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RESEARCH PAPER

Permian brachiopods from Chiapas, Mexico: new stratigraphical and paleobiogeographical insights

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Abstract
Eleven brachiopod species from the Paso Hondo Formation in the Chicomuselo region of southern Chiapas, Mexico are described. *Chonosteges cooperi* is a new species. *Dyoros* (*Tetragonetes*) *rectangulatus*, *Costispinifera rugatula*, *Echinosteges tuberculatus*, *Tropidelasma furcillatum*, *Acosarina rectimarginata*, *Tautosia transenna*, *Composita hapsida*, and *Neospirifer venezuelensis* are recorded for the first time in Mexico. The brachiopods occur in a locality to the east of the town of Monte Redondo, deposited in limestone and argillaceous limestone. The associated biota is composed of different filter feeders, with diverse invertebrates (rugose corals, microconchids, hederelloids, bryozoans, and crinoids) recorded. Lithological traits and features of the fossils allowed the facies to be assigned to a shallow open marine paleoenvironment, within a homoclinal ramp. Brachiopods recorded at the locality allow the upper levels of the Paso Hondo Formation to be correlated with the Cherry Canyon and Road Canyon formations of Texas in the United States, which have been characterized as typical stratigraphic units from the Guadalupian of North America. This information indicates that the age of the Paso Hondo Formation can be extended from the Early Permian to the Roadian (early Guadalupian), making this the first report of a formation of this age in southeastern Mexico. The presence of typical taxa from the Middle Permian in both Chiapas and Texas suggests that those regions were closely connected during the late Paleozoic, at least during the early Guadalupian. The similarity of Mexican biota to coeval faunas of Texas indicates that the brachiopods found in Chiapas occurred in the Grandian Province during the Middle Permian, which also included Texas and New Mexico, Guatemala, Venezuela, and northwest Mexico.

Keywords Brachiopoda · Paso Hondo Formation · Middle Permian · Paleoenvironment · Stratigraphy · Grandian Province

Introduction

The Southeastern Chiapas State, which borders Guatemala, is a mountainous region where mainly Carboniferous, Permian, Jurassic, and Cretaceous rocks outcrop. In particular, those of Permian age are made up of carbonates and, to a lesser extent, siliciclasts. Such rocks are associated with the Grupera (Asselian−Sakmarian), La Vainilla (Sakmarian−Artinskian), and Paso Hondo (Artinskian−Kungurian) formations, which were deposited in the Chicomuselo region during the Early Permian (Thompson and Miller 1944; Hernández-García 1973). Microfacies analysis has shown that the Paso Hondo Formation was deposited during a transgressive event, as it has facies associated with homoclinal ramp environments, such as lagoons, open waters, and mid-ramps (Torres-Martínez et al. 2017b).

The Paso Hondo Formation contains a diverse fossil biota encompassing organisms such as corals, gastropods, bivalves, cephalopods, ostracods, bryozoans, brachiopods, and crinoids, as well as foraminifera and algae (Thompson 1956; Hernández-García 1973; Buitrón-Sánchez 1977). A few of these have been found as Cisuralian specimens from Texas and New Mexico in the United States, Coahuila in the north of Mexico, and Venezuela (Mullerried et al. 1941; Thompson and Miller 1944; Kling 1960; Hernández-García 1973, Torres-Martínez et al. 2016). The age of the Paso Hondo Formation was inferred from the presence, at different levels, of the foraminifera *Staffella centralis*, *Mesoschubertella mullerriedi* (=*Schubertella mullerriedi*), *Parafusulina australis*, and *Eoverbeekina americana*, as well as

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the cephalopods *Perrinites hilli*, and *Kargalites mullerriedi* (=*Peritrochia mullerriedi*)—a set that suggested an Artinskian−Kungurian age (Mullerried et al. 1941; Thompson and Miller 1944). In this work, the brachiopod fauna of the Paso Hondo Formation is described and analyzed based on biostratigraphical information, and the pre-established criteria that were used to determine the age of the formation are discussed.

Geological setting

The rocks of the locality studied herein are made up of light gray argillaceous limestone, located between the Ishcanal and Manguito hills at 15°38′N to 15°39′N and 92°01′W to 92°02′W (Fig. 1). The Paso Hondo Formation was reported in 1944 by Thompson and Miller, who described it as a limestone and marl series that crop out at several sites along the south flank of the anticline of Chicomuselo, mainly in the southeast and west part of Paso Hondo town. The type locality occurs on the Comalapa River, near the town of the same name, in the southeast region of Chiapas, bordering Guatemala (Hernández-García 1973). The base of this formation is characterized by shale with intercalations of gray limestone. The rest of the unit is made up of limestone strata of variable thickness (up to 10 m), which can contain nodules and black flint veinlets. The limestones can consist of facies of mudstone, wackestone, packstone, or grainstone of several colors. Most are very fossiliferous, with brachiopods, mollusks, crinoids, corals, and other invertebrates found in them. In some localities, interbedded shale is common.

The total thickness of the unit is not yet known, but southwest of Chicomuselo there are sections about 600 m thick (Ibarra-Mora et al. 2006). In this context, it has been proposed that the formation could have a maximum thickness of about 1900 m (Motolinia-García et al. 2004), possibly including the La Vainilla limestone (López-Ramos 1979). Thompson and Miller (1944) assigned a Leonardian (= late Cisuralian) age to the Paso Hondo Formation based on the presence of fusulinids and cephalopods (Thompson 1956) (Fig. 2); these were considered to have been deposited in a littoral environment with lagoonal facies that intermittently became continental (Hernández-García 1973).

Material

The material described here is preserved as calcified complete shells as well as fragments and complete ventral and dorsal valves. These are housed at the National Collection of Paleontology of the Institute of Geology, National Autonomous University of Mexico. Figured and type specimens are designated in the descriptions by the prefix IGM and their assigned numbers (IGM 11107−11164). The classification and terminology used here are based on the entries in the *Treatise on Invertebrate Paleontology* for Productida

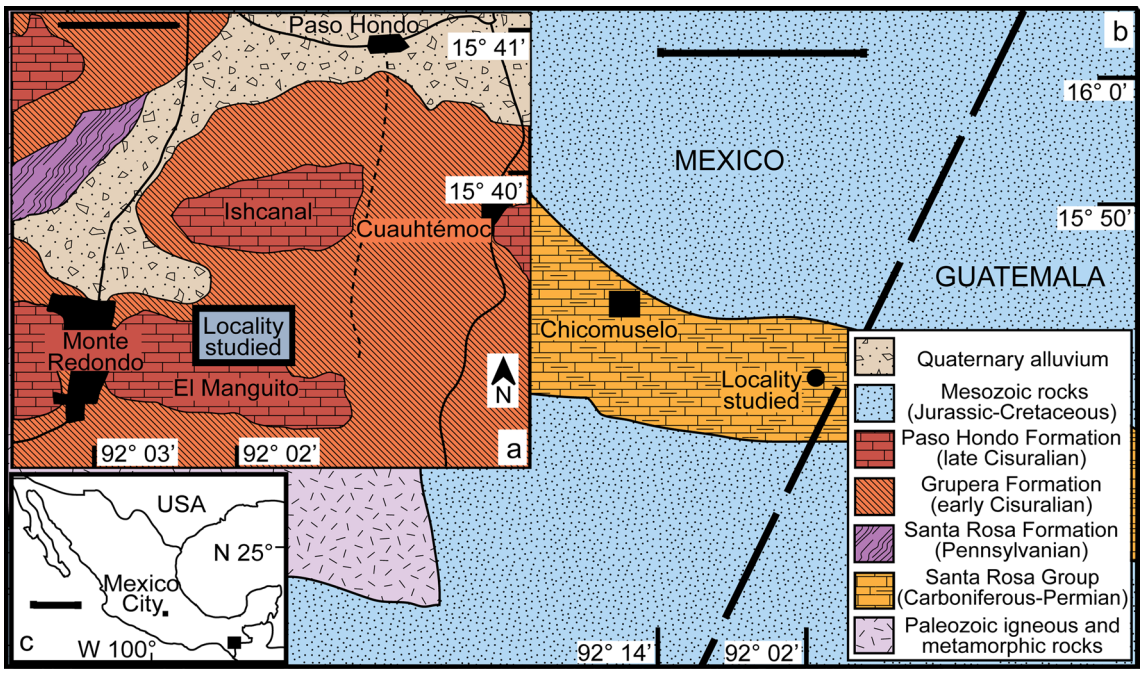

Fig. 1a–c Geological position of the studied area from the Paso Hondo Formation. **a** Locality where brachiopods occur; *scale bar* 1 km; **b** geological map of Chiapas, Mexico (modified from Weber et al. 2007); *scale bar* 25 km; **c** map of Mexico indicating the location of the Chicomuselo region; *scale bar* 500 km

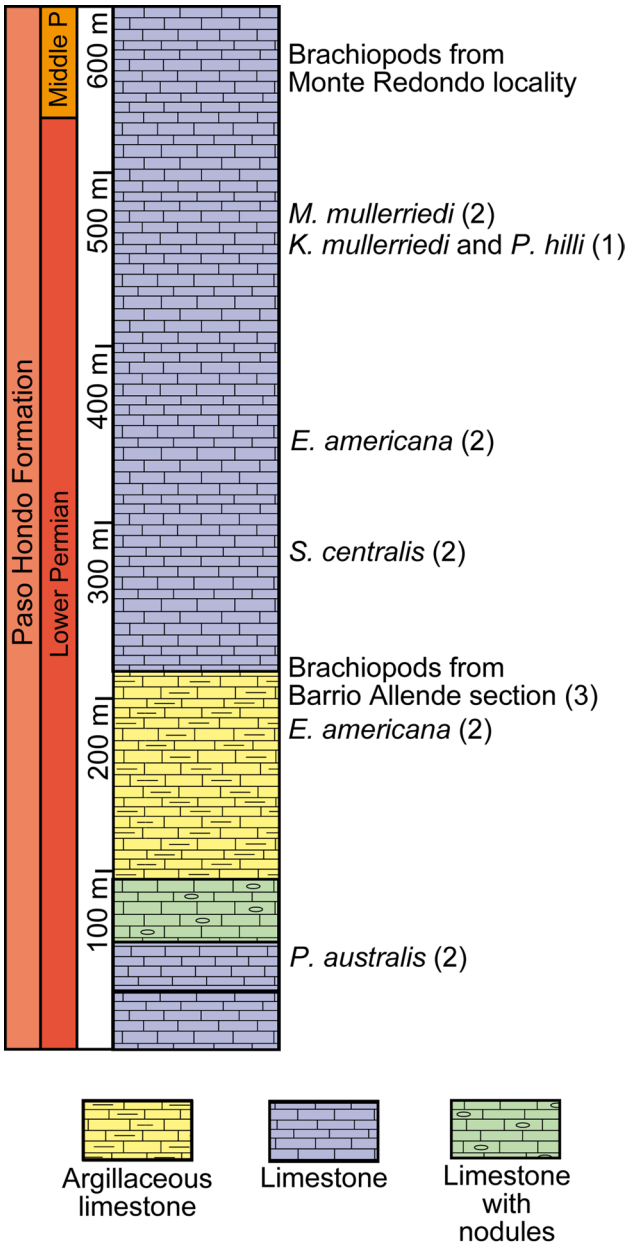

Fig. 2 Composite lithostratigraphic scheme of the Paso Hondo Formation showing the locations of fusulinids, cephalopods, and brachiopods previously recorded from the unit. The approximate stratigraphic locations of the brachiopods considered in the present work are shown. *(1)* Mullerried et al. (1941); *(2)* Thompson and Miller (1944); *(3)* Torres-Martínez et al. (2016)

(Brunton et al. 2000; Racheboeuf 2000), Orthotetida (Williams et al. 2000), Orthida (Williams and Harper 2000), Rhynchonellida (Savage et al. 2002), Athyridida (Alvarez and Rong 2002), and Spiriferida (Carter et al. 2006).

Microfacies analysis was performed for fossil-bearing rocks sampled at the locality studied. Thin sections were petrographically characterized according to the guidelines of Dunham (1962) for the classification of carbonate rocks. This analysis allowed the paleoenvironmental characteristics of the locality of the fossils to be established. Interpretations were made based on the proposed ramp microfacies types (RMF) sensu Flügel (2010), according to the homoclinal ramp model (sensu Tucker and Wright 1990; Burchette and Wright 1992; Pomar 2001).

Systematic paleontology

Class **Strophomenata** Williams, Carlson, Brunton, Holmer and Popov, 1996
Order **Productida** Sarytcheva and Sokolskaya, 1959
Suborder **Chonetidina** Muir-Wood, 1955
Superfamily **Chonetoidea** Bronn, 1862
Family **Rugosochonetidae** Muir-Wood, 1962
Subfamily **Svalbardiinae** Archbold, 1982

Genus ***Dyoros*** Stehli, 1954
Subgenus ***Dyoros*** (***Tetragonetes***) Cooper and Grant, 1975

Type species. Dyoros (*Tetragonetes*) *quadrangulatus* Cooper and Grant, 1975 (Wordian; Texas, USA).

Dyoros (***Tetragonetes***) ***rectangulatus*** Cooper and Grant, 1975
Figure 3a–c

Material. Complete calcified shell with cardinal process exposed (IGM 11107).

Description. Medium-sized shell for the subgenus, concavo-convex, subrectangular in outline with sides nearly straight. Greatest width at the hinge; length about 10.6 mm, width about 16.2 mm in the specimen. Ventral valve convex, most inflated at anterior region, posterior half slightly flattened in lateral profile. Sulcus broad and shallow, beginning about 3 mm anterior to beak. Flanks with gentle posterolateral slopes. Beak minute, umbonal region slightly swollen with oblique flanks. Reduced ears, slightly convex, at (approximately) a right angle. Interarea apsacline almost flat. Narrow hinge with short pseudodeltidium. Anterior margin truncated. Ornamentation consisting of a row of eight spines on each side of posterior margin. Dorsal valve slightly concave, mainly at posterior half, with dorsal flexure in lateral commissure. Ears concave, ill-defined. A median fold is developed, corresponding to the ventral sulcus. Interarea very narrow, hypercline, with chilidium short. Dorsal interior with low cardinal process, small and deeply excavated by a cardinal process pit, dorsally bilobated.

Remarks. Dyoros (*Tetragonetes*) *rectangulatus* has been recorded in the Cathedral Mountain and Bone Spring formations (late Early Permian), as well as Road Canyon (early

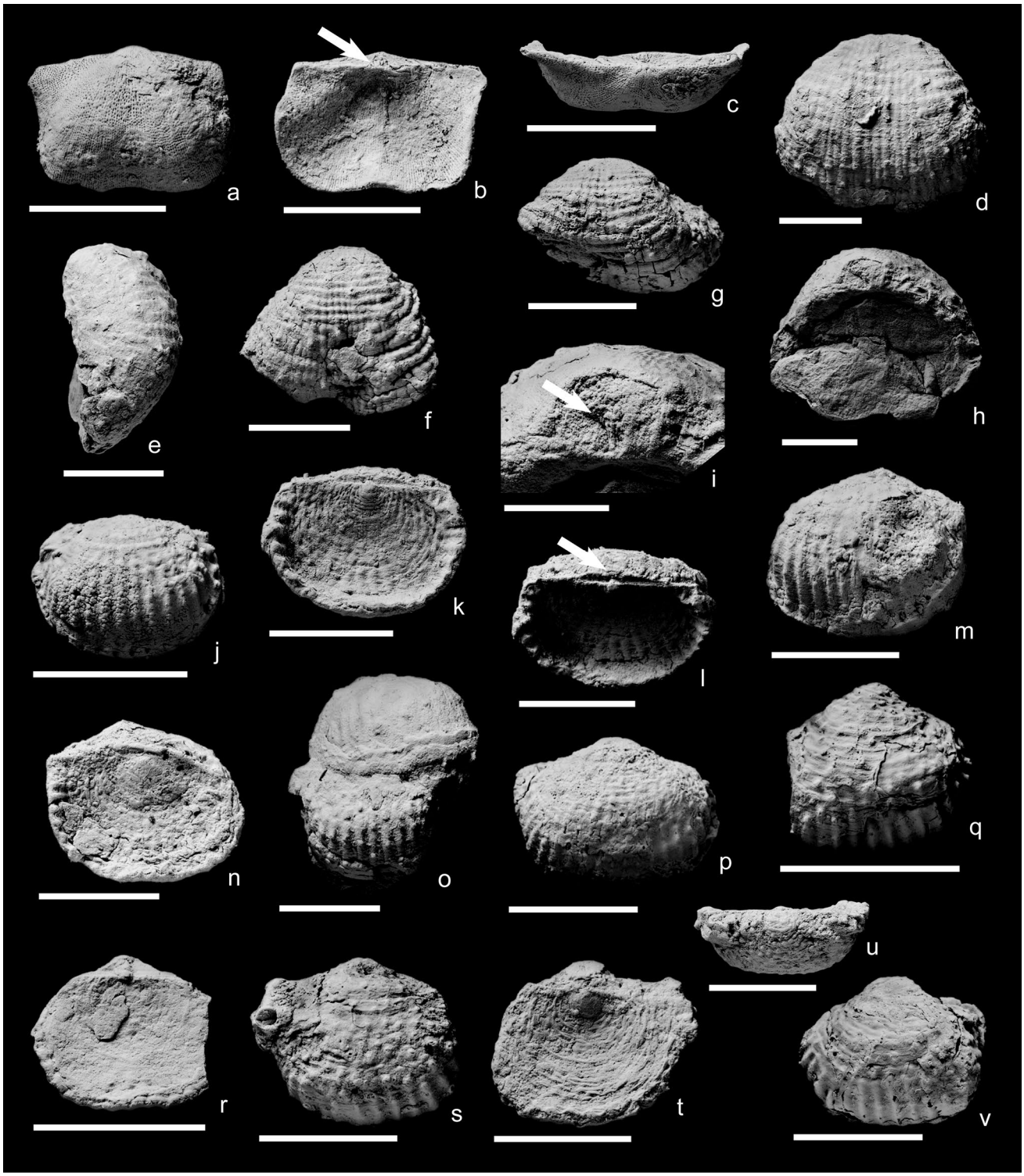

Fig. 3 **a**–**c** *Dyoros* (*Tetragonetes*) *rectangulatus* Cooper and Grant, 1975: shell in ventral (**a**), dorsal (**b**, showing the cardinal process), and posterior (**c**) view (IGM 11107). **d**–**i** *Costispinifera rugatula* (Girty 1908): shell in ventral (**d**) and lateral (**e**) view (IGM 11114); **f** ventral valve (IGM 11108); **g** ventral valve (IGM 11109); **h**, **i** shell in dorsal view with close-up of the cardinal process (IGM 11114). **j**–**p** *Chonosteges cooperi* Torres-Martínez, Sour-Tovar and Buitrón-Sánchez sp. nov.: shell in ventral (**j**), dorsal (**k**), and posterodorsal (**l**) view, showing the cardinal process (IGM 11115; holotype); shell in ventral (**m**) and dorsal (**n**) view (IGM 11116; paratype); **o** ventral valves (IGM 11118, IGM 11119; paratypes), **p** ventral valve (IGM 11117; paratype). **q**–**v** *Echinosteges tuberculatus* (King, 1931): shell in ventral (**q**) and dorsal (**r**) view (IGM 11122); shell in ventral (**s**), dorsal (**t**), and posterior (**u**) view (IGM 11123); **v** ventral valve (IGM 11125). *Scale bars* 1 cm except in **i**, where it is 0.5 cm

Middle Permian) of Texas in the United States (Cooper and Grant 1975). This species differs from *Dyoros* (*Lissosia*) *maya* of the Barrio Allende section, Paso Hondo Formation, Chiapas, Mexico (Torres-Martínez et al. 2016) by its subrectangular shape in outline with sides slightly straight, lower convexity, ears nearly at a right angle, ventral interarea apsacline, sulcus well developed, and eight spines at the hinge. This is the first report of the subgenus *Dyoros (Tetragonetes)* in Mexico.

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Suborder **Productidina** Waagen, 1883
Superfamily **Productoidea** Gray, 1840
Family **Productellidae** Schuchert, 1929 (in Schuchert and LeVene 1929)
Subfamily **Overtoniinae** Muir-Wood and Cooper, 1960
Tribe **Costispiniferini** Muir-Wood and Cooper, 1960

Genus ***Costispinifera*** Muir-Wood and Cooper, 1960

Type species. Costispinifera texana Muir-Wood and Cooper, 1960 (Wordian; Texas, USA).

Costispinifera rugatula (Girty, 1908)
Figure 3d–i

1908 *Productus subhorridus* var. *rugatulus* Girty: p. 267, pl. 30, figs. 11–12c.
1931 *Productus subhorridus* var. *rugatulus* Girty—King: p. 84, pl. 20, figs. 12, 13, 15.
1975. *Costispinifera rugatula* (Girty)—Cooper and Grant: p. 993, 994, pl. 310, figs. 62–70; pl. 312, figs. 21–24; pl. 319, figs. 1–56; pl. 321, figs. 1–9.

Material. Calcified specimens preserved as six ventral valves (IGM 11108–11113) and an additional ventral valve where dorsal internal features can be observed (IGM 11114).

Description. Large concavo-convex shell, subtrigonal in outline, with greatest width at hingeline. Deep corpus cavity. Large shell up to about 25 mm in length and 28 mm in width. Ventral valve strongly convex, geniculated, most inflated near mid-length. Long trail. Ears moderately developed. Hinge lower than greatest width. Median shallow sulcus occurs along the valve, beginning in the umbo and continuing until the anterior margin. Flanks steep. Umbo small, dorsally curved. Beak acute, protruding around 2 mm from hingeline. 9–11 irregular costae in the space of 10 mm on anterior slope. Spine bases on costae widely scattered on the valve. Strong narrow rugae on visceral disc, forming a reticulation with the costae. Long dorsal cardinal process with a median lobe posterodorsal.

Remarks The material from Chiapas displays all of the features mentioned by Girty (1908, p. 267) and Cooper and Grant (1975, p. 993) for the species, but the Mexican specimens are slightly larger than those from Texas. The material of the Paso Hondo Formation is dissimilar to *Costispinifera paucispinosa* from the Jungle Creek Formation of northern Yukon Territory in western Canada (Shi and Waterhouse 1996) in its larger size, greatest width at hingeline, more numerous costae, and arrangement of smaller spines. This is the first occurrence of *C. rugatula* in Mexico, since it has only been reported previously in the Road Canyon and Word formations, and in the Willis Ranch and Appel Ranch members of the Middle Permian of Texas (Cooper and Grant 1975).

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Suborder **Strophalosiidina** Schuchert, 1913
Superfamily **Aulostegoidea** Muir-Wood and Cooper, 1960
Family **Aulostegidae** Muir-Wood and Cooper, 1960
Subfamily **Chonosteginae** Muir-Wood and Cooper, 1960

Genus ***Chonosteges*** Muir-Wood and Cooper, 1960

Type species. Aulosteges magnicostatus Girty, 1908 (Guadalupian; Texas, USA).

Chonosteges cooperi Torres-Martínez, Sour-Tovar and Buitrón-Sánchez sp. nov.
Figure 3j–p

Etymology. In honor of Gustav Arthur Cooper, one of the greatest invertebrate paleontologists in the world.

Holotype. Complete calcified shell with cardinal process exposed (IGM 11115). Measurements in mm: length: 11.1, length along arc: 16.9, dorsal valve length: 9.3, greatest width: 14.7, hinge width: 11.2, height: 5.5.

Paratypes. Calcified specimens preserved as a complete shell (IGM 11116), four ventral valves (IGM 11117–11120), and a fragment of ventral valve with dorsal external mold (IGM 11121). Measurements: see Table 1.

Type locality and horizon. All specimens described were collected in argillaceous limestones of the Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Table 1 Shell dimensions (in millimeters) of *Chonosteges cooperi* sp. nov.

Specimen	L	LA	DV	GW	HW	H
IGM 11115	12.7	23.0	10.7	16.4	15.4	6.9
IGM 11116	13.3	24.4	–	17.0	16.8	8.0
IGM 11117	14.2[a]	25.7	–	17.5	14.0[a]	8.2[a]
IGM 11118	13.2[a]	–	–	16.5[a]	–	7.5[a]
IGM 11119	12.8[a]	–	–	15.6[a]	–	7.8[a]

L length, *LA* length along arch, *DV* dorsal valve length, *GW* greatest width, *HW* hinge width, *H* height
[a]Estimated, sample incomplete

Diagnosis. Large for genus, subrectangular to subelliptical in outline with greatest width posterior to mid-length. Ventral valve strongly geniculated at a right angle. Visceral disc slightly convex. Median sulcus weak. Length of band about 2–3 mm. Cardinal extremities at slightly greater than a right angle. Umbo obtuse by a small cicatrix. Interarea moderately long. Palintrope orthocline. Strong costae, numbering 18–22, separated by intercostal grooves broader than costae. Spines scattered on the valve, thicker in row over the band, rhizoid on cardinal extremities, and smaller on umbonal region. Narrow wrinkles on visceral disc. Dorsal valve nearly flat with visceral disc slightly convex. Length of band about 1 mm. Irregular concentric wrinkles on the valve with thin spines in row over the band. Costae on the anterior part of the valve. Broad and bilobed cardinal process.

Description. Large for genus, concavo-convex, subrectangular to subelliptical in outline with greatest width posterior to mid-length, anterior margin broadly rounded. Minute ears, not well differentiated. Ventral valve convex, more so anteriorly. Strongly geniculated at a right angle. Visceral disc slightly swollen. Median sulcus weak, beginning slightly posterior to mid-valve. Length of band about 2–3 mm. Flanks steep. Cardinal extremities short, at slightly greater than a right angle, narrowly rounded. Umbo small, obtuse by a small cicatrix of attachment. Interarea flat, moderately long. Palintrope orthocline. Ornamented by strong costae originating at geniculation, numbering 18–22, separated by intercostal grooves broader than costae. Spines occurring (1) scattered on the valve, (2) thick in row over the band, (3) rhizoid on cardinal extremities, and (4) smaller and clustered on umbonal region. Narrow and irregular concentric wrinkles on visceral disc. Dorsal valve concave, nearly flat, slightly swollen at visceral disc. Anteriorly geniculated at a right angle. Narrow band, 1 mm in length. Narrow and irregular concentric wrinkles on the entire surface. Thin spines occurring in row over the band. Costae weak and broad on anterior region, beginning in anterior part of the visceral disc. Dorsal interior with a broad and bilobed cardinal process. Other interior characters not observed.

Remarks. Chonosteges matutinus from the Skinner Ranch Formation (Artinskian) of Texas (Cooper and Grant 1975) differs from the new species by its smaller size, fairly long umbo, broader costae, narrower interspaces, mostly flat ventral valve, and flattened dorsal valve to moderately convex in anterior half. *Chonosteges pulcher* from the Cibolo, Bone Spring, and Cathedral Mountain formations (Kungurian) of Texas (Cooper and Grant 1975) is dissimilar to *C. cooperi* by its geniculation slightly less than a right angle, umbo misshapen and elongated, palintrope apsacline, sulcus deeper, and greater number of costae, with interspaces equal in width to these. *Chonosteges variabilis* from Bone Spring, Skinner Ranch, and Cathedral Mountain (Artinskian−Kungurian) formations of Texas (Cooper and Grant 1975) differs from *C. cooperi* by its semicircular shape in outline, greatest width normally at hinge, interarea short, spines on visceral disc arranged in quincunx, more numerous costae, separated by interspaces about as wide as costae, a smaller ventral band, and thicker dorsal spines. *Chonosteges costellatus* from Cathedral Mountain and Road Canyon (Kungurian−Roadian) in Texas (Cooper and Grant 1975) is dissimilar to the new species by its smaller size, greatest width usually at hinge, palintrope apsacline, coarser spines on the umbonal region, more numerous costae with interspaces of the same width, ventral band smaller, and a deeper sulcus. The genus *Chonosteges* has been recorded in different Permian localities of the United States (Cooper and Grant 1975), Guatemala (Stehli and Grant 1970), Malaysia (Leman 1994), China (Hou et al. 1979), and Japan (Shen et al. 2011), this being the first record in Mexico.

Occurrence. Roadian (argillaceous limestones of the Monte Redondo locality), Permian; Mexico.

Subfamily **Echinosteginae** Muir-Wood and Cooper, 1960

Genus ***Echinosteges*** Muir-Wood and Cooper, 1960

Type species. Aulosteges tuberculatus King, 1931 (Wordian; Texas, USA).

Echinosteges tuberculatus (King, 1931)
Figure 3q–v

1931 *Aulosteges tuberculatus* King: p. 95, pl. 27, figs. 4–7.
1931 *Aulosteges beedei* King: p. 92, pl. 25, fig. 15.
1975. *Echinosteges tuberculatus* (King)—Cooper and Grant: 848, 849, pl. 101, fig. 14; pl. 223, figs. 23, 24; pl. 224, figs. 1–10; pl. 225, figs. 1–19; pl. 226, figs. 1–18; pl. 227, figs. 1–25; pl. 228, figs. 1–43; pl. 229, figs. 20–38.

Material. Calcified specimens preserved as three complete shells (IGM 11122–11124) and a ventral valve (IGM 11125).

Description. Concavo-convex shell, subquadrate in outline, with greatest width at mid-length, and rounded anterior margin. Largest specimen approximately 11.9 mm in length and 14 mm in width. Ventral valve strongly convex, with anterior part almost steep and posterior part slightly flattened in lateral profile. Flanks steep. Short ears not well differentiated. Umbo small with short beak, suberect dorsally, the beak slightly overhanging hinge. Palintrope divided by narrow delthyrium, covered by an irregular elytridium. Interarea flattened, apsacline. Ornamentation with strong anterior costae, beginning at mid-valve, 4–5 per 5 mm on anterior margin. Narrow and irregular strong rugae in posterior half of the valve. Tubercles are scattered across the entire valve, in a quincunx arrangement over the costae and rugae. Tubercles are clustered on the ears. Dorsal valve quadrate, slightly concave, principally on visceral disc. Prominent and narrow rugae on the entire valve, forming irregular concentric grooves.

Remarks. Echinosteges tuberculatus was described by Cooper and Grant (1975, p. 848) as a large species about 58 mm in length and 59.8 mm in width. Our material is smaller than that described from Texas, with comparable measurements to juvenile specimens recorded by those authors. The species occurs in units of Texas, such as the Cherry Canyon (Getaway Member), Road Canyon, and Word (China Tank, Willis Ranch, and Appel Ranch members) formations (Cooper and Grant 1975), this being the first record in Mexico.

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Order **Orthotetida** Waagen, 1884
Suborder **Orthotetidina** Waagen, 1884
Superfamily **Orthotetoidea** Waagen, 1884
Family **Schuchertellidae** Williams, 1953
Subfamily **Streptorhynchinae** Stehli, 1954

Genus ***Tropidelasma*** Cooper and Grant, 1969

Type species. Tropidelasma culmenatum Cooper and Grant, 1969 (Asselian; Texas, USA).

Tropidelasma furcillatum Cooper and Grant, 1974
Figure 4a–c

Remarks. The calcified specimen IGM 11126 from the locality studied, Paso Hondo Formation, southeastern Chiapas, Mexico, displays diagnostic traits of *Tropidelasma furcillatum* such as: medium-sized shell, convexo-concave shape, conical, transversally subelliptical in outline with greatest width at mid-length; ventral valve elongated, concave anteriorly; beak blunt and bent; interarea flat, apsacline; broad pseudodeltidium with low lateral ridges; dorsal valve convex, more so at mid-length, subcircular in outline, a very low interarea, and ornamentation with numerous fine costae and narrow growth lines. The measurements of the specimen are about 15.9 mm in length, 14.3 mm in width, 14.2 mm in dorsal valve length, 8.9 mm in hinge width, and 7.9 in thickness, similar to those described by Cooper and Grant (1974, p. 341, pl. 53, figs. 1–5) from the Cherry Canyon Formation (Getaway Member). Previously, this species had only been recorded in localities from the Middle Permian of Texas.

Class **Rhynchonellata** Williams, Carlson, Brunton, Holmer and Popov, 1996
Order **Orthida** Schuchert and Cooper, 1932
Suborder **Dalmanellidina** Moore, 1952
Superfamily **Enteletoidea** Waagen, 1884
Family **Schizophoriidae** Schuchert and LeVene, 1929

Genus ***Acosarina*** Cooper and Grant, 1969

Type species. Acosarina dorsisulcata Cooper and Grant, 1969 (Kungurian; Texas, USA).

Acosarina rectimarginata Cooper and Grant, 1976b
Figure 4d–h

Material. Calcified specimens preserved as two complete shells (IGM 11127, 11128) and a ventral valve (IGM 11129).

Description. Medium-sized biconvex shell, subelliptical in outline, commissure rectimarginate to gently sulcate, greatest width at mid-length, similar depth in both valves. Length about 10.6 mm and width about 12.4 mm in the largest specimen. Ventral valve inflated, with greatest convexity at venter, anteriorly slightly flattened. Flanks gently sloped. Umbo

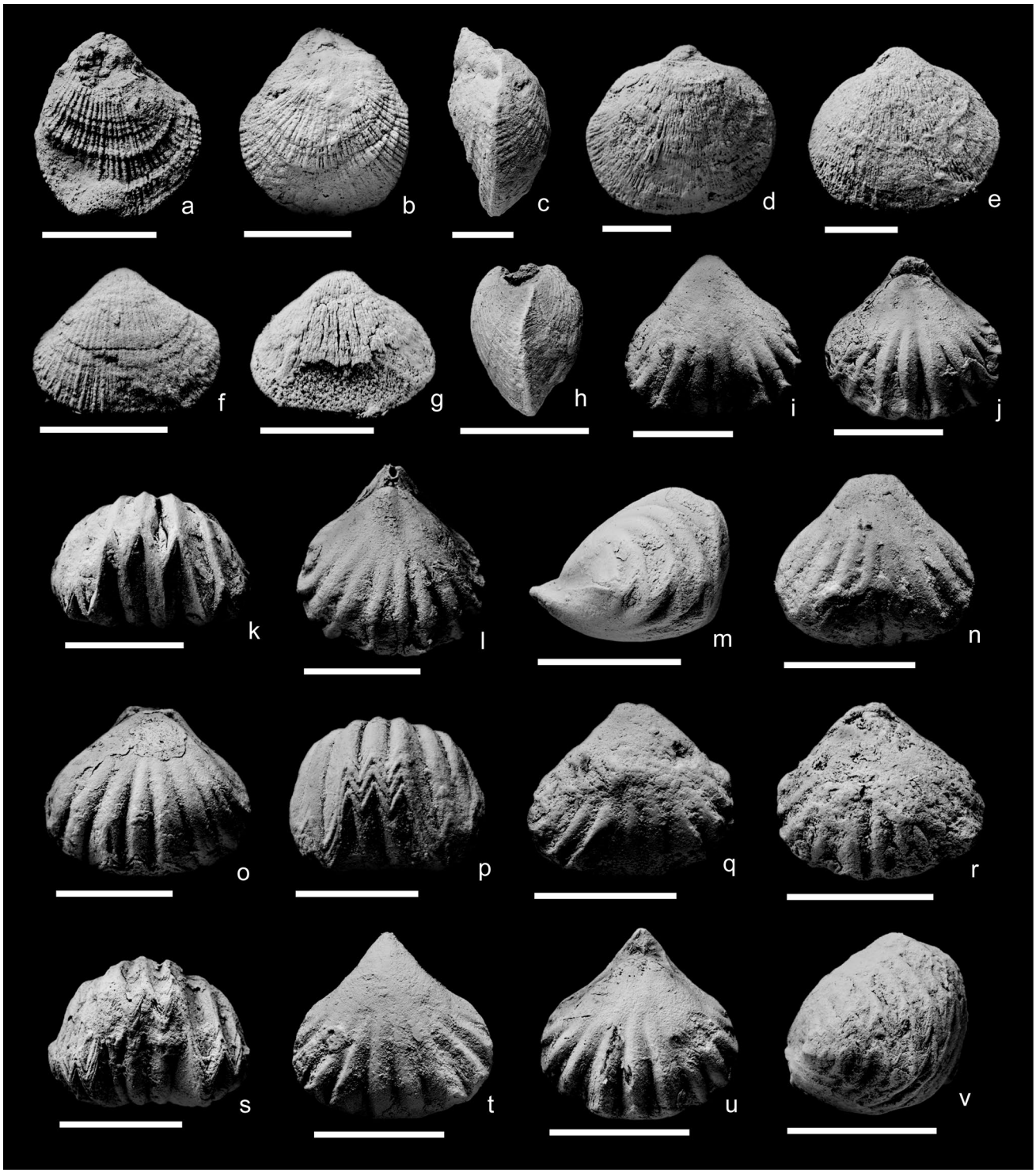

Fig. 4 **a**–**c** *Tropidelasma furcillatum* Cooper and Grant 1974: Shell in ventral (**a**), dorsal (**b**), and lateral (**c**) view (IGM 11126). **d**–**h** *Acosarina rectimarginata* Cooper and Grant 1976b: shell in ventral (**d**), and dorsal (**e**) view (IGM 11127); shell in ventral (**f**), dorsal (**g**), and lateral (**h**) view (IGM 11128). **i**–**m** *Wellerella lemasi* Cooper, 1953 (in Cooper et al. 1953): shell in ventral (**i**) and dorsal (**j**) view (IGM 11131); shell in anterior (**k**), dorsal (**l**), and lateral (**m**) view (IGM 11130). **n**–**v** *Tautosia transenna* Cooper and Grant, 1976a: shell in ventral (**n**), dorsal (**o**), and anterior (**p**) view (IGM 11137); shell in ventral (**q**), dorsal (**r**), and anterior (**s**) view (IGM 11138); shell in ventral (**t**) and dorsal (**u**) view (IGM 11139); **v** shell in lateral view (IGM 11140). *Scale bars* 1 cm, except in **c–h**, where they are 0.5 cm

moderately acute, with suberect beak. Interarea triangular. Ornamented by four costae in space of 1 mm at anterior margin, some tubular, with a few spaced concentric lamellae. Dorsal valve strongly convex, anteriorly flattened. Slightly shorter than the ventral valve. Umbo similar to opposite valve. Beak protrudes 1 mm beyond hinge. Ornamentation similar to the ventral valve.

Remarks. Acosarina rectimarginata was first described from Asselian-age (early Cisuralian) rocks of the Neal Ranch Formation of Texas (Cooper and Grant 1976b). However, the same species has been recorded in localities of other Permian ages, suggesting that its stratigraphic range extends through this period. Thus, *A. rectimarginata* has also been reported in the Hatahoko region (late Cisuralian) (Shen et al. 2011) and the Nabeyama Formation (early Guadalupian) (Tazawa et al. 2012) of Central Japan, as well as in the Changhsing Formation (late Lopingian) of South China (Shen and He 1994). This is the first report of the species in Mexico.

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Order **Rhynchonellida** Kuhn, 1949
Superfamily **Wellerelloidea** Licharew, 1956
Family **Wellerellidae** Licharew, 1956
Subfamily **Wellerellinae** Licharew, 1956

Genus ***Wellerella*** Dunbar and Condra, 1932

Type species. Wellerella tetrahedra Dunbar and Condra, 1932 (Moscovian; Missouri, Nebraska in USA and Mexico).

Wellerella lemasi Cooper, 1953 (in Cooper et al. 1953)
Figure 4i–m

Material. Seven complete calcified shells (IGM 11130–11136).

Description. Medium-sized shell, biconvex, subtriangular in outline, with rounded anterolateral margins. Anterior commissure uniplicate and serrate. Five costae on flanks. Largest specimen approximately 19 mm in length and 21 mm in width. Ventral valve convex, more so in the anterior region in lateral profile, becoming slightly flattened in the posterior half. Sulcus broad and shallow, begins at mid-length and is delimitated by steep and moderately convex flanks, ornamented by two blunt costae, beginning about 8 mm anterior to beak and extending to anterior margin, forming a trapezoidal tongue at the commissure. Flanks moderately steep. Umbo broad and gibbous. Beak slightly suberect, with an elongated submesothyrid foramen. Interior with dental plates short. Dorsal valve convex in lateral profile, with semicircular shape in anterior profile. Flanks gently sloping. Umbo blunt. Umbonal region flattened with a shallow median sulcus. Fold low and flattened, protrudes above the flanks and begins about 9 mm anterior to beak, ornamented by three very acute costae, originating at mid-length of the valve and extending until the anterior margin. Interior with median septum low and short.

Remarks. The material of Chiapas displays diagnostic features of *Wellerella lemasi* from the Monos Formation of El Antimonio, Sonora, Mexico (Cooper et al. 1953), such as its biconvex shell, subtriangular shape in outline, anterior commissure uniplicate and serrate with a trapezoidal tongue, five costae on flanks, ventral beak slightly suberect with enlarged submesothyrid foramen, dorsal valve with three costae on the fold and a shallow median sulcus in the umbonal region. Nonetheless, the specimens of the Paso Hondo Formation mainly display a fold without depressed costae, an uncommon trait in this species (Cooper et al. 1953, p. 51, 52).

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Genus ***Tautosia*** Cooper and Grant, 1969

Type species. Tautosia fastigiata Cooper and Grant, 1969 (Kungurian; Texas, USA).

Tautosia transenna Cooper and Grant, 1976a
Figure 4n–v

1955 *Wellerella*? sp. Stehli, 1955: p. 73, figs. 37–39.
1976a *Tautosia transenna* Cooper and Grant: p. 1984–1986, pl. 527, figs. 1–31; pl. 553, figs. 41–44.

Material. Six complete calcified shells (IGM 11137–11142).

Description. Shell of medium size, biconvex, subpentagonal in outline. Anterior commissure uniplicate and serrate with numerous parallel growth lines. Four low and blunt costae on flanks. Sides diverge between 80° and 90°. Large shell up 18 mm in length and 19.8 mm in width. Ventral valve strongly inflated with greatest convexity in the anterior region, slightly flattened visceral disc in lateral profile. Shallow sulcus with convex and steep flanks, beginning about 9 mm anterior to beak, extending to anterior margin, where it forms a low trapezoidal tongue; ornamented by two blunt costae that begins about 6 mm anterior to beak. Flanks moderately steep. Umbo gibbous. Beak erect and acute with an enlarged and submesothyrid foramen. Dorsal valve convex, lower than the ventral valve. Fold low, originates at

7 mm anterior to beak; ornamentation consists of three acute costae, beginning at mid-length. Flanks moderately steep. Umbonal region flattened. Interior with median septum high.

Remarks. Tautosia transenna is dissimilar to *W. lemasi* by its greater convexity, distance between the beak and the origin of the sulcus and fold, presence of numerous parallel growth lines near the commissure, fewer costae on flanks, erect beak, absence of shallow sulcus in the posterior region of the dorsal valve, and dorsal median septum high. This is the first record of the genus *Tautosia* in Mexico. *Tautosia transenna* had only been reported in localities from the Middle Permian of Texas (Cooper and Grant 1976a).

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Order **Athyridida** Boucot, Johnson and Staton, 1964
Suborder **Athyrididina** Boucot, Johnson and Staton, 1964
Superfamily **Athyridoidea** Davidson, 1881
Family **Athyrididae** Davidson, 1881
Subfamily **Spirigerellinae** Grunt, 1965

Genus ***Composita*** Brown, 1849

Type species. Spirifer ambiguus Sowerby, 1822 (Viséan; Derbyshire, England).

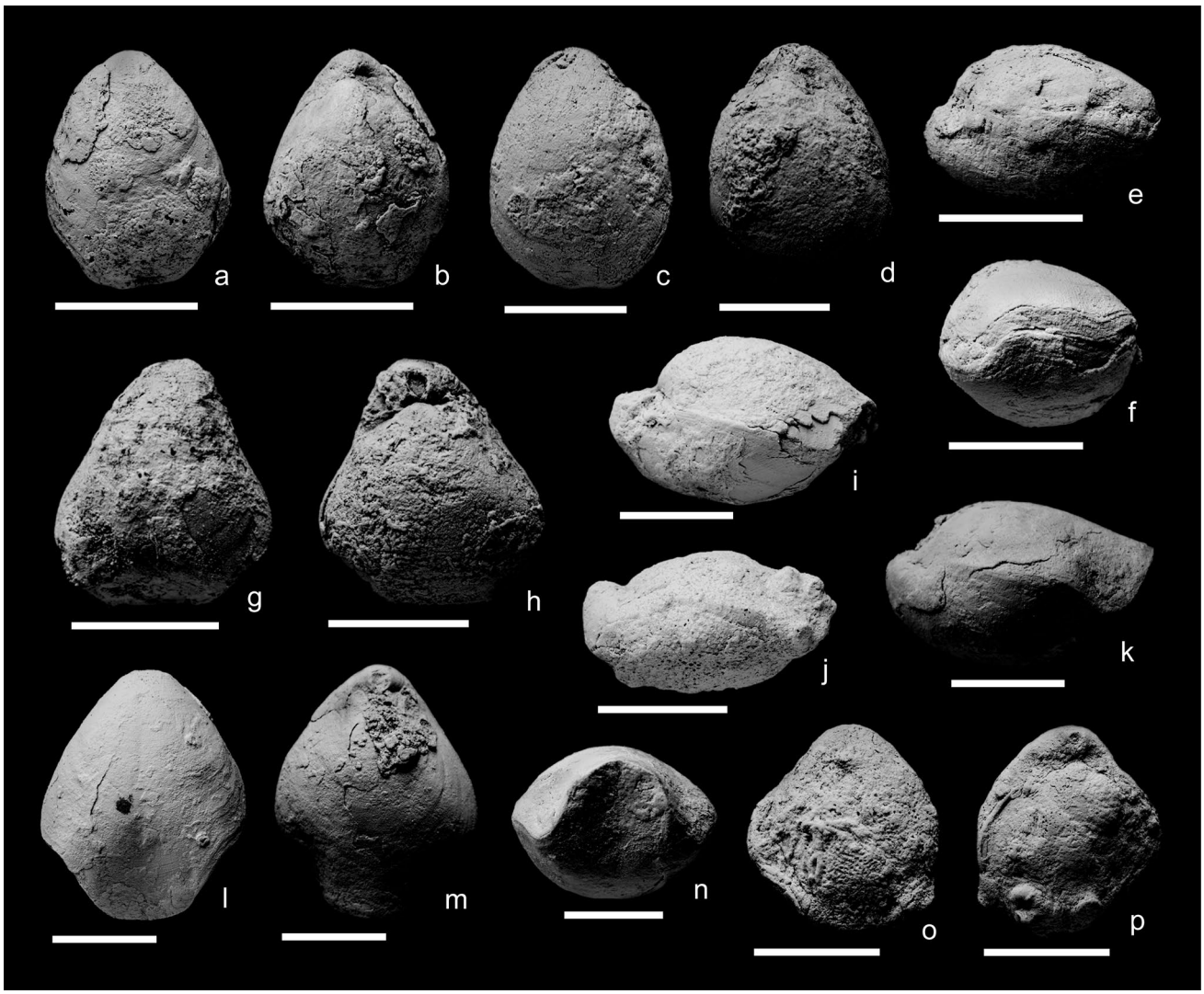

Fig. 5 **a**–**i** *Composita enormis* Cooper and Grant, 1976a: shell in ventral (**a**) and dorsal (**b**) view (IGM 11143); shell in ventral (**c**), dorsal (**d**), lateral (**e**), and anterior (**f**) view (IGM 11144); shell in ventral (**g**), dorsal (**h**), and lateral (**i**) view (IGM 11145). **j**–**p** *Composita hapsida* Stehli and Grant, 1970: **j** shell in lateral view (IGM 11150); shell in lateral (**k**), ventral (**l**), dorsal (**m**), and anterior (**n**) view (IGM 11149); shell in ventral (**o**) and dorsal (**p**) view (IGM 11150). *Scale bars* 1 cm

Composita enormis Cooper and Grant, 1976a
Figure 5a–i

1931 *Composita emarginata affinis* King: p. 128, pl. 43, figs. 12–17.
1944 *Composita emarginata affinis* King—Cloud: p. 65, pl. 18, figs. 20–22.
1976a *Composita enormis* Cooper and Grant: p. 2153, 2154, pl. 656, figs. 21–51.

Material. Six complete calcified shells (IGM 11143–11148).

Remarks. The specimens of the locality studied in the Paso Hondo Formation (southeastern Chiapas) display features from *Composita enormis* (Cooper and Grant 1976a, p. 2153, pl. 656), such as the medium to large size, biconvex shell, enlarged subovate outline; uniplicate to parasulcate commissure; anterolateral flange; convex ventral valve, most inflated in posterior region; wide and shallow sulcus in the anterior region, originating 7 mm anterior to beak; broad and arched umbo; short and suberect beak; foramen small, ovate, periphery incomplete at anterior, with slightly flanged edge; dorsal valve inflated with greatest convexity in the posterior part; fold low in the anterior region, protruding over flanks and beginning about 9–11 mm anterior to beak; umbonal region broad; beak suberect, within ventral valve; and several growth lines, more numerous near commissure of each valve. Our specimens have similar size measurements to those recorded from Texas (Cooper and Grant 1976a, p. 2153), the largest specimen being about 21 in length and 17.5 mm in width. *Composita enormis* has been reported in Guadalupian rocks from Coahuila, Mexico (Cloud 1944), and Texas in the United States (Cooper and Grant 1976a).

Composita hapsida Stehli and Grant, 1970
Figure 5j–p

Material. Calcified specimens preserved as three complete shells (IGM 11149–11151).

Remarks. The material of *Composita hapsida* from the locality studied in Chiapas is characterized by a large shell for the genus, biconvex, subovate-cardiform in outline, slightly enlarged, greatest width anterior to mid-length; commissure parasulcate; ventral valve convex, most gibbous at mid-length; shallow sulcus, posteriorly weak, but wide, moderately deep and V-shaped at anterior margin, originating about 10 mm anterior to beak; dorsal valve convex, similar to opposite valve; fold broad, forming a prominent crest, initiating anterior to mid-length; weak and narrow growth lines on both valves; and shells that reach about 24 mm in length and 19 mm in width. These are diagnostic characters of adult individuals, according to the description by Stehli and Grant (1970, p. 33, 34) for specimens from the Chochal Formation of Huehuetenango, Guatemala. *Composita hapsida* differs from *C. enormis* in its subovate-cardiform shape, absence of anterolateral flange at margin of commissure, V-shaped sulcus in the anterior region, ventral umbo dorsally curved, and prominent fold.

Order **Spiriferida** Waagen, 1883
Suborder **Spiriferidina** Waagen, 1883
Superfamily **Spiriferoidea** King, 1846
Family **Trigonotretidae** Schuchert, 1893
Subfamily **Neospiriferinae** Waterhouse, 1968

Genus ***Neospirifer*** Frederiks, 1924

Type species. Spirifer fasciger Keyserling, 1846 (Permian; Petschora, Russia).

Neospirifer venezuelensis (Gerth in Gerth and Kräusel 1931)
Figure 6a–k

1931 *Spirifer cameratus* var. *venezuelensis* Gerth in Gerth and Kräusel: p. 525, pl. 22, figs. 3, 4.
1976a *Neospirifer thescelus* Cooper and Grant: p. 2189, 2190, pl. 609, figs. 30–48, pl. 610, figs. 1–38, pl. 611, figs. 1–12, pl. 612, figs. 1–12.
1981 *Neospirifer venezuelensis* (Gerth)—Hoover: p. 100–102, pl. 9, figs. 1–13.

Material. A calcified ventral valve and its corresponding internal mold (IGM 11152), calcified specimens preserved as two complete shells (IGM 11153, 11154), nine ventral valves (IGM 11155–11163), and a dorsal valve (IGM 11164).

Description. Large-sized shell for the genus, biconvex, semielliptical to subpentagonal in outline, with greatest width at hingeline. Commissure uniplicate, slightly undulating laterally. Short lateral extensions of the hinge. Ventral valve strongly inflated, with greatest convexity posterior to the mid-valve. Flanks moderately steep. Umbo prominent with small and acute beak, strongly hooked. Umbonal slopes steep, slightly more than lateral flanks. Interarea slightly concave, narrow, and low, ornamented by fine striae intersected by horizontal lines, with sharp denticulations beginning about 3 mm lateral to hinge teeth. Delthyrium high, moderately wide, open with 50° angle. Pseudodeltidium short, located in apex of delthyrium. Sulcus deep, initiating at the beak; cross-section broadly V-shaped, broad in its front, delimited on each side by fasciculate costae in a

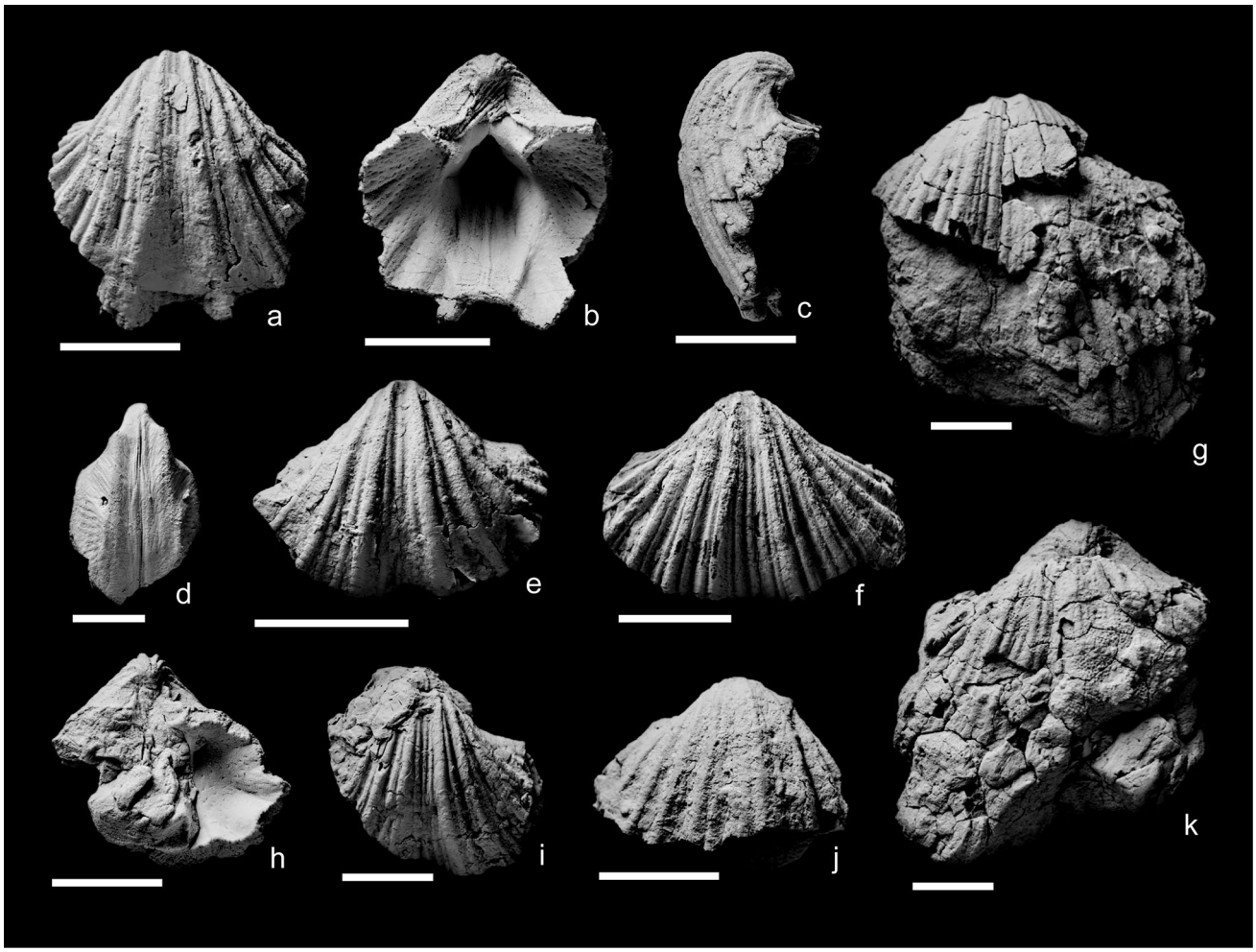

Fig. 6 **a**–**k** *Neospirifer venezuelensis* Gerth, 1931 (in Gerth and Kräusel 1931): ventral valve in ventral (**a**), dorsal (**b**), and lateral (**c**) view (IGM 11152); **d** fragment of ventral valve, interior mold (IGM 11152); **e** ventral valve (IGM 11156); **f** ventral valve (IGM 11155); **g** shell in ventral view (IGM 11153); **h** ventral valve in dorsal view (IGM 11159); **i** ventral valve (IGM 11157); **j** dorsal valve (IGM 11164); **k** shell in dorsal view (IGM 11153). *Scale bars* 1 cm except in **d**, where it is 0.5 cm

group of five. Sulcus with median costa beginning at beak. Costae fasciculate on flanks, forming groups of three to five, with median costa being larger than the side costae. Narrow, continuous, and concentric growth lines on the entire valve, interrupted by stronger and irregularly spaced growth laminae. Interior with well-differentiated dental plates with dental ridges in apical region. Teeth elongated, diverging anteriorly. Muscle field elongate oval, broad, and moderately impressed, apical portion excavated. Diductor scars large, subpentagonal, with irregular striae. Adductor marks narrow, longitudinally striated, bisected by thin median ridge. Ovarian impressions well developed at posterolateral region. Dorsal valve convex, slightly less than the ventral valve. Flanks gently convex. Interarea low. Narrow and moderately high fastigium, ornamented by four costae; median costa is bifurcating near beak. Ornamentation of flanks is similar to opposite valve.

Remarks. This form is easily distinguished from other *Neospirifer* species by its semielliptical to subpentagonal shape in outline, short cardinal extremities, arrangement of costae in fascicles with larger median costa, sulcus delimited by a strong high costa on each side, median costa in sulcus that begins at the beak, and fastigium narrow (Cooper and Grant 1976a, p. 2190). Previously, *Neospirifer venezuelensis* had been recorded in the Kungurian from the Palmarito Formation, Mérida, Venezuela (Hoover 1981) and in the Roadian from the Road Canyon Formation, Texas, USA (Cooper and Grant 1976a); this is the first record of the species in Mexico.

Occurrence. Monte Redondo locality, Paso Hondo Formation; southeastern Chiapas, Mexico. Roadian (Guadalupian).

Discussion and conclusions

Depositional paleoenvironment

During the Early Permian, the Chicomuselo region was strongly influenced by numerous changes in sea level, mainly caused by the melting of ice sheets from Gondwana (Isbell et al. 2003). The end of that ice age induced numerous regressions and transgressions in equatorial regions, triggering the formation of different marine paleoenvironments in the area. In particular, Chicomuselo has been characterized as a region where numerous carbonate environments developed, and their depositional regimes were particularly linked to homoclinal ramps (Torres-Martínez et al. 2017b).

The material described herein was preserved mostly as articulated calcified shells. The specimens were found in an autochthonous association with a variety of rugose corals and bryozoans. In addition, some brachiopods and corals are hosts of different sclerobionts, such as incrusting bryozoans, hederelloids, microconchids, and crinoids. All invertebrates were located in calcareous or argillaceous calcareous rocks that outcrop in a single bed to the east of the town of Monte Redondo. Similar associations, including those sclerobionts, have been described in Devonian localities from the Givetian of Iowa, United States (Webb and Schneider 2013), and from the Frasnian−Famennian of the Central Devonian Field, Russia (Zatoń and Krawczyński 2011).

The depositional facies of the rocks is characterized by fossiliferous wackestone with an argillaceous light brown to gray mud matrix, containing abundant bryozoans, frequent plates of crinoids, a few spines and fragments of brachiopods, scarce fragments of echinoderms, and trace ostracods. In particular, bryozoans are well preserved in longitudinal and transversal section, showing the zooecial wall fabric.

Sedimentological features of the fossil-bearing rocks, the preservation of the specimens, and the biota—mainly composed of photic-independent and stenohaline filter feeders (Pomar 2001)—allow the facies of the locality studied to be associated with an open marine environment, in particular that offshore of a homoclinal ramp. This paleoenvironment may have been characterized by normal oxygen and salinity and low-to-medium energy conditions. It seems to have been well illuminated, with an abundant nutrient supply and high productivity in the euphotic zone. The scarcity of ostracods suggests that they could have been transported from another zone.

In fact, *Dyoros* (*Tetragonetes*) *rectangulatus*, *Costispinifera rugatula*, *Echinosteges tuberculatus*, *Tropidelasma furcillatum*, *Acosarina rectimarginata*, *Wellerela lemasi*, *Composita hapsida*, *C. enormis*, and *Neospirifer venezuelensis* are species that had already been recorded in calcareous environments (Cooper et al. 1953; Stehli and Grant 1970; Cooper and Grant 1974, 1975, 1976a, b).

Implications for age assignment

The Paso Hondo Formation is known as the youngest unit from the Permian succession of Chicomuselo, Chiapas, with an Artinskian−Kungurian age. This formation has been considered one of the most fossiliferous units of the region, with a great diversity of marine fauna, such as corals, mollusks, brachiopods, bryozoans, and crinoids, as well as different groups of foraminifera. A small proportion of this biota has been described, allowing the formation to be dated. Thus, the gastropod *Waagenella crassus* (=*Belerophon (Bellerophon) crassus*) (Buitrón-Sánchez 1977), the cephalopods *Kargalites mullerriedi* (=*Peritrochia mullerriedi*) and *Perrinites hilli* (Mullerried et al. 1941), and the fusulinids *Staffella centralis*, *Eoverbeekina americana*, *Mesoschubertella mullerriedi* (=*Schubertella mullerriedi*), and *Parafusulina australis* (Thompson and Miller 1944) were correlated with the late Early Permian (late Cisuralian). However, the age range of this formation remains unclear, as *W. crassus* has been recorded from the Carboniferous to the Permian (Buitrón-Sánchez 1977); *K. mullerriedi* has been reported in the Kungurian of Mexico (Leonova 2002); *S. centralis*, *M. mullerriedi*, and *E. americana* are regional species from the Mayan Block of Artinskian−Kungurian age (Thompson and Miller 1944; Kling 1960); and *P. australis* was correlated with the *Parafusulina* zone of the Leonard Formation (Artinskian−Kungurian) but was only found in the basal levels of the Paso Hondo Formation (Thompson and Miller 1944; Kling 1960). In addition, *Perrinites hilli* is a typical cephalopod from western Pangea, but its temporal range extends from the Kungurian (late Cisuralian) to the Roadian (early Guadalupian) (Leonova 2002; Vachard et al. 2004). Taken together, the taxa have allowed the fauna to be correlated with biota of the late Cisuralian (late Early Permian) from the southern United States and western Guatemala, but none of the taxa is sufficiently reliable to establish the Kungurian (late Cisuralian) as the youngest age of the unit.

Temporal ranges of brachiopods described in this work partially coincide with the inferred age of the Paso Hondo Formation, as there are a few taxa from the late Cisuralian (Early Permian). Most of the species reported have, however, been recognized as typical taxa from the Guadalupian (Middle Permian), especially of the Roadian−Wordian. Thereby, *Dyoros* (*Tetragonetes*) *rectangulatus* has been recorded in rocks of Kungurian−Roadian age (Cooper and Grant 1975); *Costispinifera rugatula* was reported in Roadian−Wordian localities (Girty 1908; Cooper and Grant 1975); *Echinosteges tuberculatus* is recorded in the Roadian−Wordian

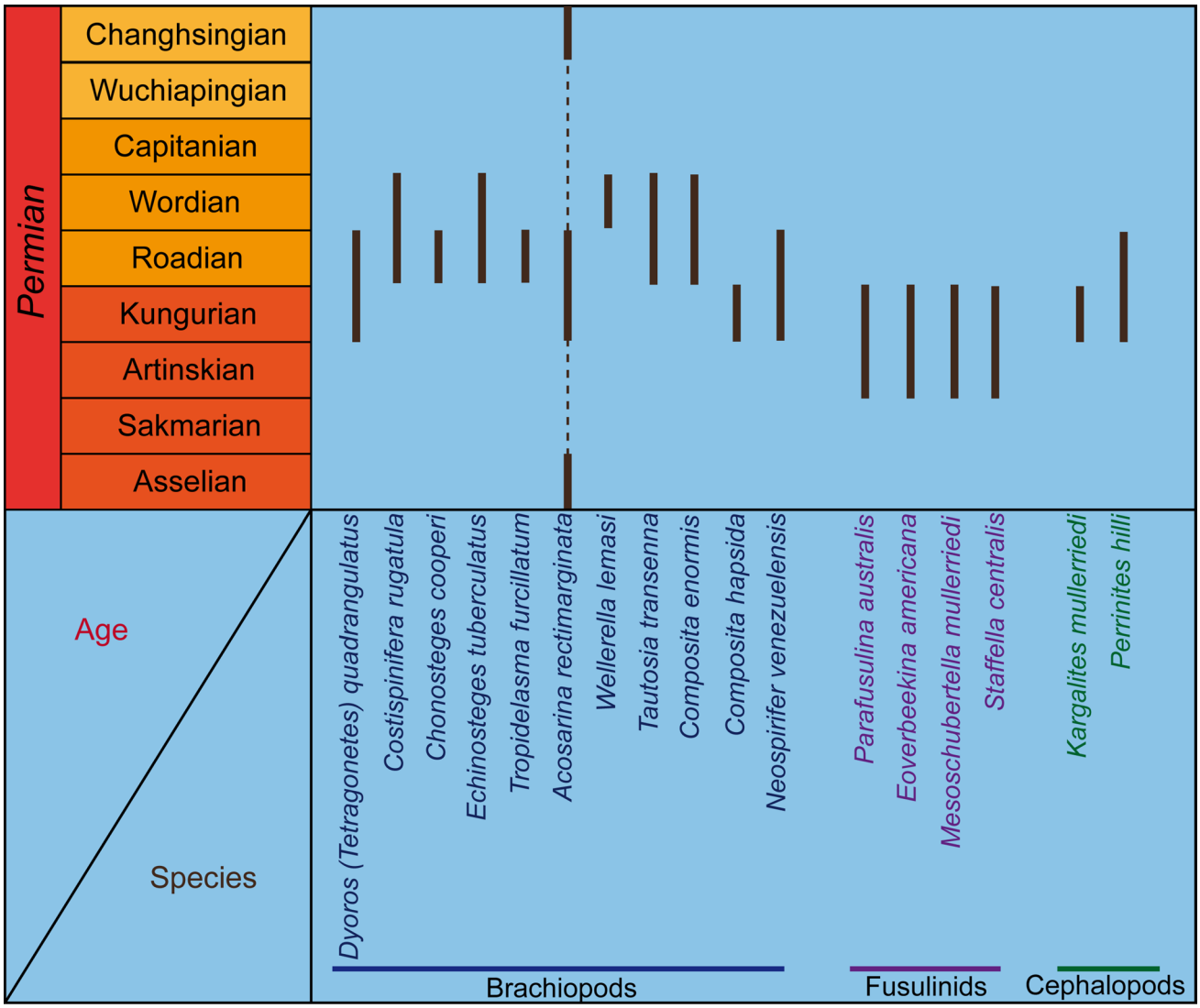

Fig. 7 Stratigraphic distributions of brachiopod species described in this work, including fusulinids and cephalopods recorded by Mullerried et al. (1941) and Thompson and Miller (1944)

(Cooper and Grant 1975); *Tropidelasma furcillatum* has been registered in Roadian rocks (Cooper and Grant 1974); *Acosarina rectimarginata* has been recorded in the Asselian (Cooper and Grant 1976b), Kungurian (Shen et al. 2011), Roadian (Tazawa et al. 2012), and Changhsingian (Shen and He 1994); *Wellerela lemasi* is recorded in the Wordian (Cooper et al. 1953); *Tautosia transenna* was reported from the Roadian−Wordian (Cooper and Grant 1976a); *Composita enormis* has been recorded in the Roadian−Wordian (Cooper and Grant 1976a); *Composita hapsida* has been associated with a Kungurian age (Stehli and Grant 1970); and *Neospirifer venezuelensis* has been reported in the Kungurian−Roadian (Cooper and Grant 1976a; Hoover, 1981) (Fig. 7).

Previously, Torres-Martínez et al. (2016) described some brachiopods from the Barrio Allende section of the Paso Hondo Formation, characterized by similar age ranges: *Dyoros* (*Lissosia*) (Artinskian−Roadian), *Hustedia shumardi* (Kungurian−Wordian), *Spiriferella propria* (Kungurian−Wordian), and *Spiriferellina tricosa* (Asselian−Roadian). Although those taxa have comparable ages, their position in the stratigraphic column (below that of the levels studied herein, as rectified in this work) and their coincidence with the foraminifer *Eoverbeekina americana* imply that they are a fauna of Kungurian age.

Species such as *D.* (*T.*) *rectangulatus*, *C. rugatula*, *E. tuberculatus*, *T. furcillatum*, *T. transenna*, *C. enormis*, and *N. venezuelensis* allow the locality studied from the Paso Hondo Formation to be correlated with the Cherry Canyon

Table 2 Previous records of the brachiopods described herein, relating to other geographic regions

Species	Texas (USA)	Huehuetenango (Guatemala)	Coahuila (Mexico)	Sonora (Mexico)	Palmarito (Venezuela)
Dyoros (T.) rectangulatus	•				
Costispinifera rugatula	•				
Echinosteges tuberculatus	•				
Tropidelasma furcillatum	•				
Acosarina rectimarginata	•				
Wellerella lemasi				•	
Tautosia transenna	•				
Composita enormis	•		•		
Composita hapsida		•			
Neospirifer venezuelensis	•				•

(Getaway Member) and Road Canyon formations of Texas in the United States (Cooper and Grant 1975, 1976a), which have been characterized as typical stratigraphic units from the Guadalupian of North America. Temporal ranges of brachiopods described herein suggest that the age of the Paso Hondo Formation extends from the Artinskian through the Kungurian (Early Permian) to at least the Roadian (Middle Permian), making this the first report of a formation of this age in southeastern Mexico. In fact, the Paso Hondo Formation has also been correlated with the Chochal Formation of Guatemala, which has been dated as Kungurian−Roadian in its Chixoy section (Kling 1960; Vachard et al. 1996).

Paleobiogeographical considerations

It has been suggested that the deposition of the Permo-Carboniferous succession of Chiapas took place between southeast of the North American Craton and northwest of Gondwana (Weber et al. 2007; Torres-Martínez et al. 2016). This succession is characterized by a lack of crystalline basement, which has hindered attempts to obtain further information on its geological history. Nonetheless, it has been proposed that the basement of the Paleozoic sedimentary units of the Chicomuselo region is most probably the Chiapas massif. This massif crops out in western and northwestern Chiapas State and is made up of igneous and metamorphic rocks (Molina-Garza et al. 1992), the oldest being of Ordovician age (Estrada-Carmona et al. 2012). However, even though various paleomagnetic and geochemical studies have been carried out to establish the geographical position of the massif during the Permian, its precise geographical location on the equatorial west side of Pangea is not known to date with any certainty (Molina-Garza et al. 1992; Weber et al. 2007). Nonetheless, the presence of several taxa in the Chicomuselo region similar to those described for New Mexico and Texas, such as fusulinids, cephalopods, and brachiopods, suggests that both the Southern United States and Chiapas had a close connection during the Late Paleozoic (Mullerried et al. 1941; Thompson and Miller 1944; Torres-Martínez et al. 2016). The apparent absence of Gondwanan taxa indicates that Chicomuselo was nearer Laurentia than another geographical region through the Early–Middle Permian (Table 2).

The provinciality of Permian brachiopods of North America was reported by Yancey (1975), who described four paleogeographical provinces in the region. One of them was the Grandian Province, which was characterized by its high percentage of endemism at the genus and species levels (Shen et al. 2009, Torres-Martínez et al. 2017a). According to Yancey (1975), the Grandian Province was composed of biota from the Texas–New Mexico region southward into Coahuila and westward into central Sonora. In this context, the records of Hoover (1981) from the Merida Andes in Venezuela; Stehli and Grant (1970) from Huehuetenango, Guatemala; Sour-Tovar et al. (2005) from Hidalgo; and Torres-Martínez et al. (2016) from Chiapas, Mexico, allow the brachiopods of these regions to be linked to coeval faunas of the Grandian Province too. Most brachiopods described herein had only previously been recorded from localities of the Middle Permian of western Texas, suggesting that the faunas of Chiapas also belonged to the Grandian Province during the Guadalupian.

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