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STRATIGRAPHY AND PALEONTOLOGY OF A SAN ANDRES FORMATION (PERMIAN, LEONARDIAN) OUTLIER, ZUNI INDIAN RESERVATION, NEW MEXICO

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Abstract—A 4.5-m-thick sequence of massive, light gray, coarsely crystalline limestone of the San Andres Formation occurs in a limited exposure south of Ojo Caliente, near the New Mexico–Arizona border. This sequence contains fossiliferous intervals near the base and top. The lower interval contains a fauna dominated by the productoid brachiopods *Peniculauris bassi* and *Rugatia occidentalis*. The upper interval contains a bivalve-scaphopod fauna with numerous nautiloids but few gastropods and brachiopods. A conspicuous element of this fauna includes exceptionally large valves of the pectinacean bivalve *Aviculopecten*? aff. *A.*? *coreyanus*. As would be expected from its location between widespread exposures of the Kaibab Formation to the west and San Andres Formation to the east, the Ojo Caliente section includes some taxa that occur in both formations. A tentative correlation of the Ojo Caliente section with the beta member (Fossil Mountain Member) of the Kaibab Formation in Arizona is supported by the presence of the brachiopods mentioned above. Subtle ecological differences in salinity, distance from shoreline and substrate probably account for the significant differences in the composition of the two Ojo Caliente assemblages.

INTRODUCTION

The San Andres Formation, of Leonardian (late Early Permian) age, is exposed discontinuously across approximately two-thirds of New Mexico (Kottlowski, 1969). Near the New Mexico–Arizona border the San Andres crops out in a small, faulted area along a monocline south of the village of Ojo Caliente (Fig. 1). Here, quarrying has created fresh exposures of a thin, 4.5-m interval of the formation. This locality is of interest because it includes one of only two small surface exposures of the San Andres in the 195 km between the northwestern outcrop limit of the San Andres (65 km to the northeast, along the southern edge of the Zuni Mountains) and the eastern limit of the correlative Kaibab Formation (130 km to the west, between Holbrook and Show Low, Arizona). The other San Andres outlier (not discussed in this paper) is a limited outcrop along the Little Colorado River about 7 km south of St. Johns, Arizona, some 55 km southwest of Ojo Caliente. This outcrop was mapped as Kaibab by Wilson et al. (1969) but was considered to be San Andres by Newell and Boyd (1975).

In addition, two intervals in the limestone sequence near Ojo Caliente are highly fossiliferous, and preservation of the fossils is better than is typical of the San Andres Formation in northern New Mexico. This outcrop has been little studied since Darton (1928) briefly described it and reported a modest number of invertebrate taxa. In this paper we document in some detail the stratigraphy and paleontology of this isolated San Andres exposure, so that it may better be related to the more extensive Kaibab and San Andres outcrops to the west and east. Fossils described and illustrated here are in the paleontology collections of the New Mexico Museum of Natural History (NMMNH), Albuquerque, New Mexico.

PREVIOUS STUDIES

Shaler (1907, p. 383, pl. 22, pl. 23, cross section D-D′) first mentioned the Permian strata that crop out south of Ojo Caliente, referring to them as "Carboniferous (Aubrey?) limestone" brought to the surface on the upthrown side of "a very low angle fault." Darton (1910, p. 32) referred to Shaler's observations and remarked that "the rock contains fragmentary fossils recognized as probably *Productus*." He (Darton, 1910, pl. 1) mapped the Permian outcrop south of Ojo Caliente as "undifferentiated Pennsylvanian."

However, 12 years later Darton (1922, p. 260, fig. 41, section B) identified these strata as Permian and assigned them to his Chupadera Formation, noting:

> In the vicinity of Ojo Caliente there is a well-marked anticlinal uplift, cut off on the west side by a fault, which brings the Mancos and Chupadera formations into contact. . . . At the axis of the uplift a small area of the top limestone of the Chupadera formation is exposed.

Sears (1925, p. 10) amplified Darton's conclusions, reporting that "fossils collected from the limestone by (Dean E.) Winchester were determined by (George H.) Girty to be of Kaibab age." Sears' (1925, pl. 2) map, actually completed by Winchester, indicated exposures of the Chupadera Formation south of Ojo Caliente along a north-south anticline with an east limb dipping 10–18°, and a west limb dipping 9°. Darton (1928, p. 142) published a list of 17 Permian invertebrate taxa as well as fish spines and plates identified by Girty from a collection made by Shaler at this outcrop. He also (Darton, 1928, p. 154–155, fig. 61) indicated, as before, that the Permian limestone south of Ojo Caliente is exposed along the axis of a north-south anticline.

Nearly three decades later, Dane and Bachman (1957; also see Dane and Bachman, 1965) first applied the name San Andres to this outcrop, showing it exposed on the upthrown, northeast side of a normal fault (note that their map fails to draw a San Andres–Chinle contact line northeast of the fault, apparently an oversight). McKee (1967, fig. 82) made brief mention of this San Andres outlier as one of several outcrops indicative of a minor marine transgression during the Leonardian. Anderson (1987), based on unpublished MF-series mapping for the U.S. Geological Survey by Gary D. Stricker, indicated that the San Andres Formation exposed south of Ojo Caliente occurs along the northeastern side of a southwest-plunging monocline (Atarque monocline: Fig. 1). He also noted that limestone was quarried here for road metal on local county roads.

GEOLOGIC CONTEXT

We collected Permian invertebrate fossils from four localities south of Ojo Caliente (Fig. 1): (1) NMMNH locality 243 in the SW¼ SW¼ SE¼ NW¼ sec. 27, T18N, R20W; (2) NMMNH locality 244 in the SW¼ SW¼ NW¼ NW¼ sec. 34, T8N, R20W; (3) NMMNH locality 245 in the NW¼ NE¼ SW¼ SW¼ sec. 27, T8N, R20W; and (4) NMMNH locality 246 in the NE¼ SE¼ NW¼ SW¼ sec. 27, T8N, R20W. The outcrop of San Andres Formation south of Ojo Caliente occupies about 2 km^2 in secs. 27, 28, 33 and 34, T8N, R20W (Fig. 1) on the Zuni Indian Reservation. Here, we measured about 4.5 m of San Andres Formation consisting of two types of limestone. The majority of the section is light gray (N7), light olive brown (5 Y 5/6) and dusky yellow (5 Y 6/4) lutite to very fine sparite (colors follow Goddard et al., 1984). The uppermost, fossiliferous limestone we observed (stratigraphic level of NMMNH localities 243 and 246; Fig. 1) is a yellowish gray (5 Y 7/2) to pale yellowish brown (10 YR 6/2) biosparite.

The base of the San Andres Formation is not exposed here, nor apparently is its upper contact with Triassic strata. Indeed, Stricker's mapping (Fig. 1; Anderson, 1987) is incorrect in showing a depositional

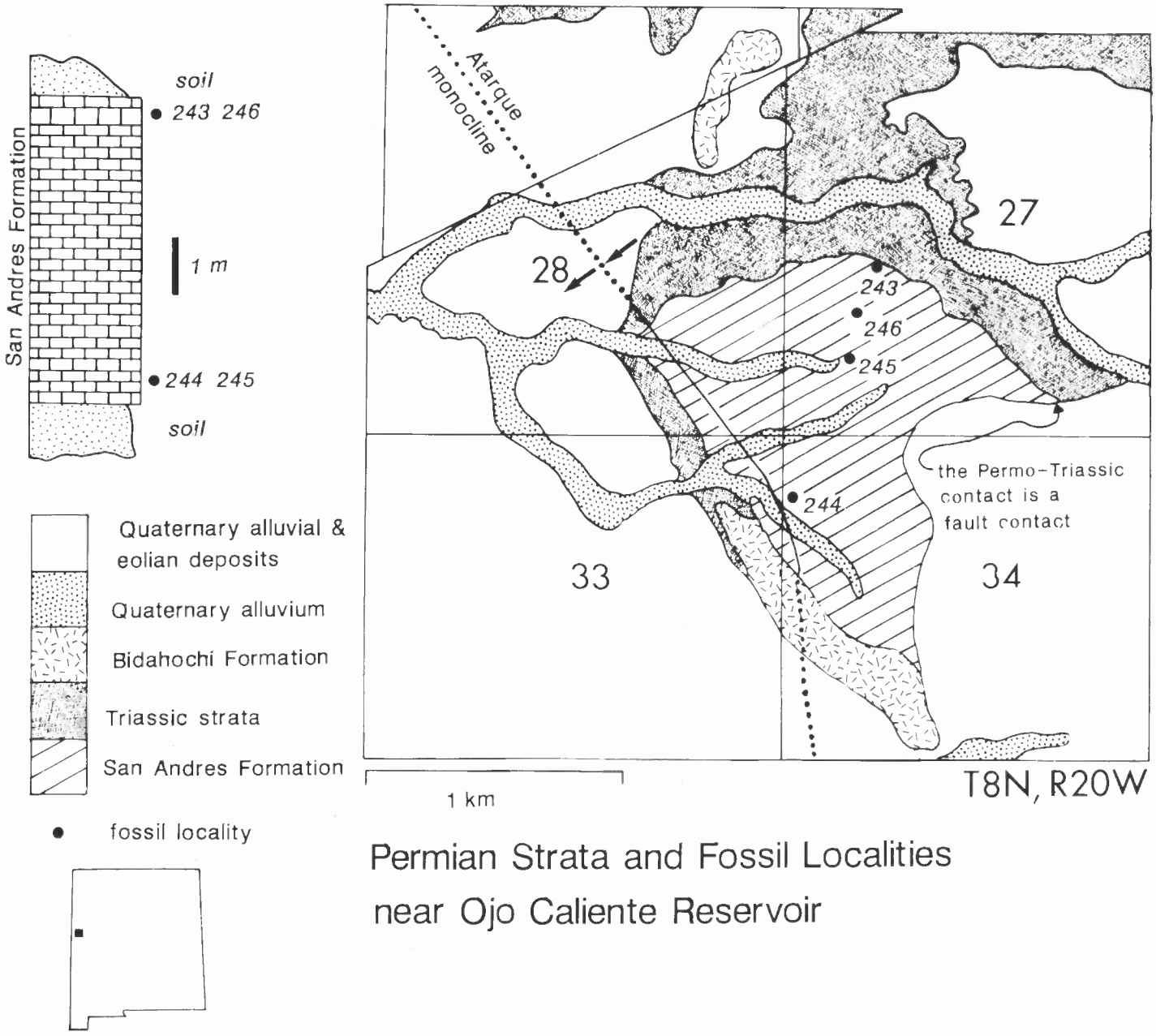

FIGURE 1. Geologic map of Ojo Caliente area, with San Andres Formation stratigraphy and fossil localities indicated (geology after Anderson, 1987).

contact between the San Andres and "lower Petrified Forest member of the Chinle Formation" in sections 27 and 28 (Fig. 1). Instead, we are convinced this contact is a fault, or series of faults, that juxtapose various Triassic units against the San Andres in this area. These Triassic units include: (1) the "mottled strata" of the Chinle Formation (Stewart et al., 1972), grayish purple (5 P 4/2), very dusky purple (5 P 2/2), pale reddish brown (10 R 5/4) and grayish orange (10 YR 7/4) sandy siltstone that crops out in the S½ SW¼ NW¼ sec. 27 and extends westward into sec. 28; (2) the Moenkopi Formation (see Hayden and Lucas, 1989), grayish red (10 R 4/2) to moderate reddish brown (10 R 4/6) arkosic lithic wackestone well exposed in the S½ SE¼ SW¼ NW¼ sec. 27; and (3) the Shinarump Member of the Chinle Formation, pale red (10 R 6/2) and very pale orange (10 YR 8/2) quartzarenite with some chert-pebble conglomerate and silicified fossil wood well exposed in the SW¼ SE¼ SE¼ NW¼ sec. 27. Strata we assign to the lower part of the Chinle (Petrified Forest Member) crop out to the north of this fault zone, in the N⅓ of secs. 27 and 28. Thus, the Permo-Triassic contact is fault controlled south of Ojo Caliente. Although it is likely that the strata of the San Andres Formation exposed here are in the upper part of the formation, their exact stratigraphic position with respect to the base of the Triassic is unclear.

PALEONTOLOGY

Introduction

Darton's (1928) faunal list (Table 1), based on identifications made by Girty, represents the only previous study of the paleontology of the San Andres outcrop near Ojo Caliente. Our relatively modest collections, described below, allow us to verify the occurrence of some of Girty's taxa and add several previously unreported taxa to the fauna. Concepts of some species reported by Girty have changed considerably since his identifications were made. However, because he was preparing monographs on New Mexico and Texas Permian faunas (e.g., Girty, 1909a, b) at approximately the same time he identified the Ojo Caliente fossils, it has been possible in some cases to determine accurately which modern names should be applied to the taxa he reported, even if ex-

TABLE 1. Taxa reported by Girty (in Darton, 1928) from the San Andres Formation near Ojo Caliente.

BRYOZOA

Stenopora sp.

BRACHIOPODA

Chonetes aff. *C. geinitzianus*

Productus ivesi

Productus occidentalis

Productus mexicanus?

BIVALVIA

Deltopecten coreyanus

Pernipecten? [sic] sp.

Pleurophorus? sp.

Pteria sp.

GASTROPODA

Bellerophon aff. *B. crassus*

Euphemus subpapillosus?

Murchisonia sp.

Phymatifer pernodosus

Pleurotomaria sp.

SCAPHOPODA

Plagioglypta canna

NAUTILOIDEA

Domatoceras n. sp.

Domatoceras sp.

VERTEBRATA

Fish spines and plates

amples were not observed in our collections. In the following paragraphs we discuss the taxa identified from this locality and illustrate typical specimens of the more common and distinctive species. Our intention is not to describe comprehensively this fauna, but rather to provide preliminary descriptive information to support our identifications, which may serve as a basis for future more detailed studies. Further study of a larger sample of fossils from this outcrop will undoubtedly result in recognition of additional species.

The fossils are distributed unequally through several intervals of the San Andres sequence, but in general they occur within light gray, coarsely crystalline, hard, massive, limestone lithologies. Much of the limestone, especially near the top and base of the sequence, is composed of calcareous shells and shell fragments, in a generally highly altered state of preservation. Steinkerns and molds are common; when present, shells are typically strongly recrystallized. These modes of preservation, together with the hard, massive limestone in which the fossils are enclosed, have hindered the study of this and other San Andres faunas in northern and central New Mexico. In contrast, some faunas of the correlative Kaibab Formation to the west are silicified, with better preservation of the skeletal morphology of the constituent organisms, and in general more is known about Kaibab faunas than northern and central New Mexico San Andres faunas.

We made our collections from two especially fossiliferous intervals of the San Andres exposure. Localities 243 and 246, near the top of the formation, are characterized by a bivalve/scaphopod/nautiloid-dominated assemblage, whereas localities 244 and 245 are low in the section and yielded abundant productoid brachiopods (Fig. 1). The taxa we identified from each locality are listed in Table 2, together with a subjective estimate of relative abundance of each taxon. Although fusulinids are lacking in the San Andres Formation in northern New Mexico and in the Kaibab Formation, the age of both formations is reliably established as late Leonardian (McKee, 1938; Baars, 1962; McKee and Breed, 1969), mainly on the basis of similarities of Kaibab/San Andres brachiopods with those of Leonardian strata in Texas.

Brachiopods

Rugatia occidentalis (Newberry)

Rugatia occidentalis is the most abundant brachiopod in the San Andres at Ojo Caliente, occurring in large numbers as the dominant invertebrate in the lower part of the section. These small productoids (Figs. 2A–G) average about 30 mm in length and are slightly to moderately wider along the hingeline. A large specimen (P3880, Fig. 2G) is about 35 mm long and 38 mm wide. The pedicle valve is strongly, but evenly, convex and displays a shallow medial sinus that begins just anterior to the beak and continues to the anterior edge of the trail, becoming less pronounced there. The sides of the valve slope steeply to the commissure. In mature specimens the beak is of moderate size and projects significantly beyond the hingeline. The ears are prominent and well set off from

TABLE 2. Biota from the San Andres Formation near Ojo Caliente. Localities 244 and 245 are approximately equivalent stratigraphically near the base of the section, and localities 243 and 246 are equivalent intervals near the top. Abundance estimates are subjective: A = abundant, C = common, U = uncommon, R = rare.

Species	Locality 244	245	243	246
BRACHIOPODA				
Composita arizonica McKee	R			R
Peniculauris bassi (McKee)	A	C		U
Rugatia occidentalis (Newberry)	A	A		R
BIVALVIA				
Aviculopecten? aff. *A.*? *coreyanus* White			U	A
Leiopteria (*Leptodesma*) sp.				A
Myalinella aff. *M. acutirostris* Newell and Burma				U
Sanguinolites? sp.				U
Schizodus canalis Branson				R
Schizodus cf. *S. texanus* Clifton				R
Solemya (*Janeia*) sp.				U
GASTROPODA				
Bellerophontidae, indet.				U
Naticopsis? sp.				U
small, high-spired forms				U
Straparollus (*Euomphalus*)? sp.				U
SCAPHOPODA				
Prodentalium canna (White)				A
NAUTILOIDEA				
Domatoceras aff. *D. bradyi* Miller and Unklesbay				C
Domatoceras sp.			R	
Stearoceras sp.			U	C
VERTEBRATA				
Fish scales/teeth				U
Fish(?) bone fragment				R

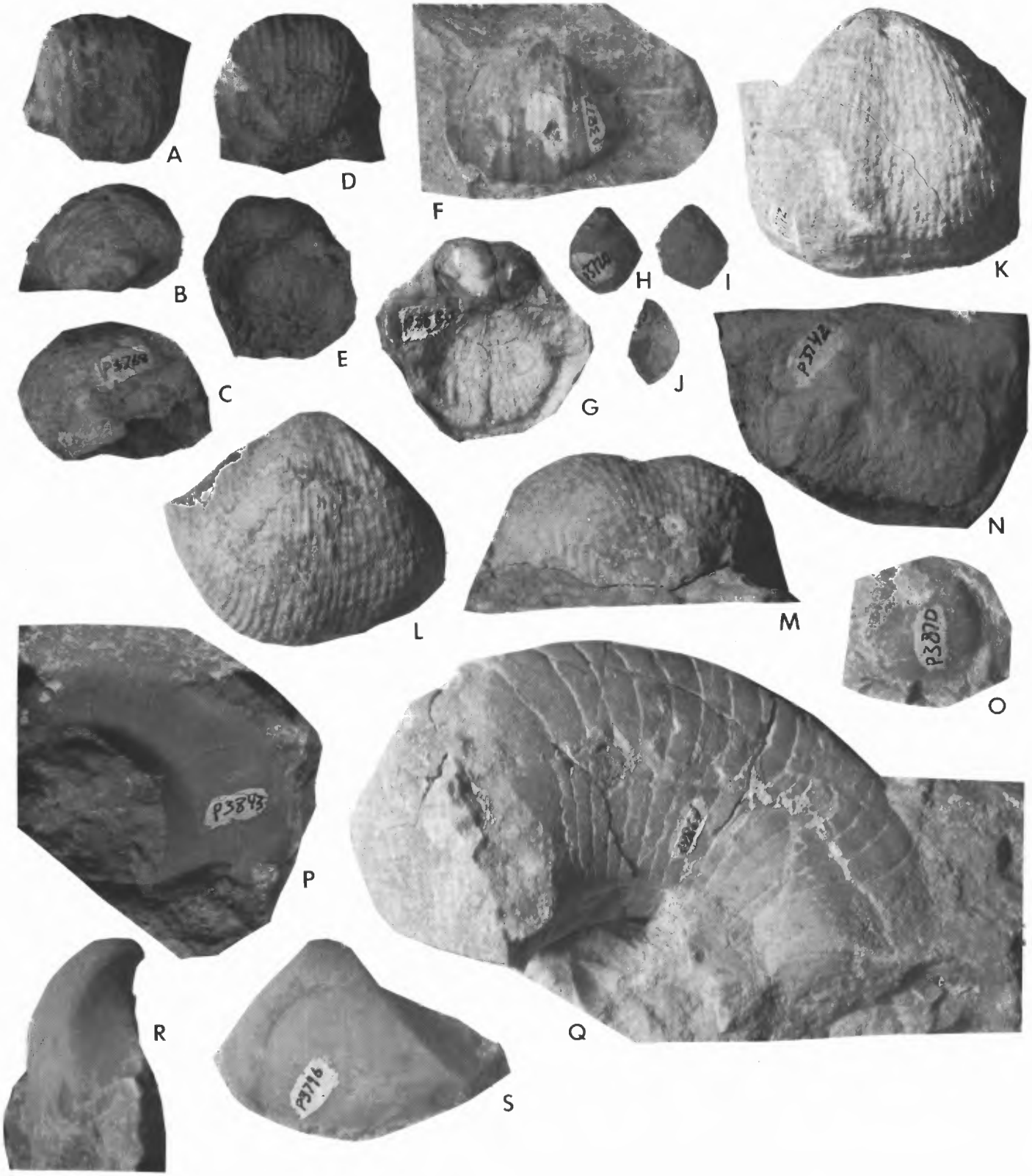

FIGURE 2. Fossils from the San Andres Formation near Ojo Caliente, New Mexico (×1 unless otherwise indicated). A–G, *Rugatia occidentalis* (Newberry): A, B, ventral and side views of pedicle valve, NMMNH-P3771, locality 244; C, D, side and posterior view of pedicle valve, NMMNH-P3768, locality 244; E, dorsal view of pedicle valve, NMMNH-P3766, locality 244; F, ventral view of pedicle valve, showing large intact spine on ear, NMMNH-P3877, locality 245; G, dorsal view of an unusually large articulated specimen, NMMNH-P3880, locality 245. H–J, *Composita arizonica* McKee, brachial valve, pedicle valve and side views of an articulated specimen, NMMNH-P3720, locality 244. K–N, *Peniculauris bassi* (McKee): K, M, ventral and posterior views of pedicle valve, NMMNH-P3712, locality 246; L, ventral view of pedicle valve, NMMNH-P3770, locality 244; N, internal surface of brachial valve, NMMNH-P3742, locality 244. O, *Schizodus* cf. *S. texanus* Clifton, right valve steinkern, NMMNH-P3810, locality 246, ×1.3. P, *Stearoceras* sp., NMMNH-P3843, locality 246. Q, *Domatoceras* aff. *D. bradyi* Miller and Unklesbay, NMMNH-P3862, locality 246. R, S, *Schizodus canalis* Branson, posterior and side views of left valve steinkern, NMMNH-P3796, locality 246.

the central portion of the valve. Ornamentation consists chiefly of strong, relatively coarse, rounded, radial costae of unequal sizes, that increase conspicuously in size anteriorly. The costae are largest on both flanks of the medial sinus (about 3 per 10 mm); those within the sinus and along the lateral surfaces of the valve are somewhat smaller. Increase in costae is not uncommon and occurs by splitting. Concentric, evenly spaced rugae are present on the visceral disc and persist to about one-fifth or one-fourth the distance to the anterior margin of the valve. These rugae are typically slightly smaller than or about equal in size to the radial costae; small nodes are present at their intersection points. Spine bases are sparse along the costae and in some specimens are virtually lacking. One or two spines are present on the ears and may be unusually large (P3877, Fig. 2F). The brachial valve is covered by matrix in nearly all specimens collected. Judging from P3880 (Fig. 2G), it is deeply concave, with reticulate ornamentation. No valve interior surfaces were observed.

Rugatia occidentalis is abundant in the Kaibab Formation (McKee, 1938; Cooper and Grant, 1975), and also occurs in the San Andres. It resembles *R. paraindica* (McKee), also from the Kaibab, but that species is larger, has a greater width-length ratio and possesses several spines on each ear (Cooper and Grant, 1975). No specimens of *R. paraindica* were identified in the Ojo Caliente section.

Peniculauris bassi (McKee)

This large distinctive productoid (Figs. 2K–N) is common in the lower part, but uncommon in the upper part of the exposed San Andres Formation at Ojo Caliente. A typical specimen (P3712, Figs. 2K, M) is 52 mm long and 60 mm wide; larger fragmentary specimens were observed. The pedicle valve of this species is wider than long, has an evenly and moderately convex profile, a shallow medial sinus and prominent ears. Its sides slope fairly steeply from the center to the commissure. Ornamentation consists of relatively fine, parallel, rounded, radial costae with little bifurcation. About 10 to 12 costae are present within 20 mm midway down the trail; interspaces are about as wide as the costae. The costae display numerous small elliptical spine bases along their length. The visceral disc also possesses numerous, wavy, concentric rugae that extend forward from the beak approximately one-third of the distance to the anterior valve margin. These rugae are prominent, somewhat larger than the radial costae and form nodes where they cross the costae. In this area unusually large spine bases are locally present.

None of our specimens include the external surface of the brachial valve, but the internal surface of a nearly complete brachial valve (P3742, Fig. 2N) is available for examination. The median septum is prominent, and the oval diductor muscle scars are aligned adjacent and parallel to both sides of the posterior part of the septum. This orientation differs from that present in most other species of *Peniculauris*, in which scars are obliquely situated relative to the median septum. The brachial ridges are large, arcuate-oval and extend antero-laterally from near the anterior margins of the diductor muscle scars. The cardinal process was not preserved in this specimen.

The Ojo Caliente specimens resemble closely those described by McKee (1938) from the Kaibab Formation of Arizona. In that formation, *Peniculauris bassi* is the most common brachiopod species and occurs in many beds. Girty (in Darton, 1928) identified a related species, *P. ivesi* (Newberry), in the Ojo Caliente fauna and in the Yeso and San Andres formations of central New Mexico (Girty, 1909b). However, McKee (1938) regarded Girty's San Andres specimens as belonging to *P. bassi*, noting that *P. ivesi* is a smaller species that differs from *P. bassi* in other aspects of shape and proportions as well. We did not observe any specimens of *P. ivesi* in our collections, but it has been reported from the San Andres Formation in the Zuni Mountains (Baars, 1962).

Composita arizonica (McKee)

A few examples of this species are present in the collections. It is relatively small, and the anterior commissure is thrown up into a fold and sulcus which is not expressed across most of the posterior part of the valves. A typical specimen (P3720, Figs. 2H–J) is 14.1 mm long, 12.0 mm wide and 8.9 mm thick. The Ojo Caliente specimens accord well with the description of the species presented by McKee (1938) based on Kaibab specimens.

Other brachiopods

In addition to *Rugatia occidentalis* and *Peniculauris ivesi* (=*P. bassi*, see above), Darton (1928) also reported *Productus mexicanus*? and *Chonetes* aff. *C. geinitzianus* from the Ojo Caliente locality. *Productus mexicanus* (of White) was identified questionably by Girty (1909b) in the San Andres Formation of southern New Mexico. King (1930) established the species *Marginifera*? *whitei* for these and similar specimens; Cooper and Grant (1975) split King's species into *Elliottella transversalis* and *Oncosarina whitei*. To further complicate matters, the taxon White called *P. mexicanus* is not the same as the species to which Shumard originally applied the name. Given this tortuous taxonomic history, identification of the small productoids Darton (1928) called *P. mexicanus*? can only be accomplished with direct examination of his specimens.

Lissochonetes geinitzianus (Waagen) is an upper Pennsylvanian to Lower Permian species known mainly from the Midcontinent (Dunbar and Condra, 1932). We are not aware of any recent reports of this species in strata as young as the San Andres. Several chonetoids are known from the Kaibab (see McKee, 1938), but as we did not observe any from the Ojo Caliente exposures we are unable to establish exactly what species was referred to as *C.* aff. *C. geinitzianus* by Darton (1928).

Bivalves

Bivalves are an abundant and conspicuous constituent of the San Andres fauna at Ojo Caliente, especially in the upper part of the formation. However, most specimens are not well preserved; incomplete steinkerns lacking or with small remnants of shell material adhering are the most common mode of preservation. Internal valve and hinge features could be observed on only a few bivalve specimens. Brief descriptions and illustrations of identified taxa are presented here; the total bivalve diversity is undoubtedly greater.

Solemya (*Janeia*) sp.

Three specimens of *Solemya* (*Janeia*) sp. are present in our collections. Two are nearly complete single valves missing only part of the posterior margin (P3807, Fig. 3B; P3896, Fig. 3C) and include part of the shell adhering to the underlying steinkern. The third (P3703, Fig. 3A) is a steinkern of the anterior half of an articulated but slightly displaced pair of valves. The larger of the two nearly complete valves (P3807) is 52 mm long and 26 mm high at the beak; the incomplete steinkern suggests an individual more than 60 mm in length.

This species possesses several distinctive features. The anterodorsal margin is conspicuously concave and the anterior margin is rather acutely rounded. The relatively low beak is situated approximately 35% of the distance from the anterior to the posterior margin. The shell is thin and displays no ornamentation aside from the obscure growth lines. A vague, rather wide depression extends vertically from the beak area to the ventral margin, producing a slight deflection of growth lines and faint emargination of that margin. Of special importance is the presence on the steinkern of a relatively deep, narrow, gently arcuate sulcus extending obliquely from the anterior side of the beak area away from the anterodorsal margin toward the middle of the anterior margin. A remnant of the shell partially covers this sulcus on P3896, indicating that it is the impression of a ridge of thickened shell material on the internal surface of the valve (Fig. 3C). No manifestation of this ridge appears on the external valve surface. This internal ridge characterizes the subgenus *Janeia*, and the sulcus it produces on the steinkern has been documented in similarly preserved late Paleozoic species from other areas (e.g., Beede, 1900, pl. 21, fig. 4).

Although several species of *Solemya* (*Janeia*) are known from the Pennsylvanian of North America, there have been few reports from the Permian. *Solemya* (*Janeia*) *parallella* (Beede and Rogers) was identified in the Kaibab of Arizona by Chronic (1952), but this species has very elongate valves and possesses a distinctive radial ornamentation that is completely lacking on the Ojo Caliente specimens. McKee (1938, pl. 15, fig. 4) illustrated an articulated specimen he identified as *Solenomya* (now *Solemya*) from the Kaibab but it is small, with nearly centrally located beaks. A second specimen assigned to *Solenomya* (McKee, 1938, pl. 15, fig. 10) appears to be closer to *Sanguinolites*? sp.

Myalinella aff. *M. acutirostris* (Newell and Burma)

This small myalinid is represented by a single left valve steinkern (P3899, Fig. 3D). It is 18 mm high, has a hinge length of 17 mm and is 27 mm along the ventral margin. Both the hingeline and ventral margin are uncurved and diverge from the sharply rounded beak at an angle of 50°. No indication of an anterior lobe below the beak was observed. The postero-dorsal margin is broadly rounded and obtuse, forming an angle of approximately 125°, whereas the postero-ventral margin is more acutely rounded. The specimen is moderately inflated, with maximum convexity above the ventral margin.

This myalinid is quite distinct from those reported from the Kaibab Formation by McKee (1938) and Chronic (1952). Its narrow, triangular shape and apparent absence of an anterior lobe suggest it belongs with *Myalinella*, but Newell (1942) emphasized the difficulty in distinguishing *Myalinella* from some species of *Septimyalina* (e.g., *S. scitula*) with poorly preserved specimens. The Ojo Caliente specimen resembles *M. meeki* (Branson) and *M. acutirostris* Newell and Burma in size and proportions. The relatively sharply rounded postero-ventral margin suggests closer affinities with the latter species (see Newell, 1942, pl. 14, fig. 17), which occurs in the Guadalupian of Texas. More specimens, ideally of several growth stages with the shell preserved, are necessary to determine more precisely the taxonomic placement of this bivalve.

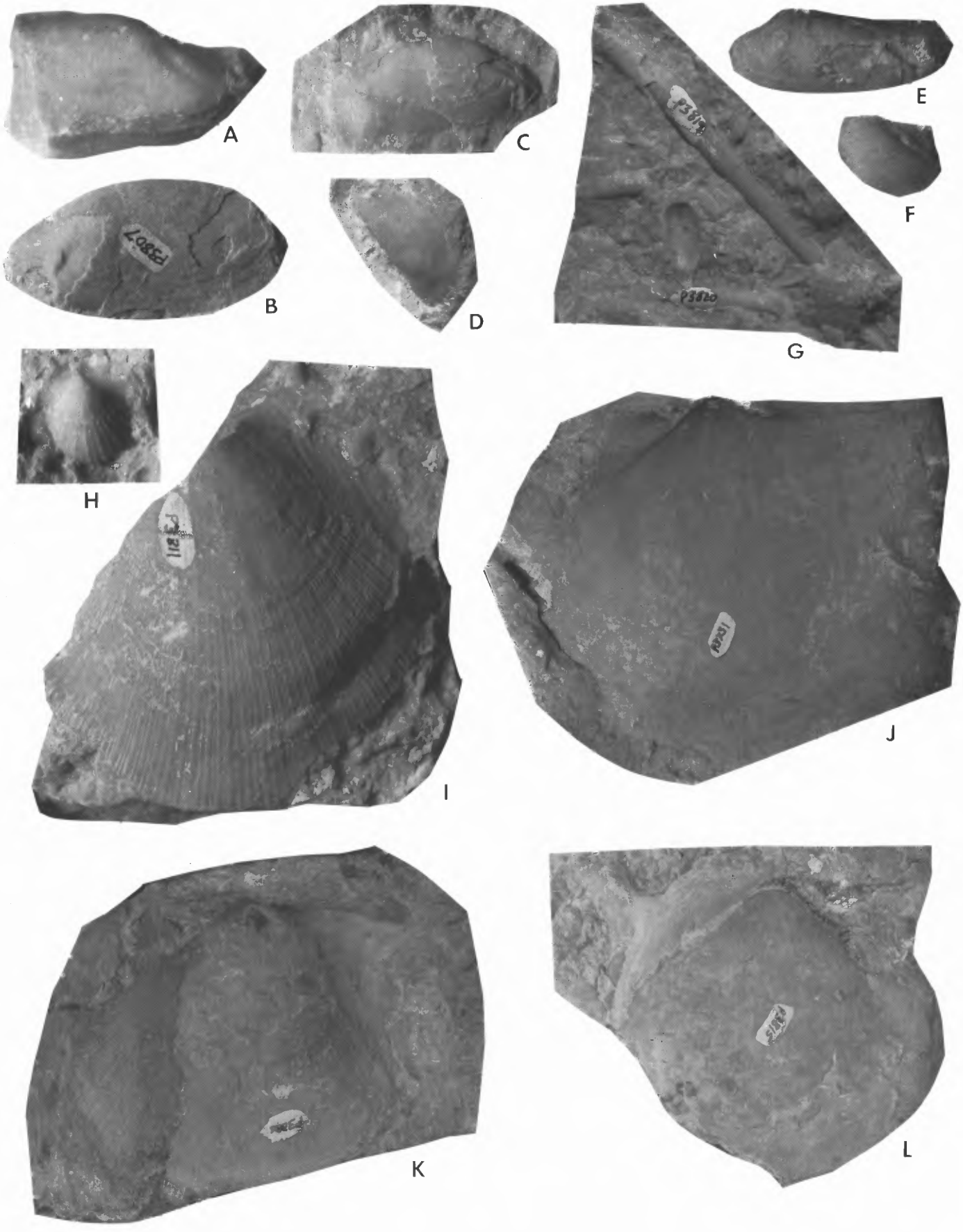
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FIGURE 3. Fossils from the San Andres Formation near Ojo Caliente, New Mexico. A–C, *Solemya* (*Janeia*) sp.: A, anterior end of right valve steinkern, NMMNH-P3703, locality 246, ×1.3; B, left valve, NMMNH-P3807, locality 246, ×1; C, right valve, NMMNH-P3896, locality 246, ×1. D, *Myalinella* aff. *M. acutirostris* Newell and Burma, left valve steinkern, NMMNH-P3899, locality 246, ×1. E, *Sanguinolites*? sp., left valve, NMMNH-P3892, locality 246, ×1.4. F, *Leiopteria* (*Leptodesma*) sp., left valve steinkern, NMMNH-P3890, locality 246, ×3. G, *Prodentalium canna* (White), incomplete specimens, NMMNH-P3819 and P3820, locality 246, ×1. H–L, *Aviculopecten*? aff. *A.*? *coreyanus* White: H, juvenile left valve, NMMNH-P3900, locality 246, ×2.3; I, incomplete left valve, NMMNH-P3811, locality 246, ×1; J, left valve steinkern, NMMNH-P3731, locality 246, ×0.67; K, incomplete left valve steinkern with some shell adhering, NMMNH-P3731, locality 246, ×0.67; L, incomplete right valve steinkern, with shell material adhering around margin, NMMNH-P3815, locality 246, ×0.67.

Leiopteria (*Leptodesma*) sp.

This small species is abundant in the upper part of the San Andres near Ojo Caliente and is probably the bivalve referred to *Pteria* sp. by Girty (in Darton, 1928). Specimens are mainly steinkerns, and a typical individual (P3890, Fig. 3F) is 6.0 mm long and 4.3 mm high. They are characterized by a strongly inflated valve of moderate length, with a low but prominent posterior auricle that extends nearly to the posterior end of the valve. No ornamentation was observed. Of the small Permian members of the subgenus, the Ojo Caliente specimens most resemble *Dozierella* sp. 1 of Chronic (1952) (*Dozierella* is a synonym of *Leiopteria*) and *L.* (*L.*) *parva* of White (1877). However, the specimens at hand appear to be more strongly inflated and to possess a larger posterior auricle than those taxa. Clifton (1942) referred White's (1877) specimens to *L.* (*L.*) *gouldii* (Beede), a Guadalupian species, but judging from Newell's (1940) comprehensive description of that species it is larger (10–20 mm long), more elongate, and possesses a relatively smaller posterior auricle than the Ojo Caliente specimens. In view of the paucity of preserved shell material and absence of information on the hinge teeth, no attempt is made to assign these specimens to a species.

Aviculopecten? aff. *A.*? *coreyanus* (White)

The largest and most conspicuous bivalves in the Ojo Caliente San Andres assemblage are numerous specimens of an unusually large aviculopectinid. Complete articulated specimens were not observed but many specimens comprise most of a single valve, and both left and right valves are represented. These bivalves are preserved as steinkerns with little to most of the recrystallized shell adhering to them. Maximum length of a large left valve is estimated at 130+ mm; height appears to be equal to or slightly less than length. The hingeline is straight and long, and approximately equals the greatest longitudinal expansion of the main body of the valve. The large posterior auricle merges with the posterior valve margin smoothly and with relatively little emargination. The periphery of the body of the valve is acline and virtually circular.

The left valve (Figs. 3I–K) is strongly convex for the genus, especially across the umbonal area. The anterior umbonal slope near the hingeline is rather steep, whereas the posterior slope is very gentle and merges smoothly with the posterior auricle. Ornamentation (Fig. 3I) consists of numerous, closely spaced, radial costae, of several ranks. About 25 costae occur within a length of 20 mm at a position along the valve midline about three-fourths of the distance from the beak to the ventral margin. A complete valve would have as many as 150 costae. Primary costae are broad, low, and nearly flat; secondary and tertiary costae are progressively smaller, narrower, and less broadly rounded. A few fourth-order costae are present as thin, sharp structures along the flanks of adjacent costae. Size and shape differences between primary, secondary and tertiary costae are gradational, but are clearly evident upon close inspection. Considerable variation in costae size is evident across all parts of the valve. Costa increase is by intercalation, but even small costae may extend separately for most of the distance across the surface of the valve, with increase in size ventrally being very gradual.

Costa size decreases abruptly from the body of the valve to the posterior auricle. About 20 fine, narrow, relatively widely spaced, muted riblets adorn this auricle, becoming fainter toward the posterior and dorsal margins. Concentric, lamellate growth lines are well-developed across the posterior auricle but become less conspicuous on the body of the valve. The anterior auricle is not well preserved on any specimen, but appears to be smaller, less expanded and more emarginate than the posterior auricle. Ornamentation on the anterior auricle is unknown.

The right valve (Fig. 3L) is significantly flatter than the left valve. Little shell material is retained on any of the right valve steinkerns available, but what remains is sufficient to demonstrate that the posterior auricle, at least, is unornamented. Internal valve and hinge features are not well displayed on the specimens examined. A nearly complete left valve steinkern (P3731, Fig. 3J) has a deep, narrow, linear furrow immediately below and parallel to the hingeline margin, on both sides of the beak. These indicate the presence of a pair of symmetrical cardinal teeth, each widening slightly toward the beak. The nature of the resilifer and other hinge structures is not known.

Two small pectinacean valves appear to represent juveniles of *A.*? aff. *A.*? *coreyanus*. The best preserved individual (P3900, Fig. 3H) is a small left valve about 9 mm in length and width. Ornamentation consists of prominent, narrow, sharp, widely spaced primary costae, with smaller secondary and faint tertiary costae intercalated between them. These costae are more widely separated, sharper and display more conspicuous size differences than the costae on mature valves of *A.*? aff. *A.*? *coreyanus*. However, this ornamentation pattern correlates well with trends observed from the ventral margin toward the beak on mature specimens; unfortunately, none of the large specimens retains shell ornamentation in the beak area, making direct comparison impossible.

The shape, ornamentation, large size and prominent posterior auricle of these specimens agree well with the specimens of *A.*? *coreyanus* described and illustrated by White (1877) from "Carboniferous" (actually Permian) strata near Fort Wingate, New Mexico. Descriptions of *A.*? *coreyanus* from the New Mexico Permian (White, 1877; Girty, 1909b; Newell, 1937) are based upon few specimens, all of which are at most half the size attained by the Ojo Caliente valves. Girty (in Darton, 1928) reported *A.*? *coreyanus* from this locality, and although no reference was made to unusually large size, we assume that he was referring the large forms described here to that species. It is likely that these specimens are simply large individuals of *A.*? *coreyanus*, a species known previously only from much smaller individuals. As we have not examined the type specimens and because some aspects of the morphology of the Ojo Caliente specimens are as yet unknown, we do not positively assign them to *A.*? *coreyanus*. Newell (1937) noted that the poorly known right valve of this species may be devoid of radial ornamentation, which would remove it from *Aviculopecten*. We are unable to clarify the nature of right valve ornamentation at this time, but our impression is that radial ornamentation is either lacking or muted.

The Ojo Caliente specimens also resemble *A. kaibabensis* Newell. This large species reaches a height of 75 mm and has a strongly convex left valve and an unusually low posterior umbonal slope. Ornamentation consists of numerous, closely spaced, relatively coarse radial costae, with the primary costae being slightly more pronounced than the others. Figures of *A. kaibabensis* (Newell, 1937; Chronic, 1952) indicate that its ornamentation is very similar to that of the Ojo Caliente specimens. The posterior auricle of *A. kaibabensis* is seemingly not as pronounced as that of *A.*? *coreyanus*, and the convexity of the left valve is perhaps somewhat greater. The right valve of both species is smooth or only obscurely ornamented. Neither Newell (1937) nor Chronic (1952) compared the two species, but except for the differences noted above they appear to be very close.

Although several workers have reported *A.*? *coreyanus* from the San Andres Formation in New Mexico, we are aware of no reports of this species from the Kaibab of Arizona, and only one (Hewett, 1931) from the Kaibab or Toroweap Formation of southern Nevada. On the other hand *A. kaibabensis* has never been reported from the San Andres of New Mexico. This may suggest that the two species represent a geographically gradational complex of large aviculopectens characteristic of Leonardian strata in the New Mexico–Arizona area. McKee (1938, pl. 42, unnumbered and uncaptioned figure) figured a Kaibab shell fragment of a large pectinacean of a size comparable to that of the Ojo Caliente specimens, but its ornamentation is coarser, and the ribs are more sharply rounded and widely separated.

Schizodus canalis (Branson)

A single, nearly complete left valve steinkern (Figs. 3R, S) agrees in all respects with specimens of *S. canalis* described and illustrated by Newell and Boyd (1975, fig. 46) from the San Andres outlier south of St. Johns, Arizona. The specimen is 43.6 mm long and 32.7 mm high. Length/height is 1.33, slightly greater than the average (1.27) for the St. Johns collection.

Schizodus cf. *S. texanus* Clifton

A nearly complete right valve (Fig. 2O) measuring 17 mm long and 14.5 mm high displays the generally elongate shape of *S. texanus*. The beak is sharp, prominently elevated, and situated near the anterior margin of the valve. The postero-dorsal margin descends steeply from the beak and then curves upward with posterior expansion of the valve. The posterior margin of the valve is not preserved.

White (1877, pl. 11, fig. 6) reported as *S. wheeleri* two larger specimens with similar shape from "Carboniferous" (actually Permian) rocks near Ft. Wingate.

Chronic (1952) noted *S. texanus* (to which White's specimens were referred) in the Kaibab of northern Arizona, and Newell and Boyd (1975) stated that the species is widespread in both the San Andres and Kaibab formations, and is abundant in the St. Johns, Arizona outcrop. Clifton's (1942) type collection of *S. texanus*, from Leonardian units in Texas and southern New Mexico, displays moderate variation in shape; the holotype has a generally convex postero-dorsal margin below the beaks that appears similar to that of the Ojo Caliente specimen. Because this specimen is incomplete and solitary we cannot be certain that it is *S. texanus*. *Schizodus canalis* has a much less extended posterior margin and carinate posterior ridge.

Sanguinolites? sp.

Several poorly preserved incomplete specimens are referred questionably to *Sanguinolites*. The best preserved specimen (P3892, Fig. 3E) is an elongate, low, laterally compressed left valve about 30 mm long and 12 mm high at the beak. The beak is low and situated about 0.25 of the distance from the anterior to the posterior end. Ornamentation is restricted to faint, widely spaced concentric growth wrinkles. The dorsal post-umbonal part of the valve is only obscurely set off from the rest of the valve by a slight increase in convexity and the hint of a weak radial ridge. The posterior valve margin is evenly rounded and probably gaped slightly. This valve closely resembles *Sanguinolites*? sp. of Chronic (1952) from the Kaibab Formation of Arizona, but differs in having a straight rather than vaguely convex antero-dorsal margin and a less distinct post-umbonal area. Both differences may be the result of preservational variations. The specimen identified as *Solenomya* sp. by McKee (1938, pl. 15, fig. 10) is also similar to the Ojo Caliente specimens. The proportions and shape of *Sanguinolites*? sp. resemble *Wilkingia rothi* (Newell) from the Whitehorse Formation of Texas. However, that species possesses a sulcus extending obliquely from the beak to the posterior valve margin and radial rows of small papillae on the valve, neither of which were observed on the Ojo Caliente specimens.

Gastropods

Gastropods are uncommon in the Ojo Caliente sequence and their remains are restricted to steinkerns. We observed steinkerns of a small *Naticopsis*?, a small bellerophontid, a medium- to high-spired form, and portions of the whorls of a large *Straparollus* (*Euomphalus*)?.

Although Darton (1928) did not cite *Naticopsis* from this fauna, he did note the presence of several other taxa: *Euphemus subpapillosus*?, *Bellerophon* cf. *B. crassus*, *Phymatifer pernodosus*, *Pleurotomaria* sp. and *Murchisonia* sp. We did not collect identifiable representatives of any of these species, but some discussion of them is included here, in order to reach reasonable conclusions about their identity according to current taxonomic concepts.

Euphemus subpapillosus, now *Euphemitopsis subpapillosa* (White), was originally described from the Kaibab and equivalent formations in Utah and Arizona. Girty (1909b) reported it from the San Andres Formation of the Caballo, Fra Cristobal and San Andres Mountains in southern New Mexico, and it ranges widely in Lower Permian formations from Wyoming to northern Mexico (Knight, 1953; Yochelson, 1960).

Bellerophon crassus Meek and Worthen is a large Middle Pennsylvanian species. Girty (1909a) reported it from the Permian of the Glass Mountains, but his specimens are now considered to be *Bellerophon deflectus*, a species established on the basis of specimens from the Kaibab Formation of Arizona (Chronic, 1952). Yochelson (1960) noted the resemblance between *B. crassus* and *B. deflectus*, and it is very likely that Darton's (1928) report of *B.* aff. *B. crassus* based on Girty's identification refers to *B. deflectus*. Although not mentioned by Chronic (1952), the large bellerophontid illustrated by McKee (1938, pl. 21, fig. 7) from the alpha member of the Kaibab appears to be *B. deflectus*.

Phymatifer pernodosus is the name applied to a large, nodose *Euomphalus* reported by early workers (e.g., Girty, 1909b) from the Permian Aubrey Group and San Andres Formation of Arizona and New Mexico. Yochelson (1956) pointed out that *Straparollus* (*Euomphalus*) *pernodosus* is confined to Middle Pennsylvanian strata, and is part of a series of nodose species that culminates with *S.* (*E.*) *kaibabensis* Chronic. Chronic (1952) noted the strong resemblance between the two species and reported *S.* (*E.*) *kaibabensis* from the San Andres as well as the Kaibab formations. It is thus likely that the report of *Phymatifer pernodosus* by Darton (1928) from the Ojo Caliente locality refers to *S.* (*E.*) *kaibabensis*.

Nothing more definite can be said about the specimens reported as *Murchisonia* and *Pleurotomaria*. In the early part of this century these names were applied to a wide variety of gastropods now referred to numerous genera. Examination of the specimens would be required in order to identify them more accurately.

Scaphopods

Prodentalium canna (White)

This scaphopod, long known as *Plagioglypta canna* from numerous Permian units throughout the western U.S., is among the most abundant fossils in the San Andres exposures at Ojo Caliente. All of the specimens we collected are incomplete (typically the apical and apertural ends are missing), some are crushed, and the shells are heavily recrystallized. The shells are characterized by their long, narrow, uncurved, conical shape, circular cross section, and smooth external surfaces. Measurements of two of the largest specimens are: length, 90+ mm; maximum diameter, 8 mm; diameter near apex, 2 mm (P3819, Fig. 3G), and length, 88+ mm; maximum diameter, 8.5 mm; diameter near apex, 2.2 mm (P3860). Yancey (1973) noted that large complete specimens may reach a length of 200–250 mm and a diameter of 20 mm. The shells of the Ojo Caliente specimens are relatively thick, averaging 2.0 to 2.5 mm in thickness at the wide ends of these specimens. *Prodentalium canna* is common to abundant in several intervals of the Kaibab Formation in Arizona (McKee, 1938; Chronic, 1952), and has been reported from the San Andres Formation in southern New Mexico (e.g., Girty, 1909b).

This species was long assigned to *Plagioglypta*, mainly on the basis of its apparently smooth, unornamented external shell surface. However, Yancey (1973), in re-examining White's type specimens, noted the presence of fine longitudinal ribbing externally and transferred the species to *Prodentalium*, a designation followed by subsequent workers. This ribbing is not present on most specimens because of post-mortem abrasion, poor preservation and/or weathering.

Nautiloids

Nautiloids are among the most common and conspicuous fossils in the Ojo Caliente section. However, as is typical of nautiloids elsewhere in the Kaibab and San Andres formations, preservation is usually as steinkerns, with little of the original shell remaining, and complete specimens are extremely rare. Little additional study of San Andres and Kaibab nautiloids has been accomplished since Miller and Youngquist's (1949) monograph on North American Permian nautiloids (see McKee and Breed, 1969 and Kues, 1987, for reviews). Most of the more than a dozen species known from these formations were established more or less typologically on the basis of a few incomplete specimens, typically steinkerns, and thus the species and to some extent genus-level taxonomy can only be regarded as provisional. Here we briefly describe and illustrate the forms collected from the Ojo Caliente exposures, but refrain from definite species assignments.

Domatoceras aff. *D. bradyi* Miller and Unklesbay

Several steinkerns of a medium-sized nautiloid with narrow chambers and a vertically rectangular cross section are similar in most features to *Domatoceras bradyi*. The most complete specimen (P3862, Fig. 2Q) consists of most of the last and part of the penultimate whorl of a shell that was an estimated 130 mm in diameter. The whorls are laterally compressed, measure about 48 mm high and 35 mm wide at the first septum, and widen slightly dorsally. The lateral whorl surface is flat to very gently convex and curves evenly and fairly abruptly across the ventrolateral shoulder to a nearly flat venter. The umbilical shoulder is gently rounded, and the umbilicus is shallow. The diameter of the umbilicus is estimated at about 45% of the total shell diameter. Nodose ornamentation is absent. The sutures are closely spaced (about 9 in a distance equal to the height of a whorl) and gently undulatory, forming shallow lobes across the venter and lateral whorl surface, and shallow, slightly more strongly curved and narrower saddles across the ventrolateral and umbilical shoulders. The siphuncle is displaced ventrally and located approximately midway between the center and ventral margin of the septa.

In most features these Ojo Caliente specimens are virtually identical to the specimens of *D. bradyi* described by Miller and Youngquist (1949). However, *D. bradyi* possesses a sharp, narrow lira along the midline of the venter, a structure lacking in the Ojo Caliente specimens. Because Miller and Youngquist (1949) had only five specimens of *D. bradyi* available for study, the significance and prevalence of this unusual feature cannot be adequately assessed. *Domatoceras bradyi* is known from the Kaibab Formation of northern Arizona and the San Andres Formation of the Sacramento Mountains area, south-central New

Mexico. A related San Andres species, *D. walteri* Miller and Unklesbay, possesses obscure, sparse nodes and grooved ventrolateral shoulders, both lacking in the Ojo Caliente specimens. *Stearoceras sanandreasense* (Miller, Dunbar and Condra) is superficially similar to *D. bradyi*, but has a wide, low whorl cross section and a more centrally located siphuncle.

Stearoceras sp.

Several incomplete steinkerns are characterized by a roughly quadrate whorl cross section, relatively sharply rounded ventrolateral and umbilical shoulders, and a deep umbilicus. In general these specimens indicate a nautiloid of medium size, perhaps 100 to 125 mm in maximum diameter. They possess a flat to gently convex lateral whorl surface, which rounds evenly but somewhat abruptly across the ventrolateral shoulder to a gently convex venter. The curvature of the umbilical shoulder is about equal to or somewhat sharper than that of the ventrolateral shoulder. In addition, the umbilical shoulder is more sharply rounded on smaller, earlier whorls than on the last whorl. One specimen (P3843, Fig. 2P) possesses incipient, low, elongate, widely spaced nodes along the ventrolateral shoulder.

Sutures are transversely oriented and relatively widely spaced; about 5 or 6 occur in a distance equal to the height of a whorl. They develop very gentle, broad lobes across the venter, narrower, more strongly curved saddles at the ventrolateral shoulders, broad, moderately arcuate lobes across the lateral whorl surface, and restricted saddles across the umbilical shoulder before descending with little or no flexure across the umbilical wall.

None of the specimens is complete enough to allow accurate measurements of whorl dimensions. Whorl cross sections appear to be about as high as wide. Only one specimen (P3881) preserved part of the shell adhering to the steinkern. The shell on the last whorl of this specimen is about 2 to 3 mm thick and displays numerous, closely spaced growth lines. On this specimen the umbilical shoulder of the penultimate whorl is considerably sharper than on the succeeding whorl. In general, the surface topography of the steinkern appears to reflect the external shell morphology well.

In most features these specimens appear similar to a group of Lower Permian nautiloid species assigned by Miller and Youngquist (1949) to *Stearoceras*, e.g., *S. aberrans* (Miller and Unklesbay), *S. simplex* (Hyatt) and *S. militarium* (Hyatt). These species are characterized by rather angular whorls, sharply curved at the ventrolateral and umbilical shoulders—quite unlike the inflated, evenly convex whorl surfaces of the type species, *S. gibbosum* (Hyatt). The obscure nodes on P3843 and the somewhat angular, quadrate cross section of these specimens also suggest a trend toward the typical morphology of *Metacoceras*.

Two incomplete steinkerns (P3884 and P3885) closely resemble the specimens described above but possess more inflated whorls and less sharply rounded shoulders. In these features they approach the external shell form characteristic of *S. rotundatum* (Miller and Unklesbay). P3884 is a small specimen with a diameter of approximately 65 mm, and a whorl cross section that is wider (30 mm) than high (25 mm). P3885 has a diameter of at least 115 mm; only a small portion of the last whorl is preserved.

The gradational variation in morphology of even these few specimens is pronounced. Additional collections of Kaibab and San Andres nautiloids are needed in order to ascertain the degree of intraspecific variation within species of *Stearoceras* and related genera, and to better define the status of established species that were based on only a few, incomplete steinkerns.

DISCUSSION

In contrast to the conclusion of McKee (1938), Leonardian marine environments represented by the Kaibab and San Andres formations extended continuously from east-central Arizona through west-central New Mexico (Rascoe and Baars, 1972). The fauna of the San Andres exposure near Ojo Caliente includes elements of both formations, especially among the brachiopods, scaphopods and nautiloids. Our modest sample of invertebrates is not distinctive or diverse enough to allow exact correlation with specific intervals of the Kaibab and San Andres outcrops to the west and east; most taxa are either relatively long ranging in these formations or too poorly known to assess their ranges precisely. The abundance of the brachiopod *Peniculauris bassi* and virtual restriction of *Rugatia occidentalis* to limestones of the beta member (Fossil Mountain Member) of the Kaibab in Arizona (McKee, 1938) suggest a tentative correlation.

As noted earlier, the stratigraphic position of the thin Ojo Caliente exposure within the San Andres Formation or relative to the unconformity at the base of overlying Triassic units cannot be determined locally. Baars (1962) reported a mollusc-brachiopod fauna restricted to the limestones in the upper 12 m of a 29-m-thick section of the San Andres Formation about 5 km south of Fort Wingate (70 km northeast of Ojo Caliente). He also noted that the lower half to two-thirds of the San Andres in the Zuni Mountains is composed of dolomites, shales, siltstones and sandstones, whereas the upper half to one-third of the formation is typically a massive, cliff-forming limestone. Thus, it seems reasonable to believe that the Ojo Caliente limestone exposure represents part of the upper half to one-third of the San Andres Formation in west-central New Mexico.

The Ojo Caliente San Andres sequence includes two distinctive fossiliferous horizons. The upper interval contains a diverse assemblage dominated by bivalves and scaphopods, with significant numbers of nautiloids but few brachiopods. The lower interval is dominated by the abundant productoid brachiopods *Peniculauris bassi* and *Rugatia occidentalis*. Paleoecological analysis of Kaibab faunas (e.g., McKee, 1938; Nicol, 1944, 1965; Chronic, 1952; McKee and Breed, 1969) have demonstrated the occurrence of several broadly defined associations of species. Kaibab scaphopods, for example, (*Plagioglypta* faunule of Nicol, 1944) are most numerous in facies interpreted as nearshore, euryhaline environments, where they are mainly associated with abundant bivalves and gastropods but relatively few brachiopods (McKee, 1938; see also Bretsky and Bermingham, 1970). In contrast, brachiopod-dominated assemblages (e.g., *P. bassi* fauna of McKee, 1938; *Dictyoclostus* faunule of Nicol, 1944) have been interpreted as representing more stenohaline, open-marine environments. Bivalves such as *Aviculopecten* and nautiloids also indicate normal marine, offshore conditions, although nautiloids could have floated into and been preserved in nearshore euryhaline environments.

Such broad paleoecological interpretations cannot be applied uncritically to the two Ojo Caliente San Andres assemblages. There is little lithological difference between the coarse-grained limestones containing both assemblages, and thus no obvious sedimentological indications are present suggesting significant variations in the environments. The substrate on (or in) which both faunas lived was probably composed of fine, soft, lime mud, locally with high densities of shells and fragmented bioclasts, deposited in generally quiet conditions. During the time of San Andres deposition in west-central New Mexico the Ojo Caliente area was relatively close to the northern shoreline of the Leonardian sea (Rascoe and Baars, 1972), and deposition of San Andres sediments (in the nearby Zuni Mountains) occurred in conditions ranging from hypersaline lagoons, nearshore shallow environments dominated by terrigenous mud and sand, and normal-marine, carbonate shelf environments. The thin San Andres limestone sequence preserved near Ojo Caliente, however, appears to represent an offshore, essentially normal-marine phase of deposition.

Both Ojo Caliente assemblages lived in these offshore carbonate environments. The lower productoid assemblage is similar to brachiopod dominated faunas in the Kaibab except for the absence of the sponges that are so common in Kaibab faunas. This assemblage reflects normal-marine, stenohaline conditions. The upper assemblage, however, is not exactly comparable to any reported Kaibab assemblage, but the taxa most closely resemble forms from the alpha (Harrisburg) member (Beus, personal commun., 1989). Although this assemblage is dominated by presumably nearer-shore, euryhaline bivalves and scaphopods, the occurrence of abundant large *Aviculopecten* valves and a surprisingly high number of nautiloids suggests that salinity cannot have varied much from normal marine salinity. The conspicuous difference in the composition of the two Ojo Caliente assemblages must reflect variations in the ecological conditions (such as salinity, distance from shoreline, substrate) in which they lived, but this variation was subtle and at present cannot be definitely related to one or more specific environmental parameters.

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