Neospiriferinid brachiopods (Spiriferida, Trigonotretidae) from Ixtaltepec Formation, Pennsylvanian of Oaxaca State, Southern Mexico

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The brachiopods of the Subfamily Neospiriferinae (Order Spiriferida) *Neospirifer dunbari*, *N. pantojai* n. sp., *N. amplia* n. sp., *Septospirifer mazateca* n. sp. and ?*Septospirifer* sp. are described for Pennsylvanian rocks of southern Mexico. The material was recovered from the type section of the Ixtaltepec Formation, near the town of Santiago Ixtaltepec, in Oaxaca State. Mexican *Neospirifer* species are associated with the *Neospirifer cameratus-dunbari* lineage, a typical North American group, and their presence in Oaxaca confirms the Morrowan-Desmoinesian age for the Ixtaltepec Formation and the faunistic similarity that exists between Carboniferous faunas from southern Mexico and those from the Midcontinent region of North America. *Septospirifer* species represent the first record of the genus for Mexico and the third occurrence worldwide. □ *Brachiopods*, *Mexico*, *neospiriferids*, *Neospirifer*, *Pennsylvanian*, *Septospirifer*.

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The genera included in the Subfamily Neospiriferinae, as proposed by Carter *et al.* (1994), represent a group of brachiopods for which a clear taxonomic position has not yet been reached among brachiopod workers. In particular, this is the case for taxa described as typical of North America and that composed the *Neospirifer cameratus–dunbari* group as they possess unique and distinctive morphological characters, such as a very peculiar internal structure and smooth costae. These characteristics may determine their re-assignation to a different genus than *Neospirifer* as originally described for the Permian of Eurasia (Poletaev 1997). The taxonomic position of the representatives of the genus *Septospirifer* Waterhouse (1971) has also been discussed and it has been suggested that the genus should be included in the Subfamily Spiriferinae because of the type of apical apparatus and costae (Poletaev 1997). Three of the species described in this paper may be related to the *Neospirifer cameratus–dunbari* group and a fourth species may be assigned to the genus *Septospirifer*. The description of these taxa will contribute with additional information to clarify the final taxonomic position of these brachiopods.

Geographical setting

Fossils described in this work were collected in the type section of the Ixtaltepec Formation (17°30′–17°35′N/97°05′–97°10′W) approximately 500 m to the north of the town of Santiago Ixtaltepec, in the Municipality of Nochixtlan, Oaxaca (Fig. 1).

Stratigraphic and palaeoenvironmental settings

The region of Santiago Ixtaltepec is characterized by one of the most extensive sequences of Paleozoic rocks in Mexico (Fig. 2). This sequence rests upon the so-called Oaxacan Complex, which is comprised by metamorphic rocks of Precambrian age between 1000 to 1200 million years old (Fries *et al.* 1962).

The oldest Paleozoic unit is the Tiñú Formation of Cambrian–Ordovician age (Pantoja-Alor & Robison 1967; Robison & Pantoja-Alor 1968; Pantoja-Alor 1970; Sour-Tovar & Buitron 1987; Sour-Tovar 1990; Navarro-Santillán *et al.* 2002). The Santiago Formation

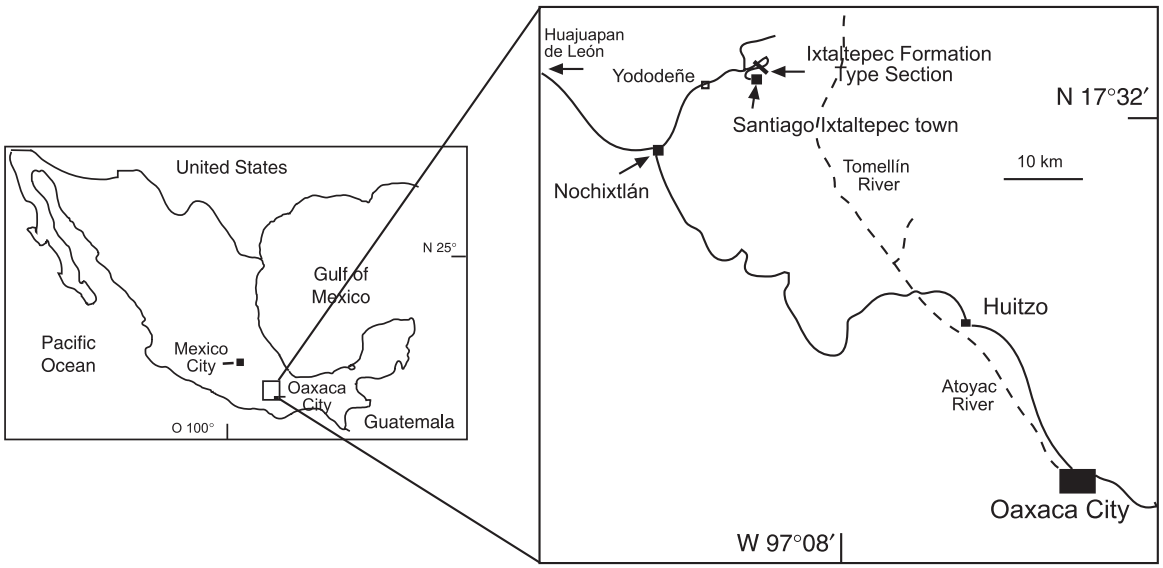

Fig. 1. Geographic location of the Ixtaltepec Formation type section, where specimens of neospiriferids have been collected.

of Early Mississippian (Osagean) age and 67 m in thickness (Navarro-Santillán *et al.* 2002) is located on top of the Tiñú Formation in a clear angular unconformity. The Ixtaltepec Formation of Lower-Middle Pennsylvanian age (Quiroz-Barroso & Perrilliat 1997; Sour-Tovar & Martinez-Chacón 2004) is placed on top of the Santiago Formation in an angular unconformity. The Ixtaltepec Formation is nearly 600 m thick and has been divided into two members: the first (157 m) is composed of argillaceous intercalations, sandstone, limestone and sandy limestone deposits and the second is initially composed of 350 m of calcarenite, shale, and an alternation of shale and sandstone with small stratified layers of igneous rocks. The top part of the second member (almost 100 m) is represented by sandy shales and an alternation of shale and sandstone.

Several strata of the second member of the Ixtaltepec Formation contain abundant invertebrate faunas including the brachiopods described in this work. Among those faunas, bivalves represent the most diverse taxonomic group (Quiroz-Barroso & Perrilliat 1997, 1998), although the number of specimens of brachiopods is higher. Also, it is possible to find abundant bryozoans and crinoids, some trilobites, and cephalopods, among other invertebrates. The Ixtaltepec Formation, according to its sedimentological characteristics and the stratigraphic distribution of the fossil associations, is thought to represent deposition in a wide range of sedimentological environments from prodelta, through reef and peri-reef lagoon, to offshore neritic environments with a high affluence of fine terrigenous sediments.

Systematic palaeontology

Repository data and terminology

Specimens described herein are housed in the Museum of Paleontology at the Faculty of Sciences of the Universidad Nacional Autónoma de México. They are catalogued with the abbreviation FCMP/E1 and their respective reference numbers. The classification used is that proposed by Carter *et al.* (1994), and the morphologic terms are those noted by Williams *et al.* (1997) and Williams & Brunton (1997).

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams *et al.*, 1996

Class Rhynchonellata Williams *et al.*, 1996

Order Spiriferida Waagen, 1883

Suborder Spiriferidina Waagen, 1883

Superfamily Spiriferoidea King, 1846

Family Trigonotretidae Schuchert, 1893

Subfamily Neospiriferinae Waterhouse, 1968

Genus *Neospirifer* Fredericks, 1919

Type species. – *Spirifer fasciger* Keyserling, 1846 (Lower Permian, Russia).

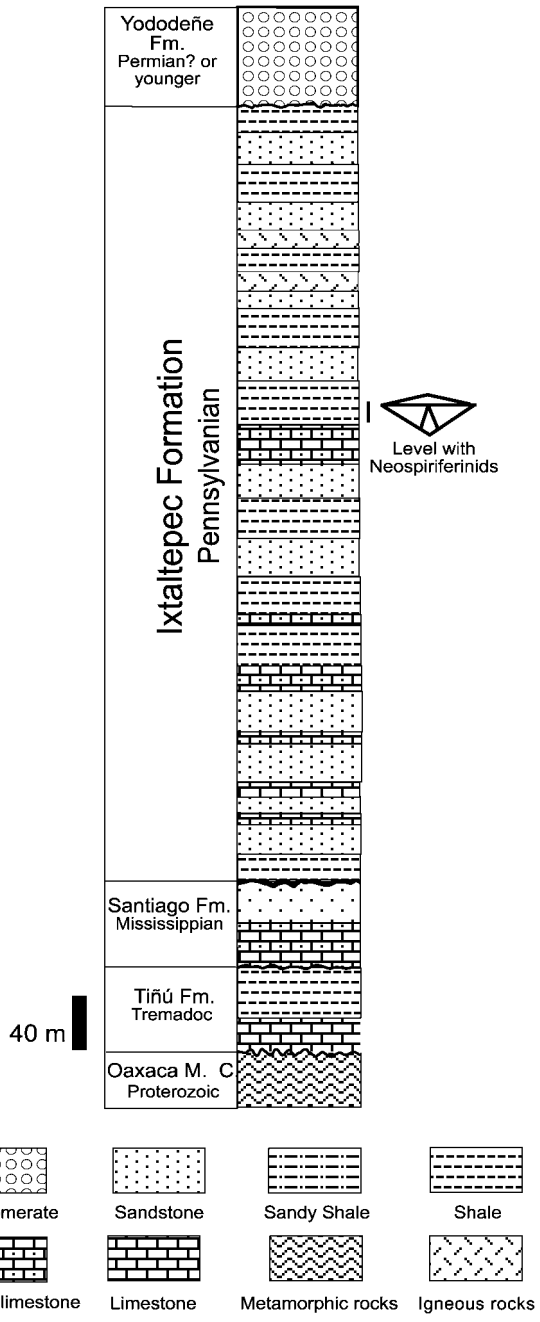

Fig. 2. Stratigraphy of Palaeozoic outcrops from Santiago Ixtaltepec area. Beds with neospiriferids are located 370 m above the base of the Ixtaltepec Formation.

***Neospirifer dunbari* King, 1933**

Fig. 3A–H

1933 *Neospirifer dunbari* King, p. 441.
1967 *N. dunbari dunbari* King – Spencer, 1967, pp. 22–23, figs 13–14.

Description. – Large shells are up to 52 mm in length and 74 mm in width; biconvex; triangular in dorsal outline; transverse to alate with maximum width along the hinge line; cardinal extremities acute and triangular. Gently convex longitudinally; cardinal area low and deep, transversely extended. Shell surface totally covered with imbricate concentric lines; costellate with fasciculate, rounded, thin costellae on both valves (Fig. 3C, D); parasulcate anterior commissure. Ventral valve convex; curved and slightly elevated umbo; striate wide and high apsacline interarea; cardinal process with triangular wide delthyrium; slightly deep ventral sulcus with 9–12 costellae; median costa and two lateral costellae originating at umbo and bifurcating towards the middle of the valve; lateral flanks with 18–20 thin costellae. Dorsal valve moderately convex; wide and sub-triangular median fold with short linguiform anterior termination with 10–13 costellae derived from a median costa and two well-defined costellae bifurcating laterally; lateral flanks with 19–22 costellae. Ventral interior with large sub-triangular dental plates; well-developed dental adminicula; thin and long cyrtomatodont teeth; large and triangular muscle field with small diductor muscle scars, thinning towards the posterior region, and very wide adductor muscle scars. Dorsal interior with low and narrow notothyrium with striate ctenophoridium; narrow and long dental sockets; short and thin crural bases; very short and thin median septum.

Discussion. – Specimens of *N. dunbari* from Oaxaca have the typical morphological characters originally described by King (1933) for the species. However, the arrangement of costellae on both valves is distinctive for these forms, allowing a distinction to be made between previously described specimens for this species in North America. *N. dunbari* can be easily differentiated from other similar taxa, such as *Neospirifer praenuntius* Easton, 1962, *Neospirifer cameratus* Morton, 1836, *Neospirifer goreii* Mather, 1915 and *Neospirifer triplicatus* var. *gibbosus* Dunbar & Condra, 1932. *N. praenuntius* is more transverse in dorsal outline. *N. cameratus* has a narrower and more compact cardinal process partially covered by a plate (see Hoare 1961). *N. goreii* has a more curved ventral umbo and costellae only display fasciculation at the posterior region. *N. triplicatus* var. *gibbosus* has a slightly transverse shell, the cardinal area is larger and both valves are strongly convex.

Material. – Seven internal moulds of ventral valves (FCMP/E1-1720, E1-1954, E1-1956, E1-1994, E1-1995, E1-1997, E1-1998), five external moulds of ventral valves (FCMP/E1-1455, E1-1731, E1-1966, E1-1979, E1-1985), ten internal moulds of dorsal valves (FCMP/E1-639, E1-1719, E1-1747, E1-1948, E1-1949, E1-1959, E1-1963, E1-1964, E1-1965, E1-1992) and five external moulds of dorsal valves (FCMP/E1-1716, E1-1718, E1-1723, E1-1962, E1-1983).

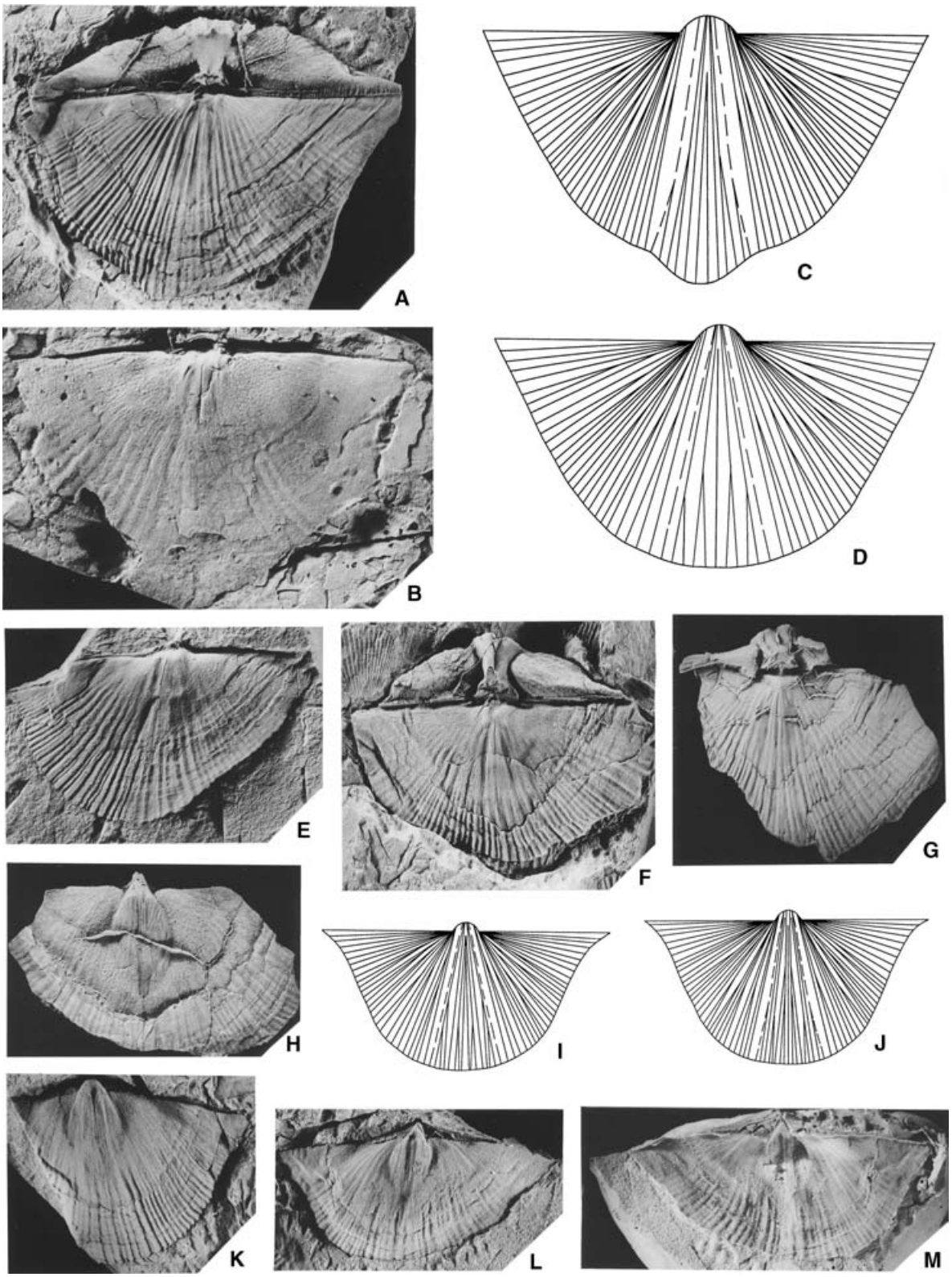

Fig. 3. ☐A–H. *Neospirifer dunbari* ☐A. Dorsal valve with the posterior region of ventral valve, internal mould, FCMP/E1-1747. ☐B. Dorsal valve, internal mould, FCMP/E1-1719. ☐C. Costellation of dorsal valve. ☐D. Ventral valve, costellation. ☐E. Dorsal valve, composite mould, FCMP/E1-1992. ☐F. Dorsal valve with the posterior region of ventral valve, internal mould, FCMP/E1-1947. ☐G. Dorsal valve, composite mould, FCMP/E1-1998. ☐H. Ventral valve, composite mould, FCMP/E1-1994. ☐I–M. *Neospirifer pantojai* n. sp. ☐I. Ventral valve, costellation. ☐J. Dorsal valve, costellation. ☐K. Ventral valve, internal mould, FCMP/E1-1987. ☐L. Ventral valve, internal mould, juvenile specimen, FCMP/E1-1988, holotype. ☐M. Rubber mould of FCMP/E1-1988. All pictures ×1.

***Neospirifer pantojai* n. sp.**

Fig. 3I–M

Holotype. – E1-1988; ventral valve, internal mould.

Derivation of name. – After Jerjes Pantoja-Alor, Mexican geologist who discovered the Palaeozoic outcrops from Nochixtlán region.

Diagnosis. – *Neospirifer* with tranverse shell and short alate cardinal extremities; dorsal fold with 13 fasciculate costellae; ventral sulcus with 12–15 costellae.

Description. – Medium-sized shells up to 35 mm in length and 60 mm in width; biconvex; triangular in dorsal outline; moderately transverse in adult forms but strongly transverse in juveniles; maximum width along the hinge line; cardinal extremities short and alate. Gently convex longitudinally; cardinal area low and deep, transversely extended. Shell surface costellate with sub-rounded, fasciculate, bifurcating, thin costellae on both valves (Fig. 3I, J); parasulcate anterior commissure. Ventral valve are strongly convex; incurved and slightly elevated umbo; moderately high apsacline interarea; cardinal process with narrow triangular delthyrium; slightly deep and narrow ventral sulcus with 12–15 costellae, derived from three simple costellae originating at the umbo; lateral flanks with 17–18 thin costellae, derived from 9–11 costellae by bifurcation from the posterior region. Dorsal valve is slightly convex; wide, low and subtriangular median fold with 13 costellae, derived from 5 simple costellae originating at the umbo; lateral flanks with 15–18 thin costellae, derived from 8–11 costellae by bifurcation from the posterior region. Ventral interior thick, sub-triangular and very short dental plates; not well-developed dental adminicula; thin and short cyrtomatodont teeth; small and striate muscle field with rhombic in shape diductor muscle scars and small adductor muscle scars.

Discussion. – The new species *N. pantojai* can be compared to *N. triplicatus* var. *alatus* Dunbar & Condra, 1932, *N. latus* Dunbar & Condra, 1932 and *N. thescelus* Cooper & Grant, 1976, which are the most similar taxa because of their transverse shells with alate cardinal extremities. *N. triplicatus* var. *alatus* has sub-angular and strongly fasciculate costellae, more extended cardinal extremities, and a median dorsal fold with only 7–8 costellae. *N. latus* has acute or sub-rounded cardinal extremities, higher number of costellae (16–20 on dorsal fold and 15–19 in the ventral sulcus), and different pattern of fasciculation. *Neospirifer thescelus* has a deeper ventral sulcus, fascicles in bundles of four or more costellae and strong non-continuous growth lamellae. *N. pantojai* can be differentiated from specimens of *N. dunbari* from the same locality because of the alate cardinal extremities, number of costellae in the ventral sulcus and lateral flanks and the rhombic shape of diductor muscle scars.

Material. – Four internal moulds of ventral valves (FCMP/E1-1987, E1-1988 (holotype), E1-1989 and E1-2004) and one external mould of a dorsal valve (FCMP/E1-1990).

***Neospirifer amplia* n. sp**

Fig. 4A–G

Derivation of name. – The species name refers to its large extension at hinge line.

Holotype. – FCMP/E1-1946, ventral valve, composite mould.

Paratype. – FCMP/E1-1945, dorsal valve internal mould.

Diagnosis. – *Neospirifer* extremely transverse, with width twice the length at hinge line; angular cardinal extremities; ventral sulcus with a well-defined median costa and two lateral costellae deriving into 7–9 thinner costellae; dorsal fold with 10–12 costellae.

Description. – Large shells up to 26 mm in length and 92 mm in width; biconvex; triangular in dorsal outline; extremely transverse, with width twice the length at hinge line; strongly angular cardinal extremities. Slightly convex longitudinally; cardinal area low and deep, transversely extended. Shell surface costellate with fasciculate, sub-rounded, thin costellae on both valves (Fig. 4E, F); parasulcate anterior commissure. Ventral valve convex; incurved and moderately elevated umbo; wide and high apsacline interarea; cardinal process with triangular narrow delthyrium; slightly deep and wide ventral sulcus with a well-defined median costa and two lateral costellae deriving into 7–9 thinner costellae; lateral flanks with 18–21 thin costellae, derived from 9–12 costellae by bifurcation from the posterior region. Dorsal valve moderately convex; wide and triangular median fold with 10–12 costellae; lateral flanks with 17–20 costellae, derived from 9–11 costellae by bifurcation from the posterior region. Ventral interior large, thick, rounded dental plates; small dental adminicula; thin and short cyrtomatodont teeth; large and rhombic in shape muscle field but triangular and deeper towards the posterior region. Dorsal interior with low and narrow notothyrium with striate ctenophoridium; narrow and short dental sockets; very short and thin crural bases; short and thin median septum.

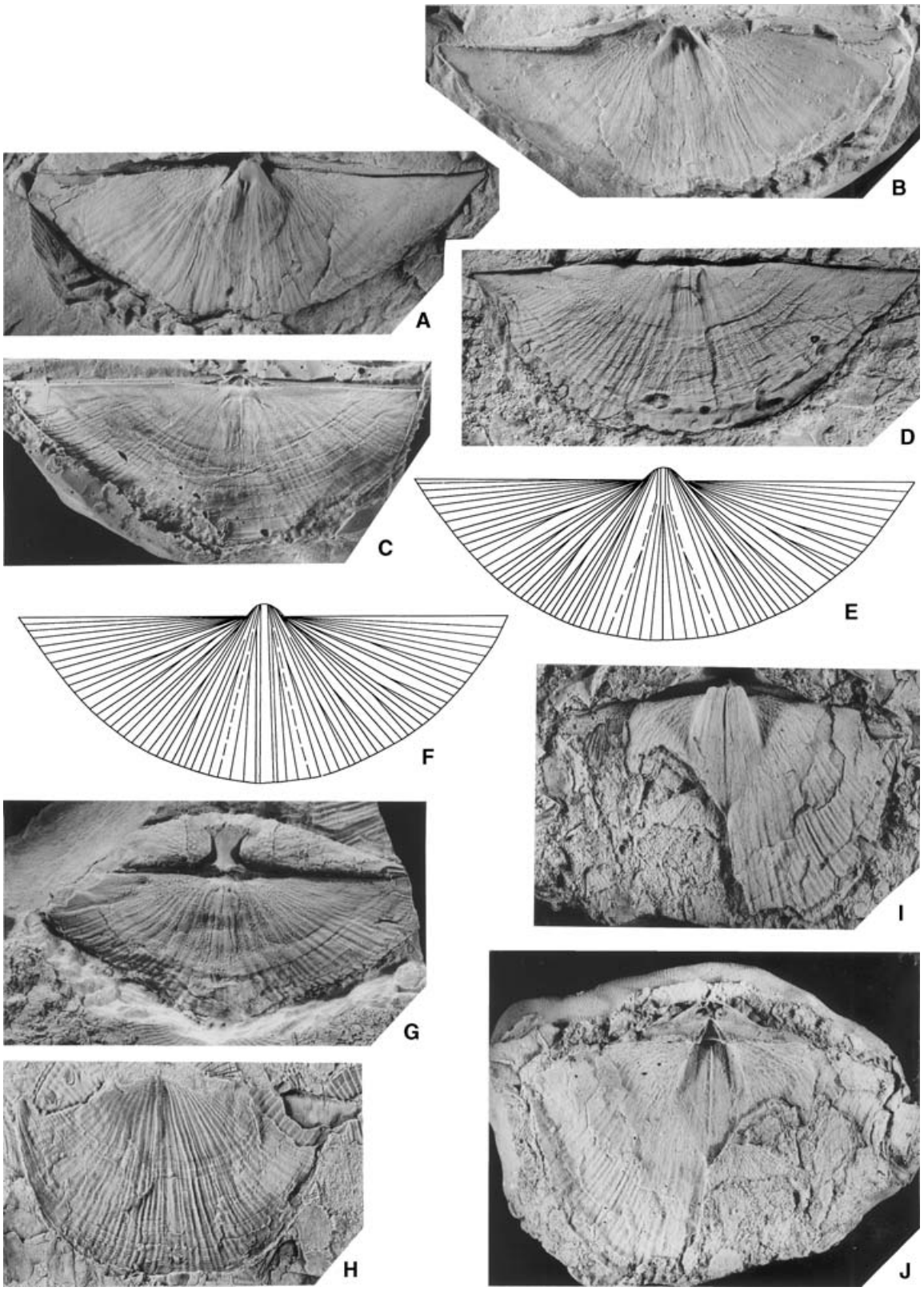

Fig. 4. □A–G. *Neospirifer amplia* n. sp. □A. Ventral valve, composite mould, FCMP/E1-1946, holotype. □B. Rubber mould of FCMP/E1-1946. □C. Rubber mould of FCMP/E1-1974. □D. Dorsal valve, composite mould, FCMP/E1-1960. □E. Dorsal valve, costellation. □F. Ventral valve, costellation. □G. Dorsal valve with the posterior region of ventral valve, internal mould, FCMP/E1-1945, paratype. □H–J. *Septospirifer mazateca* n. sp. □H. Dorsal valve, external impression, FCMP/E1-1952. □I. Ventral valve, internal mould, FCMP/E1-1953, holotype. □J. Rubber mould of FCMP/E1-1953. All pictures ×1.

Discussion. – The new species, *N. amplia*, can be easily differentiated from other species of *Neospirifer* described in this work and in regions of North America because shells are extremely transverse with width twice the length at hinge line (for additional comparison to *N. goreii*, *N. cameratus*, *N. triplicatus* var. *latus* and *N. latus*, see previous discussion for *N. dunbari* and *N. pantojai*). *N. amplia* can be differentiated from *N. kansasensis* (Dunbar & Condra 1932) as the later species has a dorsal fold with 18–22 costellae, very deep ventral sulcus and 80–90 costellae on dorsal valve. In addition, *N. amplia* is compared to similar forms described outside North America, such as *N. campbelli* (Roberts *et al.* 1976) and *Neospirifer senilis* (Roberts *et al.* 1976). *N. campbelli* has a biconvex shell but with unequal convexity of both valves, rounded cardinal extremities, and narrow adductor muscle scars. *N. senilis* has a prominent bifurcating costa on the dorsal fold, bifurcating or trifurcating costellae on dorsal flanks and in the ventral sulcus.

Other material. – One internal mould of ventral valve (E1-1957), six external moulds of ventral valves (FCMP/E1-1728, E1-1958, E1-1961, E1-1976, E1-1977, E1-1978), seven internal moulds of dorsal valves E1-1950, E1-1960, E1-1967, E1-1968, E1-1974, E1-1975, E1-1984), and three external moulds of dorsal valves (FCMP/E1-1955, E1-1969, E1-1986).

Genus *Septospirifer* (Waterhouse, 1971)

Type species. – *Septospirifer tatondukensis* Waterhouse, 1971 (Permian, Canada).

***Septospirifer mazateca* n. sp.**

Figs 4H–J, 5A–D

Derivation of name. – The species name derives from national mazateco in reference to people who live in Mazateca region, northeast of Oaxaca State.

Holotype. – FCMP/E1-1953, ventral valve, internal mould.

Diagnosis. – *Septospirifer* with rectimarginate shell, angle of cardinal extremities of 50 to 60 degrees; ventral sulcus slightly deep; costellae moderately thick; diductor muscle scars wide and adductor muscle scars very wide.

Description. – Large shells up to 54 mm in length and 86 mm in width with maximum width at hinge line; biconvex; sub-triangular in dorsal outline; short alate cardinal extremities with angle of 50 to 60 degrees in respect to the hinge line. Shell surface costellate with fasciculate, bifurcating, sub-rounded and moderately thick costellae on both valves (Fig. 5C, D); parasulcate anterior commissure. Ventral valve convex; incurved and slightly elevated umbo; wide and high apsacline interarea; slightly deep and wide ventral sulcus with 15–17 costellae, derived from seven costellae by bifurcation from the posterior region; lateral flanks with 19–21 costellae, derived from 7–10 costellae by bifurcation from the posterior region. Dorsal valve slightly convex; elevated, very wide, and sub-triangular median fold with 15–17 costellae, derived from nine costellae by bifurcation at the umbo; lateral flanks with 17–21 costellae, derived from 8–10 costellae by bifurcation at the umbo. Ventral interior with low and moderately large thick dental plates; not well-developed dental adminicula; large muscle field with wide adductor muscle scars and small diductor muscle scars thinning towards the posterior region; median septum very long and thin.

Discussion. – The presence of a median septum in the interior of the ventral valve is the diagnostic morphological character to differentiate the genus *Septospirifer* from other genera of neospiriferinid brachiopods. Although this is the criterion chosen by Waterhouse (1971), there are reports prior to his work where the presence of this ventral septum was described in species of the genus *Neospirifer* (Hoare 1961; Sturgeon & Hoare 1968).

Septospirifer mazateca is compared to other described species of *Septospirifer*, such as *S. tatondukensis* (Waterhouse 1971), *Septospirifer sarcinatus* (Lee & Gu 1976), and *Septospirifer extensus* (Lee & Gu 1976). *S. tatondukensis* has a deep ventral sulcus, angle of cardinal extremities of 35 to 40 degrees, and wide diductor and narrow adductor muscle scars. *S. sarcinatus* has not a rectimarginate shell and it has thinner costellae and rounded cardinal extremities. *S. extensus* has a very prominent dorsal fold, very thin costellae and acute cardinal extremities.

Material. – One internal mould of ventral valve (FCMP/E1-1953, holotype). Four external moulds of ventral valves (FCMP/E1-99, E1-142, E1-148, E1-2000), one external mould of a ventral valve, FCMP/E1-1951 and two external moulds of dorsal valves (FCMP/E1-1723, E1-1952).

?*Septospirifer* sp.

Fig. 5E–L

Description. – Medium-sized shells up to 24 mm in length and 62 mm in width with maximum width at

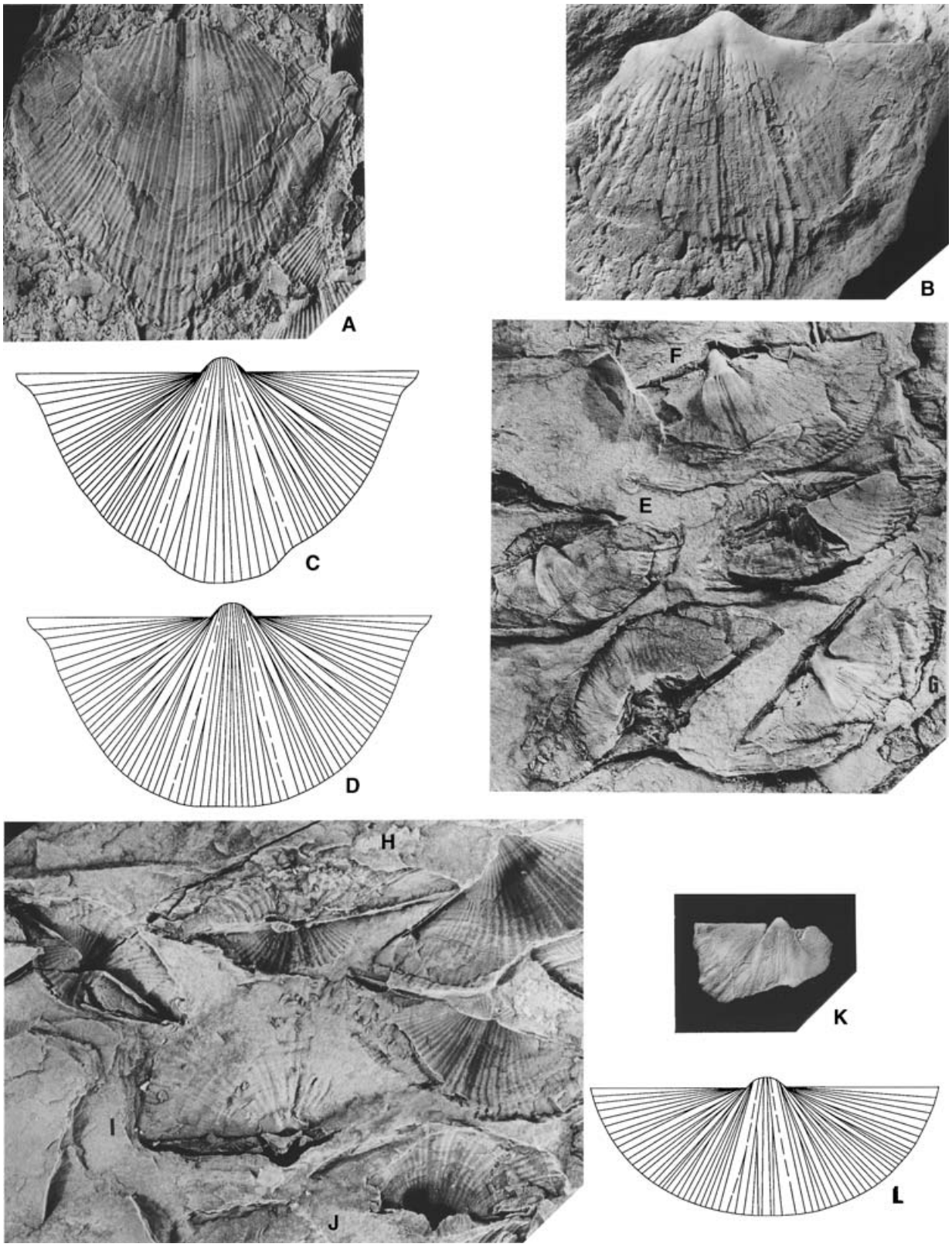

Fig. 5. □A–D. *Septospirifer mazateca* n. sp. □A. Ventral valve, external impression, FCMP/E1-1951. □B. Ventral valve, external mould, FCMP/E1-2000. □C. Ventral valve, costellation. □D. Dorsal valve, costellation. □E–L ?*Septospirifer* sp.; □E. Ventral valve, internal mould, FCMP/E1-1971. □F. Ventral valve, composite mould, FCMP/E1-1970. □G. Ventral valve, internal mould, FCMP/E1-1972. □H. Dorsal valve, external impression, FCMP/E1-2002. □I. Dorsal valve, internal mould, FCMP/E1-2005. □J. Ventral valve, external impression, FCMP/E1-1980. □K. Posterior fragment of ventral valve, internal mould, FCMP/E1-1991. □L. Ventral valve, costellation. All pictures ×1.

hinge line; biconvex; sub-triangular in dorsal outline; transverse; short alate cardinal extremities with angle of 70 to 80 degrees in respect to the hinge line. Shell surface costellate with fasciculate, bifurcating, sub-rounded, and moderately thin costellae on both valves (Fig. 5H); parasulcate anterior commissure. Ventral valve convex; incurved and slightly elevated umbo; striate and high apsacline interarea; slightly deep and wide ventral sulcus with 7–10 costellae bifurcating from three costellae, median plication not divided, at the posterior region; lateral flanks with 19–22 costellae. Dorsal valve slightly convex; low and narrow median fold with 8–10 costellae. Ventral interior with short and wide dental plates; not well-developed dental adminicula; large muscle field with not well-developed medium-sized adductor muscle scars and medium-sized diductor muscle scars thinning towards the posterior region; faint impression of a possible median septum. Dorsal interior with a notothyrium with striate ctenophoridium; very short and thin crural bases.

Discussion. – Specimens described herein are assigned with doubts to the genus *Septospirifer* as the presence of a median septum in the interior of the ventral valve is not clear. These specimens differ from those belonging to *Septospirifer mazateca* because they have more transverse shells, shorter alate cardinal extremities, and fewer costellae in the ventral sulcus. For additional comparison to other species of *Septospirifer*, see previous discussion for *S. mazateca.*

Material. – Six internal moulds of ventral valves (FCMP/E1-1970, E1-1971, E1-1972, E1-1973, E1-1991, and E1-2003); one composed mould of ventral valve (FCMP/E1-1980); two internal moulds of ventral valves (E1-1981, E1-1982); one internal mould of dorsal valve (E1-2005); and one external impression of dorsal valve (FCMP/E1-2002). Specimens E1-2003 and E1-1980 present the central-posterior region of the dorsal valve.

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