. 1, 2.

1952 *Productus concinnus* Sowerby; Sarytcheva & Sokolskaya, p. 137, pl. 37, fig. 184.

1979 *Productus concinnus* Sowerby; Martínez-Chacón, p. 173, pl. 16, fig. 17; pl. 17, figs. 1–10.

Material. A composite mold, with part of ventral external mold and part of dorsal internal mold (FCMP 1214).

Description. Medium-size shell, with greatest width at the trail and deep corpus. Medium shell up to 31 mm in length and 40 mm in width. Ventral valve convex, greatest convexity in posterior region. Long trail, extended laterally. Visceral disc slightly geniculated. Median shallow sulcus vanishes toward the anterior margin. Flanks steep. Small umbo strongly incurved. Ornamented by complete costae, beginning at the beak and well developed until the trail, with few bifurcations, 12 occurring per 10 mm over the posterior region of the trail. Few rugae on the visceral disc, forming a reticulation with the costae. Scattered spines over valve cluster of numerous spines on flanks. Ventral interior not observed. Dorsal interior with wide diaphragm area. The diaphragm is concentric around the visceral disc. Median septum is long, anteriorly narrow and posteriorly stout, extending two-thirds length of valve. The lateral ridges diverge slightly from the hinge, curving around inside ears until reaching the lateral margin. Scars of adductor muscles elongate and suboval in outline.

Occurrence. Ixtaltepec Formation, level API-2, Arroyo de las Pulgas type section. Visean (Middle Mississippian).

Remarks. The specimen of Nochihtlán resembles *Productus concinnus* from the Valdeteja Formation (Lower Bashkirian) of the Cantabrian Mountains described by Martínez-Chacón (1979, p. 173). This species has been recorded in Belgium (Visean), England, Russia (Visean/Bashkirian) and the Cantabrian Mountains (Bashkirian) (Martínez-Chacón, 1979). This is the first report of *Productus concinnus* in Mexico.

Tribe RETARIINI Muir-Wood & Cooper, 1960

Antiquatonia Miloradovich, 1945

Type species. *Productus antiquatus* Sowerby, 1821. Derbyshire, England. Visean (Middle Mississippian).

Antiquatonia sp.
(Figures 3H–I)

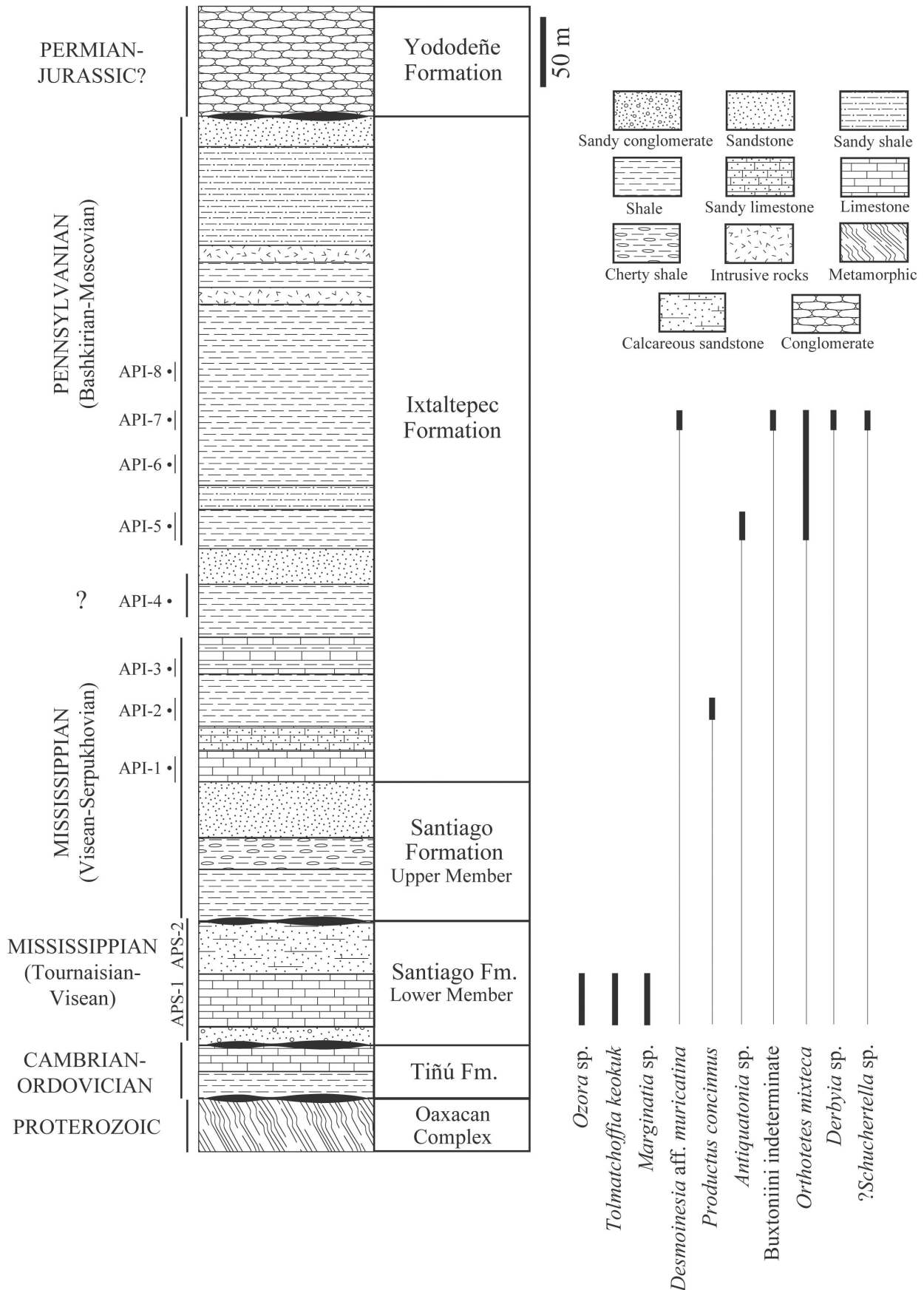


Figure 2. Stratigraphy of the Paleozoic outcrops from Santiago Ixtaltepec region. Wider dark lines represent the stratigraphic level where brachiopods were found and thin ones are guidelines. **Abbreviations:** API, Arroyo de las Pulgas Ixtaltepec; APS, Arroyo de las Pulgas Santiago.

Material. A ventral internal mold with external impression (FCMP 1215).

Description. Ventral valve strongly convex, more so at mid-length, not geniculated. Subrectangular in outline, with greatest width anterior to hingeline. Large up to 26 mm in length and 44 mm in width. The sulcus is shallow, begins in the umbo, and extends towards the anterior margin. Ears large and strongly arched. Umbo shallow and broad. Beak protruding. The ornamentation consists of subequal costae, entire, usually bifurcated, 10 in space of 10 mm on the trail. Concentric rugae on posterior region. Spines over costae occurring (1) scattered on the valve, (2) in simple row parallel to hingeline, and (3) in row in the base of umbo. Interior not observed.

Occurrence. Ixtaltepec Formation, level API-5, Arroyo de las Pulgas type section. Bashkirian–Moscovian (Lower–Middle Pennsylvanian).

Remarks. The specimen of *Antiquatonia* sp. displays similar features to *Antiquatonia portlockiana* (Norwood & Pratten) and *Antiquatonia hermosanus* (Girty) from the Burgner Formation (Moscovian) of Missouri (Hoare, 1961, p. 53, 56, respectively). Our material is similar to that of Missouri in the ventral valve convex, strongly arched ears, concentric rugae in posterior region, and spines on each side of the base of umbo and simple row of spines parallel to hingeline. However, *Antiquatonia* sp. differs from *A. portlockiana* in the broad umbo, protruding beak, shallow sulcus, more numerous costae per 10 mm on the trail, and a weak posterior reticulation as well. Moreover, the Oaxacan specimen is dissimilar of *A. hermosanus* by its protruding beak, convergent costae absent, more number of bifurcated costae and fewer spines parallel to hingeline. The lack of internal features, a complete trail and dorsal valves did not allow us to relate the material to any previously described species.

Subfamily DICTYOCLOSTINAE Stehli, 1954
Tribe DICTYOCLOSTINI Stehli, 1954

Ozora Carter, 1990

Type species. *Ozora genevievensis* Carter, 1990. Illinois, United States. Visean (Middle Mississippian).

Ozora sp.
(Figures 3J–L)

Material. Two ventral internal molds (FCMP 1216, 1217) and a dorsal external mold (FCMP 1218).

Description. Medium-sized shell, subrectangular in outline, greatest width at hingeline. Medium shell up 36 mm in length and 33 mm in width. Ventral valve strongly convex with corpus cavity elevated. Short and slightly convex ears. Median sulcus moderately deep, beginning about 1 cm anterior to beak and continuing until anterior margin, more broad at anterior border. Flanks diverge 70°, descending towards the ears. Ornamented by costae that increase by both bifurcation and intercalation, which are fine on the visceral

disc and strong on the trail, 10–12 per 10 mm over the anterior margin. Concentric rugae on the visceral disc. Spines on the costae, on flanks and the trail, other in parallel row to the hingeline. Dorsal valve slightly concave, almost flat, anteriorly geniculate. Trail short. A median fold is developed corresponding to the ventral sulcus, initiating in the visceral disc and extending to anterior margin where it becomes broad. The ornamentation is similar to that of the ventral valve, but the rugae are prominent, forming a reticulation. Interior not observed.

Occurrence. Santiago Formation, Lower Member, Arroyo de las Pulgas type section. Tournaisian (Lower Mississippian).

Remarks. The specimens studied are related with *Ozora* from the Tournaisian (Lower Mississippian) of the United States. The material displays diagnostic features of the genus, such as the strongly inflated shape, geniculated, median sulcus moderately developed, corpus cavity elevated, reticulation on the visceral disc, spines on flanks, trail and near hinge, and dorsal valve strongly geniculated (Carter, 1990, p. 226). The material resembles *Ozora genevievensis* Carter, (1990, p. 227–229), but the poor conservation do not allow us to identify it with more certainty. This is the first record of *Ozora* in Mexico.

Subfamily BUXTONIINAE Muir-Wood & Cooper, 1960
Tribe BUXTONIINI Muir-Wood & Cooper, 1960

Buxtoniini genus and species indeterminate
(Figure 3M)

Remarks. The material consists of an internal mold of ventral valve (FCMP 1219) from the Ixtaltepec Formation, level API-7 (Bashkirian–Moscovian), Arroyo de las Pulgas type section. The specimen displays a small size with about 31 mm in length and 40 mm in width. Subcircular in outline, geniculated. Slightly convex, mainly at the umbo. Deep corpus cavity. Moderately long trail. Large ears flattened and separated from umbonal slopes by a shallow concave flexure, extending towards the anterolateral margins like a bordering flange. Median sulcus weak, beginning about 7 mm anterior to beak, and continuing until anterior margin. Umbo short, protruding 1 mm across hingeline. Irregular costae on the entire valve, weak on posterior region and absent on the ears, 11 occurring in the space of 10 mm on anterior slope, increased anteriorly by intercalation. Narrow rugae on the entire valve, except on the umbo. As well as, swollen elongate spine bases, widely scattered, in rows on lateral margins and clustered on the ears. The specimen resembles *Kochiproductus* Dunbar, 1955, or an allied genus of the tribe Buxtoniini. The material of Ixtaltepec differs from *Kochiproductus* from the lower Permian of Arctic regions, Mongolia, North and South America (Brunton *et al.*, 2000), in its smaller size, lower convexity, costae anteriorly more notorious, rugae prominent on ventral valve, and the different arrangement of spines. This could be a new genus but until now, there are not more specimens to reliably compare.

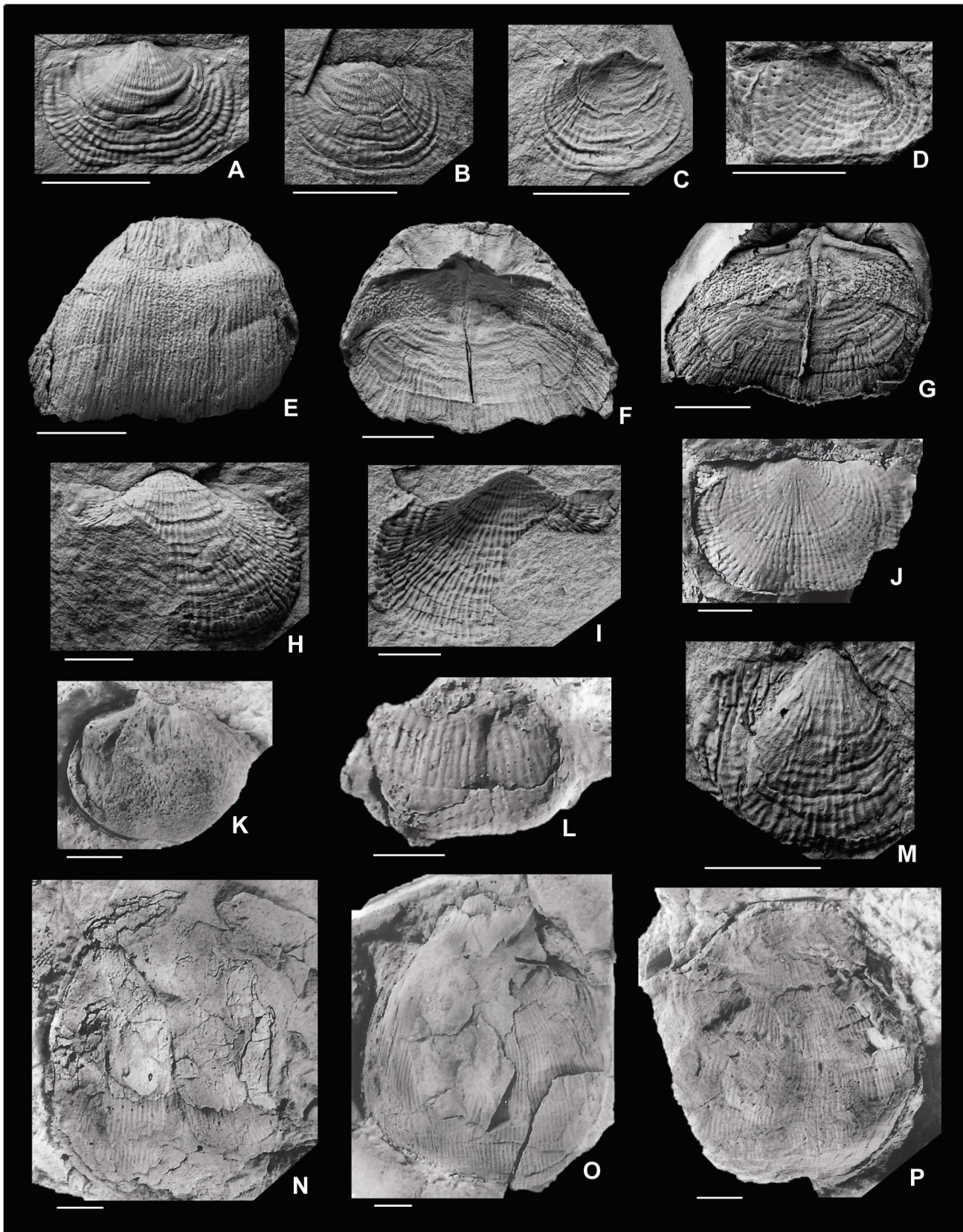


Figure 3. A–D, *Desmoinesia* aff. *muricatina*, A, ventral internal mold (FCMP 1211); B, C, ventral internal and external molds (FCMP 1212); D, ventral external mold (FCMP 1213). E–G, *Productus concinnus*, ventral external (E), dorsal internal (F) and rubber cast of dorsal internal mold (G) (FCMP 1214). H, I, *Antiquatonia* sp. ventral internal and external molds (FCMP 1215). J–L, *Ozora* sp., J, dorsal external mold (FCMP 1218); K, ventral internal mold (FCMP 1216); L, ventral internal mold (FCMP 1217). M, Buxtoniini genus and species indeterminate, ventral internal mold (FCMP 1219). N–P, *Tolmatchoffia keokuk*, N, ventral internal mold (FCMP 1220); O, ventral internal mold (FCMP 1221); P, ventral internal mold (FCMP 1222). Scale bars = 10 mm.

Tribe TOLMATCHOFFIINI Sarytcheva *et al.*, 1963

Tolmatchoffia Frederiks, 1933

Type species. *Productus robustus* Tolmatchoff, 1924. Kuznetsk, Russia. Tournaisian (Lower Mississippian).

Tolmatchoffia keokuk (Hall, 1858)
(Figures 3N–P)

1858 *Productus setigerus?* var. *keokuk* Hall, p. 639, pl. 19, figs. 4b–c.

1927 *Productus* aff. *keokuk* (Hall); Girty, p. 64, pl. 23, figs. 3–6.

1931 *Productus keokuk* (Hall); Hewett, p. 19.

1967 *Tolmatchoffia keokuk* (Hall); Sando, p. 541.

1990 *Tolmatchoffia keokuk* (Hall); Kammer *et al.*, p. 419.

2014 *Tolmatchoffia keokuk* (Hall); Carter *et al.*, p. 270, figs. 6A–F.

Material. Four ventral valves (FCMP 1220–1223) and a dorsal internal mold (FCMP 1224).

Description. Large concave-convex shell, corpus deep, subovate with greatest width in the anterior region. Slightly longer than wide. Large shell up to 80 mm in length and 60 mm in width. Ventral valve strongly convex with venter almost flattened. Gently spreading trail. Steep flanks. Weak to shallow median sulcus begins at mid-length of visceral disc and extends to end of trail. Short and slightly convex ears. Umbo massive, curve and rounded, protruding slightly across hingeline. Entire costae on the valve with some bifurcations on the trail, 9–11 per 10 mm in the anterior region, separated by narrow and rounded intercostal grooves. Concentric faint rugae on the visceral disc. Spines occurring beside the costae (1) in concentric rows on the trail, and (2) clustered on the flanks and ears. Dorsal valve slightly concave, subcircular in outline, with greatest width at mid-length. Small and rounded umbo. The ornamentation is poorly visible but is similar to that of the ventral valve.

Occurrence. Santiago Formation, Lower Member, Arroyo de las Pulgas type section. Tournaisian (Lower Mississippian).

Remarks. The Oaxacan specimens are related with *Tolmatchoffia* by distinctive traits of the genus, such as their large shell, almost planoconvex shape, greatest width in the anterior region, corpus deep, gently spreading trail, umbo massive, extending slightly beyond hingeline, ears small, scattered spines on ventral valve (commonly concentric on ventral trail and crowded on ears and flanks) and slightly developed rugae (Muir-Wood & Cooper 1960, p. 290; Brunton *et al.*, 2000, p. 502). The material resembles especially *Tolmatchoffia keokuk*, recorded in the Keokuk Limestone from Tournaisian of Iowa and Illinois in the United States (Hall, 1858, p. 639). According to Hall (1858), this species displays an ovoid shell, hingeline equaling or less than the greatest width, broad and shallow sulcus, umbo very prominent, entire rounded costae that are about equal to the spaces between them, bifurcating anteriorly, and bases of small tubular spines,

crowded in cardinal margins and ears. The genus occurs in the Lower Mississippian of United States in Iowa (Hall, 1858), Idaho (Girty, 1927), Wyoming (Sando, 1967), Missouri and Illinois (Kammer *et al.*, 1990), as well as in Eurasia and northern Africa (Brunton *et al.*, 2000). This is the first report of the genus in Mexico.

Marginatia Muir-Wood & Cooper, 1960

Type species. *Productus fernglenensis* Weller, 1909. Missouri, United States. Tournaisian (Lower Mississippian).

Marginatia sp.
(Figures 4A–C)

Material. Two ventral internal molds (FCMP 1225, 1226).
Description. Medium-sized ventral valve, subquadrate in outline, strongly geniculated, curved trail. Medium up to 28 mm in length and 26 mm in width. Flanks steep. Broad and shallow sulcus on venter and trail. Umbo small. The ornamentation consists of entire costae, 10–12 per 5 mm at mid-length, with some bifurcations on the anterior region. Narrow and regular rugae over visceral disc, four in space of 5 mm at mid-length, forming a reticulation with the costae. Spines widely scattered on the trail and flanks.

Occurrence. Santiago Formation, Lower Member, Arroyo de las Pulgas type section. Tournaisian (Lower Mississippian).

Remarks. The specimens of the Santiago Formation display certain features described by Muir-Wood & Cooper (1960), such as the subquadrate shell in outline, ventral valve convex with slightly sulcate venter, curved trail, flanks steep, entire costae, spines on trail, and narrow rugae on visceral disc, forming a reticulation with the costae. *Marginatia* has been reported in numerous localities from the Tournaisian/lower Visean (Lower–Middle Mississippian) of the world, being the material herein described the first record of the genus in Mexico.

Order ORTHOTETIDA Waagen, 1884
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily ORTHOTETOIDEA Waagen, 1884
Family ORTHOTETIDAE Waagen, 1884

Orthotetes Fischer de Waldheim, 1850

Type species. *Orthotetes radiata* Fischer de Waldheim, 1850. Kaluga, Russia. Visean (Middle Mississippian).

Orthotetes mixteca Sour-Tovar & Quiroz-Barroso, 1989
(Figures 4D–I, K)

1989 *Orthotetes mixteca* Sour-Tovar & Quiroz-Barroso, p. 10, pl. 3, figs. 1a–d.

2008 *Orthotetes mixteca* Sour-Tovar & Quiroz-Barroso; Buitrón-Sánchez *et al.*, p. 7.

Material. A ventral internal mold (FCMP 1227), two dorsal

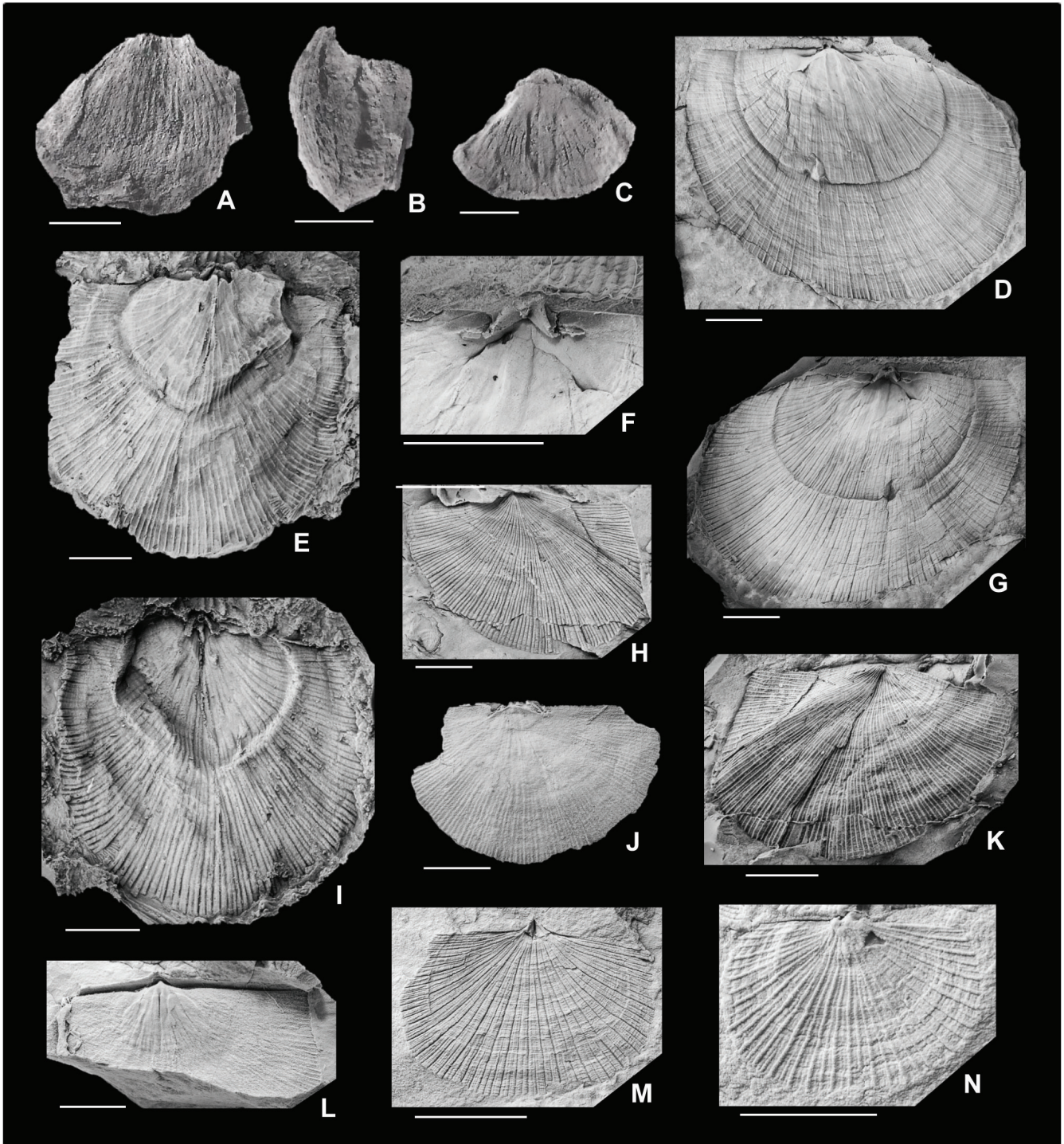


Figure 4. A–C, *Marginatia* sp., A, B, ventral internal mold in ventral and lateral view (FCMP 1225); C, ventral internal mold (FCMP 1226). D–I, *Orthotetes mixteca*, D, G, dorsal internal mold (D) and rubber cast (G) (FCMP 1228); E, I, ventral internal mold (E) and rubber cast (I) (FCMP 1227); F, close up of cardinal process from FCMP 1228; H, K, dorsal external and internal molds (FCMP 1229). J, L, *Derbyia* sp., J, dorsal internal mold (FCMP 1230); ventral internal mold (FCMP 1231). M, N, *Schuchertella* sp., M, ventral external mold (FCMP 1233); N, dorsal internal mold (FCMP 1234). Scale bars = 10 mm.

internal molds (FCMP 1228, 1229) and a dorsal external mold (FCMP 1229).

Description. Large to medium shell, elliptic in outline, resupinate. Greatest width at mid-length. Large shell up to 52 mm in length and 48 mm in width. Ventral valve slightly convex in lateral profile, most inflated in posterior region.

Cardinal extensions subquadrate. Umbo small, protruding slightly across hingeline. Interarea anacline with about 45° to 50°. Ornamentation consists of radial costae, 34–36 occur in 10 mm at anterior margin, parvicostallate in arrangement slightly irregular, that is a first order costa followed by two third order costae, after a second order costa followed by

two third order costae and a first order costae. Concentric and fine growth lines on the entire valve. Concentric rugae on the valve, mainly in the posterior region. Interior with high median septum, extended to two-thirds length of valve, embracing by large muscle scars, flabellate. Dental ridges converge with the median septum, forming a small delthyrial chamber. Dorsal valve slightly convex, being more inflated at mid-length. Interarea vestigial. Ornamentation similar to ventral valve but the growth lines are regular on the entire valve. Interior with small-corrugated chilidium. Cardinal process well-developed and socket ridges recurved.

Occurrence. Ixtaltepec Formation, levels API-5, API-6 and API-7, Arroyo de las Pulgas type section. Bashkirian–Moscovian (Lower–Middle Pennsylvanian).

Remarks. The specimens of *Orthotetes mixteca* collected in recent years allowed us to observe morphological traits that had never been reported for the species in previous works. The description in this manuscript complements the original taxonomic features of the Mexican species recorded by Sour-Tovar & Quiroz-Barroso (1989, p. 10, pl. 3).

Family DERBYIIDAE Stehli, 1954

Derbyia Waagen, 1884

Type species. *Derbyia regularis* Waagen, 1884. Salt Range, Pakistan. Guadalupian (middle Permian).

Derbyia sp. (Figures 4J–L)

Material. An internal mold of shell (FCMP 1230), a ventral internal mold (FCMP 1231) and a ventral external mold (FCMP 1231).

Description. Small to medium-sized shell, subcircular to subelliptic shape in outline, resupinate and uniplicate. Greatest width at mid-length with a smaller hingeline. Cardinal extensions subrounded. Medium shell up 24 mm in length and 27 mm in width. Ventral valve slightly convex in the posterior region, becoming slightly concave anteriorly. Interarea anacline with an angle of 40°. Triangular delthyrium with about 70°. Numerous radial costae on the entire valve, thin in a parvicostellate arrangement, with a first order costa followed by three costae of second order and a first order costa, 37–39 in a space of 10 mm in the anterior margin. Irregular concentric growth lines and regular rugae on the valve. Interior with ventral muscle area wide and short, ventral muscle scars flabellate and bisected by median septum. Dorsal valve slightly convex. Ornamentation is similar to opposite valve. Interior with cardinal process short and chilidium not observed.

Occurrence. Ixtaltepec Formation, level API-7, Arroyo de las Pulgas type section. Bashkirian–Moscovian (Lower–Middle Pennsylvanian).

Remarks. The material was assigned to *Derbyia* because of different diagnostic traits of the genus, such as the distorted shape of the shell, commissure uniplicate, ornamentation of

bifurcated and intercalated fine costae, with several growth lines, ventral muscle area wide and short, with median septum, as well as a short cardinal process (Cooper & Grant, 1974, p. 289; Williams *et al.*, 2000, p. 657). *Derbyia* sp. differs from *Orthotetes mixteca* in its smaller size, more numerous costae and rugae, different parvicostellate arrangement, smaller ventral muscle area and absence of chilidium.

Family SCHUCHERTELLIDAE Williams, 1953 Subfamily SCHUCHERTELLINAE Williams, 1953

Schuchertella Girty, 1904

Type species. *Streptorhynchus lens* White, 1862. Missouri and Illinois, United States. Visean (Middle Mississippian).

?*Schuchertella* sp. (Figures 4M–N)

Material. A ventral internal mold (FCMP 1232), a ventral external mold (FCMP 1233) and a dorsal internal mold (FCMP 1234).

Description. Small-sized schuchertellinid, subcircular to subrectangular in outline, resupinate, almost flat. Greatest width anterior to the hingeline. With about 15 mm in length and 22 mm in width. Cardinal extensions subrounded, slightly acute. Ventral valve slightly convex in the posterior region, becoming concave anteriorly. Interarea anacline of about 85°. Delthyrium triangular in angle approximate of 30°. Pseudodeltidium convex. Numerous radial costae on the entire valve, 24–28 per 10 mm in the anterior border, irregularly parvicostellate. Concentric growth lines and irregular rugae over the valve. Dorsal valve slightly convex, mainly in the posterior region. Ornamentation similar to the ventral valve but with weak growth lines.

Occurrence. Ixtaltepec Formation, level API-7, Arroyo de las Pulgas type section. Bashkirian–Moscovian (Lower–Middle Pennsylvanian).

Remarks. The specimens studied are related with the Subfamily Schuchertellinae by their rectimarginate shape, costellate with concentric ornamentation, pseudodeltidium convex and linear dorsal interarea (Williams *et al.*, 2000). These traits added to the external ornamentation and a ventral interarea anacline suggest that the material belongs to the genus *Schuchertella*. However, poor preservation and lack of muscle scars prevented us to do a reliable assignment. ?*Schuchertella* sp. differs from *Orthotetes mixteca* and *Derbyia* sp. in its smaller size, fewer number and different arrangement of costae and more numerous rugae.

DISCUSSION

Ozora sp., *Tolmatchoffia keokuk* and *Marginatia* sp. were found in the APS-1 unit, a basal level of the Santiago Formation. This unit is composed by limestone with intercalations of calcareous sandstone and contains a varied fossil association, mainly constituted of photic-independent

biota (bryozoans, brachiopods and crinoids) (Pomar, 2001). These taxa were preserved as disarticulated calcified specimens. The type of fauna, preservation of fossils and calcareous features of the bearing rocks have allowed to relate the depositional setting with a peri-reef environment. The presence of the genera *Ozora* and *Marginatia* and the species *Tolmatchoffia keokuk* in lower beds of the Santiago formation confirms the Tournaisian–Visean age of the bearing strata, previously inferred by the brachiopods *Lamellosathyris lamellosa* and *Torynifer pseudolineatus* (Navarro-Santillán *et al.*, 2002).

Productus concinnus was found at API-2 level of the Ixtaltepec Formation, characterized by shale strata with intercalations of calcareous shale. Herein highlight the presence of diverse brachiopods (Torres-Martínez & Sour-Tovar, 2012, 2016a, b), bivalves (Quiroz-Barroso & Perrilliat, 1997, 1998), crinoids (Villanueva-Olea & Sour-Tovar, 2015), and other groups of invertebrates, which were associated in a peri-reef community. In this level, the occurrence of the brachiopods *Orbiculoidea caneyana* (Torres-Martínez & Sour-Tovar, 2016a), *Ovatia muralis* (Torres-Martínez & Sour-Tovar, 2012), *Inflatia inflata* (Torres-Martínez & Sour-Tovar, 2016b), *Stegacanthia bowsheri* and *Undaria* sp. (Torres-Martínez & Sour-Tovar, 2018) have allowed to assign the age of the bearing rocks to the Visean (Middle Mississippian). Likewise, the presence of *Productus concinnus* in the Visean of Mexico coincides with the previous records of this species from the Visean–Bashkirian of Europe (Martínez-Chacón, 1979).

Antiquatonia sp. and *Orthotetes mixteca* were deposited at API-5, composed by shale and siltstone, and characterized by the presence of abundant chonetidines (Sour-Tovar & Martínez-Chacón, 2004) and neospiriferins (Torres-Martínez *et al.*, 2008). It has been inferred that these brachiopods were accumulated *post-mortem* in a subtidal environment, which was subject to seasonal variations of energy and high input of terrigenous. The finding of brachiopods *Neochonetes (N.) granulifer* (Sour-Tovar & Martínez-Chacón, 2004) and *Neospirifer dunbari* (Torres-Martínez *et al.*, 2008) have allowed to relate this level with a Bashkirian–Moscovian age (Early–Middle Pennsylvanian).

Finally, *Desmoinesia* aff. *muricata*, *Orthotetes mixteca*, *Derbyia* sp. and *Schuchertella* sp. were found at API-7 which has the most diverse fossil association of the Ixtaltepec Formation. This is made up of argillaceous strata, maybe deposited in an intertidal or a peri-reef environment. The age of this level has been confirmed by the presence of *Orbiculoidea missouriensis*, *O. capuliformis* (Torres-Martínez & Sour-Tovar, 2016a), *Neochonetes (N.) granulifer* (Sour-Tovar & Martínez-Chacón, 2004), *Reticulatia huecoensis* (Torres-Martínez & Sour-Tovar, 2016b), *Echinaria knighti*, *Linoproductus platyumbonus*, and *Linoproductus prattenianus* (Torres-Martínez & Sour-Tovar, 2012); all of them typical species of the Lower–Middle Pennsylvanian (Bashkirian–Moscovian) of North America.

Paleobiogeographical considerations

Previously, it has been suggested in several works that there is a strong affinity among the Carboniferous invertebrates of Santiago Ixtaltepec and coeval faunas from diverse localities of the Mid-Continent region, central-eastern of the United States (*i.e.* Quiroz-Barroso & Sour-Tovar, 1996; Quiroz-Barroso & Perrilliat, 1997, 1998; Sour-Tovar *et al.*, 1996; Navarro-Santillán *et al.*, 2002; Torres-Martínez & Sour-Tovar, 2016b). However, some recent works have also proved that this similarity decreases with the age of the faunas. Porrás-López (2017) made a paleogeographical analysis of productidines from the Carboniferous of Oaxaca, based on the application of similitude indices (Simpson, Sorensen, and Jaccard). This study demonstrated that during the Mississippian the resemblance of Oaxacan faunas were mainly with North American invertebrates; nonetheless, there are many cosmopolite genera. The same work states that at the end of the Mississippian the similarity with taxa from the United States increased, reaching a strong regionalization during the Pennsylvanian.

The genus *Ozora* and the species *Tolmatchoffia keokuk* are relatively common taxa from localities of the Mid-Continent, and their records in Oaxaca suggest that there was a geographic connection between both regions at least since the Early Mississippian. In contrast, *Marginatia* is considered a cosmopolitan taxa of low-latitudes.

The presence of *Productus concinnus* suggests that during the Middle Mississippian (Visean) the Santiago Ixtaltepec region was also connected to Europe by means of a marine connection. The rest of productidines and orthotetoids brachiopods herein described occur in Pennsylvanian strata. *Antiquatonia*, *Orthotetes*, *Derbyia* and *Schuchertella* are considered as cosmopolite genera in the Late Carboniferous, and their presence in several localities of the Mid-Continent is very common. Their records in the Santiago Ixtaltepec region increase the faunal similitude values between Pennsylvanian localities of the United States and Oaxaca.

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