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Paleontology, Taphonomy and Paleoecology of the Palmarito Formation (Permian of Venezuela)

by

Peter R. Hoover

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CONTENTS

Abstract 5
Resúmen 5
Acknowledgments 5
Introduction 6
The Palmarito Formation
  Regional Setting 8
  Historical Setting 10
  Biostratigraphic Correlation 13
Lithic and Faunal Analysis
  Introduction 17
    Lithic Description Techniques 17
    Faunal Lists 18
    Taphonomy 18
    Paleoecology 19
  Collecting Localities
    Locality 1 19
    Locality 2 20
    Locality 3 21
    Locality 4 22
    Locality 5 23
    Locality 6 24
    Locality 7 26
    Locality 8 26
    Locality 10 27
    Locality 11 28
    Locality 13 29
Depositional Environments 31
Organism/Substrate Relationships 31
Permian Ratio 33
Sampling Efficiency Index 35
Introduction to Systematic Paleontology
  Philosophical Considerations 37
  Format 38
  Terminology 38
  Type Repositories 39
  Measurements 39
Brachiopod Systematic Paleontology
  Family **Craniidae** Menke 39
  Family **Schizophoriidae** Schuchert and LeVene 40
  Family **Derbyiidae** Stehli 41
  Family **Meekellidae** Stehli 47
  Family **Rugosochonetidae** Muir-Wood 49
  Family **Aulostegidae** Muir-Wood and Cooper 55
  Family **Cooperinidae** Pajaud 57
  Family **Rhamnariidae** Muir-Wood and Cooper 59
  Family **Marginiferidae** Stehli 62
  Family **Paucispiniferidae** Muir-Wood and Cooper 66
  Family **Linoproductidae** Stehli 70
  Family **Retariidae** Muir-Wood and Cooper 72
  Family **Echinoconchidae** Stehli 74
  Family **Dictyoclostidae** Stehli 74
  Family **Lyttoniidae** Waagen 82
  Family **Pontisiidae** Cooper and Grant 84
  Family uncertain (**Rhynchonellacea**) 87
  Family **Retziidae** Waagen 88
  Family **Athyrididae** McCoy 93
  Family **Ambocoeliidae** George 96
  Family **Elythidae** Frederiks 98
  Family **Spiriferidae** King 100
  Family **Reticulariinidae** Cooper and Grant 102
  Family **Dielasmatidae** Schuchert 104
  Family **Pseudodielasmatidae** Cooper and Grant 105
  Family **Cryptonellidae** Thomson 106
References Cited 109
Plates 117
Index 128

LIST OF ILLUSTRATIONS

Text-figure — Page

1. Maps showing location of eleven Palmarito Formation fossil assemblages 7
2. Similarity coefficient matrix for brachiopod genera in Palmarito Formation fossil assemblages 14
3. Dendrogram showing similarities in brachiopod generic composition among Palmarito Formation fossil assemblages 15
4. Brachiopod occurrences and taphonomic indices in eleven collecting localities within the Palmarito Formation ..... foldout inside back cover
5. Habitat-type distributions for species and individuals in Palmarito Formation brachiopod assemblages ... 32
6. Permian Ratio for brachiopods, calculated for well-known localities of marine Permian fossils, plotted against latitude 34
7. Permian Ratio and Sampling Efficiency Index for nine Palmarito Formation and 35 Road Canyon Formation articulate brachiopod assemblages 35
8. Sampling Efficiency Index for Permian articulate brachiopod assemblages, calculated for well-known collecting localities, plotted against latitude 36
9. Shape variation of dorsal valves of four samples of *Cooperina* from the Permian of West Texas and Venezuela 59
10. Comparison of shell form of two population samples of *Echinauris bella* Cooper and Grant (1975) 64
11. Scattergrams of dimensions of two population samples of *Hustedia hyporhachis* n. sp. from Venezuela and one population sample of *Hustedia consuta* Cooper and Grant (1976b) from West Texas 92–93

LIST OF TABLES

Table — Page

1. Occurrences of brachiopod genera in Palmarito Formation fossil assemblages 14
2. Comparison of brachiopod generic composition of the Palmarito Formation and of selected Permian biostratigraphic units in the West Texas region 14
3. Comparison of brachiopod generic composition of Palmarito Formation fossil assemblages and (or) assemblage groups, with West Texas stratigraphic units 16
4. Genera and families of Arnold collection Palmarito Formation brachiopods identified by H. M. Muir-Wood and P. R. Hoover 17
5. Results of rock constituent analyses of Venezuelan marine Permian rocks containing appreciable numbers of silicified fossils 32
6. Habitat-type classification of Palmarito Formation brachiopod genera 33
7. Familial affinities of Palmarito Formation brachiopod genera 35
8. Permian Ratio and Sampling Efficiency Index of Palmarito Formation articulate brachiopod assemblages 35
9. Measurements of dorsal valves of *Cooperina inexpectata* Termier, Termier and Pajaud (1966) from locality 6, Palmarito Formation 60–61
10. Statistics calculated from measurements of dorsal valves of two species of *Cooperina* Termier, Termier and Pajaud (1966) 61

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PALEONTOLOGY, TAPHONOMY AND PALEOECOLOGY OF THE PALMARITO FORMATION (PERMIAN OF VENEZUELA)

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ABSTRACT

The Palmarito Formation of the Venezuelan Mérida Andes is late Early and early Late Permian (Roadian–Wordian) in age, and contains a well-preserved, diverse fauna including many forms of a distinctly Tethyan aspect. Its carbonate sediments were deposited in a variety of marine, warm-water shelf environments, under variable energy conditions. Values of both diversity (as Stehli's Permian Ratio) and sampling efficiency (as his Sampling Efficiency Index) for Permian brachiopods are enhanced by bulk collections of rock containing silicified fossils. On a global scale, the observed southward decline in sampling efficiency is chiefly a result of less intensive study of faunas in southern regions. No parameter relating substrate character to faunal composition was found. The brachiopod fossil fauna includes 32 genera of which three (*Stauromata, Costicrura,* and *Anaptychius*) are new, 44 species of which 12 (*Derbyia auriplexa, Derbyia deltauriculata, Dyoros acanthopelix, Stauromata esoterica, Xenosteges minusculus, Rugatia intermedia, Spinifrons grandicosta, Collemataria venezuelensis, Hustedia hyporhachis, Costicrura minuta, Aneuthelasma globosum* and *Anaptychius minutus*) are new, and two subspecies of previously described species, one of which (*Peniculauris subcostata latinamericana*) is new. Internal structures of a new chonetacean brachiopod genus are developed by application of new serial peel reconstruction techniques.

RESUMEN

La Formación Palmarito de los Andes Merideños de Venezuela es de edad Pérmico Inferior alto a Superior bajo (Roadian–Wordian), y contiene una fauna diversa y bien preservada, incluyendo muchas formas de un aspecto distintivamente Tethiano. Sus sedimentos calcáreos fueron depositados en una variedad de ambientes marinos, de aguas cálidas y someras, debajo de varios condiciones energéticas. Los valores de diversidad (expresada como la "Permian Ratio" de Stehli) y de la eficiencia de muestreo (expresada como su "Sampling Efficiency Index") fueron mejorados para los braquiópodos Pérmicos por colecciones másivas de rocas que contienen fósiles silicificados. En una escala global, la declinación que se observa hácia el sur en la eficiéncia de muestreo se debe principalmente al estudia menos intensivo de faunas en las regiones septentrionales. No se ha podido hallar ningún parámetro que relacione el carácter fino del sustrato a la composición faunística. La fauna fósil de braquiópodos incluye 32 géneros, de los cuales tres (*Stauromata, Costicrura* y *Anaptychius*) son nuevas, 44 especies de las cuales 12 (*Derbyia auriplexa, Derbyia deltauriculata, Dyoros acanthopelix, Stauromata esoterica, Xenosteges minusculus, Rugatia intermedia, Spinifrons grandicosta, Collemataria venezuelensis, Hustedia hyporhachis, Costicrura minuta, Aneuthelasma globosum* y *Anaptychius minutus*) son nuevas, y dos subespecies de especies previamente descriptas, de las cuales una (*Peniculauris subcostata latinamericana*) es nueva. La estructura interna de un nuevo género de braquiópodos (Chonetacea) es descubierta por la aplicación de una nueva técnica por láminas seriadas.

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This work is dedicated to my wife Caroline, for remaining sympathetic to me and my chosen profession.

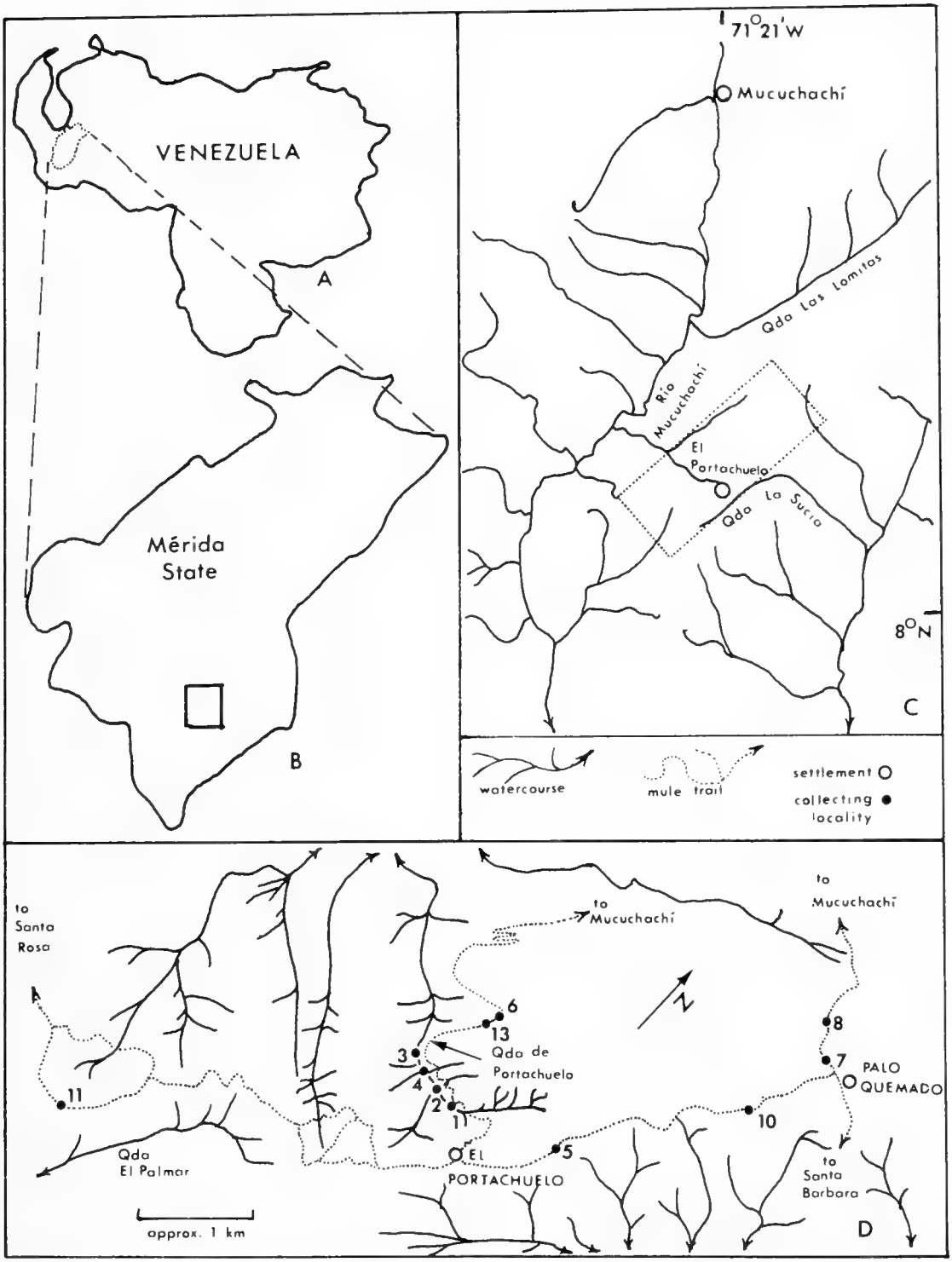
INTRODUCTION

For several years paleontologists and biologists have been interested in the global diversity patterns of marine organisms, particularly those that can be used in interpretation of the fossil record (Stehli, 1957; Fischer, 1960; Stehli *et al.*, 1969; Waterhouse and Bonham-Carter, 1975). Stehli (1971) has related latitudinal taxonomic diversity gradients to the distribution of families of thermally-tolerant cosmopolitan, and thermally-sensitive endemic Permian articulate brachiopods. He found measured diversity to be highly variable, and devised a statistic, the *Permian Ratio*, that minimized diversity variations caused by inadequate sampling. This ratio is defined as:

$$\frac{\Sigma - C}{C}$$

where Σ = the total number of brachiopod families identified, and C = the number of globally cosmopolitan families identified at that locality. By making the number of cosmopolitan forms less significant, the statistic increases the significance of the endemic (and thermally-sensitive) forms recovered. *Permian Ratio* values (see Text-fig. 6), plotted against latitude, increase from the poles toward a maximum near, but north of the present Equator. Some low-latitude stations have anomalously low *Permian Ratio* values. Stehli also observed that sampling efficiency, as measured by the percentage of possible global cosmopolitan families recovered at any locality, declined toward the south from about 30° North latitude. A potentially fruitful line of investigation was to try to determine, through the study of new collections, if anomalously low *Permian Ratio* values at a selected equatorial station were due to sampling inadequacy, and, if so, in what ways sampling could be improved. I also hoped to explain why otherwise cosmopolitan families were missing.

Central and South America are comparative unknowns, in terms of Permian brachiopods. South of Mexico, well-documented Permian brachiopod faunas of Tethyan aspect are known only from Guatemala and from the Titicaca region of Peru and Bolivia. Formal description and illustration are necessary prerequisities for use of a fauna in diversity studies, as they enable an investigator to verify taxonomic assignments for himself. Between Guatemala, at 16° North latitude, and Peru, at 7° South latitude, numerous faunas had been reported in faunal lists, but none had been comprehensively treated. When the opportunity for study there arose, I undertook a rigorous system-



Text-figure 1.—Maps showing location of the eleven Palmarito Formation fossil assemblages collected for this study.

atic, taphonomic and paleoecologic survey of the fossils, especially the brachiopods, of the Permian Palmarito Formation of the southwestern Venezuelan Andes, at approximately 8° North latitude.

During the rainy season—June and July—of 1971 a reconnaissance expedition to the type area of the Palmarito Formation was undertaken. This area is located about 250 kilometers south of the city of Mérida, Venezuela (Text-fig. 1), and at that time was reached by jeep, mule and foot from that city. Samples from as

many fossiliferous exposures as possible were taken: the main purpose was to find those exposures that promised optimal sampling, by means of collection of silicified fossils. Forty-one localities sampled during that field season yielded about 500 kilograms of rock and fossils that was returned to the United States for study. During the remainder of that year and the two following, specimens were prepared, and the most promising localities earmarked for re-collection. The next field season—March through April, 1973—came at the end of a protracted dry season in Venezuela, making access to localities easier than it had been previously, and many of the logistic hardships encountered in 1971 were eased. Nine of the original 41 localities were re-sampled in bulk: several additional samples that looked promising were taken as well. Approximately 1300 kilograms of fossil-bearing matrix from the Mérida Andes was returned from the 1973 season. No mapping was undertaken, because field time was limited, and because preliminary mapping had already been done by agencies of the Venezuelan government.

The results of the study are several. The brachiopod specimens used in preparation of Arnold's 1966 faunal list for the Palmarito Formation were re-examined. It was determined that the brachiopod diversity had been overestimated and that many identifications not only were incorrect but also biostratigraphically misleading. Examination of Arnold's collections, in combination with those made by the author, showed the unit to be largely of latest Early Permian (*sensu* Grant and Cooper, 1973) rather than Permocarboniferous age, in the type area.

Examination of all available fossil assemblages recovered from the author's collections showed that the Palmarito fauna is truly Tethyan in aspect and that its previously reported temperate character was probably largely a result of the comparative rarity of the hard substrates necessary for the attachment of many endemic Tethyan brachiopod forms. The decline in Sampling Efficiency Index southward from about 30° North was determined to be in great part a result of less intensive study of those faunas, but no definitive test of causal relationships could be made. Attempts to find a quantitatively measurable parameter that could relate substrate character and faunal composition were unsuccessful, but one character tested—silt/clay ratio of insoluble residues—may be an indicator of energy regime (Hoover, 1976b). The Palmarito assemblages sampled are inferred to have been deposited in a variety of warm-water shelf environments, from beach or bar to level bottom below wave base.

The entire fauna is reported in the form of faunal lists, while the brachiopod fauna is identified, described and figured, and is discussed in terms of its biostratigraphic, paleoecologic, taphonomic and paleogeographic significance. The brachiopod fauna includes 32 genera of which three are new, 44 species of which 12 are new and 2 subspecies of previously existing species, one of which is new.

THE PALMARITO FORMATION

Regional Setting

It is generally agreed that late Paleozoic marine sediments in the Western Hemisphere were deposited in a geosynclinal basin or series of basins. The form of this trough, however, is unclear, although several hypotheses have been proposed. These may be separated into two groups, whose basic difference lies in the disposition of the present Caribbean Islands. In Permian continental reconstructions, these troublesome fragments, for which no Late Paleozoic paleomagnetic data are available, most commonly have been placed within a reduced Caribbean Sea. For example, the hypotheses of Carey (1958) and Freeland and Dietz (1971) place most of Mexico in the position of the present Gulf of Mexico in pre-drift time, and rotate the pre-Mesozoic Yucatan and Central American basement blocks to produce a Late Paleozoic continental mass in the Gulf Region. In the last decade, another family of hypotheses has arisen that seem to require less strain on both imagination and the laws of physics. Hamilton (1966), Walper and Rowett (1972) and van der Voo *et al.* (1976), assume an opposite sense of rotation of the region which appears as an overlap in the "Bullard Fit" (Bullard *et al.*, 1965), and place the resultant southern tip of Mexico off the west coast of South America. This produces a more intimate pre-Mesozoic connection of the southern Appalachian, Ouachita, Mexican-Central American and northern Andean geosynclinal belts, which in turn helps to explain the great faunal similarity of the Palmarito and its stratigraphic equivalents in North America. Paleomagnetic studies necessary to test the sense of rotation of the critical Central American and Caribbean fragments have not been made, as rocks of suitable age and type have not been examined from many parts of that region (Hicken *et al.*, 1972). It is hoped that future paleomagnetic studies, in combination with pertinent Upper Paleozoic faunal studies such as this one, will provide data that can be used in such a test.

Permocarboniferous sediments were deposited over a great area of Central and South America, but this time was not one of extensive oceanic development,

relative to the Early Paleozoic. In addition, known and studied exposures of marine Upper Paleozoic rocks in the area are rather limited. Many parts of the region have been affected by severe diastrophism since Permian time, so that much Upper Paleozoic sedimentary section has been removed by uplift and consequent erosion, or faulting. Great thicknesses of fossiliferous strata have been metamorphosed to the degree that fossils can no longer be recognized and identified. Without such aids, the depositional age of the units cannot be determined directly.

Many known fossil localities in the region are not fully exploited, in part due to poor accessibility, thick vegetative cover, high degree of slope and rapid weathering. Until recently, little detailed geological investigation had been carried out in many of these areas, except in connection with petroleum company operations. Recent literature syntheses and the work of national geological surveys or ministries of mines, in combination with the International Stratigraphic Lexicon project, have aided in the resolution of many of these problems.

Though on present latitudinal coordinates, Texas lies north of the Equator and far from exposures of the Palmarito, it is a proper place to begin a more detailed regional discussion. The Permian strata of West Texas and adjacent New Mexico have been studied assiduously since Shumard (1858, 1859) made his original reports. Most portions of the diverse fauna have been reported in monographic form. The brachiopods alone have been treated in four monographic studies (Girty, 1909; R. E. King, 1931; Stehli, 1954; Cooper and Grant, 1972, 1974, 1975, 1976a, 1976b, 1977). Because of this concentrated and detailed study, and the vast amount of comparative material available (over 72 tons of matrix collected and processed since 1939 at the USNM alone), the West Texas sections have become a Western Hemisphere standard for both faunal comparison and stratigraphic correlation in the Lower, and lower Upper Permian. Stratigraphic terminology used in later discussions follows that of Cooper and Grant (1972).

Palmarito-equivalent strata are known from many areas in Mexico (Lopez-Ramos, 1969), along the course of the Paleozoic geosyncline that follows the axis of that country. Lopez-Ramos reported 28 studied marine Permian localities in Mexico, extending from Sonora in the north to Chiapas in the south. The sedimentary histories of the exposures differ, tending to support the separation of these areas during the Late Paleozoic.

Two sections in Mexico have received rigorous faunal treatment. Cloud (*in* R. E. King *et al.*, 1944) studied the exposures at Las Delicias, Coahuila, where the section consists of limestones, mudstones, sandstones and conglomerates, and spans the Permian from Wolfcampian to apparent Ochoan-equivalents. Over 3000 m of section are exposed. Cooper *et al.* (1953) examined the marine Permian exposures at El Antimonio in western Sonora. Strata of Word age exposed there are about 500 m thick.

The basinal complex in Mexico continues through Guatemala and British Honduras and may extend into the Caribbean along the trend of the Cayman Ridge and Bartlett Trough (Dengo and Bohnenberger, 1969). Although these southernmost Permian marine exposures in Central America have been known since the pioneer studies of Sapper (1937), relatively few have been investigated paleontologically. Stehli and Grant (1970) reported a diverse brachiopod fauna from the Chochal Limestone, of the Department of Huehuetenango, Guatemala, that shows close similarities to the Palmarito fauna. This unit, now placed within the regionally more applicable Santa Rosa Group (Clemons *et al.*, 1974) has been correlated with the Leonard Formation of the West Texas area, on the basis of brachiopods (Stehli and Grant, 1970), fusulinids (Henbest, *in* Roberts and Irving, 1957; Kling, 1960) and ammonoids (Glenister, *pers. comm.*, 1974). Hoffstetter (1960) reported a Permian fauna from the Macal Series of the Santa Rosa Group of Belize, but presented only a faunal list. No Upper Paleozoic marine rocks have been reported from the Caribbean virgation. Following the apparent structural trend into the South American continent, the first rocks of this character encountered are those of the Palmarito Formation. The Palmarito, like many Permian Tethyan units in the Western Hemisphere, consists of a predominantly clastic, terrigenously-influenced lower shaly member and a predominantly marine upper limestone member, which ranges in age from Late Leonardian to Early Guadalupian. Rocks of similar lithic character from the Sierra de Perijá in Colombia (Trumpy, 1943), contain a fauna of sponges, foraminifera, crinoid remains, brachiopods, gastropods and cephalopods (Burgl, 1973). To the writer's knowledge only the foraminifera (Miller and Williams, 1945) and cephalopods (Thompson and Miller, 1949) of this area have been systematically treated in the literature. Exposures of questionable Permian age have been reported from other areas within Colombia (Burgl, 1973; Stehli, *pers. comm.*, 1974), but none has yielded significant faunal data.

Upper Paleozoic marine rocks of the Macuma Formation are known in one outcrop and one well in the Cutucu Mountains south of Quito, Ecuador. A fauna

of Pennsylvanian age including brachiopods, bryozoans, and crinoid remains was recovered from the lower part of the unit (Dozy, *in* Tschopp, 1956) and two Pennsylvanian foraminifera were recovered from the lower part of the thicker upper member (Baggelaar *in* Tschopp, 1953). The uppermost 150–200 m of the unit has yielded a brachiopod-bryozoan fauna to which Goldschmid (*in* Tschopp, 1953) assigned a latest Pennsylvanian to Early Permian age. Stehli (*pers. comm.*, 1974) has mentioned the existence of Permian red beds in Ecuador, but no other marine strata are known.

The Upper Paleozoic section is relatively complete in Peru. Mississippian, Pennsylvanian and Permian strata have been identified (Newell, Chronic *et al.*, 1953) but only the Pennsylvanian and Permian are demonstrably marine. Mississippian strata previously reported (Murphy *in* Megard *et al.*, 1971) as marine, have, on reconsideration (Murphy, *pers. comm.*, 1974) been assigned to the Pennsylvanian. The Pennsylvanian marine strata are equivalent in age to the Itaituba Formation of Brazil.

The Copacabana Group in Peru as well as in much of Bolivia and adjacent Argentina and Chile, has previously been considered equivalent in age to some lower portions of the Palmarito (Newell, Chronic *et al.*, 1953; Arnold, 1966).

Outside the above areas, the record of holomarine Permian in South America is poor. Between 50° and 52° South latitude, in the Madre de Dios Archipelago of Chile, fusulinids that indicate an age ranging up into the Permian have been recovered from a thick (ca. 5000 m) series of limestones (Cecioni, 1956; Douglass and Nestell, 1976). Cecioni reported the presence of a rich and well-preserved fauna in addition to the foraminifera, but included no descriptions or illustrations. Meyerhoff (1970) considered this unit to document deposition in warm water and thus to be an extension of the Permian Tethyan belt. Such a conclusion appears unwarranted on the basis of fusulinid evidence alone, as fusulinids themselves are not indicators of warm-water conditions (Ross, 1967; Dunbar, 1973).

There were, in addition to the marine deposits in what might be termed the Upper Paleozoic Andean geosyncline, other contemporary marine deposits, within and between the relatively stable cratonic areas of South America. Local submergences and incursions at cratonic borders periodically allowed minor sedimentary deposits to accumulate. Itaituba-equivalent (mid-Pennsylvanian) strata are apparently widespread in parts of Brazil, Argentina, Paraguay and Uruguay, but Palmarito-equivalent beds (which do not overlap with Itaituba-equivalents) are not nearly so ubiquitous. None has been noted in cratonic areas north of southern Brazil. Parts of the Passa Dois Series of Argentina contain Permian marine strata (Frakes *et al.*, 1969) but their associated faunas, closely associated with glacial deposits, are clearly of Boreal affinities.

Palmarito-equivalent strata are widely but systematically distributed in the Western Hemisphere. Pre-Mesozoic continental configurations may have been such as to place some now separate localities relatively closer together. It is tempting to think that such pre-drift configuration hypotheses might be tested using faunal diversity data, but present analytic refinements cannot sufficiently reduce the noise level in the data. The new hypotheses do, however, aid in explanation of the great similarity in faunal composition found in many of the faunas within the Western Hemisphere marine Permian, because their present great latitudinal spread is most likely a Mesozoic artifact brought about by continental plate movements.

Historical Setting

The first investigator to consider the relatively undeformed Paleozoic strata of the Venezuelan Andes in detail was Christ (1927), who reported on the geologic section exposed along the trail from Mucuchachí to Santa Barbara de Barinas (Text-fig. 1). Christ divided strata of from Archaean to Tertiary age into six series. Of these, only three, the Mucupatí, Palmarito and Lomita Series, are pertinent here. Christ sent the Palmarito Series fossils to the museum at Basle, Switzerland, where they were studied and later reported on by Gerth (*in* Gerth and Kräusel, 1931).

Specimens referred to *Fusulina* and *Spirifer* were the only ones described and illustrated, a dubious distinction which they have, with a single exception (Hoover, 1975), maintained to the present day. Gerth (p. 524) recognized the presence of silicified fossils ("*teilweise verkieselte Fossilien*") in the unit, but never mentioned that these might provide a better sampling of the fossil fauna. He concluded that, on the basis of correlations with Bolivia and Asia, the Palmarito Series could not be younger than Late Carboniferous.

Englemann (1935) cited three more Palmarito localities along the Transandean highway in the state of Táchira, but contributed nothing further to the stratigraphy, lithology or paleontology of the unit. Schuchert (1935) reviewed work on the unit to date and concurred in the view that it was of Late Carboniferous age. Hedberg and Sass (1937) dedicated a single two-line sentence to the presence of fusulinids in a limestone in the upper reaches of the Río Palmár, Zúlia

state. This appears to have been the first mention of possible Palmarito equivalents in the Sierra de Perijá.

In the following year a dispute began which confused the picture of the Venezuelan Upper Paleozoic for several years. The Palmarito in the type section was both under- and overlain by coarser-grained reddish sedimentary rocks. The only fossils commonly found in either of these sandy units were in the limestone cobbles that locally formed a basal conglomerate within the overlying Lomita Series. Fusulinids, common in these cobbles, may have been the basis for Christ's assignment of a questionable Permian age to the bottom of the Lomita Series. The lithologic similarity of the Mucupatí and Lomita Series made the Palmarito Series easy to identify (the only non-redbed) in the type area, but also, in this area where stratigraphically continuous exposures were exceptional, it encouraged confusion of the sandy units.

This may be what started the controversy over the age of the Mucupatí Series. Kehrer (1938) collected in the type area of the Palmarito and Mucupatí Series in the 1930's. During this trip he collected fossils from "various localities in the sandstones within Christ's Mucupatí Series." A poorly preserved molluscan fauna indicated to him and to Kehrer, "Cretaceous . . . rather than Devonian age for the Mucupatí Series." (Kehrer, 1938, p. 50)

Oppenheim (1937) complicated the situation by supporting Kehrer's age for the Mucupatí and renaming this Cretaceous unit the Sabaneta Group. Christ's Lomita Series became the "Red Formations," hardly a distinctive name in that area, and one which happily has not been repeated in the literature. To these units he assigned a Lower Jurassic to Cretaceous age. He had apparently not known the exact details of Kehrer's work, because he based the post-Paleozoic age of his Sabaneta Group on the absence of diagnostic Paleozoic marine fossils and on the presence of plant remains. Kündig (1938) mentioned Kehrer's ideas about the Cretaceous age of the Mucupatí Series, "inofficially [*sic.*] called the Sabaneta Group," but cited (p. 29) an exposure of the Palmarito Series that showed transitional contact with his underlying Sabaneta Series (=Mucupatí of Christ, 1927).

Because no definite locality for Kehrer's collections was given, and no lithic data other than that cited above was available, the problem probably can never be completely resolved. The existence in such a tectonically complex region as the type area of the Palmarito of a fault sliver of a much younger, lithologically similar unit, surrounded by Sabaneta strata, is a distinct possibility. Alberding (1956) may have settled the Mucupatí/Sabaneta controversy by suggesting that the term "Mucupatí" be considered invalid, since in the literature it consisted of at least two units of distinct ages, in fault contact. Because it had originally been considered Devonian (Christ, 1927), and has recently been shown to be of Carboniferous and Permian (Pierce *et al.*, 1961) as well as Cretaceous (Aguardiente and Tomon Formations of Sutton, 1946) age, its stratigraphic utility was indeed compromised.

Kehrer (1938) presented a suite of fossils from the Palmarito Series that had been collected along a new trail between Palmarito and Sabaneta. He inferred that there was a high probability that a large portion of the Palmarito in the type area was of Permian age, perhaps extending down into the Late Carboniferous in its lower portions. Kehrer noted the great similarity of the Sabaneta to the Girón Series (an apparent equivalent to Christ's Lomita Series, introduced by Hettner, 1892). He assigned an Early Carboniferous age to the Sabaneta.

Schaub (1944) mentioned the occurrence of fusulinids of "schwagerinoid" type in loose blocks of limestone that formed part of the basal conglomerate of the La Quinta Formation and described them as having been derived from the Palmarito Formation. In his opinion, the wall structure of the fusulinids indicated Middle Pennsylvanian to Permian age.

The Upper Paleozoic in Venezuela is not confined to the Mérida Andes. Liddle (1946), in his book on the geology of Venezuela and Trinidad, included the second major review article on the Palmarito. He discussed in detail work he had done along the Río Cachirí in the Sierra de Perijá (state of Zúlia). There he described a section about 500 m thick, principally micaceous shales and sandstones, with a basal conglomerate. The uppermost 17 to 25 m of this section was reddish-stained dark limestone, containing crinoid columnals, *Rhombopora* or *Alveolites*, and an unidentified spiriferoid brachiopod. He assigned the section to the "Upper Permian" and correlated it with the Palmarito Formation of the Mérida Andes. The age of this unit is still in question, because the locality is difficult to pinpoint, and because field relationships in the Sierra de Perijá are far from clear. Gonzales de Juana (1951) suggested that only the uppermost reddish limestone should be attributed to the Palmarito, and that the rest of the sequence was better referred to as a Sabaneta equivalent (of Permocarboniferous age). De Rivero (1956) suggested that the redbeds might represent the La Quinta Formation, in fault contact with the overlying Palmarito Limestone, as suggested by the presence of limestone blocks in the basal conglomerate of the redbeds. Hea and Whitman (1960) also placed this portion within the La Quinta Forma-

tion. Liddle mentioned as indirect evidence of the presence of Permocarboniferous in the Sierra de Perijá, float containing *Dictyoclostus liddlei* Harris, in the Caño del Oeste of the Río Cachirí, and fusulinids in the upper reaches of the Caño Pescado, an affluent of the Río Palmár. The former is not referable to any Palmarito dictyoclostid genus, and probably is not of Permian age. The fusulinids may have been the same as those mentioned by Hedberg and Sass (1937).

Sutton (1946) discussed the Palmarito of the type area in the Mérida Andes, and measured the thickness of the unit as 1800 m. He did not, however, differentiate the Sabaneta from the Palmarito, which explains the great thickness given.

Thompson and Miller (1949) described fusulinids and cephalopods from both the Palmarito and apparent time-equivalent strata in Colombia. These were apparently the same units, though in different localities, as those described by Trumpy (1943) from Colombia. Gonzales de Juana (1951) formalized the formational status of the Palmarito, and designated outcrops of sparsely fossiliferous dark limestones near the city of Mérida (state of Mérida) as Palmarito equivalents. From some of his samples from that area, Sellier de Civrieux (1951) identified, in association with *Parafusulina,* a species of the foraminiferan *Globivalvulina,* which he considered most similar to forms from the Upper Guadalupian of West Texas.

Pierce *et al.* (1961) discussed eleven marine fossiliferous Paleozoic localities from the southeastern sector of the Mérida Andes. Though most of these were already in the literature, all were enhanced by the detailed attention given them. Most localities were in structurally deformed areas, and although the fauna recovered in any single place was usually smaller than that in the relatively undeformed type area, the combined faunal listing is both impressive, and suspect. On the bases of fusulinid and other faunal evidence, the age of the unit is from mid-Pennsylvanian to early Late Permian. Measured sections yielded formational thicknesses from 200 to about 1200 m. The only section other than those in the type region from which a diverse Palmarito fauna was reported was the Carache area in the state of Trujillo.

Shell and Creole (1964) mentioned the Palmarito Formation in a long article dealing mainly with older units in the Mérida Andes. They did not take issue with previous conclusions about the age or extent of the Palmarito, but did mention that on the basis of palynological investigations, the Sabaneta Formation was largely of Permian age, with only the lower part of possible Carboniferous age.

Arnold (1966) described the Sabaneta sequence from several localities in the Mérida Andes. He detailed the lithologic characters observed in all sections, and arrived at age assignments that do not disagree materially with those of previous investigators. Extensive faunal lists given for three localities are based on samples taken in connection with the measurement and detailed description of stratigraphic sections.

Shagam and Hargraves (1970), in an investigation of Permocarboniferous redbeds (Sabaneta and Mérida facies) in the Mérida Andes, considered the Sabaneta to underlie the Palmarito in its entirety, rather than contacting it diachronously, as had been suggested by Arnold. This concept was discussed further by Shagam (1972).

Interest in the Palmarito over the last decade has not been centered on its faunal composition, but rather on its precise stratigraphic relationships and correlations, as these relate to the Paleozoic and subsequent development of the Andean region. At present there are two opposed hypotheses concerning Paleozoic sedimentation in this region. One, proposed by Arnold (*in* Shell and Creole, 1964; Arnold, 1966) suggested that Paleozoic sedimentation there occurred in two time periods, separated by a period of uplift, non-deposition and some deformation. The first of these sedimentary cycles he called the Lower Paleozoic cycle, which included the deposition of the Caparo Formation and its northern lateral equivalent, the Mucuchachí Formation, in Ordovician and early Silurian time. Unconformably overlying these, the Permocarboniferous continental Sabaneta Formation and its lateral shelf facies equivalent, the Palmarito, were deposited.

The opposing hypothesis of W. R. Smith (*in* Shell and Creole, 1964; see also Shagam, 1968; Martín B., 1968; Shagam and Hargraves, 1970; Shagam, 1972) showed a lower Paleozoic sedimentation cycle during which the Caparo, El Horno and Mireles Formations, among others, were deposited. This episode was followed by emergence during the Devonian and Mississippian. A second Paleozoic sedimentation cycle, roughly within the same basin, included the Mérida, Mucuchachí and Sabaneta facies, lateral equivalents of roughly the same age, overlain by the northern and southern facies of the Palmarito Formation, with the intervening basinal facies of Palmarito-equivalent age missing.

These two models differ mostly in the age assignment of the Mucuchachí Formation, a sparsely fossiliferous sequence of shales, phyllites and slates. In the latter explanation the Palmarito southern facies covers a longer time span than does the northern, implying a transgression of the Palmarito marine environment

from south to north, during Late Pennsylvanian time. It also shows a short hiatus within the Palmarito section in the south, and between the Palmarito and Mérida facies in the north, representing a period of nondeposition and (or) erosion, near the Pennsylvanian–Permian boundary.

The concept of the Palmarito Formation has undergone remarkably little alteration since Christ's first formal description, while the section around it has been considerably changed. This is probably due to several causes. The type area of the formation is remote, and few direct observations have been made since 1927. Fossils are considered to provide an objective means of determining relative position in a time scale, and while the Palmarito is replete with well-preserved fossils, with two exceptions (Gerth and Kräusel, 1931; Hoover, 1975), none have ever been described and figured. Thus, the real affinities of the fossils remain poorly understood. The Palmarito is lithologically conspicuous, as it is naturally defined by under- and overlying redbed units. In other areas it is less distinctive lithologically, but can be recognized easily when fossils are present. To field geologists working in the Mérida Andes, recovery of fusulinids indicates the presence of the Palmarito Formation. The extrapolation of this philosophy to the other macrofossils found in association with the fusulinids has led to problems in correlation, especially with the Permocarboniferous units exposed in the Sierra de Perijá. Typical Palmarito shelf faunas have not been reported, to my knowledge, from the Venezuelan portion of the Sierra de Perijá. That units of a similar age do exist close by in Colombia has been established by fusulinid and cephalopod evidence.

BIOSTRATIGRAPHIC CORRELATION

No attempt at biostratigraphic correlation of the Palmarito fossil fauna with non-Western Hemisphere Tethyan Permian faunas is here attempted. The similarity of the Venezuelan forms to those from West Texas is so striking that more far-reaching correlation would in essence be a global correlation of West Texas rather than Venezuelan forms; an exercise of dubious significance, considering the comprehensive works on this subject already presented by others (*e.g.*, Cooper and Grant, 1972; Grant and Cooper, 1973).

The brachiopod fauna of the Palmarito Formation includes at least 32 genera and 44 species, of which 3 genera, 12 species and a single subspecies are described here as new. The names used in classification of these taxa are drawn from study of the available literature, but lean heavily on a recent monograph on the West Texas brachiopods (Cooper and Grant, 1972, 1974, 1975, 1976a, 1976b, 1977). This seems justified by the following: (1) Grant and Cooper (1973) have demonstrated the existence of trans-longitudinal "provinciality" in the Upper Permian: regions within which correlation is enhanced and between which correlation is difficult. There is no reason to doubt that such divisions extend lower in the section. (2) The West Texas sections appear to be the most continuous and accessible expanse of Permian strata in the Western Hemisphere, and are considered the standard for the hemispherical marine Permian. (3) The diverse fauna recovered there during the past hundred or more years of study can better elucidate age and facies relationships of the Palmarito Formation than can geographically closer, yet less well understood faunas in Central and South America, such as the Copacabana Group of Peru and Bolivia (Newell, Chronic, *et al.*, 1953; Samtleben, 1971) and the Chochal of southeastern Mexico, Guatemala and British Honduras (Stehli and Grant, 1970; Kling, 1960).

Because my study was primarily faunal in emphasis, sampling localities were selected to (1) lie within the lithologically-defined boundaries of the Palmarito Formation and (2) contain a high concentration of recoverable fossils, preferably silicified. Low on the list of priorities (and probabilities) was knowledge of the exact stratigraphic position of a sample within a measured section. The collection area has been mapped on a small scale, and at least one stratigraphic section has been competently measured in the vicinity of the type section (Arnold, 1966), but the mapping is schematic, and the section offers few recognizable landmarks for use in sample location. The true stratigraphic position of individual samples can rarely be determined in the field.

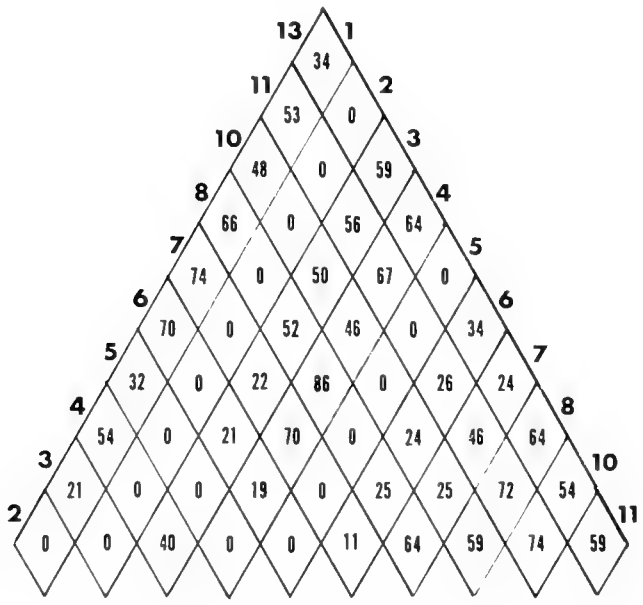
Although it has been stressed (Grant and Cooper, 1973) that age determinations should ideally be made on the basis of the entire preserved fauna, only the brachiopods are extensively employed here. The biostratigraphic significance of the remainder of the fauna is dealt with briefly at the end of this section.

As a first step in correlation, the brachiopod genera of the Palmarito Formation were compared with those recovered from each of several of the well-defined stratigraphic units of West Texas. Data for the latter were derived from Cooper and Grant (1972, 1974, 1975, 1976a, 1976b, 1977) and from collections at the National Museum of Natural History (Washington, D.C.). The Otsuka Coefficient* was used as a standard

* The number of items (genera) shared by the two units compared, divided by the square root of the product of the number of items in each unit.

of comparison, because it appears to reduce the bias inherent in comparing samples of different sizes (for discussion of the various binary coefficients which might have been employed, and their attributes, see Cheetham and Hazel, 1969). The use of the genus as a standard in this and following comparisons for correlative purposes follows the rationale of Grant and Cooper (1973, p. 573). The results of the above comparison appear in Table 2. This shows that although all similarity levels are low, the highest level of similarity lies between the Palmarito Formation and the Road Canyon and Cathedral Mountain Formations of West Texas.

In Table 1, one can readily appreciate the great difference in brachiopod generic composition between Locality 6 and all other Palmarito Formation localities. This suggested the desirability of determining how many distinctive generic assemblages of brachiopods existed within the Palmarito Formation. To do this I calculated the similarity in generic composition of brachiopod assemblages at sampled localities within the Palmarito, and then systematically compared these groups with brachiopod assemblages from finer stratigraphic subdivisions in the better-known West Texas region. Again using the Otsuka Coefficient, the genera recovered at each locality were compared to those from every other locality, and the results were plotted as a similarity matrix (Text-fig. 2). While this matrix contains all the information needed to determine the degree of similarity among the localities, it lacks visual



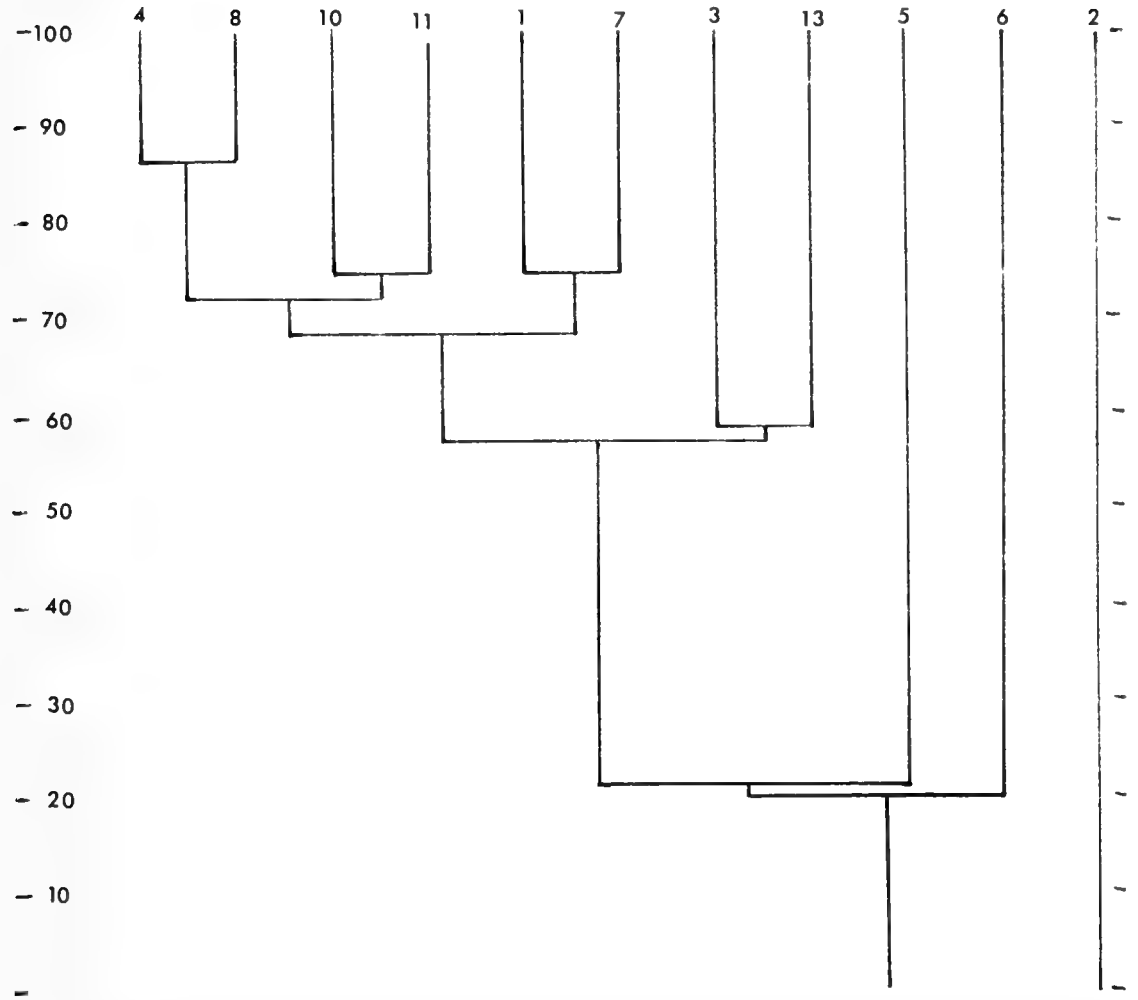
Text-figure 2.—Similarity coefficient matrix for brachiopod genera in Palmarito Formation fossil assemblages. Large numbers represent localities; smaller numbers are Otsuka Coefficient × 100.

Table 1.—Occurrences of brachiopod genera in Palmarito Formation fossil assemblages. × = presence; – = absence.

	Localities										
Genera	1	2	3	4	5	6	7	8	10	11	13
Acosarina	–	–	–	–	–	–	×	–	–	–	–
Anaptychius	–	–	–	–	–	×	–	–	–	–	–
Anemonaria	×	–	–	–	–	–	–	–	×	×	–
Aneuthelasma	–	–	–	–	–	×	–	–	–	–	–
Chonetinetes	–	–	–	×	–	–	–	×	–	–	×
Cleiothyridina	–	–	×	–	–	–	–	–	–	–	–
Collemataria	–	–	–	–	–	×	–	–	–	–	–
Composita	×	–	×	×	–	–	×	×	×	×	×
Cooperina	–	–	–	–	–	×	–	–	–	–	–
Costicrura	–	–	–	–	–	×	–	–	–	–	–
Derbyia	–	–	×	×	–	×	–	×	×	×	×
Dyoros	–	×	–	–	–	–	–	–	–	–	–
Echinauris	×	–	–	×	–	×	×	×	–	×	×
Holotricharina	–	–	–	×	–	–	–	×	×	×	×
Hustedia	×	–	×	–	–	×	–	×	×	×	×
Kutorginella	×	–	–	×	–	–	×	×	–	×	–
Meekella	–	–	×	×	–	–	×	×	–	×	–
Neophricadothyris	×	–	–	–	–	–	×	×	–	–	–
Neospirifer	×	–	–	×	–	–	×	×	–	–	–
Oligothyrina	–	–	×	–	–	–	–	–	–	–	×
Paucispinifera	–	–	–	–	–	–	–	×	–	–	–
Peniculauris	×	–	–	–	×	–	–	–	–	–	–
Petrocrania	–	–	–	–	–	×	–	–	–	–	–
Pontisia	–	–	×	–	–	–	–	×	×	×	–
Ramavectus	–	–	–	–	–	–	–	–	–	×	–
Rugatia	×	–	–	×	–	–	×	×	×	×	–
Spinifrons	–	–	×	×	–	–	–	×	–	×	×
Spiriferellina	–	–	×	–	–	–	–	–	–	–	–
Stauromata	×	–	–	×	–	–	×	×	–	–	–
Texarina	–	–	–	–	–	–	–	–	–	×	–
Xenosteges	–	–	–	–	–	×	–	–	–	–	–
Total Genera	10	1	9	11	1	10	9	15	7	13	8

Table 2.—Comparison of brachiopod generic composition of the Palmarito Formation and of selected Permian biostratigraphic units in the West Texas region. Values are expressed as Otsuka Coefficient × 100; N = total number of genera included in given biostratigraphic unit.

	Palmarito Formation, all localities [N = 31]
Capitan and Bell Canyon Fms. (Guadalupian) incl. all mbrs. [N = 73]	29
Cherry Canyon, Getaway & Word Fms., incl. all mbrs. (Lower Guadalupian) [N = 81]	32
Road Canyon Fm. (Upper Leonardian) [N = 88]	41
Cathedral Mountain Fm. (Leonardian) [N = 83]	38
Skinner Ranch, Taylor Ranch, Hueco and Hess Fms. (Upper Wolfcampian) [N = 81]	33



Text-figure 3.—Dendrogram showing similarities in brachiopod generic composition among Palmarito Formation fossil assemblages. Figure derived by weighted-pair grouping of similarity coefficient matrix shown in Text-figure 2.

clarity. To overcome this problem, the matrix was "clustered," using the weighted-pair grouping method (Bonham-Carter, 1967; Text-fig. 3). The limitations of the method employed, which include an imposition of hierarchal structure on the data, and the lesser significance of clustering when the units compared (localities) consist of small numbers of items (genera) (Stehli and Wells, 1971), have been recognized, and are considered balanced by the more immediate visual intelligibility provided by the dendrogram. To appreciate the distortion imposed on the similarity matrix at low levels of association, it should be noted, by comparing Table 1 and Text-figure 3, that while localities 2 and 5 consist of a single genus each, locality 5 appears more similar to most others than does locality 6, which contains ten genera.

From the dendrogram, four localities or groups of localities were selected to be used as units for further comparisons. The first group included localities 1, 4, 7, 8, 10 and 11: the second, third and fourth groups were localities 3, 13 and 6, respectively. Localities 2 and 5 were not considered because of the negligible fauna recovered. The four Palmarito groups were compared to six stratigraphic entities in the West Texas region (Table 3). While most of the similarity of Palmarito brachiopods to Lower and Middle Leonardian Texas forms comes from the first group, that group's closest association is with the Road Canyon Formation fauna. The closest associations of the other three groups are with West Texas strata younger than Road Canyon: localities 3 and 6 with the Willis Ranch Member of the Word Formation and locality 13 with the Road Canyon Formation and the China Tank Member of the Word Formation.

The brachiopod fauna as a whole (Table 7) has largely Late Leonardian or Early Guadalupian affinities. This is in strange contrast to the faunal aspect presented by Arnold (1966); based on identifications by H. M. Muir-Wood (Table 4). My own reassessment of the brachiopod genera present in this collection (Table 4) is strikingly different, and profoundly affects the apparent familial composition of that suite (see discussion under "Permian Ratio"). Arnold stated (p. 2378) that Dr. Muir-Wood had indicated the age of the unit to be Early Permian. A comparison of the genera she reported with those from several West Texas stratigraphic units, again using the Otsuka Coefficient, showed the greatest faunal similarity with the *Uddenites*-bearing shale zone that lies at the base of the Wolfcampian Series (Hoover, 1976a, pp. 61, 127).

Brachiopods, though more intensively studied in this report, do not constitute the entire Palmarito fossil fauna. The other fossils recovered include bryozoans, cephalopods, chitons, corals, crinoids, echinoids, fusulinids, gastropods, ostracods, pelecypods, sponges and trilobites. These elements were forwarded to qualified workers for examination. The bryozoans, chitons, corals, crinoids, echinoids, ostracods and sponges present no more diagnostic stratigraphic information than terms ranging from "Upper Paleozoic" to "Lower Permian," but center about the latter degree of refinement.

Cephalopods were recovered from several of the Palmarito localities sampled. Drs. Furnish and Glenister, of the University of Iowa, and one of their students, Dr. Chunsun Lee, kindly identified various coiled nautiloids from locality 1, and orthocone nautiloids like *Mooreoceras* from several localities. Of greater biostratigraphic importance, however, were the identification of *Perrinites hilli* at locality 4, and another locality (Field No. PRH-71-VE-12) nearby. This form was described by Miller and Williams (1945) from the Perijá Peninsula of Colombia, and is similar to specimens from the Chochal Limestone in Guatemala (collected by F. G. Stehli) and in Chiapas, Mexico (collected by Müllereid). A Late Leonardian age is most likely for the deposits containing this form. Lee (1975) has identified (at loc. 10) *Martoceras subinterrupta*, a form previously reported only from the Upper Artinskian [Baigendzhinian] of the Urals, roughly equivalent in age to the Cathedral Mountain Formation of West Texas (Waterhouse and Piyasin, 1970).

Evidence from the fusulinids (Douglass, *pers. comm.*, 1975) tends to support these ages. Fusulinids were recovered from two localities in the Palmarito: one, a short but indeterminate distance down section from locality 4, and the other from locality 6. Those from the former locality were similar to *Parafusulina durhami*, and to *Schwagerina setum*, but differ from the latter in their larger proloculus and the presence of cuniculi. These characters suggest a Leonardian age for rocks at that locality. Those from locality 6 proved to be a new species of *Parafusulina*, similar to *P. sellardsi*, but slightly less advanced than that form, and indicative of latest Leonardian or possibly earliest Wordian age.

Table 3.—Comparison of brachiopod generic composition of Palmarito Formation fossil assemblages and (or) assemblage groups, with West Texas stratigraphic units. Values expressed are Otsuka Coefficient × 100; N = total number of genera included.

	Palmarito Formation Fossil Assemblages			
	1, 4, 7, 8 10 & 11 [N=20]	3 [N=9]	13 [N=8]	6 [N=10]
Word Formation Appel Ranch Mbr. [N = 56]	24	22	19	25
Word Formation Limestone Lens between Willis Ranch and Appel Ranch Mbrs. [N = 53]	28	23	19	26
Word Formation Willis Ranch Mbr. [N = 63]	25	25	18	28
Word Formation China Tank Mbr. [N = 62]	26	21	23	20
Road Canyon Formation [N = 88]	38	21	23	20
Cathedral Mountain Formation [N = 83]	34	22	19	21

Most of the gastropods (Yochelson, *pers. comm.*, 1975) indicated an age of Late Pennsylvanian or Permian, but one, *Cylicioscapha*, from locality 11, is typical of rocks equivalent in age to the Road Canyon or Word Formations of West Texas.

The pelecypods appear North American in aspect, and one, *Schizodus canalis*, which appears at Palmarito localities 1 and 8, appears elsewhere only in Road Canyon Formation age-equivalents, supporting a latest Leonardian age for the lower portions of the Palmarito (Newell, *pers. comm.*, 1975).

Trilobite fragments recovered from localities 10 and 13 were identified (Chamberlain, *pers. comm.*, 1975) as species of *Anisopyge*, which appears in the Leonardian and Guadalupian of North and Central America.

In summary, most of the biostratigraphic indicators recovered point to a Late Leonardian or earliest Gua-

dalupian (Roadian to Wordian World Stage of Grant and Cooper, 1973) age, though there are indications (fusulinids and ammonites) that locality 10 may be somewhat older (Baigendzhinian World Stage of Grant and Cooper, 1973).

LITHIC AND FAUNAL ANALYSIS

INTRODUCTION

All localities from which fossils were collected for this study were visited during July 1971 and April 1973. All lie within, or in close proximity to the type section of the Palmarito Formation, in the Arzobispo Chacón district of the state of Mérida, Republic of Venezuela (Text-fig. 1).

Lithic Description Techniques

Due to the variety of rock types collected, several methods of lithic description were employed. All rocks were described in the field, and the usual field characteristics noted. These included geographic and stratigraphic position, where these could be determined, thickness and attitude of beds, color, gross mineralogy and bedding characters, fossil content and extent of exposure or outcrop. At localities 1 and 2 no further description was possible, since the rock was so friable that it could not be transported intact to the laboratory. A slab approximately 0.5 cm thick was cut from rocks taken from localities 3, 4, 5, 6 (block C), 7, 8, 10, 11 and 13. The plane of the cut was oriented normal to bedding if the latter could be ascertained. Both sides of the slabs were polished and X-rayed. The X-radiographs were used as aids in the determination of depositional texture. The slabs, oiled or wetted, were also examined with a binocular microscope. Where possible (locs. 3, 4, 5, 6 (block C), 7, 10, 11 and 13) a representative chip (approximately 1×2 cm) of each rock type was made into a doubly-polished thin section, using the techniques of Moreland (1968). These sections, used in determinations of microstructure, mineralogy and depositional texture, were examined with a standard petrographic microscope. The slides were also analyzed by X-ray diffraction, to determine approximately the relative proportions of calcite, dolomite and quartz present. Rocks containing silicified brachiopod fauna were subjected to a rock constituent analysis to test correlation of lithic and paleoenvironmental parameters. Results were summarized by Hoover (1976b). A by-product of the analysis was the discovery that the dark color of many of the rock samples was due to hydrocarbon infiltration. When the samples were dissolved large oil slicks formed on the liquid and container surfaces and the insoluble residues were much lighter in color. Solid residues (carbonized plant fragments, pyrite) indicative of a euxinic depositional environment were not recovered.

The descriptive terminology used follows two schemes: compositionally, the carbonates are characterized by the Folk (1962) classification; in terms of depositional texture the Dunham (1962) classification is employed.

Table 4.—Genera and families of Arnold collection Palmarito Formation brachiopods identified by H. M. Muir-Wood and P. R. Hoover. Familial assignments follow the usage of the Treatise (Williams *et al.*, 1965). See Hoover (1976a) for more detailed identifications.

Genera Identified by H. M. Muir-Wood	Family Assignment
Meekella	Meekellidae
Lissochonetes	Chonetidae
Neochonetes	Chonetidae
Quadrochonetes	Chonetidae
Avonia	Overtoniidae
Marginifera	Marginiferidae
Echinauris	Marginiferidae
Kozlowskia	Marginiferidae
Productus	Productidae
Bathymyonia	Echinoconchidae
Waagenoconcha	Echinoconchidae
Juresania	Buxtoniidae
Antiquatonia	Dictyoclostidae
Peniculauris	Dictyoclostidae
Rugatia	Dictyoclostidae
Squamaria	Dictyoclostidae
Cancrinella	Linoproductidae
Hustedia	Retziidae
Composita	Athyrididae
Neospirifer	Spiriferidae
Phricodothyris	Elythidae
Dielasma	Dielasmatidae

Genera Identified by P. R. Hoover	Family Assignment
Meekella	Meekellidae
Dyoros	Chonetidae
Holotricharina	Overtoniidae
Echinauris	Marginiferidae
Kutorginella	Marginiferidae
Echinoconchidae	Echinoconchidae
Ramavectus?	Buxtoniidae
Peniculauris	Dictyoclostidae
Rugatia	Dictyoclostidae
Spinifrons	Dictyoclostidae
Anemonaria	Linoproductidae
Paucispinifera?	Linoproductidae
Hustedia	Retziidae
Composita	Athyrididae
Neospirifer	Spiriferidae
Neophricadothyris	Elythidae

Faunal Lists

Although a resume of the brachiopod fauna of each locality appears as a part of Text-figure 4, a separate presentation within the discussion of each locality gives a better concept of the entire bed assemblage. The number following each brachiopod species indicates the minimum number of individuals that could have provided the number of valves and shells observed. The initials in parentheses accompanying other taxa refer to the individuals who were kind enough to provide identifications within their own areas of expertise (see "Acknowledgments"). Where no other information is given, the identification is mine.

Taphonomy

In recent years there has been increasing interest in the taphonomic history of fossil organisms and their remains (*e.g.*, Lawrence, 1968; Boyd and Newell, 1972; Erdtmann and Prezbindowski, 1974). Post-death processes contribute in great measure to the final aspect of the fossil assemblage as seen by the investigator. Although Boyd and Newell define taphonomy as "mode of entombment," I consider it to include all post-death alterations in the remains of a once-living organism, including not only its interactions with living organisms and with the chemical and physical environment, but also changes wrought by the investigator during sampling and preparation.

The mode and extent of breakage of fossils, by whatever means or cause, is often held to be significant in inferring the environment of deposition of fossils (*e.g.*, Waterhouse and Piyasin, 1970). Observations of recent shelf benthos would indicate that bioturbation might be a significant disruptive influence, but Thayer (1979) suggests that the high diversity of sessile benthos adapted to life on soft substrates may be related to a smaller number of bioturbating organisms, and hence a lower incidence of bioturbation below the Permo-Triassic boundary. The environment of deposition is, however, only one place where that destruction may occur. The bumps, jars and abrasions of aqueous transport and the packing of fossils during deposition must account for some of the observed shell injuries. Compaction of the unconsolidated or partially consolidated sediment column places stresses on the enclosed shells that may result in crushing or breakage. Later tectonic movements, accompanied by slippage, flow or breakage, can, in fossiliferous rocks, easily break the enclosed fossils. Such broken fossils may later be recemented in their crushed forms by precipitates from fluids passing through the rocks. Fossils are often broken during collection; a common expression of this is the decortication of calcareous fossils that are cracked out of a calcareous matrix. During etching, crushing of silicified specimens by each other, the surrounding rock or insoluble residues, or by the buildup of carbon dioxide gas within the shells, is not uncommon. For all of the above reasons it is important that the paleontologist who would be a paleoecologist be interested in, and report to colleagues on the methods under his (her) control that were used in the various stages of collection and preparation, in order to assess the damaging effects those operations may have had on the fossils described.

Boyd and Newell (1972) discussed a Permian assemblage consisting largely of silicified pelecypods, assumed to have been originally composed of the same aragonitic or high-magnesium calcite shared by most of their modern relatives. These chemically unstable remains were altered in ways that are rarely duplicated among roughly contemporary brachiopods, because the latter are thought to have been composed in life of more stable low-magnesium calcite. Chave (1964) and Lawrence (1968) have dealt at length with the chemical causes and preservational implications of differences in carbonate shell mineralogy. The articulate brachiopods, among carbonate-shelled Permian marine invertebrates, are the most likely candidates for preservation, in terms of chemical stability of original shell material.

As my study deals largely with silicified fossil assemblages, at least a cursory discussion of silicification seems in order. The mechanism of silicification is unclear, although it has been suggested (Emery and Rittenberg, 1952; Siever, 1962) that changes in the partial pressure of CO_2 and in pH that accompany the decomposition of organic soft tissues in sea water or interstitial fluids could provide a proper chemical regime for replacement of calcite by silica or *vice versa*. Palmarito fossils provide evidence that at least two distinct silicification mechanisms operated there. Apparently the percentage of magnesium replacing calcium in the mineral calcite, and the crystal structure of the two forms of calcium carbonate (calcite and aragonite) play a part in determining the susceptibility of original carbonate shell to either or both dissolution and replacement by silica during diagenesis (Chave, 1964). As a result of diagenetic changes, the extent of magnesium substitution in the calcite lattice may change within a single shell, so that a variable susceptibility to silicification exists. When this is so, silicification may be incomplete or selective, and fossils like those of *Echinauris* cf. *E. lappacea* Cooper and Grant (1975) (loc. 8), may be formed. In these (see Pl. 5, figs.

18, 19) the exterior of the ventral valve and a mold of the inside of the dorsal valve are silicified. The hollow interior of the fossil is lined by drusy silica, and retains no vestige of original organic structure. Boyd and Newell (1972) suggested an alternative origin of such fossils. They invoke geode-type infilling of voids in semi-consolidated or consolidated sediments by silica-bearing solutions. Another mode of silicification involves the filling of such a leached-out void by calcareous micrite, which is subsequently silicified. This process forms natural casts composed of numerous discrete grains, rather than continuous opaline silica. The micrite apparently enters these voids *via* partings along bedding, breaks in the consolidated sediments, or *via* erosionally re-exhumed extremities of the voids themselves. Both types of silicification have been observed in Palmarito Formation fossils. Only the first occurs commonly among the articulate brachiopods, the other being largely limited to the molluscs.

Several kinds of data were collected to assess the importance of the energy regime of the depositional environment, and other taphonomic factors in producing the breakage observed in any assemblage. Relative numbers of dorsal and ventral valves, and articulated shells of each species recovered were noted (see Text-fig. 4). The minimum number of individuals to which the observed valves might be attributed was noted as an aid in determining the significance of each count. Waterhouse and Piyasin (1970) and Sheehan (1978) have noted that such numbers and the valve ratios derived therefrom can be quite misleading unless further qualified. The architecture of Permian brachiopods was so variable that shells of different genera were differentially resistant both to breakage and disarticulation after death. Most productids probably disarticulated quite readily after death, there being little skeletal hinge structure to keep the valves together. In addition, the dorsal valve in this group tends to be less massive and more fragile than its ventral counterpart, and is more commonly broken or missing. The globose spiriferidines (*e.g., Hustedia, Composita, Neophricadothyris*) are commonly found articulated, since their complex articulatory hinge structure was sufficient to keep the valves together under considerably greater current or wave activity. Most other types of brachiopods fall between these two extremes. Subjective estimates of wear on shell were made, both from whole specimens and polished thin sections.

Paleoecology

Taphonomy and paleoecology are really two parts of the same inferential process: the study of taphonomy permits the selective removal of some of the bias that hinders complete understanding of the paleoecology of a fossil assemblage. Many authors have recognized and defined fossil communities, and in doing so have relied heavily on the relative abundances of the various species present. They have stressed that there must be convincing evidence of *in situ* deposition, before inferences concerning community type can be drawn, but Lawrence (1968) among others, has stressed that transportation is probably not nearly so important a factor as simple preservation. He estimated that 40 to 70 percent of a living community may be elminated from the fossil record by non-preservation alone. Thayer (1979) however, suggests there may be less postmortem non-preservation in Paleozoic than in modern benthic deposition. The extremely complex taphonomic histories of the various Palmarito fossil assemblages have probably altered, in no recognizably systematic way, the percentage composition of the original living community. For this reason no attempts were made here to analyze the significance of relative abundances of fossils unless these numerical abundance differences were striking.

Exposure of the Palmarito in isolated exotic blocks makes comparisons of large-scale lateral or vertical changes in species or assemblages impossible. Even within the type and reference sections of the formation, one cannot be certain of the original relative stratigraphic position of samples, because severe structural deformation has taken place. Paleoautecological reconstructions here are limited to comparisons, however distant, with living representatives of the phylum, inferences from preserved morphology and associated organisms and sediments. Most of these subjects are covered in the individual systematic discussions. Within the Palmarito samples some paleosynecological inferences can be drawn. These are discussed under "Permian Ratio" and "Sampling Efficiency Index."

COLLECTING LOCALITIES

Locality 1 consists of one wall of the stream bed near the head of a small stream locally known as the Quebrada de Portachuelo (Quebrada Queveda of Arnold, 1966), roughly 100 m downstream (up section) from the highest redbed layer of the Sabaneta Formation, which is the base of the Palmarito Formation (see Text-fig. 1). The rock exposed is a petroliferous, dark gray, fossiliferous, fissile siltstone, containing occasional small lenses of silty limestone. A block of about one cubic m, which had slipped down from the wall and lay close to its base in the stream bed, formed the actual site of collection. Fossils were removed by hand from the weathered rock over an area of about

one square m, through a stratigraphic thickness of about one-half m. They were preserved entirely by calcite permineralization, and all were dark gray to black in color. Although the friability of the rock prevented the return of bulk samples to the laboratory, field examinations allowed determination that the rock was compositionally a biomicrite. Draping of sedimentary laminae around more resistant skeletal grains (crinoid stems, ramose bryozoa) indicated that soft-sediment deformation had taken place, and that in terms of depositional texture the rock was a packstone. The crushed shells of many of the more fragile fossils confirmed this. Fossil collections returned to the laboratory were cleaned using an S. S. White Airbrasive, and delicate structures were developed using common mechanical techniques. Among the fossils recovered from the locality were:

BRACHIOPODS

Anemonaria? cf. *A. sublaevis* (King)	1
Composita cf. *C. pilula* Cooper and Grant	1
Echinauris cf. *E. liumbona* Cooper and Grant	5
Hustedia sp.	1
Kutorginella cf. *K. umbonata* (Muir-Wood and Cooper)	1
Neophricadothyris cf. *N. crassibecca* Cooper and Grant	7
Neospirifer venezuelensis (Gerth)	4
Peniculauris subcostata latinamericana n. ssp.	29
Rugatia occidentalis (Newberry)	33
Stauromata esoterica n. gen. and sp.	9

BRYOZOA

Timanotrypa? sp. (OLK)
indeterminate ramose, encrusting and fenestellid forms

CEPHALOPODS
(WMF; BFG)

coiled nautiloids aff. *Titanoceras-Metacoceras-Fordiceras*

CORALS
(CTS)

Lophophyllidium aages (Jeffords)
indeterminate lophophyllidiids?

ECHINODERMS

Haertocrinus? sp. (calyx plate) (JJB)
columnals

GASTROPODS
(ELY)

Straparollus (*Euomphalus*) sp. indet.
?*Taosia* sp. indet.

PELECYPODS
(NDN)

Megadesmus cf. *gryphoides*
Schizodus canalis Branson

Most brachiopods and other fossils were severely crushed, but the fragments were rarely dispersed. This crushing was most commonly dorsoventral in the brachiopods, but occurred in many other orientations. The rarity of fragment dispersion suggests that the destructive mechanism was loading and compression of soft sediment prior to lithification, rather than current or wave action. The dark color of the rock at this and most other Palmarito localities is probably entirely the result of hydrocarbon infiltration (see discussion under "Lithic Description Techniques"), and no inferences of euxinic conditions in the depositional environment are made. The high percentage of muds which make up the rock might ordinarily be taken as evidence of a low energy regime in the depositional environment, but the asymmetry of the valve distributions of the brachiopods (Text-fig. 4) suggests that moderate wave or current energy conditions were present. The abundant bryozoans may have served as baffles to currents near the bottom, trapping finer sediments and providing protected places where organisms adapted to quieter habitats could thrive. Many of the brachiopods show traces of a diverse epifauna, of which only a very few body fossils have been preserved. Bioturbation by vagile organisms (gastropods, pelecypods), in addition to current activity and post-depositional loading, may have contributed to shell breakage (but see Thayer, 1979, for arguments opposing this). None of the fossils shows much abrasion, suggesting that asymmetry of the valve distributions is a function of current activity within the local environment rather than transport from outside. The total assemblage does not appear to have been severely crowded, as no shell asymmetry indicative of growth under crowded conditions was observed that could not be attributed to taphonomic processes or a natural proclivity of the organism for such a mode of growth (*e.g.*, *Hustedia*). The depositional environment is interpreted as having been close to the life environment of the organisms preserved, and to have been located in shallow, warm water of moderate current activity, probably below wave base.

Locality 2 lies in the Quebrada de Portachuelo, about 100 m downstream (up section) from locality 1 (Text-fig. 1). The rock from which the fossils were collected is a petroliferous dark gray shale, with thin (ca. 5 cm thick) intercalated lenses of calcareous siltstone. Although the rock was so friable that no samples could be transported intact to the laboratory for sectioning or slabbing, the rock could easily be called a biomicrite in compositional terms. There is evidence of soft-sediment deformation, in the dorsoventral crushing of many fossils, and the resultant depositional texture could be termed a wackestone or incipient packstone, depending on the local fossil density. The actual collecting site lay directly within the side wall

of the stream bed: the size of the area collected was about one m parallel to and one-half m normal to bedding. All fossils collected were preserved by calcite permineralization, and in addition were heavily infiltrated by hydrocarbons, giving them a uniformly dark color. The shale proved unusually adherent, and consequently considerable amounts of material were cleaned by etching in 52% hydrofluoric acid, using an adaptation of a technique developed for ostracods by Sohn (1956). This dissolved the siliceous shales and converted the calcite shells to fluorite. The resulting pseudomorphs were semi-transparent (Pl. 2, figs. 17–22) and allowed inspection of some internal details, but the conversion to fluorite unfortunately also involved an increase in (crystal) unit cell size, so that specimens over about 1 cm in length were invariably broken, while smaller specimens were commonly decorticated. Among the fossils recovered were:

BRACHIOPODS

Dyoros acanthopelix n. sp. 120
indeterminate productidine fragments 3

ECHINODERMS

columnals

OSTRACODS
(IGS)

Acratia? sp.
Bairdia (*sensu lato*) spp.
Cavellina sp.
Ceratobairdia? sp.
Healdia sp.
Hollinella spp.
indeterminate ostracods (3 types)

Most of the brachiopod fragments have been dorsoventrally crushed, probably as a result of soft-sediment compaction by loading. The valve distribution (Text-fig. 4) is symmetrical, indicating that although some shells were disarticulated, few if any were destroyed. Most of the disarticulation probably resulted from hydrofluoric acid etching and concomitant size increase. Examination of specimens in the rock before etching revealed few if any disarticulated specimens, other than those produced by splitting of the shale. There is no evidence of the sort of wear that would be incurred in transport from outside the environment of deposition. That environment is interpreted as having been in shallow water of low current energy, with a soft substrate. The absence of pediculate or cemented brachiopods may indicate that the initial grain size of the carbonate sediment was very small, so that no real support for a holdfast organ like a pedicle existed. This inference may in turn be supported by the overwhelming dominance of a single form whose flattened valves made it peculiarly adapted to life on a soft substrate.

Locality 3 lies within the Quebrada de Portachuelo, at the brink of the first high (over 5 m drop) waterfall encountered when proceeding downstream from the head of the stream (Text-fig. 1). Samples were collected over a lateral distance of one m through a stratigraphic interval of about one m. The rock, assignable to the Upper Palmarito limestones as conceived by Arnold (1966), occurs in thick to massive beds, separated by partings of medium gray calcareous siltstone. The limestones are dense, petroliferous, dark gray silty limestones, compositionally biomicrites. The rocks do not appear to have been compacted by soft-sediment deformation as have some others in the Palmarito, and in terms of depositional texture are wackestones. In addition to calcareoous and silicified skeletal grains, clasts include sand- and silt-sized anglular quartz and rock fragments, and numerous small siliceous spheres. These latter may be of volcanic origin. Much of the rock is laminated, and included within the laminae are numerous euhedral dolomite rhombs. Cracks of probable tectonic origin cutting both rock and fossils have been filled by calcite. All fossils collected from this locality were silicified and were prepared for study by hydrochloric acid etching. The quality of the silicification is very good, and no geode-fillings or micrite envelopes of the type described by Boyd and Newell (1972) were observed. Among the fossils recovered were:

BRACHIOPODS

Cleiothyridina cf. *C. nana* Cooper and Grant 2
Composita cf. *C. pilula* Cooper and Grant 3
Derbyia sp. 2
Hustedia hyporhachis n. sp. 20
Meekella skenoides Girty 33
Oligothyrina? sp. 34
Pontisia cf. *P. stehlii tumidosa* Cooper and Grant 33
Spinifrons? cf. *S. grandicosta* n. sp. 1
Spiriferellina cf. *S. hilli* (Girty) 29

BRYOZOA
(OLK)

indeterminate fistuliporids

CORALS
(CTS)

indeterminate solitary rugose forms

ECHINODERMS

columnals

GASTROPODS
(ELY)

Anomphalus n. sp.
Apachella aff. *A. franciscana* (Chronic)
Apachella sp. indet.
?*Cibecuia* sp. indet.

Dichostasia complex Yochelson
Discotomaria cf. *D. basisulcata* Batten
Discotropis sp.
?*Lamellospira* sp.
Orthonema sp. indet.
Straparollus (*Euomphalus*) sp. indet.
"*Strobeus*" sp. indet.
Worthenia sp. indet.
new genus of high-spired gastropods
?pleurotomariaceans (2 genera)

SPONGES
(JKR)

Colospongia sp.
Cystothalamia sp. (nov.?)
Defordia cf. *densa* Finks
Girtyocoelia cf. *dunbari* King, 1943
Girtyocoelia n. sp.

The valve distributions of brachiopods with equivalently durable dorsal and ventral valves are noticeably symmetrical (Text-fig. 4). There was probably little transport: the fossils lived near where they were buried. Although the fossils were extensively fragmented, most of this can be attributed to post-burial taphonomic processes. Cracks that pervade the rock were formed after lithification and are probably of tectonic origin. During etching, the secondary, crack-filling calcite between separated portions of many shells was dissolved and the valves when recovered, were broken.

The sea floor here is interpreted as a combination of hard and soft substrates. Initially it had a soft mud bottom. Some of the brachiopods recovered (*Composita, Cleothyridina, Hustedia, Spinifrons*?) are clearly adapted to life on such a substrate. The settlement of such potentially large siliceous sponges as *Defordia,* probably initially on the living or dead shells of the above brachiopods, provided larger areas of hard substrate to which other forms might attach. Indeed, numerous specimens of *Meekella* and *Spiriferellina* (both pediculate forms: see Schümann, 1969) have been recovered partially overgrown by sponge tissue near the beak, suggesting that these forms lived attached to the sponges. The dark color of the limestone is probably entirely the result of hydrocarbon infiltration, and not of euxinic conditions in the depositional environment, but the presence of dolomite rhombs in some sedimentary laminae may indicate that the water there had been somewhat hypersaline, and that access to open ocean water was limited. If negative evidence can be admitted, no open water forms such as ammonoid cephalopods were found in the residues, and none was observed in polished slabs or sections. In addition, none of the vagrant pelecypods found at other Palmarito localities were recovered. The environment of deposition is interpreted as having been one of moderate to low current energy, in warm, shallow water, possibly with restricted access to the open ocean.

Locality 4 lies within the Quebrada de Portachuelo about 100 m upstream (down section) from locality 3 (Text-fig. 1). The area sampled comprises about 2 m laterally and one m normal to bedding. The rocks are exposed in the side wall of the stream bed, and lie almost vertical. They consist of thin- to medium-bedded silty limestones, intercalated with thin-bedded calcareous siltstones. Compositionally a biomicrite, in terms of depositional texture the rock would be classified as a packstone. In addition to the large numbers of calcareous and silicified skeletal grains present, the rock contains many sand- and silt-sized siliceous spheres, which may be of volcanic origin. Also present are abundant fine, needle-like calcitic forms that are interpreted as calcareous and (or) calcified (originally siliceous) sponge spicules. Large bodies (up to 10 cm in largest diameter) of consolidated sediment with thin silicified rinds occur commonly within otherwise laminar limestones. The finer sediments outside are draped and compressed around them, but this may be due to the weight of these large bodies rather than to loading by overlying sediments. Recovered fossils are partially or totally silicified, the former being the more common. Although many calcareous fossils were also present, none was recovered, as the fossils were prepared for study by etching in dilute hydrochloric acid. No silicified micrite envelope casts were found. Since the limestones here were among the muddiest encountered, etching was quite slow, and the few mm of decalcified silt produced during a week's etching were removed from the dried block using an S. S. White Airbrasive unit. Among the fossils recovered were:

BRACHIOPODS

Chonetinetes cf. *C. varians* Cooper and Grant	3
Composita cf. *C. pilula* Cooper and Grant	11
Derbyia auriplexa n. sp.	2
Derbyia cf. *D. complicata* Cooper and Grant	1
Derbyia sp.	1
Echinauris cf. *E. liumbona* Cooper and Grant	13
Holotricharina hirsuta Cooper and Grant	8
Kutorginella cf. *K. umbonata* (Muir-Wood and Cooper)	14
Meekella skenoides Girty	6
Neospirifer venezuelensis (Gerth)	1
Rugatia intermedia n. sp.	2
Spinifrons? cf. *S. grandicosta* n. sp.	1
Stauromata esoterica n. gen. and sp.	1

BRYOZOA

indeterminate ramose and fenestellid forms

CEPHALOPODS
(WMF; BFG; CSL)

Perrinites hilli

ECHINODERMS

columnals

GASTROPODS
(ELY)

Goniasma sp. indet.
Palaeostylus sp. indet.
"*Worthenia*" cf. *W. corrugata* H. Chronic
new genus aff. *Taosia*

PELECYPODS
(NDN)

Parallelodon sp.

The only brachiopods from which substantial numbers of complete shells were recovered were those which could have lived comfortably on a soft muddy substrate. The valve distribution of *Meekella* (Text-fig. 4) is unusual. At locality 4, mostly dorsal valves were recovered, in contrast to locality 3, in which subequal numbers of both valves were found. It is inferred that the population of *Meekella* sampled at locality 4 grew and lived elsewhere, and that the disarticulated dorsal valves were transported a short distance to this soft-substrate burial environment. The fragmentation or relatively poor preservation of many of the fossils cannot be entirely attributed to either partial silicification or faulty preparation, but rather to transportation of dead shells from elsewhere. This suggests that the deposit is largely allochthonous. Judging from the fine sorting and coarsely graded bedding seen in thin section and polished slab, the environment of deposition was one of moderately strong current and (or) wave action, although the alternation between thin, fossil-barren siltstones and thin, sparsely fossiliferous silty limestones, and the lack of abrasive wear on most fossils indicate that the duration of high energy conditions was not long. Soft sediment deformation appears to have been minimal here, that observed being mostly around the numerous bodies of consolidated sediment, here interpreted as rip-up clasts, which could have produced load structures, such as draped, compressed sedimentary laminae, by virtue of their own weight. These are interpreted as having been deposited in shallow, warm water, above a soft substrate, but near to the area from which the fossil debris recovered was derived. The rip-up clasts and the presence of disarticulated valves of such relatively strongly articulated brachiopods as *Meekella* indicates that a moderately strong current regime of short duration ("storm") would be a likely agent of transportation and production of rip-up clasts. Similar deposits in the Ordovician of Quebec (Bretsky and Bretsky, 1975), the Devonian of New York (Bowen, Rhoads, and McAlester, 1974) and the Jurassic of Morocco (Ager, 1974) have been interpreted as having been caused by storms.

Locality 5 consists of a large (ca. eight cubic m) exotic boulder that lies along the mule trail between El Portachuelo and Palo Quemado, about one-quarter the distance from the former to the latter (Text-fig. 1). Several sample blocks were removed from the surface of this boulder. The block lies within exposures of the Sabaneta Formation, and was clearly derived from inaccessible Palmarito Formation outcrops upslope. The rock is a medium-gray, massive, petroliferous limestone which in the field appeared to contain numerous large silicified productids. Accordingly, large amounts of the rock were collected. Unfortunately the silicification was poor and only a single identifiable specimen of a brachiopod was recovered. In polished slab the rock is essentially featureless, with only the occasional randomly oriented, partially silicified shell standing out. In thin section however, one can see that most of the dark coloring present is caused by infiltrated hydrocarbons, and that most of the grains present are not silicified. With the exception of the few stringers of coarse silt- and clay-sized material, the sedimentary grains are of sand-size or larger. Most are skeletal in origin, but rare dolomite rhombs are present in the sand-sized fraction of the sediment. Compositionally the rock would be a calcarenite; in terms of depositional texture a packstone. Many intergranular boundaries are fused, and numerous stylolites have apparently served as pathways for hydrocarbon migration. Among the fossils recovered in etching or observed in polished slab or thin section were:

BRACHIOPODS

Peniculauris subcostata latinamericana n. ssp. 1

CEPHALOPODS

indeterminate large orthocone and coiled nautiloids

FORAMINIFERA
(RCD)

Geinitzina sp.
Globivalvulina sp.
Pachyphloia sp.
indeterminate textulariid

GASTROPODS
(ELY)

Apachella sp.
Bellerophon (?*Pharkidonotus*) sp. of Yochelson, 1960
Naticopsis cf. *N. obla us* Winters
Orthonema sp. indet
Palaeozygopleura sp. indet.

Straparollus (*Euomphalus*) sp. indet.
Taosia sp. indet.
"*Yunnania*" sp. indet.

The rock appears to have been somewhat compacted, probably by the same force that compacted the assemblages at localities 1, 2, 7, and 11, but here the sediments (calcareous sands) were mechanically competent and reacted to the stress by the welding of some grain boundaries and the formation of stylolites. The rarity of fine particle sizes and the moderately good sorting of the calcareous grains in the sand- and gravel-size fractions indicate that this rock may have originated as a bar deposit. Certainly high energy conditions are indicated, to abrade and sort the fragments to this degree. The larger silicified fossils present (brachiopods, cephalopods, gastropods) are interpreted as having been derived from some outlying environment, in much the same way that pelecypods are washed onto well-sorted modern beaches. The absence of much terrigenous material in the rock suggests that either the adjoining land was of low relief, or that this was a bar rather than a beach deposit. The environment of deposition probably lay within wave base, in very shallow water, and indeed may have been in part emergent. The dolomite present may indicate limited access to open ocean environments. The absence of sedimentary structures characteristic of beach or bar sands may be due to extensive bioturbation by the gastropods (or other organisms that have not been preserved as fossils).

Locality 6 consists of a rolled exotic block located beside the mule trail that connects El Portachuelo and Mucuchachí. This trail closely follows the eastern flank of the Quebrada de Portachuelo (Text-fig. 1). The entire block comprises about two cubic m. When first discovered (1971) the block was almost entirely covered by vegetation, and only a small sample was removed from its top. Laboratory recognition of its peculiar fossil fauna prompted re-collection of large samples from the bottom (block A), middle (block B), and top (block C) when I revisited the locality in 1973. All three levels appeared in the field to be framework-supported, thick-bedded, petroliferous, light gray to tan silty limestones, bearing numerous finely silicified fossils. These limestones were separated by inconspicuous, thin (ca. 1 cm thick) siltstone partings. The fossils were recovered from all blocks by hydrochloric acid etching. Beyond valve separation of shells of the easily disarticulated productaceans, little taphonomic alteration has disrupted the fossil assemblage. None of the fossils shows signs of abrasive wear, and most asymmetric valve distributions are explainable by either differential structural stability of the two valves involved, or by susceptibility of the valves to current transport. Thin-section and polished slab analysis shows all three blocks to be compositionally spicular biomicrites, and, in terms of depositional texture, wackestones or boundstones. Among the fossils recovered from the three blocks were:

BLOCK A

BRACHIOPODS

Anaptychius minutus n. gen. and sp. 24
Aneuthelasma globosum n. sp. 15
Collemataria venezuelensis n. sp. 45
Cooperina inexpectata Termier, Termier and Pajaud 57
Costicrura minuta n. gen. and sp. 20
Hustedia hyporhachis n. sp. 13
Petrocrania teretis Cooper and Grant 11
Xenosteges minusculus n. sp. 36

BRYOZOA

indeterminate ramose and fenestellid forms

GASTROPODS (ELY)

Holopeiform gastropod indet.
New genus aff. *Orthonema*
New genus of high-spired gastropods
Pleurotomariacean gastropod indet.

PELECYPODS (NDN)

Pegmavalvula gloveri Newell and Boyd

SPONGES (JKR)

Defordia cf. *densa* Finks
Guadalupia(?) sp.

BLOCK B

BRACHIOPODS

Anaptychius minutus n. gen. and sp. 6
Aneuthelasma globosum n. sp. 24
Cooperina inexpectata Termier, Termier, and Pajaud 13
Costicrura minuta n. gen. and sp. 6
Hustedia hyporhachis n. sp. 4
Rhynchonellacea, family uncertain 2
Xenosteges minusculus n. sp. 5

BRYOZOANS

indeterminate ramose and fenestellid forms

CORALS

indeterminate solitary rugose forms

FUSULINACEANS (RCD)

Parafusulina cf. *P. sellardsi*

GASTROPODS (ELY)

Orthonema sp.
Platyworthenia sp.

New genus aff. *Taosia*
New genus of high-spired gastropods

PELECYPODS
(NDN)

Pegmavalvula cf. *gloveri* Newell and Boyd

SPONGES
(JKR)

Defordia cf *densa* Finks
Guadalupia cf. *williamsi* King

VERMES
(ELY)

two or more forms of *Spirorbis* or similar attached worm tubes

BLOCK C

BRACHIOPODS

Anaptychius minutus n. gen. and sp.	21
Aneuthelasma globosum n. sp.	38
Cooperina inexpectata Termier, Termier, and Pajaud	99
Costicrura minuta n. gen. and sp.	30
Derbyia sp.	1
Echinauris bella Cooper and Grant	1
Hustedia hyporhachis n. sp.	20
Petrocrania teretis Cooper and Grant	2
Rhynchonellacea, family uncertain	4
Xenosteges minusculus n. sp.	130

BRYOZOA

indeterminate ramose and fenestellid forms

CORALS

indeterminate solitary rugose corals
small fragment of tabulate coral ?*Acaciapora* sp. (CTS)

GASTROPODS
(ELY)

?*Orthonema* sp. indet.
Holopeiform gastropod indet.
New genus of high-spired gastropods
Pleurotomariacean gastropod indet.

OSTRACODS
(IGS)

Cavellina? sp.
Hollinella sp.
Roundyella sp.
indeterminate bairdiids

PELECYPODS
(NDN)

Acanthopecten sp.
Girtypecten sp.

SPONGES
(JKR)

Defordia cf. *densa* Finks

VERMES
(ELY)

two or more forms of *Spirorbis* or similar attached worm tubes

Although the faunules recovered from the three blocks at locality 6 are similar, they are not identical. Numbers of brachiopod individuals probably better reflect intensity of picking of the acid-insoluble residues than real diversity: relative numbers of individuals within the faunules may be more significant. All three blocks contain faunas that are largely adapted to life on a hard substrate. The tiny *Costicrura* is similar to *Cruricella* Grant (1976) from Thailand. Grant (1976, pp. 189–190) suggests that that small pediculate form lived closely appressed to a hard substrate, so closely indeed that in order to open its valves it would have had to relax its pedicle. When solidly fixed, beaks of both valves would have been in contact with the substrate, making shell gape impossible. *Costicrura* may well have shared this habit. Certainly it is found only in association with extensive hard substrates such as those provided by the sponge *Defordia*. Few free-living brachiopods are present in the assemblages. Only those generally conceded to be among the hardiest of Tethyan forms (*e.g.*, *Hustedia*) lived on the soft substrate in this assemblage, and most others adapted to that substrate were probably derived from outside. Most of the brachiopods lived above the sea floor, attached to sponges. The three blocks sampled at locality 6 probably represent three microenvironments within a larger incipiently biohermal environment. Block A is best characterized by the presence of the lyttoniid *Collemataria*, which appears nowhere else in the Palmarito Formation. Block B contains numerous specimens of *Parafusulina*, which is absent from both blocks A and C. Block C is characterized by the pelecypods *Acanthopecten* and *Girtypecten*, rather than *Pegmavalvula*, which appears in the other two blocks. The basic substrate is apparently the same in all three places: a soft substrate of biomicrite upon which sponges and clams have provided a secondarily hard surface. It would be tempting to suggest that a factor like salinity, energy, or depth differences was responsible for these apparently discontinuous distributions, but it is more likely to have been a complex combination of such factors. It is likely that the three microenvironments were contemporaneous and laterally discontinuous, patterns that are reflected in vertical section. The fine calcareous biomicrite that forms the basic soft substrate here probably settled out when moderately strong currents struck such effective baffles as the fenestellid bryozoans and anastomosing sponges. These currents were probably the agent that produced the asymmetrical valve distributions (Text-fig. 4) in all but the most tightly articulated forms (*e.g.*, *Anaptychius*). The environment of deposition is interpreted to have been in shallow, warm water, of mod-

erate current activity. The lack of noticeable amounts of terrigenous material suggests that it was not near a shoreline of high relief. It appears to have been in a less restricted area than that represented by locality 3, as it lacks the dolomite rhombs so prevalent there.

Locality 7 was a paving stone in the mule trail between Palo Quemado and Mucuchachí, about 1 km northwest of Palo Quemado, and about 200 m toward Palo Quemado from the small chapel locally known as Capilla de la Santa Cruz de Palmarito (Text-fig. 1). This is on the old trail connecting Mucuchachí and Santa Barbara de Barinas, and the locality lies within the type section of the Palmarito Formation as defined by Christ (1927). Although out of place there, the rock sampled is definitely from within the formation. The outcrop from which it was derived, however, could not be located. The block was about one m square and one-fourth m thick, and consisted of a dark gray, petroliferous, fossiliferous, fissile, very silty limestone. Field examination using dilute HCl discovered no silicified fossils, but crackouts were so promising that a large amount of material (almost the entire block) was collected. Preparation was entirely by mechanical methods. In thin-section and polished slab examinations, the rock proved to be heavily infiltrated by hydrocarbons that probably accounted for most of its dark color. Within the sand and silt fractions there was primitive sorting, and some thin graded beds (on the scale of the thin-section), but in general the rock was poorly sorted. Compositionally a biomicrite, it contained large numbers of apparent sponge spicules and abundant angular skeletal and quartz grains and rock fragments scattered through the micritic groundmass. The rock showed signs of having suffered soft-sediment deformation: laminar fine sediments draping over clasts, crushing normal to bedding, and considerable apparent recrystallization and welding at intergranular boundaries had taken place. In terms of depositional texture the rock is a packstone. Few brachiopods showed an asymmetrical valve distribution (Text-fig. 4). Among the fossils recovered from this locality were:

BRACHIOPODS

Acosarina? sp.	1
Composita cf. *C. pilula* Cooper and Grant	6
Echinauris cf. *E. liumbona* Cooper and Grant	93
Kutorginella cf. *K. umbonata* (Muir-Wood and Cooper)	1
Meekella skenoides Girty	1
Neophricadothyris cf. *N. crassibecca* Cooper and Grant	150
Neospirifer venezuelensis (Gerth)	16
Rugatia occidentalis (Newberry)	1
Stauromata esoterica n. gen. and sp.	16

BRYOZOA

indeterminate fenestellids

CORALS (CTS)

Lophophyllidium sp.

ECHINODERMS

columnals

Although there is some disarticulation of the fossil brachiopod shells recovered at locality 7, the large percentage of fine micritic matrix seems to indicate that the environment of deposition was one of relatively low current energy. Most of the breakage or distortion of shells observed can be attributed to soft-sediment deformation, probably due to sedimentary loading. Shells are not severely abraded: both primary and secondary layers of most shells can be discerned in thin-section. The abundance of angular quartz and rock fragments suggests that the depositional environment was close to a shoreline of moderate relief, in shallow, warm water.

Locality 8 lies in the side wall of the mule trail connecting Palo Quemado and Mucuchachí, about 200 m toward Mucuchachí from a small chapel locally known as Capilla de la Santa Cruz de Palmarito (Text-fig. 1). This is on the old Santa Barbara de Barinas–Mucuchachí mule trail, within the type section of the Palmarito Formation as defined by Christ (1927). The volume sampled here was about one-half cubic m. The rock at this locality had been totally leached of soluble carbonates to a depth of over one m, so that although the rock would texturally be a wackestone, or in compositional terms a biomicrite, it contained no calcite or dolomite. Fossils from this strange matrix were recovered in surface collections and by cutting them from the dried silt residues with the aid of dental tools and an S. S. White Airbrasive unit. Most specimens were silicified, but many leached calcareous individuals left beautifully detailed molds. These were collected if they represented rare forms or added significant features to those taxa represented by silicified specimens. In addition to the fossils, numerous large bodies (up to 10 cm in largest diameter) of consolidated sediment, with thin silicified rinds, occurred commonly within the surrounding finer laminar sediments. Pinching and compression of these finer laminae was probably due to loading either by these large clasts themselves, or by the accumulated sediment column, while the sediments were still relatively plastic. Among the fossils recovered were:

BRACHIOPODS

Chonetinetes cf. *C. varians* Cooper and Grant	3
Composita cf. *C. pilula* Cooper and Grant	76
Derbyia auriplexa n. sp.	1
Derbyia cf. *D. complicata* Cooper and Grant	4
Echinauris cf. *E. liumbona* Cooper and Grant	11
Holotricharina hirsuta Cooper and Grant	4
Holotricharina? sp. A	1
Hustedia sp.	1
Kutorginella cf. *K. umbonata* (Muir-Wood and Cooper)	16
Meekella skenoides Girty	3
Neophricadothyris cf. *N. crassibecca* Cooper and Grant	42
Neospirifer venezuelensis (Gerth)	1
Paucispinifera? cf. *P. sulcata* Cooper and Grant	4
Pontisia stehlii Cooper and Grant	6
Rugatia intermedia n. sp.	30
Spinifrons grandicosta n. sp.	4
Stauromata esoterica n. gen. and sp.	3

BRYOZOA

indeterminate ramose and fenestellid forms

CORALS
(CTS)

Lophophyllidium sp. aff. *L. spinosum* Jeffords

ECHINODERMS

indeterminate cidaroid (echinoid) spines and plates (PMK)
columnals

GASTROPODS
(ELY)

Kinishbia sp.
Meekospira sp. indet.
Straparollus (*Euomphalus*) aff. *S.* (*E.*) *kaibabensis* H. Chronic
New genus allied to *Orthonema*

PELECYPODS
(NDN)

Schizodus canalis Branson

SPONGES
(JKR)

indeterminate sponges

Soft sediment deformation in the rock at locality 8 was probably quite minor, and limited to that occurring below the large bodies that are here interpreted as storm-derived rip-up clasts. Most shell breakage observed can be explained by either or both transportation and abrasion near the site of deposition (Text-fig. 4). The only brachiopods at all well preserved are those (*e.g., Neophricadothyris, Composita, Derbyia*) that appear to be adapted to life on a soft substrate. Many of the valves of *Neophricadothyris* however, consist solely of beaks, suggesting that the more fragile portions of the valves were abraded away. High energy pre-depositional current or wave activity must be invoked to account for the condition of these fossils. The environment of deposition is inferred to have been in shallow, warm water near wave base, in an area affected by periodic storms.

Locality 10 is situated along the mule trail that connects El Portachuelo and Palo Quemado (Text-fig. 1). The rock is exposed in and on both sides of the trail itself, about 100 m south of the house locally known as "Altamira" (owned in 1971 by Silvestre Gutiérrez). Although several m in extent, this exposure is probably a large exotic block, as most surrounding rocks are reddish and greenish sandstones referable to the Sabaneta Formation. The block itself consists of rather thin (5–15 cm thick) beds of a slightly silty dark gray limestone, separated by thinner (ca. 1 cm thick) partings of gray siltstone. The collection area covered about two m laterally and one m normal to bedding. Both lithologies are abundantly fossiliferous. Dominant forms recognized in the field are the brachiopods *Hustedia* and *Derbyia*. These fossils and many others are finely silicified, and were prepared for study by etching in dilute hydrochloric acid and removal of the dried decalcified silt residues with an S. S. White Airbrasive unit. Some of the globular forms (*e.g., Hustedia*) contained silicified laminar geopetal structures. Some cephalopods, gastropods and pelecypods were preserved as apparent silicified micrite envelopes. In thin-section and polished slab the rock is clearly a biomicrite, with occasional thin bands of fine sandy material. The shells do not appear to have been compacted by soft-sediment deformation, and although the rock is grain-supported in places, it contains a considerable percentage of mud. In terms of depositional texture it is a wackestone. Some shell breakage occurred as a result of decalcification during etching of crack-fillings of tectonic origin. Among the fossils recovered were:

BRACHIOPODS

Anemonaria sublaevis (King)	29
Composita cf. *C. pilula* Cooper and Grant	5
Derbyia deltauriculata n. sp.	34
Holotricharina? sp. A	1
Hustedia hyporhachis n. sp.	335
Pontisia stehlii Cooper and Grant	4
Rhynchonellacea, family uncertain	5
Rugatia intermedia n. sp.	1

BRYOZOA

indeterminate ramose and fenestellid forms
"*Lyropora*" sp.

CEPHALOPODS

Mooreoceras-like orthocone nautiloid (WMF; BFG)
Martoceras subinterrupta (Krotov, 1885) (CSL)

CORALS
(CTS)

Lophophyllidium sp. cf. *L. pelaeum* (Jeffords)
?*Acaciapora* sp.

ECHINODERMS

columnals

GASTROPODS
(ELY)

?*Ananias* sp. indet.
Apachella sp. indet.
?*Bellerophon* sp. indet.
Euphemites aequisulcatus H. Chronic
Euphemites cf. *E. exquisitus* Yochelson
Glyptospira sp. indet.
Kinishbia sp.
Naticopsis sp. indet. (2 subgenera)
Onycochilus sp. indet.
Orthonema sp.
Retispira sp. indet.
"*Soleniscus*" sp. indet.
Straparollus (*Euomphalus*) aff. *S.* (*E.*) *kaibabensis* H. Chronic
Worthenia sp. indet.
New genus of high-spired gastropods
New genus of high-spired gastropods with changing spire angle

PELECYPODS
(NDN)

Pseudomonotis sp.
Sanguinolites sp.

TRILOBITES
(CKC)

Anisopyge perannulata (Shumard) Girty, 1909

The shells from this locality have suffered very little from post-depositional soft substrate deformation. The dark color of the rock, like that of most Palmarito lithologies, is due to interstitial infiltration by hydrocarbons that is clearly secondary. Although there is some breakage and separation of the easily disarticulated productids, the extremely delicate dorsal valves of such forms as *Anemonaria* are often preserved in their entirety (Text-fig. 4). This suggests that current activity was not strong in or near the depositional environment, and that the assemblage is mostly a biocoenose. The attitude of many fossils (*e.g., Derbyia, Hustedia, Lophophyllidium*) suggests that this locality represents at least in part an only slightly disturbed living assemblage. The fossil assemblage consists entirely of forms adapted to life on muddy substrates, and there are no cemented forms. The presence of geographically widespread nektonic forms (the cephalopod *Martoceras subinterrupta* and the *Mooreoceras*-like orthocone nautiloid) suggests that there was access to the holomarine environment, and that locality 10 lay offshore from any local reef-like development. Most specimens of the paucispiniferid *Anemonaria* were recovered during the etching of a single small block. This is interpreted to indicate that the spatial distribution of such forms was discontinuous and patchy, since postmortem transport would have entailed more breakage and wear than is observed in these delicate forms. *Derbyia* too seems patchily distributed, but not in so clear cut a manner as *Anemonaria*. Specimens of *Hustedia* appear discontinuously distributed as well: some individuals of both it and *Derbyia* are markedly atypical or asymmetrical, indicating growth in dense populations, yet some blocks collected contain few individuals of either. The diversity of gastropod types and the presence of trilobite remains suggest a vigorous infauna whose bioturbatory activities may have contributed to some of the valve fragmentation observed. The environment of deposition, and for most of the organisms preserved, the life environment, is interpreted as having been in shallow, warm water below wave base, on a soft muddy bottom, with clear access to open ocean, and relatively far offshore.

Locality 11 consists of several exotic blocks lying up a steep slope from a disused mule trail that connects the small settlements of El Portachuelo and Santa Rosa (Text-fig. 1). It lies on the west flank of the Quebrada Palmar, near the head of that stream. The rocks are repeated intercalations of thin- to medium-bedded, dense, dark gray, petroliferous fossiliferous silty limestones and thinner, fossil-poor calcareous siltstones. The contacts between limestone and siltstone are somewhat undulatory but are persistent as far as they can be traced (tens of m in some of the largest blocks). There are two distinct lithic types within the limestone itself, which are revealed in thin-section and polished slab: one is a relatively unfossiliferous biomicrite, which is poorly sorted and in places laminar; the other is a very fossiliferous muddy calcarenite, and texturally is locally either a packstone or grainstone. Most of the clasts in both rock types are skeletal in origin: those in the grainstone are considerably more rounded and abraded. The fossils recovered were all silicified, many of them imperfectly. Silicified micrite envelope casts of chiton plates, cephalopods, gastropods, and pelecypods are common. The assemblage was prepared for study by etching in dilute hydrochloric acid, and subsequent removal of the dried silt residues using hand tools and an S. S. White Airbrasive unit. The asymmetry of valve distributions and general condition of the fossils indicates that there had been considerable taphonomic abrasion, if not transportation. Among the fossils recovered were:

BRACHIOPODS

Anemonaria? cf. *A. sublaevis* (King) 4
Composita cf. *C. pilula* Cooper and Grant 6
Derbyia cf. *D. filosa* Cooper and Grant 9
Echinauris cf. *E. lappacea* Cooper and Grant 20
Holotricharina? sp. A 1
Hustedia hyporhachis n. sp. 43
Kutorginella cf. *K. umbonata* (Muir-Wood and Cooper) 5
Meekella skenoides Girty 1
Pontisia stehlii Cooper and Grant 17
Rhamnariidae cf. *Ramavectus* sp. 1
Rugatia intermedia n. sp. 4
Spinifrons? cf. *S. grandicosta* n. sp. 7
Texarina? cf. *T. wordensis* (King) 5

BRYOZOA

indeterminate ramose and fenestellid types

CEPHALOPODS
(WMF; BFG)

Mooreoceras-like orthocone nautiloid

CHITONS
(AGS)

indeterminate chiton plates

CORALS
(CTS)

Lophophyllidium sp.

ECHINODERMS

columnals

GASTROPODS
(ELY)

Anomphalus sp. indet.
Apachella aff. *A. franciscana* (Chronic)
Apachella sp.
"*Colpites*" sp. indet.
Cylicioscapha sp.
Glyptotomaria sp. indet.
Glyptospira sp. indet.
holopeiform gastropod indet.
Kinishbia sp.
?*Meekospira* sp. indet.
Onycochilus sp. indet.
Orthonema sp.
Straparollus (*Euomphalus*) aff. *S.* (*E.*) *kaibabensis* H. Chronic
Taosia sp.
new genus aff. *Taosia*
new genus allied to *Orthonema*
new genus of high-spired gastropods
open-coiled vermitiform pleurotomariacean, genus new

PELECYPODS
(NDN)

Astartella sp.
Aviculopecten sp.
Guizhoupecten sp.
Nuculopsis sp.
Parallelodon sp.
Pegmavalvula cf. *gloveri* Newell and Boyd
Pseudomonotis sp.
Pseudopermophorus sp.
Sanguinolites sp.
Streblochondria sp.

SPONGES
(JKR)

Colospongia sp.
Cystothalamia sp. (nov.?)
Defordia cf. *densa* Finks
Girtyocoelia sp.
Haplistion cf. *H. aeluroglossa* Finks, 1960
hexactinellid root tuft
Wewokella (?) sp.

Most specimens of the diverse fauna recovered from this locality come from the relatively thin packstone-grainstone layers, which consist almost entirely of severely abraded skeletal fragments. Far less worn, broken or abraded shells are found outside of these layers: the faunal composition of the muddier portions is essentially the same as that in the packstones, but fossils are far less abundant. This suggests that the more fossil-rich layers are simply localized concentrations derived from the same environment, the result of periodically elevated energy conditions. The silty layers that intervene between the limestones, however, are almost barren of fossils, and contain only an occasional *Hustedia* or *Composita,* brachiopods that are almost ubiquitous in the Palmarito (Text-fig. 4). These siltstone laminae are interpreted as fines that have been winnowed out of the packstone-grainstone layers. The shells found in the siltstones are probably those generalist forms that first settled on the soft substrate when the energy regime had returned to lower levels.

The fauna as preserved is one of the most diverse in the Palmarito, but no one element is dominant. It appears that most of the forms have been derived from another life environment and are here allochthonous. Although no rip-up clasts such as those seen at localities 4 and 8 were observed, some of the rocks seen here (the packstone-grainstone layers and siltstones) could be ascribed to the local winnowing action of periodic storms, which would segregate the skeletal debris and micritic matrix on the sea floor. Preserved portions of an apparently diverse assemblage of bioturbators (chitons, gastropods, some pelecypods) may have aided in comminution of skeletal debris, but cannot be responsible for the sorting observed. The environment of deposition is interpreted as having been in shallow, warm water, near wave base, over a soft substrate, in an area subject to periodic storms.

Locality 13 consists of a large (ca. 100 kg) rounded exotic block which lay beside the mule trail connecting El Portachuelo and Mucuchachí, about 200 m toward

El Portachuelo from locality 6 (Text-fig. 1). No exposures of similar rocks could be located on inspection of the surrounding area. The boulder showed no obvious bedding laminations, and was a dense, dark gray to black, petroliferous, silty limestone, without the siltstone partings common to most other samples collected in this study. In polished slab examination, there were suggestions of bedding along which hydrocarbon infiltration had proceeded. Thin-section examination showed the rock to be compositionally a biomicrite, with dolomite rhombs in addition to skeletal clasts, and in terms of depositional texture a wackestone. It had not been secondarily compacted as had many other Palmarito samples, and the fossils recovered from it were without exception exquisitely preserved by fine silicification (see Pl. 4, fig. 55). All recovered fossils were prepared by etching in dilute hydrochloric acid, and removing the small quantity of adherent silt residues using an S. S. White Airbrasive unit. Valve distributions of some easily disarticulated productaceans like *Echinauris* were markedly asymmetrical (Text-fig. 4). This may in part be explained by the comparative fragility of the dorsal valve in such forms. Most other valve distributions were symmetrical. Among the fossils recovered were:

BRACHIOPODS

Chonetinetes cf. *C. varians* Cooper and Grant	4
Composita cf. *C. pilula* Cooper and Grant	8
Derbyia auriplexa n. sp.	7
Derbyia sp.	4
Echinauris bella Cooper and Grant	377
Holotricharina? sp. A	1
Hustedia hyporhachis n. sp.	89
Oligothyrina? sp.	2
Spinifrons grandicosta n. sp.	2

BRYOZOA

indeterminate fenestellids

CHITONS
(AGS)

indeterminate chiton plates

CORALS

indeterminate solitary rugose form

GASTROPODS
(ELY)

Anomphalus sp. indet.
Apachella sp.
Discotropis sp. of Yochelson, 1960
cf. *Donaldina* sp. indet.
Glabrocingulum sp. indet.
Glyptospira sp. indet.
Goniasma sp. one
Goniasma sp. two
Kinishbia sp. indet.
Meekospira sp. indet.
Naticopsis sp. (new subgenus)
Orthonema sp.
Taosia sp.
?*Worthenia* sp. indet.
holopeiform gastropod indet.
low-holopeiform gastropod
open-coiled ?pleurotomariacean
high-spired genus indet.
new genus of high-spired gastropods
sinistral gastropod indet.

PELECYPODS
(NDN)

Sanguinolites sp.
Pseudomonotis sp.

TRILOBITES
(CKC)

Anisopyge ?inornata Girty (*in* Lee and Girty, 1909)

The exquisite preservation of such delicate spinose forms as the *Echinauris* and *Holotricharina* here suggests that deposition took place under conditions most favorable for fine preservation (rapid burial in soft sediment, perhaps under reducing conditions). The lack of breakage by soft sediment compaction suggests that the rocks were deposited close to the end of Palmarito deposition, and that the overlying column of marine sediments was thin. The symmetric valve distribution (Text-fig. 4) of most faunal elements suggests that taphonomic alteration was minimal. The comparative fragility of the dorsal valve of the *Echinauris* easily explains the asymmetric distribution seen in that form. The ventral valve is protected from breakage by a forest of spines that almost completely surrounds it. Muir-Wood and Cooper (1960, p. 45) suggested that some accumulations of marginiferids (like *Echinauris* here: see Pl. 4, fig. 55), that included shells in almost every possible orientation, may have been biocoenoses. The spines covering the ventral valve hang over the commissure to such a great extent that the shell would have been supported above the soft substrate, and able to carry on life processes in clear water, in almost any position. It may be that the hollow, mantle-filled spines also served as springs to cushion the jars and blows encountered as the shells were rolled about the sea floor by currents. The comparatively large number of specimens of this form collected here is probably best explained by the manner in which the spines of *Echinauris* entangle one another. Obviously this sort of habit led to localized and discontinuous populations on the sea floor. Pre-lithification breakage of the entire fossil assemblage at this locality was minor. The environment of deposition is interpreted as having been a soft-substrate bottom, with little relief, below wave base in warm water, perhaps restricted

from ready access to open ocean conditions. The presence of chitons, gastropods, certain pelecypods and trilobites suggests the presence of an infauna that may in part have been responsible for any shell disarticulation that occurred. Bioturbation, if present (see Thayer, 1979), was extensive, as few traces of bedding laminae, and no burrows or feeding traces now remain.

DEPOSITIONAL ENVIRONMENTS

Pierce *et al.* (1961) and Arnold (1966) have demonstrated that the Sabaneta and Palmarito Formations (or facies) are records of a marine transgression from southeast to northwest across the Mucuchachí depositional basin in Permian time. The Sabaneta represents the continental facies of this transgression and the Palmarito the marine facies. None of the rocks and fossils analyzed here indicate deposition in other than marine conditions, but some (locs. 3, 5 and 13) indicate that access to open ocean may have been restricted locally. Almost all the assemblages are characteristic of soft, muddy substrates. In only three (locs. 3, 5 and 6) are there indications of other conditions. In the environment of locality 5, energy conditions were probably too severe to allow settlement of attached forms on the winnowed calcarenite substrate, but at localities 3 and 6, hard-bottom assemblages colonized sponge substrates. At locality 3, hypersaline conditions may have prevented optimal development of the full potential of brachiopod diversity provided by organic hard substrates in the Tethyan realm. At locality 6, however, holomarine conditions were present, and greater diversity could develop. The faunal differences in the three samples from that locality are probably due to a variety of causes, notably the patchy distribution that is characteristic of tropical organisms. The periodic storms inferred from sediment characters in the Upper Palmarito Formation may have acted as environmental stresses deterrent to bioherm formation on the scale of those seen in the age-equivalent Cathedral Mountain and Road Canyon Formations of the West Texas region.

ORGANISM/SUBSTRATE RELATIONSHIPS

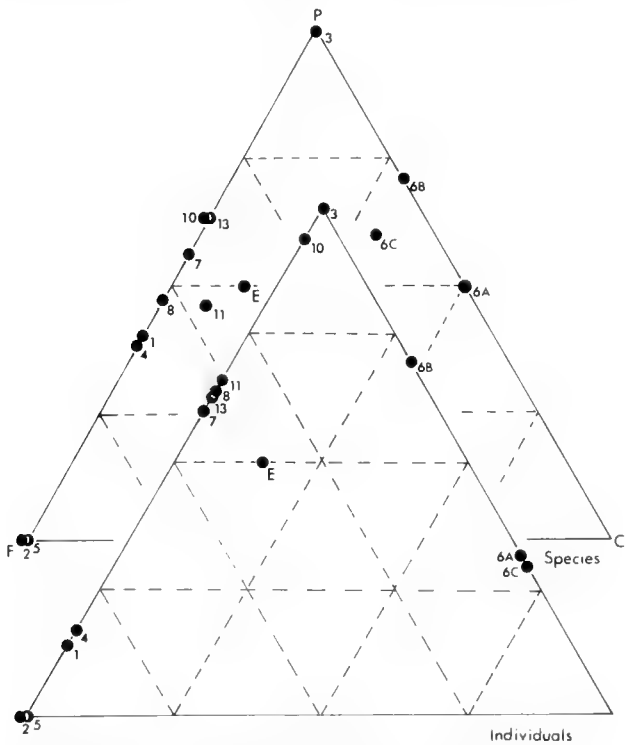
Stehli (1971) suggested that in tropical regions soft-substrate environments may act as a secondary stress, after temperature, limiting the distribution of some Permian Tethyan articulate brachiopods. One object of my study was to determine if there were some objectively measurable parameter that could be related meaningfully to the character of the substrate on which these brachiopods lived. A measure of the size-frequency distribution of sedimentary particles was one logical possibility (Hoover, 1976b). The easily measured sand/silt ratio was not employed, since in the Palmarito the sand and coarser particles commonly are skeletal in origin, and are variably silicified. Some are lost in etching, so that the weight percent of recoverable sand is meaningless as a measure of original sediment grain-size distribution. A potentially more useful parameter that appeared likely to remain intact through lithification and diagenesis was the ratio between silt- and clay-sized particles in the hydrochloric acid-insoluble residues. The silt/clay ratio should reflect substrate character as a partial record of the energy regime and (or) current activity. A higher energy regime or episodic activity should leave a lithic record with a higher silt/clay ratio than that of a quiet environment or episode, since higher energies would preferentially remove the finer particles. The only Palmarito rocks useful for such studies were those that contained appreciable numbers of silicified fossils. It was assumed that silicification equally affected all sizes of fine particles, so that the insoluble residues remaining after etching would reflect in a consistent way the size-distribution of the parent sediment. It was also assumed that originally non-carbonate fines were either minor, or had the same or similar size-frequency distributions as the calcareous sediments, and that the percentage of clay-sized particles agglomerating to form silt-sized particles was approximately the same in both insoluble residues and parent sediment.

Much of the Palmarito is characterized by repeated intercalations of thin limestones and thinner shales. Where possible both lithic types were sampled at each collecting locality, and analyzed separately. Analytical techniques and calculations were discussed by Hoover (1976a).

In most Palmarito localities an interesting result of the analysis was that shales had higher silt/clay ratios than the limestones they separated (see Table 5). Everywhere that this relationship held, the shales contained much less diverse brachiopod assemblages than did the limestones. In places where this relationship did not hold (locs. 6A and 10) the shale assemblage was equally as diverse as that of the surrounding limestone. The shales (assuming the silt/clay ratio does indeed reflect energy conditions) are thus interpreted as having been produced by the winnowing effect of localized higher energy conditions. The few fossils found within them are the most common forms (*Hustedia* and (or) *Composita*), which apparently either could live under rather harsh conditions, or were the first to resettle the free substrate when energy conditions returned to lower levels. The shale at localities

6A and 10 is interpreted as the result of a change in sedimentation rate, rather than energy conditions, which would not change the size-distribution of the substrate grains or materially alter the habitat of the brachiopods that lived there. The intercalated limestones and shales of the Palmarito suggest a periodicity of such higher energy episodes. Ager (1974: Jurassic of Morocco), Bowen, Rhoads, and McAlester (1974: Devonian of New York), and Bretsky and Bretsky (1975: Ordovician of Quebec) noted similar deposits and interpreted them as storm deposits. Tending to support this contention for the Palmarito are the apparent rip-up clasts seen in the limestones of assemblages 4 and 8 (see "Lithic and Faunal Analysis").

It was originally hoped that the silt/clay ratio might be correlated with brachiopod habitat type, which should in turn be controlled in part by substrate. To this end, the Palmarito brachiopod genera were separated into three classes by habitat type: pediculate, free-living and cemented (Table 6). The percentage of the total bed assemblage in each class was calculated (for both species and individuals) and plotted on a triangular diagram (Text-fig. 5). The proper position of some genera in this admittedly simplistic division is questionable. Schümann (1969) has shown that many of the Orthotetacea, including such Palmarito forms as *Meekella* and *Derbyia*, were not cemented to the substrate but rather attached by a short byssus-like pedicle, which penetrated the ventral beak through numerous tiny holes. These two genera are here arbitrarily assigned to the pediculate class.



Text-figure 5.—Habitat-type distributions for species and individuals in Palmarito Formation brachiopod assemblages. Localities are numbered. F = free-living, supported on soft substrate by spines or shell; P = attached to hard or soft substrate by functional pedicle; C = cemented or closely appressed to hard substrate; E = entire brachiopod fauna (all localities).

Table 5.—Results of rock constituent analyses of Venezuelan marine Permian rocks containing appreciable numbers of silicified fossils. See Hoover (1976a) for discussion of calculations and analytical techniques. L = limestone analysis; S = shale analysis; Rep. = replicate analysis.

Locality and Gross Lithology	Percent Soluble Carbonate and Organic Fraction	Percent Insoluble Inorganic (sand-size or coarser)	% Silt/ % Clay (insoluble and inorganic)	Silt/Clay Ratio (by weight)
3_L	91.9	6.7	0.9/0.5	1.86
3_S	49.9	48.8	1.0/0.3	3.73
4_L	75.1	18.0	5.0/1.9	2.56
4_S	66.5	25.3	6.6/1.6	4.64
5_L	97.5	0.5	1.1/0.9	1.17
$6A_L$	89.2	6.8	2.3/1.6	1.42
$6A_L$ (Rep.)	89.8	6.5	2.1/1.6	1.27
$6A_S$	70.6	17.9	6.9/4.6	1.50
$6C_L$	87.4	7.9	2.9/1.8	1.65
10_L	87.9	5.2	4.0/2.8	1.43
10_S	65.2	22.9	5.9/6.0	0.99
11_L	87.0	10.3	1.8/0.9	1.90
11_S	67.5	19.6	9.3/3.6	2.56
13_L	94.9	1.3	2.1/1.7	1.22

Text-figure 5 emphasizes the difference in taxonomic and habitat-type composition between the incipiently biohermal fauna at locality 6 and all others in the Palmarito. As can be seen by a comparison of the silt/clay ratios (Table 5) and the habitat-type diagrams (Text-fig. 5), there is no correlation between the two. Within the variation attributable to experimental error (Hoover, 1976a), the silt/clay ratio of soft-bottom assemblages such as locality 10 are identical to those from the demonstrably hard-bottom incipiently biohermal assemblages of locality 6. It is difficult to differentiate soft- from hard-bottom assemblages on sedimentological grounds in carbonate rocks. It appears that, at least in the Palmarito, hard bottom assemblages arise on soft substrates, by initial growth of populations of large sponges (*e.g.*, *Defordia* sp.). These forms were able to grow, once established on a comparatively small hard substrate such as a shell, and to increase in size far beyond the margins of the original attachment surface. They could grow out along the surface of soft substrates and project upward into the water column as well. They thus provided

Table 6.—Habitat-type classification of Palmarito Formation brachiopod genera. Pediculate = attached to the substrate by a functional pedicle during most or all of life; Cemented = anchored by ventral valve, ventral beak, or rhizoid spines, usually to some "hard" surface; Free = lying loose on the substrate, there supported by the ventral valve, commonly also by specially oriented spines or processes.

Pediculate	Cemented	Free
Acosarina?	*Collemataria*	*Anemonaria*
Anaptychius	*Cooperina*	*Chonetinetes*
Aneuthelasma	*Petrocrania*	*Dyoros*
Cleiothyridina	*Ramavectus?*	*Echinauris*
Composita	*Xenosteges*	*Holotricharina*
Costicrura		*Kutorginella*
Derbyia		*Paucispinifera?*
Hustedia		*Peniculauris*
Meekella		*Rugatia*
Neophricadothyris		*Spinifrons*
Neospirifer		*Stauromata*
Oligothyrina?		
Pontisia		
Spiriferellina		
Texarina?		

niches for several phyla of attached forms (including several families of endemic Tethyan brachiopods) which could not otherwise survive in a soft-substrate environment. Thus the hard-bottom niches that many of the Tethyan brachiopods occupy are not reflected by measurable parameters of the sediment grain-size frequency distribution, nor do these seem to correlate with the distribution of the sponges, which act to establish greatly enlarged hard substrate areas.

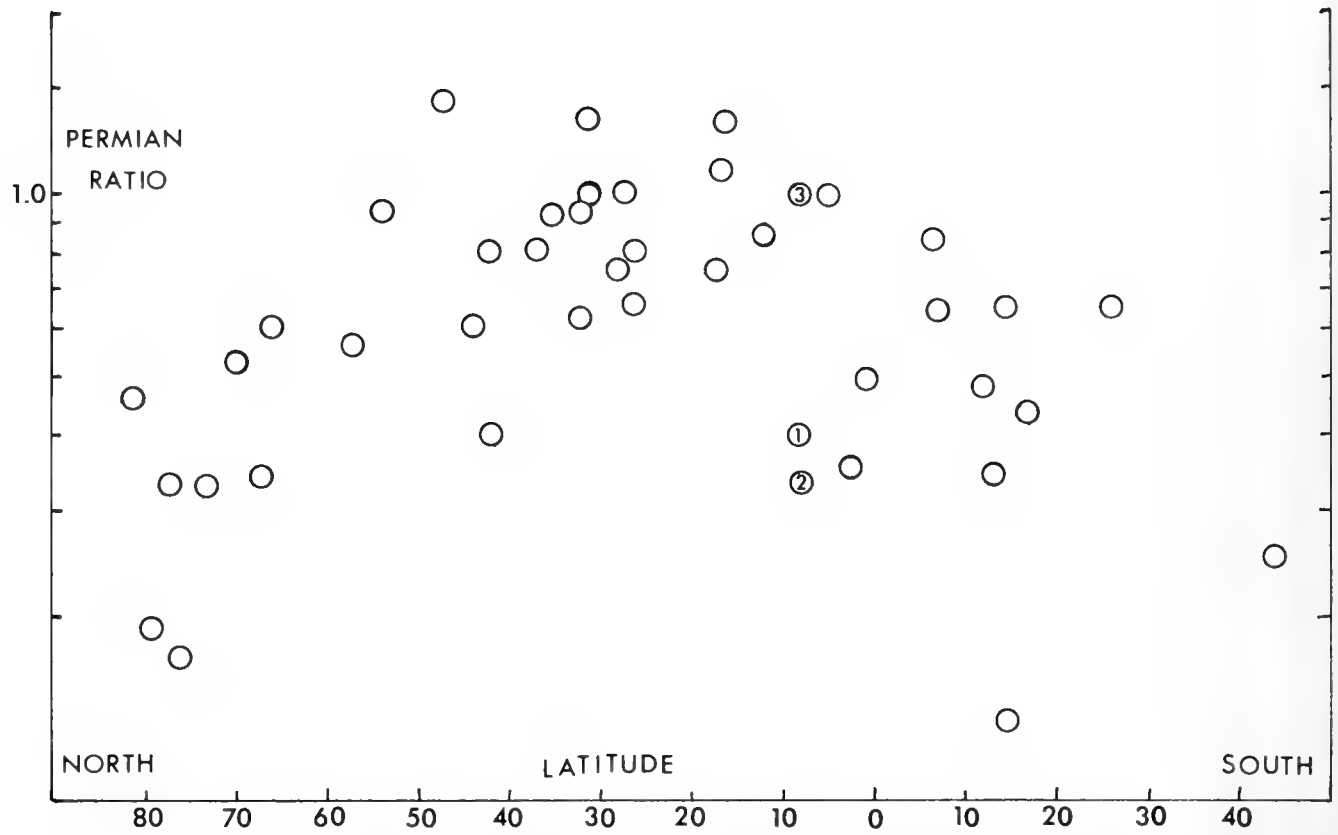
It is instructive to compare the thermally-based latitudinal distribution of Permian articulate brachiopods to their habitat types. The Road Canyon Formation of West Texas (roughly equivalent in age to the Palmarito [see Biostratigraphic Correlation]) contains 34 families of articulate brachiopods. Of these, 16 are globally cosmopolitan, while 18 are limited mostly to low latitudes. Slightly less than half of the cosmopolitan families are adapted to life on a soft substrate, and no cemented forms are truly cosmopolitan in their Permian distribution. Among the Tethyan endemic families, however, one-third are cemented in habitat-type, and only a single free-living family is represented (in the Road Canyon assemblages sampled). Thus the high familial diversities recorded in many Permian Tethyan fossil brachiopod assemblages reflect the presence of organic hard substrates that provided the necessary niche space for diversification.

PERMIAN RATIO

Stehli (1971, 1973) related the thermally-controlled latitudinal taxonomic diversity gradient to the distribution of families of thermally-tolerant cosmopolitan (Boreal and Austral) and thermally-sensitive endemic (Tethyan) Permian articulate brachiopods. He found 16 families that had been recovered from most Permian brachiopod faunas, all over the world. These he designated Cosmopolitan Dominant families. They were (according to the classification used in the *Treatise* [Williams *et al.*, 1965]): the Schuchertellidae, Orthotetidae, Chonetidae, Marginiferidae, Echinoconchidae, Buxtoniidae, Dictyoclostidae, Linoproductidae, Stenoscismatidae, Rhynchoporidae, Athyrididae, Spiriferidae, Spiriferinidae, Bachythyrididae, Elythidae and Dielasmatidae (Stehli and Grant, 1971, p. 504). The difference between the number of families of Permian brachiopods recovered from a locality and the number of Cosmopolitan Dominant families recovered there, divided by the latter number, Stehli termed the "Permian Ratio" for brachiopods (1970, p. 3330). This ratio was employed instead of pure diversity in discussions of latitudinal diversity variations, as it reduced somewhat the sampling bias inherent in some of the collections, and acted as a temperature-sensitive indicator. A value for the Permian Ratio was calculated for each known brachiopod fauna, and plotted against latitude (Stehli, Douglas and Newell, 1969, fig. 2; Stehli, 1970, fig. 16; Text-fig. 6). Recent latitudes are used in preference to any of several paleomagnetically-based paleolatitudinal frameworks, (1) to provide direct comparison with relevant previous papers (*e.g.*, Stehli, 1970), and (2) to avoid the controversy that would follow the use of any one of the paleomagnetic schemes currently in favor (cf. Habicht, 1979; Scotese *et al.*, 1979). My usage of a recent latitudinal coordinate should in no way be construed as a denial of the sea-floor spreading and continental drift hypotheses. Although there is considerable spread in the values, there is clearly a trend upward from the pole toward a maximum close to the present equator. The fauna of the Palmarito, as it was known prior to this study (*i.e.*, from Arnold, 1966; Pierce *et al.*, 1961), provided the data for point 1 in Text-figure 6.

This fauna was not included in Stehli's figures, as he had used only those which were described and figured, so that he might personally ascertain familial assignments. It happened by chance that the specimens on which Arnold's faunal list had been based came (*via* the identifier (Dr. H. M. Muir-Wood) and Dr. A. J. Boucot) to be in the collections of the National Museum in Washington, D.C. Dr. Muir-Wood's identification labels still accompany the specimens. Conditions were thus ideal for a taxonomic re-evaluation of the fossils (Hoover, 1976a).

Each identified brachiopod in the Arnold Collection



Text-figure 6.—Permian Ratio for brachiopods, calculated for well-known localities of marine Permian fossils, plotted against latitude. Point ① represents the Palmarito fauna as reported by Arnold (1966); point ② represents that collection as re-examined herein; point ③ represents the entire suite of Palmarito Formation brachiopods available for this study. Data were derived from Stehli, 1970; Samtleben, 1971; Stehli, *pers. comm.*, 1973; this study.

was re-examined and identified in the light of knowledge gained through study of my own collections. Considerable generic reassignment resulted (see Table 4) and a second, revised value for the Permian Ratio of the fauna was calculated, and plotted as point 2 of Text-figure 6.

The classification used throughout this study is, at the family level, very close to that of Cooper and Grant (1972, 1974, 1975, 1976a, 1976b, 1977). In order that the Permian Ratio values calculated for the entire fauna might be comparable with those previously calculated, the taxa presented in this study were reassigned at the family level, to accord with the *Treatise* classification (Table 7). This third value for the Permian Ratio for Palmarito brachiopods is plotted as point 3 in Text-figure 6. One of the goals of this study was more rigorous definition of the inflection point of the curve in the plot of Permian Ratio *vs.* Latitude (see Text-fig. 6). The addition of two or three points to the curve cannot accomplish that. This portion of the study shows however, that the Permian Ratio of such tropical faunas as the Palmarito can be enhanced by more comprehensive collecting, and that the brachiopod fauna, in terms of familial diversity, is Tethyan in character, and not temperate as had been suspected (Newell, *pers. comm.*, 1972).

I also wanted to determine the source of the dramatic increase in the apparent taxonomic diversity of the Palmarito brachiopod fauna shown in Text-figure 6. Table 8 shows Permian Ratio values for both Dr. Muir-Wood's and my own analyses of Arnold's collections, as well as for individual collecting localities in the present study. It is striking that, of the twelve non- Cosmopolitan Dominant families in the entire fauna, eight are represented in a single locality (locality 6) and that only three of these appear elsewhere in the formation as presently known. Without the *chance* discovery of this block (which probably would not have been sampled in a normal stratigraphic study, as it is patently out of place and not located within a measurable stratigraphic section), the Permian Ratio value for the entire fauna would have been drastically reduced (see Table 8).

Table 7.—Familial affinities of Palmarito Formation brachiopod genera. Both the familial assignment used in the Systematic Paleontology section of this study and that used in the *Treatise* (Williams *et al.*, 1965) are given. [ ] surround the probable family assignment of genera described since 1965. Inarticulate brachiopods (*e.g.*, *Petrocrania*) are not used in calculation of Permian Ratio or Sampling Index.

Genus	Family in this study	Family in *Treatise*
Petrocrania	Craniidae	Craniidae
Ascosarina?	Schizophoriidae	Enteletidae
Derbyia	Derbyiidae	Orthotetidae
Meekella	Meekellidae	Meekellidae
Dyoros	Rugosochonetidae	Chonetidae
Stauromata	Rugosochonetidae	[Chonetidae]
Chonetinetes	Rugosochonetidae	[Chonetidae]
Xenosteges	Aulostegidae	Aulostegidae
Cooperina	Cooperinidae	[Strophalosiidae]
Ramavectus?	Rhamnariidae	Buxtoniidae
Echinaurus	Marginiferidae	Marginiferidae
Echinoconchidae	Echinoconchidae	Echinoconchidae
Anemonaria	Paucispiniferidae	[Linoproductidae]
Paucispinifera?	Paucispiniferidae	Linoproductidae
Holotricharina	Linoproductidae	[Overtoniidae]
Kutorginella	Retariidae	Marginiferidae
Peniculauris	Dictyoclostidae	Dictyoclostidae
Rugatia	Dictyoclostidae	Dictyoclostidae
Spinifrons	Dictyoclostidae	Dictyoclostidae
Collemataria	Lyttoniidae	[Lyttoniidae]
Pontisia	Pontisiidae	[Wellerellidae]
Hustedia	Retziidae	Retziidae
Cleiothyridina	Athyrididae	Athyrididae
Composita	Athyrididae	Athyrididae
Costicrura	Ambocoeliidae	[Ambocoeliidae]
Neophricadothyris	Elythidae	Elythidae
Neospirifer	Spiriferidae	Spiriferidae
Spiriferellina	Reticulariinidae	Spiriferinidae
Aneuthelasma	Dielasmatidae	[Dielasmatidae]
Oligothyrina?	Pseudodielasmatidae	Labaiidae
Anaptychius	Cryptonellidae	[Mutationellidae]
Texarina?	Cryptonellidae	[Cryptonellidae]

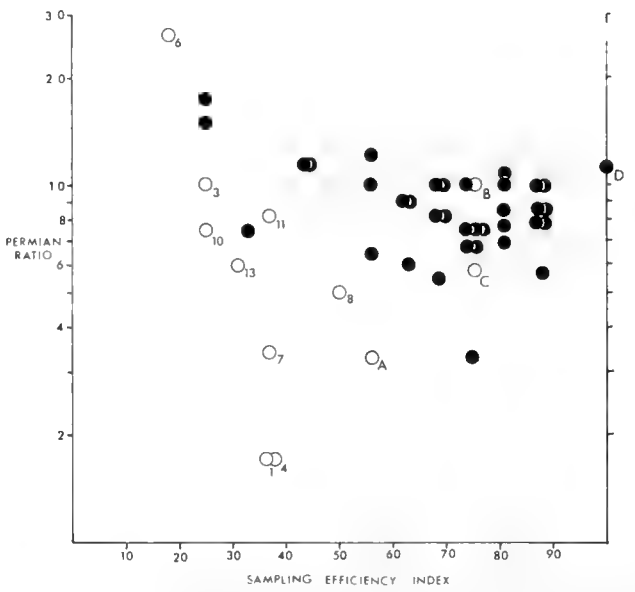
SAMPLING EFFICIENCY INDEX

Stehli (1970, p. 3327) and Stehli and Grant (1971, p. 504) presented as a rough measure of the efficiency of sampling (for Permian articulate brachiopods) the ratio of the number of Cosmopolitan Dominant families found, to the number expected (16). It is instructive to look at the sampling efficiency index (SEI) in combination with the Permian Ratio (PR), as they are closely related (see Text-fig. 7). This figure shows the poor sampling efficiency in the Palmarito relative to the intensively investigated (roughly age-equivalent) Road Canyon Formation of the West Texas region.

A rough estimate of the advantage of silicification over calcareous permineralization as a mode of preservation can be gained by looking at the SEI of otherwise similarly constituted assemblages in the Pal-

Table 8.—Permian Ratio and Sampling Efficiency Index of Palmarito Formation articulate brachiopod assemblages. Families are assigned according to the *Treatise* classification (Williams *et al.*, 1965; see Table 7).

Assemblages	Total Number of Families	Cosmopolitan Dominant Families	Permian Ratio	Sampling Efficiency Index
Arnold Collection (as identified by Muir-Wood)	14	10	0.40	0.63
Arnold Collection (as identified by Hoover)	12	9	0.33	0.56
locality 1	7	6	0.17	0.37
locality 2	1	1	0.00	0.06
locality 3	8	4	1.00	0.25
locality 4	7	6	0.17	0.37
locality 5	1	1	0.00	0.06
locality 6	11	3	2.67	0.18
locality 7	8	6	0.34	0.37
locality 8	12	8	0.50	0.50
locality 10	7	4	0.75	0.25
locality 11	11	6	0.83	0.37
locality 13	8	5	0.60	0.31
Entire Fauna	24	12	1.00	0.75
Entire Fauna (less loc. 6)	19	12	0.58	0.75



Text-figure 7.—Permian Ratio and Sampling Efficiency Index for nine Palmarito Formation (Venezuela) and 35 Road Canyon Formation (West Texas) articulate brachiopod assemblages. Open circles = Palmarito Formation assemblages (numbered); solid circles = Road Canyon Formation assemblages; A = Arnold collection as re-examined herein; B = entire Palmarito Formation collection; C = Palmarito Formation assemblages, except assemblage 6; D = 35 Road Canyon Formation assemblages.

marito (Table 8; see "Biostratigraphic Correlation"). While it should be noted that no one locality is very efficiently sampled, the maximum SEI attained by silicified assemblages, such as that at locality 8 (=0.50) is not equalled by the non-silicified assemblages (locs. 1 and 7 = 0.37), even though these were as diligently sampled (according to a subjective estimate of effort expended). For faunal sampling, the collection of large amounts of silicified faunas wherever found within a unit is superior (in terms of the SEI) to the strictly stratigraphic attack, where samples of all exposed rocks are taken in a single or several sections, but along as continuous exposures as possible. In addition to making collections of that sort, those interested in the biostratigraphic implications of a fauna might do well to make collections of promising float blocks. It has been demonstrated that the SEI obtained by a combination of these methods is superior to that obtained by using a single one (my collection total SEI = 0.75; Arnold's collection total SEI [re-examined] = 0.56).

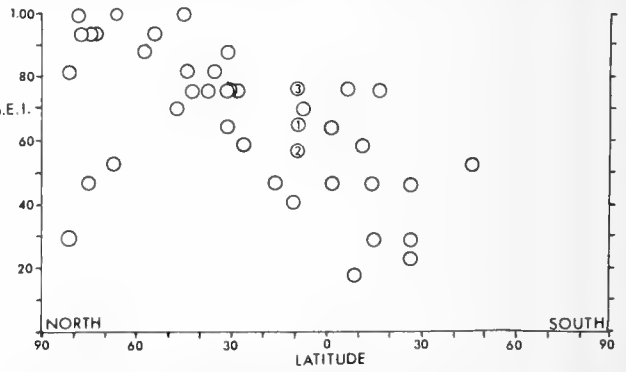
Four Cosmopolitan Dominant Permian articulate brachiopod families were not identified in any of the Palmarito material available for study: the Schuchertellidae, Stenoscismatidae, Rhynchoporidae and Brachythyrididae. *Rhynchopora,* the only Permian rhynchoporid genus, was reported by Pierce *et al.* (1961) in the Carache area of the state of Trujillo, Venezuela, but since neither specimens, illustrations nor descriptions were given, this occurrence cannot be considered valid data for this study. The inherent unreliability of even generic identifications in faunal lists is emphasized not only by my re-examination of the Arnold Collection (Hoover, 1976a), but also the fact that, to most investigators, such a list is relatively useless unless accompanied by the name of the person responsible for it.

A few of the specimens from locality 6 that were assigned to "Rhynchonellacea, family uncertain" bore some resemblance to stenoscismatids. There were, however, no preserved interiors, or vestiges of the anterolateral stolidium characteristic of the family, so that not even tentative assignment to that group could be made. The majority of the inferred substrates encountered in the Palmarito (soft-bottom) are interpreted as suitable for the establishment of populations of stenoscismatids, so that some other factor (resulting in non-occurrence, non-preservation or non-collection) must be responsible for their absence.

Although several small apparent juvenile orthotetaceans were found at localities 3, 4 and 6, only one appeared to exhibit the recurved erismata of the Schuchertellidae. The small size and coarse silicification of this single specimen, however, made even tentative assignment to that family unjustified.

Several Tethyan brachythyridid genera are known in the Western Hemisphere, but their occurrence is almost entirely limited to North America. The family is known from other continents, however, and is widespread in the Boreal and Austral regions. Four genera are known in the West Texas region: *Eliva, Elivina, Eridmatus* and *Spiriferella.* Of these only *Spiriferella* occurs in rocks of an age thought to be equivalent to the Palmarito strata (Roadian) and there it occurs in only two of 34 localities surveyed. Perhaps, as Grant (1976) has suggested, connections with Boreal populations of *Spiriferella* were closed at this time, preventing easy access to the south. In Mexico the genus is known from the Monos Formation, thought to be a time-equivalent of the Word Formation of West Texas (Cooper *et al.,* 1953). It has not been recovered further south in the Americas, and it may be that it is not truly cosmopolitan in its distribution.

There are several possible reasons for the apparent non-occurrence of certain Cosmopolitan Dominant families. Stehli and Grant (1971, p. 505, text-fig. 3; reproduced here in Text-fig. 8) note that the SEI decreases southward across latitude, beginning this decline at about 30° North latitude. They suggest that this phenomenon may be due to "deeper tropical weathering, less intensive study and the increase of small, difficult to collect forms in the Tethyan assemblage." The first of these suggested reasons at least is not applicable to the Palmarito. Locality 8 consists of rocks so deeply weathered that although the limestone



Text-figure 8.—Sampling Efficiency Index for Permian articulate brachiopod assemblages, calculated for well-known collecting localities, plotted against latitude. Point ① represents the Palmarito Formation brachiopod assemblage as reported by Arnold (1966); point ② represents that collection as re-evaluated herein; point ③ represents the entire suite of Palmarito brachiopods available for study. Data from Stehli and Grant, 1971; this study.

depositional fabric and texture remain intact, they contain no soluble carbonate whatsoever. Yet this locality provided the highest SEI of any in the formation, and was represented by the greatest number of brachiopod families. Some tiny forms may have been lost, but in the silty limestones so common in the marine Permian of Central and South America, extensive natural leaching provides good opportunity for the formation of external and internal molds. At locality 8, some of the calcite in the specimens had been silicified, so that preservation is in the form of external and internal molds and silica replacements.

Less intensive study is a real factor: many southern hemisphere exposures are not only relatively poorly exposed and remote, but are far from major study centers. The high SEI's reported to the north of 30° North probably reflect two things. The Boreal Permian brachipod fauna consists to a great extent of large, easily recovered, commonly preserved, massive forms, due to the proclivity (suggested by Stehli and Grant, 1971, p. 507) for such forms to be characterized by late maturity, slow growth and individual longevity, so that faunas composed largely of Cosmopolitan Dominant families could easily be fully sampled (16 out of 16). Tethyan faunas from the Boreal/Tethyan boundary down to about 30° North lie within the area where the great majority of persons interested in the study of such forms live, and (with the exception of Australia and New Zealand), the combination of good exposures and interested investigators is not present south of that latitude. Less intensive study may also be a result of the different modes of sampling, discussed above, which can significantly alter both the Permian Ratio and Sampling Efficiency Index.

In contrast to Boreal or Austral ones, Tethyan assemblages certainly do include smaller, more delicate forms. Collection of silicified assemblages, however, should (as in the Palmarito) allow recovery and recognition of the tiniest, most delicate brachiopods (*e.g., Costicrura minuta,* loc. 6; see Pl. 8, figs. 41, 44).

There are other possibilities. Using the Palmarito as an example, we may compare assemblages from present-day tropical regions to those from temperate regions of the Western Hemisphere (West Texas). Against the nearly total exposure, moderately steeply-dipping beds and relatively high relief, and relatively easy access and short travel distance from research centers of the West Texas exposures, contrast the structurally complicated, vegetatively overgrown, distant, relatively less accessible beds of equivalent age in Venezuela. It has been suggested (McCall, *pers. comm.,* 1975) that the decline may be due to the equatorward decrease in eurytopic forms. Bulk sampling and the use of the family as the taxonomic base should reduce a large part of such bias.

Warme (1969) has remarked that "regardless of the geometry of spacing [of samples] it is unlikely that any sample of reasonable size will include all individual species living in a given [tropical] habitat." This of course becomes less applicable at higher taxonomic levels until at the family level one should be able to sample all families present within a more modest sample size. But what is this optimum sample size? Grant (1971) has shown that the number of species of silicified brachiopods identified in the Road Canyon Formation of West Texas increased directly in proportion to the amount of rock collected. He unfortunately gives no data as to how much was collected from each locality, but has assured me (Grant, *pers. comm.,* 1975) that the average exceeded the 50–100 kg range of samples from the Palmarito. In the Palmarito it was often impossible to sample even this much at a single locality, due to the logistics of removing and transporting that much material.

Cooper (*pers. comm.,* 1975) has remarked that individual bioherms in the West Texas Permian tend to have highly individual fossil faunas at the species level, thus tending to support Warme's contentions in the fossil record. In the Palmarito, only locality 6 could be considered as incipiently biohermal, as contrasted to the commonness of these structures in the Road Canyon Formation, its closest West Texas correlative (see "Biostratigraphic Correlation"). I suspect many more as yet uncollected such deposits may exist within the Palmarito exposures. The chance, however, of collecting all such deposits is smaller than that of collecting all types of biostromes or incipient bioherms in a more accessible, better exposed situation. Thus the second of Stehli and Grant's suggested reasons for lowered sampling efficiency in the southern hemisphere is probably largely responsible for that decline. Although such a decline is reversible, through intensive work and a more faunally-oriented sampling program (see Text-fig. 8, points 1, 2 & 3), it is questionable whether that reversal would ever become financially or physically feasible.

INTRODUCTION TO SYSTEMATIC PALEONTOLOGY

PHILOSOPHICAL CONSIDERATIONS

The concept of the species, the basic unit of taxonomy, has been succinctly defined, for living organisms, in terms of reproductive capability. In the fossil

record, however, our frequent inability to distinguish individual time planes confidently in the rocks often means that rather than dealing with contemporaneous distinct species, we are concerned with variably-sized segments of evolving lineages. Since evolution, whether it moves gradually or in a saltatory fashion, is a process in which both organisms and their interrelationships change, the species concept becomes increasingly abstract as our power of time-resolution decreases. The most common unit of sampling in the fossil record is the formation. Shaw (1964), among many others, has demonstrated that formation boundaries may be diachronous, and that the distribution of fossils within such a unit is not necessarily isochronous. Inherent in the common belief that in paleontology we are indeed dealing with organisms divisible into species analogous to biological species, is the assumption that the evolutionary change taking place in a lithic unit or units is small: our gauge of this change is, and must be morphologically based.

The paleontologist today would normally concede that he (she) tries in some measure to think of the fossils he studies as once-living organisms. This becomes a basic problem in classification: should one attempt somehow to approximate the range of variation implied in the biological species concept, or should one describe and differentiate morphological variants? In the case of the Permian brachiopods one might think there would be little choice. A vast majority of these organisms represent stocks that have no modern representatives. Soft parts are rarely preserved and their form is rarely indicated. Yet the axiom of the working paleontologist to "think of fossils as once-living organisms" leads us to infer soft parts to clothe these partial skeletons.

One possible solution to this problem would be to give strictly morphologically-based taxa special sorts of names. This has been done in the study of miospores and ichnofossils, but, although desirable, it seems an impractical solution to the problem faced by the invertebrate paleontologist.

Brachiopods exhibit homeomorphy to a great degree, *i.e.*, a Mississippian and a Permian productid brachiopod, or two geographically distant Permian brachiopods may exhibit strikingly similar external or internal characters. The inter-relationships of paleontology and biostratigraphic and evolutionary studies, however, may require that such forms be given distinct names that have more temporal and spatial than morphological foundations (for a fuller discussion of this problem, see [among others] Bell, 1950).

In sum, a morphological classification would be simpler in terms of describing objects, if no further use was to be made of them. We cannot do this because we do envision inferential uses of fossils. We thus make the apparently valid assumption that forms sufficiently separated in time cannot represent close genetic relatives (because this might suggest retrograde evolution within a lineage, and we assume that exact retrograde evolution is highly unlikely) and that the conspecificity of geographically distant forms is suspect. A practical justification of this assumption is biostratigraphy. Genera or species with large gaps in their temporal distributions are biostratigraphically troublesome.

At any time, only a limited number of brachiopod morphologies can exist in the niches available. Temporal homeomorphs, while a systematic and biostratigraphic problem, can be useful in making paleoecological inferences, as the they may imply adaptation of (assumed) different stocks to similar environmental conditions.

Morphospecies, at least species of Permian brachiopods described here, have different ranges of variation. In the "Comparison" sections following, each species is carefully differentiated from others in its genus, to justify its claim of morphologic uniqueness. A more important reason for this intellectual exercise is to show how closely one form may be morphologically (and, by inference, genetically) related to another.

Species names are simply handles for convenient discussion of time segments of evolving lineages. More often than not, real evolutionary significance lies with groups of several, rather than single species. As an entire lineage becomes better understood, specific names as such become less significant or necessary.

Format

In general the taxonomic hierarchy above the family level is simply stated, and generally follows the classification scheme of Cooper and Grant (1972, 1974, 1975, 1976a, 1976b, 1977). Simple diagnoses of families and subfamilies are considered sufficient here. Detailed generic descriptions are included only for new taxa. Individual species are always considered in detail.

Terminology

The jargon words peculiar to brachiopod systematics, as for any other descriptive art, are numerous, and hopefully more precise than the word-combina-

tions they replace. Those used here follow Muir-Wood and Cooper (1960), the *Treatise* (Williams *et al.*, 1965) and the recent monographic study of the West Texas Permian brachiopods (Cooper and Grant, 1972, 1974, 1975, 1976a, 1976b, 1977).

Type Repositories

The initials of the type repositories cited in the following text are explained below:

USNM = National Museum of Natural History, Smithsonian Institution
Washington, D.C. 20560, U.S.A.

MMH = Ministerio de Minas e Hidrocarburos (*now* Ministerio de Energía)
Dirección de Geología
Caracas, Venezuela

NMB = Natürhistorisches Museum Basel
Basel, Switzerland

Measurements

The measurements of the brachiopods presented in the following section are standard except where otherwise defined, and follow the usage of Muir-Wood and Cooper (1960, pp. 18–20). In the tables of measurements, various subscripts have been employed as qualifications:

b = *broken:* Used where the shell is broken at one or both extremities of a linear measurement. Unless further qualified, measurements so marked should not be taken as typical.

c = *crushed:* Used where complex breaks and (or) obvious distortions of the shell, not explainable in terms of the organism's life processes, have occurred. Unless further qualified, measurements so marked should be considered atypical.

e = *estimated:* Used when the author has estimated the measurement, based on reasonable restoration of breakage, crushing or other distortion.

h = *half-measurement:* Used in the measurement of bilaterally symmetrical features (*e.g.*, hinge width of a productid) when one extremity is damaged. The measurement made is one-half that given in the table.

BRACHIOPOD SYSTEMATIC PALEONTOLOGY

Phylum **BRACHIOPODA** Dumeril, 1806

Class **INARTICULATA** Huxley, 1869

Order **ACROTRETIDA** Kuhn, 1949

Suborder **CRANIIDINA** Waagen, 1885

Superfamily **CRANIACEA** Menke, 1828

Family **CRANIIDAE** Menke, 1828

Discussion.—The Craniidae are the only inarticulate brachiopods that are commonly recovered by the hydrochloric acid etching technique. Their original calcitic composition probably accounts for their silicification in common with the articulates.

Genus **PETROCRANIA** Raymond, 1911

Diagnosis.—

Attached, pedicle valve thin; brachial valve conical, ornament of concentric growth lines, in some simulating ornament of host; characterized by pair of sigmoidal dorsal *vascula lateralia*, secondary canals branching off laterally; posterior adductors larger than anterior, margin of valves not thickened. (Rowell, 1965, p. H290)

Type Species.—*Craniella meduanensis* Oehlert, 1888, p. 102.

Occurrence.—*Petrocrania* has been recovered from rocks ranging in age from Middle Ordovician through Permian in Europe, North America and Asia. It is uncommon in the Permian, but this is probably in part due to lack of both interest and recognition.

Comparison.—Among Permian Craniidae, *Petrocrania* differs from *Crania* Retzius (1781) and *Philhedra* Koken (1889) which bear ornament of radial costellae, *Lepidocrania* Cooper and Grant (1974), which bears strongly lamellose concentric ornament with rare spines, and *Acanthocrania* Williams (1943), which bears a roughly radial ornament of short spines, in its nearly smooth ornament of concentric growth lines.

Discussion.—The inarticulate brachiopods play a very small part in the total brachiopod fauna in the Upper Paleozoic. One reason they are overlooked is that their stratigraphic range is commonly great: as biostratigraphic indicators they are comparatively poor.

Petrocrania teretis Cooper and Grant
Plate 1, figures 1–6

Petrocrania teretis Cooper and Grant, 1974, p. 250, pl. 28, figs. 17–25.

Description.—

Small, smooth, variable cones with rounded sides and anterior; posterior side usually straight. Cones varying from nearly flat to high and misshapen, usually low; beak off center, from one-third to two-fifths of length from posterior margin. Posterior slope gentle; median region somewhat swollen and having steeper sides than the long anterior slope. Surface smooth except for slight irregularities inherited from host. Anterior adductor scars larger than posterior adductors which are marginal. (Cooper and Grant, 1974, p. 250)

Measurements (in mm).—

	Length	Width	Thickness
LOCALITY 6, BLOCK A:			
USNM 220974 (dorsal valve)	2.7_{be}	2.7	0.7
USNM 220975 (dorsal valve)	3.5	3.9	1.2
USNM 220976 (dorsal valve)	3.8	4.0	0.8
MMH-DG-501 (dorsal valve)	4.2	4.6	1.2
USNM 220977 (dorsal valve)	4.5	4.7	1.0
USNM 220978 (dorsal valve)	5.6	6.2	$0.3_{?c}$
LOCALITY 6, BLOCK C:			
USNM 220979 (articulated valves)	3.3	3.3	1.1
USNM 220980 (articulated valves)	4.3	4.5	1.6_{c}

Occurrence.—*Petrocrania teretis* Cooper and Grant occurs in the West Texas region where it was first described from the Cherry Canyon and Word Formations of Early Guadalupian age. In the Palmarito Formation it has been recovered in the assemblages at locality 6, blocks A and C, where it is rare. An Early Guadalupian age for these Palmarito assemblages is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Small, subcircular, depressed conical *Petrocrania.*

Types.—Figured Specimens: USNM 220975, USNM 220979; Measured Specimens: USNM 220974–220980, MMH-DG-501.

Comparison.—*P. teretis* may be distinguished from *P. diabloensis* Cooper and Grant (1974) and *P. exasperata* Cooper and Grant (1974) by its smaller size, and from *P. septifera* Cooper and Grant (1974) by its lack of a dorsal median septum. The *vascula lateralia,* said by Rowell (1965, p. H290) to characterize the genus, cannot be discerned in either Venezuelan or West Texas individuals referred to *P. teretis.*

Discussion.—In contrast to the long ranges and consequent stratigraphic uselessness of many of the inarticulate brachiopods, *P. teretis* appears to be easily recognized by its small size and smooth exterior, and is comparatively restricted in its time range. The specimens recovered from block C of locality 6 (USNM 220979, USNM 280980) consist of articulated valves. Although this is the first occurrence of a *Petrocrania* ventral valve in the Western Hemisphere, its significance is minor since the conjoined valves cannot readily be separated.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block A)	—	11	—	fine silicification
6 (block C)	2	—	—	fine silicification

Class **ARTICULATA** Huxley, 1869
Order **ORTHIDA** Schuchert and Cooper, 1932
Suborder **ORTHIDINA**
Schuchert and Cooper, 1932
Superfamily **ENTELETACEA** Waagen, 1884
Family **SCHIZOPHORIIDAE**
Schuchert and Levene, 1929

Genus **ACOSARINA** Cooper and Grant, 1969

Type Species.—*Acosarina dorsisulcata* Cooper and Grant, 1969, p. 2, pl. 5, figs. 19–23.

Diagnosis.—Small Schizophoriidae with rectimarginate to sulcate anterior commissure and low ventral median septum.

Occurrence.—*Acosarina* has been recovered in the West Texas region alone, in beds ranging in age from latest Pennsylvanian (Gaptank Fm.) to Guadalupian (Word Fm.). It is likely that its geographic range might further be extended, since it probably includes many forms previously described as *Rhipidomella* Oehlert (1890) or *Orthotichia* Hall and Clarke (1892).

Comparison.—*Acosarina* is assigned to the Enteletacea on the basis of its punctate shell, ornament of tubular costellae, and juxtaposition of ventral median septum and dental plates. Among Permian genera, its fairly wide hinge and fully developed palintropes in both valves distinguish it effectively from *Rhipidomella,* while its short dental plates and low, elongate ventral median septum differentiate it from *Orthotichia.* It is distinguished from *Schizophoria* King (1850) by the conservatism of internal structures in the ventral apex.

Acosarina? sp.
Plate 1, figures 7–9

Description.—Small, somewhat rostrate schizophoriid, having relatively wide, straight hingeline, rounded outline, and hollow tubular costellae. Ventral interarea high, with narrow delthyrium. Ventral interior having dorsally directed teeth, triangular in section, supported anteroventrally by short dental plates. Thin median septum arising at apex, widening and becoming higher anteriorly, terminating anterior to ends of dental plates.

Dorsal valve unknown.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height
LOCALITY 7				
USNM 220981	11.0_{b}	8.0_{h}	10.3_{h}	4.8_{e}

Occurrence.—The single partial ventral valve here tentatively assigned to *Acosarina* was recovered from locality 7. It was first recognized on the basis of its tubular costellae. Its more diagnostic interior details were later mechanically prepared.

Diagnosis.—Schizophoriid ventral valve with fairly wide hinge, tubular costellae, short dental plates and long, low median septum.

Types.—Figured and Measured Specimen: USNM 220981.

Comparison.—(see generic discussion) The Palmarito specimen is only provisionally assigned to the genus because it is unknown whether the relative strength of dental plates and median septum in the ventral valve were altered during preparation, and because only a single partial ventral valve was found.

Discussion.—This specimen cannot unequivocally be assigned to *Acosarina*: indeed, on strictly morphological grounds, it could be ascribed to *Orthotichia*. The known stratigraphic range of *Orthotichia* in West Texas extends only through the Bone Spring Formation (Leonardian), while that of *Acosarina* in the same area extends through the Lower Guadalupian Word Formation. The majority of the fauna preserved at locality 7 is most similar to uppermost Leonardian (Roadian) faunas in the West Texas area (see Table 3). In view of the great overall similarity between the Texas and Venezuelan Permian faunas, the differing ranges of the two genera there, and the present similarity of ventral valve internal arrangements of the Palmarito specimen to *Acosarina,* it is tentatively assigned to that genus.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
7	—	—	1	calcite permineralization

Order **STROPHOMENIDA** Öpik, 1934

Suborder **STROPHOMENIDINA** Öpik, 1934

Superfamily **DERBYIACEA** Stehli, 1954

Family **DERBYIIDAE** Stehli, 1954

Subfamily **DERBYIINAE** Stehli, 1954

Genus **DERBYIA** Waagen, 1884

Type Species.—*Derbyia regularis* Waagen, 1884, p. 594, pl. 53, figs. 1, 2, 4. Genolectotype by Hall and Clarke (1892).

Diagnosis.—Derbyiinae having prominent single ventral median septum directly joined near sub-pseudodeltidial apex, without dental plates or spondylium.

Occurrence.—*Derbyia* has been recovered from most of the world's continents, and may be said to have a cosmopolitan distribution in the Early Permian, although its specific diversity is quite low in Boreal regions. The genus is known from Mississippian through Permian rocks, though it reaches its peak of specific diversity in the Late Pennsylvanian and Permian.

Comparison.—The character of the ventral median septum readily distinguishes *Derbyia* from other Permian genera of the Derbyiinae. In *Licharewiella* Sokolskaya (1960), the ventral median septum is continuous anteriorly with a high transverse ridge; in *Nothopindax* Cooper and Grant (1974), the septum does not reach the valve floor. Outgrowths of the dental ridges onto the median septum of *Derbyia* may produce a shallow secondary "spondylium," which should not be confused with the primary spondylium of the Orthotetidae.

Discussion.—A complete and exhaustive discussion of the history and relationships of the genus *Derbyia* is presented elsewhere (Cooper and Grant, 1974, p. 289ff.), and it would be pointless to enlarge greatly upon it here. There are, however, certain asepcts of species assignment within the genus that must be dealt with.

Presence or absence of secondary plications, which has been used even in supraspecific distinctions [*e.g.*, *Derbyia* (*Plicatoderbyia*) Thomas (1937)], appears in itself to have no taxonomic significance even at the specific level (Cooper and Grant, 1974; Cooper, 1975), such features being present in several otherwise well-differentiated species of *Derbyia*. The outline and relative dimensions (shape) are important taxonomic features at the species level, although many species exhibit considerable variation around a norm. Certain species [*e.g.*, *Derbyia laqueata* Cooper and Grant (1974)] are defined as having rather wide ranges of variation in shape. Perhaps of more widespread usage in specific differentiation is primary surface ornament.

Ornamentation in *Derbyia* consists chiefly of costellae of various sizes and cross-sectional shapes. A misleading specific character is the density of costellation, which, as measured, is a gauge of *both* the size and the density of packing of the costellae. An additional problem is that this feature is commonly measured in terms of number of costellae in a five mm distance. Although the distance from the beak at which the measurement is taken is commonly stated

as well, the number of costellae reported can vary considerably depending on the orientation of the line.

Interior details are quite variable in many Orthotetidina, yet may also be considered in specific diagnoses. This practice is only reliable when a large suite of conspecific specimens is available for study. It follows that reliable specific identifications within the genus can only be made when suitably large collections are available, unless the taxon is externally quite distinctive (*e.g., Derbyia auriplexa,* n. sp.).

Derbyia auriplexa new species
Plate 1, figures 30–36

Etymology of Name.—L. *auri* = ear; L. *plexus* = braided.

Description.—Medium-sized for genus, thin-walled, unequally biconvex shell; dorsal valve more convex than ventral. Extremely auriculate, widest at hinge. Lateral margins constricted anterior to ears, diverging anteriorly to about midvalve; anterior commissure rectimarginate in dorsal or ventral aspect. Definite dorsal sulcus, arising just anterior to umbo, continuing to anterior margin, commonly interrupted by humps or dimples. Ornament of fine costellae (17–18 in five mm at 10 mm distance from dorsal umbo) increasing anteriorly by intercalation; costellae acute in section, anteriorly sinuous. Concentric growth lines generally absent, but strongly overlapping concentric growth lamellae sporadically developed, producing step-like breaks in surface. Surface secondarily "braided," with alternating humps and dimples. Costellae may arise, die out, split or coalesce on dimples or hollows, strengthening "braided" effect.

Ventral valve low, planar to rounded triangular in lateral aspect, irregularly rounded in anterior aspect; greatest height about one-fourth shell length anterior of beak. Interarea apsacline, dorsoventrally striate, generally low, triangular, but commonly produced ventrally in beak area; pseudodeltidium long, narrow, triangular in outline, rounded to flat-topped in dorsal aspect, having smooth crest without median longitudinal groove.

Dorsal valve convex in lateral aspect, convex to bilobate in anterior aspect. Umbo low, rounded, produced slightly posterior to hingeline.

Ventral interior having strong, anteriorly directed hinge teeth, triangular in cross-section, supported posteriorly by anteriorly divergent dental ridges. Low broad median swelling on underside of pseudodeltidium, dividing secondary spondylium into two parts. Long, thin, high median septum, scimitar-shaped in lateral aspect, having high point at about midlength, arising in delthyrial apex at junction of sub-pseudodeltidial median ridge and dental ridges, extending anteriorly about one-third to one-half valve length. Muscle scars large, ovate, smooth to striate, without callus rims. Interior otherwise smooth, but reflecting gross exterior ornament of dimples and humps.

Dorsal interior having large cardinal process supported by long, thin erismata that bend slightly laterad near dorsal ends. Low anteroventrally cuspate dentifers crossing entire outer faces of erismata; thin brachiophores, square in lateral aspect, extending a few mm anteriorly from erismata, just dorsal of dentifers. Myophore bilobate, deeply cleft mesially, each lobe having posterior median slit, internally crenulate to denticulate distally. Chilidial plates low, disjunct, separated by deep anteroposterior groove. Dorsal interarea very low, having short swellings, which may function as fulcral plates, just laterad of chilidial plates. Low, distinct angular myophragm, flanked by ovate, striate to flabellate muscle scars, arising below cardinal process, continuing anteriorly about one-fourth shell length.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height or Thickness	Surface Length	Material
LOCALITY 13						
USNM 220982 (holotype)	27.0_c	41.6_{hc}	31.4_h	15.5	—	(articulated valves)
USNM 220983	34.5	60.0_h	41.0_c	14.0	50.0	(dorsal valve)
USNM 220984	34.6_h	64.0_h	37.6_h	9.0_c	—	(ventral valve)
USNM 220985	38.8	63.0_c	38.6	19.0	57.0	(dorsal valve)
USNM 220985	45.0_c	60.0_h	47.0_h	12.7	—	(ventral valve)

Occurrence.—*D. auriplexa* was recovered in good condition only from locality 13. Several partial ventral interareas and shell fragments with the characteristic bumpy ornament were recovered from locality 8. A single dorsal valve was recovered from locality 4. Localities 8 and 13 are poorly defined stratigraphically but locality 4 is well-defined as within the Upper Limestone Member of the Palmarito Formation.

Diagnosis.—*Derbyia* of moderate size with strongly braided, bumpy ornament and well-defined exaggerated ears.

Types.—Holotype: USNM 220982; Figured Specimens: USNM 220982, USNM 220983, USNM 220984; Measured Specimens: USNM 220982–220985.

Comparison.—The only form closely related to *D. auriplexa* is *D. cincinnata* Cooper and Grant (1974), from the Cathedral Mountain and Road Canyon Formations (Leonardian) of West Texas. *D. cincinnata* is in general not auriculate, and none of the specimens of that species in the National collections shows the uniformly extreme auriculation of the Venezuelan form. Internal features of the two species are quite similar, though they vary in a manner typical of the genus. They share the characteristic external ornament.

Discussion.—A Leonardian-equivalent age for the portion of the Upper Palmarito Formation that contains *D. auriplexa* is not inconsistent with other lines of faunal evidence.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
4	1	1	—	fine silicification
8	—	—	1	fine silicification
13	1	6	4	fine silicification

Derbyia cf. **D. complicata** Cooper and Grant
Plate 1, figures 10–16

cf. *Derbyia complicata* Cooper and Grant, 1974, p. 296, pl. 81, figs. 4–38; pl. 88, figs. 1–6.

Description.—Medium-sized, small- to medium-sized for genus, planoconvex to slightly biconvex, quadrate, commonly auriculate shell having mesially indented anterior margin and distinct dorsal sulcus. Hingeline straight, commonly widest part of shell. Surface ornament of alternating costellae and costae, commonly one costa to every four or five costellae. Costae best developed on visceral lobes of both valves, absent nearer hinge and within dorsal sulcus. Commonly seven costae on each side of dorsal sulcus and a like number on ventral valve, a single one mesial there. Costae and costellae crenulate, produced distally, forming crenulate and irregularly serrate margins. Costae of markedly uneven strength.

Ventral valve planar to weakly convex, with slight to pronounced auriculation. Greatest height at or just anterior to beak. Interarea apsacline, triangular, flat to slightly concave, smooth to faintly dorsoventrally striate, having triangular delthyrium apically filled by distinct small pseudodeltidium. Pseudodeltidium smooth, lacking median groove or prominence.

Dorsal valve moderately convex, broadly bilobate, greatest height at about midvalve.

Ventral interior having strong, anteriorly directed hinge teeth, triangular in section, supported posteriorly by distinct rounded dental ridges. Low, slender median septum arising anterior to delthyrial apex and extending to about one-fourth shell length. Muscle scars indistinct, smooth, flanking median septum. Surface smooth, but having deep radial furrows mirroring external costae, extending from distal margins of muscle attachment area to commissure. Anterolateral margins somewhat serrate.

Dorsal interior having small cardinal process supported by anteriorly divergent erismata; erismata curving slightly posteriorly at distal ends. Dentifers low, subtle, produced anteroventrally as relatively large thin brachiophores. Myophore bilobate, cleft mesially, with short, internally crenulate slits on posterior faces of lobes, producing effective quadrilobation; posteriorly U-shaped in section. Chilidial plates comparatively large, triangular, overhanging low, narrow dorsal interarea posteriorly, and bases of myophoral slits anteriorly. Short median keel lying between chilidial plates in median groove of cardinal process. Surface generally smooth; many radial striae reflecting exterior costellae. Muscle scars indistinct, smooth, flanking low median rise that is an internal expression of exterior sulcus.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height or Thickness	Material
LOCALITY 4					
USNM 220986	12.8	19.0_b	17.1	4.3	(dorsal valve)
LOCALITY 8					
USNM 220987	15.3_e	26.6_h	18.9_h	4.5_e	(ventral valve)
USNM 220988	21.5	30.2_b	30.3	10.7	(articulated valves)

Occurrence.—D. complicata has been recovered only from the Cathedral Mountain and Road Canyon Formations in the West Texas region. In the Palmarito Formation *D.* cf. *D. complicata* is rare: a single articulated specimen and several partial ventral valves were taken from locality 8, while a single partial dorsal valve was found at locality 4. The Leonardian age indicated by similarity of the two forms is not inconsistent with other biostratigraphic indicators for those two Palmarito localities.

Diagnosis.—Small auriculate *Derbyia* with strong and unequal crenulate costellae and radial plications.

Types.—Figured and Measured Specimens: USNM 220986–220988.

Comparison.—D. cf. *D. complicata* may be recognized best by its auriculate hinge, weakly to strongly crenulate, uneven radial ornament, and well-developed chilidial plates. It is clearly differentiable from other Palmarito forms of the genus: *Derbyia auriplexa* n. sp. has clearly non-crenulate radial ornament with superposed "braiding" of humps and dimples; *D. deltauriculata* n. sp. has more regular, non-crenulate costellae; *Derbyia* cf. *D. filosa* Cooper and Grant (1974) is much larger. In the West Texas collections from which *D. complicata* was first described, it seems most closely related to *D. laqueata* Cooper and Grant (1974), *D. texta* Cooper and Grant (1974) and *D. crenulata* Girty (1909). The first is admitted by its authors to be "one of the most variable and least unified of the Glass Mountains species of *Derbyia*" (Cooper and Grant, 1974, p. 306). Some specimens in the Glass Mountains share the development of primary and secondary radial ornament, but none exhibit crenulation of that ornament. *D. texta* is commonly smaller and more compact that *D. complicata,* and its radial ornament tends to be somewhat coarser, and complicated by its more obvious concentric ornament. *D. crenulata* often bears two sizes of radial ornament, but the costae are all of roughly the same strength, in contrast to their uneven expression in *D. complicata.*

Discussion.—The form of the pseudodeltidium of the Venezuelan form is questionable; it is only preserved as a small triangular plate in the apex of one of the Palmarito specimens. It may well have originally been larger and more prominent.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
4	—	1	—	fine silicification
8	1	—	3	fine silicification

Derbyia deltauriculata new species
Plate 1, figures 17–28

Etymology of Name.—Gr. *delta* = the Greek letter Δ = an equilateral triangle; L. *auriculatus* = auriculate; eared.

Description.—Small to medium sized for genus, thin-walled planoconvex to unequally biconvex shells having straight hingeline and broad dorsal sulcus. Commonly but not invariably widest at hinge; outline semicircular, quadrate, cardioid or irregular commonly modified by attachment. Shell commonly auriculate; ears small, equilaterally triangular. Surface finely costellate (13 costellae in 5 mm at 20 mm from dorsal beak, increasing to 18–19 in 5 mm in zones of intercalation), costellae commonly alternate in size, increasing anteriorly by intercalation in no systematic pattern. Costellae distinct, having straight sides and rounded crests, of various sizes along any growth line. Concentric ornament commonly limited to overlapping lamellae, best expressed on distal portions of valve.

Ventral valve planar to slightly convex, having apical cicatrix of attachment. Greatest height at or just anterior to beak. Beak pointed, produced slightly posterior to hinge. Interarea flat to slightly concave, smooth, with surficially undifferentiated apparent perideltidium and narrow rounded pseudodeltidium, latter bearing consistent distinct median groove; dorsoposterior surface of pseudodeltidium thus appearing bilobate. Anterior margin of pseudodeltidium straight or

concave, with or without median salient corresponding to supra-pseudodeltidial median groove.

Dorsal valve moderately to strongly convex. Anterior commissure straight or slightly indented; greatest height at about midvalve.

Ventral interior having strong anteriorly directed hinge teeth, triangular in section. Dental ridges, narrower than teeth, running from distal edge of tooth base to delthyrial apex. Subpseudodeltidial median ridge present, commonly produced anteriorly as salient, beyond anterodorsal pseudodeltidial margin. Median septum long, slender, scimitar-like, highest point commonly opposite anterior ends of hinge teeth. Muscle scars flabellate, anteriorly raised on slight pads, commonly with lobate rims, flanking median septum to its anterior termination. Remainder of interior surface smooth, except crenulate or radially grooved at anterolateral margins.

Dorsal interior having relatively small cardinal process supported by short, fragile, laterad-curving erismata. Dentifers short, low. Chilidial plates disjunct, robust, reflexed over very low dorsal interarea. Lateral extensions of chilidial plates acting as fulcral plates. Cardinal process myophore bilobate, having short median cleft, each lobe bearing slit on posterior face. Myophore posteroventrally U-shaped in section, effectively quadrilobate. Low, broad, indistinct median rise, separating indistinct smooth muscle scars, reflecting exterior sulcus. Anterior and lateral margins radially grooved to crenulate. Remainder of interior surface smooth to faintly striate, striae mirroring external ornament.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height	Material
LOCALITY 10					
USNM 220989	—	20.2	19.2	4.0	(ventral valve)
USNM 220990	14.1	28.6_h	20.0	5.1	(dorsal valve)
USNM 220991	15.2	25.0_h	22.0	6.4	(dorsal valve)
USNM 220992	16.5	30.8_h	27.2_h	4.5	(ventral valve)
USNM 220993 (holotype)	20.9	35.3	27.1	4.8	(ventral valve)

Occurrence.—This species was recovered only from locality 10, where it is abundant.

Diagnosis.—Medium-sized auriculate *Derbyia* with transverse outline, regular alternating straight costellae and distinct broad dorsal sulcus.

Types.—Holotype: USNM 220993; Figured Specimens: USNM 220991, USNM 220993–220996; Measured Specimens: USNM 220989–220993.

Comparison.—*Derbyia deltauriculata* n. sp. is easily distinguished from the other Palmarito species of that genus: from *D.* cf. *D. complicata* Cooper and Grant (1974) by its smooth costellae; from *D. auriplexa* n. sp. by its evenly costellate surface; from *D.* cf. *D. filosa* Cooper and Grant (1974) by its small size. The common Bolivian Permian species, *D. buchi* (d'Orbigny, 1842) is easily distinguished by its more circular outline, coarser radial ornament, and the rarity of auriculation in that form. In all characters but auriculation, *D. deltauriculata* closely resembles the North American species *D. crassa* (Meek and Hayden, 1858), especially some forms from the Permian (Wolfcampian) of Kansas. Specimens collected by G. A. Cooper in 1953 from the Florena Shale Member of the Beattie Limestone (USNM Acc. No. 199311) show striking similarities to the Palmarito species. They are not so auriculate, but are more so than the typical *D. crassa*. This form, not formally identified or described, may be intermediate between *D. crassa* and *D. deltauriculata*, and is easily distinguished from the several subspecies of *D. crassa* erected by Dunbar and Condra (1932) by its auriculation.

Discussion.—The type of *D. crassa* is of unknown stratigraphic position, but specimens referred by Dunbar and Condra (1932) to this species are from units in the North American mid-continent which are from mid-Desmoinesian to mid-Virgilian in age. The specimens intermediate in auriculation between *D. crassa* and *D. deltauriculata* mentioned above are of mid-Wolfcampian age equivalent strata. It may be that auriculation is a character which developed in the *D. crassa* stock during the Upper Paleozoic, but there are at present insufficient data to make more than this suggestion.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
10	4	26	30	fine silicification

Derbyia cf. **D. filosa** Cooper and Grant
Plate 2, figures 1–6

cf. *Derbyia filosa* Cooper and Grant, 1974, p. 300, pl. 82, figs. 1, 2, 11–36.

Description.—Large, planoconvex to biconvex shells having straight hingeline; greatest height at or just anterior to umbo. Outline semi-circular. Greatest width at or just anterior to hingeline; slightly auriculate or not. Ornament of fine costellae of roughly uniform height, acute in section, separated by flat-bottomed troughs. Costellae arising at beak and increasing anteriorly by intercalation, in four to five unsystemati-

cally distributed generations; from 10 to 16 costellae, commonly 11 to 12, in a five mm distance. Surface may be secondarily dimpled, bumpy or braided, more commonly distally.

Ventral valve beak asymmetrically produced and pursed or not, having apical cicatrix of attachment that may or may not obscure radial ornament. Interarea flat, triangular, apsacline, anteroposteriorly faintly striate. Convex pseudodeltidium, filling most of delthyrium, exhibiting smoothly concave anterior margin and concentric growth lamellae.

Dorsal valve commonly gently, rarely strongly convex, greatest height at or posterior to midvalve. Umbo produced slightly beyond hingeline.

Ventral interior having strong hinge teeth, triangular in section, directed anteriorly, buttressed interiorly by long dental ridges; ridges diverging anteriorly at about 30° on inner face of interarea. Vault of pseudodeltidium having low, rounded, median longitudinal ridge, merging posteriorly with larger base of median septum. Rounded, excavate bilateral fossae (=secondary spondylium of Cooper and Grant, 1974) formed at junction of sub-pseudodeltidial median ridge, dental ridges and median septum. Median septum high, thin, extending anteriorly only to anterior margin of diductor muscle scars. Muscle scars smooth, indistinct; interior surface otherwise smooth.

Dorsal interior having large cardinal process and long thin erismata. Latter bearing low dentifers that do not extend dorsad to hinge. Hinge sockets well-defined by dentifers, erismata, hingeline and low broad swelling on lateral slope of erismata anterior to dentifers. Lateral lobes of cardinal process joined dorsad to broad disjunct chilidial plates. Plates, separated by deep mesial groove, anterodorsally overhanging reduced dorsal interarea as thin reflexed lips. Cardinal process myophore bilobate ventrally, lateral lobes deeply excavate anteroposteriorly on dorsal faces; lobes U-shaped in posterior aspect. Inner faces of myophoral slits crenulate to denticulate, with definite lipped rims. Large muscle field, apparently smooth or striate and contained by erismata; may be divided by low, rounded median ridge, in some specimens extending up onto cardinal process shaft.

Measurements (in mm).—

	Length	Hinge Width	Height	Material
LOCALITY 11				
USNM 220997	—	77.0_h	15.2	(ventral valve)
USNM 220998	60.9	85.0_h	—	(ventral valve)

Occurrence.—In the West Texas region where it was first described, *D. filosa* has been recovered from the Road Canyon, Word and Cherry Canyon Formations, of Late Leonardian and Early Guadalupian age. In the Palmarito Formation it is known only from locality 11. A Late Leonardian to Early Guadalupian age for the beds at that locality is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Large *Derbyia* having weak, relatively widely spaced costellae and a strong, reflexed bilobate chilidium.

Types.—Figured Specimens: USNM 220998–221001; Measured Specimens: USNM 220997–220998.

Comparison.—*D. filosa* is characterized by its flattish ventral valve, strong, relatively uncrowded costellae, auriculate hinge and short plates which join the median septum to the dental ridges. While the Palmarito form shares most of these characters, the expression of the ears cannot be ascertained in the extremely limited number of complete specimens available, and the costellae seem uniformly weaker than those of West Texas *D. filosa*. The Venezuelan form may be distinguished from most other species of *Derbyia* by its large mature size and its relatively widely spaced costellae; its prominent bilobate reflexed chilidium distinguishes it from otherwise similar forms like *D. informis* Cooper and Grant (1974), *D. nasuta* Girty (1909) and *D. pannucia* Cooper and Grant (1974).

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
11	1	8	4	medium-grained silicification

Derbyia sp.
Plate 1, figure 29

Discussion.—Specimens of both juvenile and adult *Derbyia* exhibiting the diagnostic single ventral median septum, but lacking either sufficiently good preservation or adequate numbers of specimens for specific identification were recovered from localities 3, 4, 6 (block C) and 13. Mature specimens (beak area of a single ventral valve) were found only at locality 4. All other material was complete or partial valves, mostly ventral.

Types.—Figured Specimen: USNM 221002.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	—	2	—	fine silicification
4	—	1	1	fine silicification
6 (block C)	—	—	1	fine silicification
13	—	3	4	fine silicification

Family **MEEKELLIDAE** Stehli, 1954

Genus **MEEKELLA** White and St. John, 1867

Type Species.—*Plicatula striato-costata* Cox, *in* Owen, 1857, p. 568, pl. 8, fig. 7.

Diagnosis.—Meekellidae in which the dental plates meet the floor of the ventral valve without joining.

Occurrence.—*Meekella* has been recovered from all the Americas, Europe, Asia and parts of southeast Asia. It is known from uppermost Desmoinesian to Upper Guadalupian equivalent rocks, although its most cosmopolitan distribution was reached in the Lower Permian, when its range extended to the edges of the Boreal realm (Stehli and Grant, 1970). It has not been recovered from Africa or Australia, and it is expected that future studies will maintain its largely Tethyan affinities.

Comparison.—*Meekella* is the only genus of the Meekellidae to be recovered from the Palmarito. It may easily be distinguished from most other meekellid genera by the internal details of the ventral valve, and from *Niviconia* Cooper and Grant (1974) by the relative conservatism of its articulatory and visceral supportive apparatus.

Discussion.—*Meekella* is represented in the Palmarito by a single, variable species that is identified on the basis of several very small suites of specimens. Cooper and Grant (1974, p. 352) have succinctly summarized one great difficulty in identification of species of *Meekella*: "Species of *Meekella* . . . are highly variable." Interior details, while important for generic differentiation, are notoriously unreliable in specific taxonomy, since both cardinal process and dental apparatus change so remarkably during the course of ontogeny of a single individual. Exterior details used extensively in specific identifications may be masked or missing in some specimens, and indeed may appear only in certain growth stages of the animal. Taxonomically significant parameters of many species of *Meekella* vary over wide ranges, the norm of which is difficult to determine without the aid of a large number of specimens. The poor preservation of small numbers of specimens of the Venezuelan forms thus allow specific identification in only a single case.

Meekella skenoides Girty
Plate 2, figures 7–16

Meekella skenoides Girty, 1909, p. 206, pl. 30, figs. 8, 9; R. E. King, 1931, p. 56, pl. 7, figs. 6–8; Newell, Rigby *et al.*, 1953, pl. 21, fig. 1; Cooper and Grant, 1974, p. 370, pl. 99, figs. 40–41; pl. 101, figs. 9–13; pl. 104, figs. 1–10; pl. 108, figs. 6–10; pl. 115, figs. 1–32; pl. 116, figs. 1–8.

Meekella difficilis Girty, 1909, p. 206, pl. 30, fig. 10 (*non* R. E. King, 1931, p. 53, pl. 4, figs. 16, 17; pl. 5, fig. 1).

Description.—Medium to large-sized, small to medium-sized for genus, moderately to strongly biconvex, inequivalved, having high conical ventral and bowl-like dorsal valves. Outline transversely oval to subcircular; commonly widest at about midlength. Hingeline short, straight; commissure rectimarginate, serrate. Surface ornament of fine costellae (commonly five in a one mm distance); costellae increasing anteriorly, commonly by intercalation, rarely by splitting. Oblique-sided angular plicae, superposed on costellae, arising about eight mm from dorsal or ventral umbones, increasing anteriorly in width and height, not number; very rarely bifurcating, six to eight on each flank, from 13 to 16 per valve. Plicae strongest at anterior margin, becoming obsolete posteriorly and laterally.

Ventral valve shallow to deep, most commonly deep, up to two-thirds as high as wide, cone-like, having apical to subapical cicatrix of attachment; greatest height commonly just anterior to beak. Interarea small, high, smooth, triangular to curved triangular, commonly symmetric in small, apparent juvenile specimens, commonly asymmetric in larger, apparently more mature individuals. Triangular delthyrium completely filled by pseudodeltidium that is laterally bounded by striae at delthyrial margin and has a distinct rounded monticulus with mesial groove. Anterior margin of pseudodeltidium straight, concave if broken.

Dorsal valve swollen, commonly one-half as high as wide; greatest height at one-third to one-half valve length from beak. Slightly auriculate, tiny triangular ears extending as thin plates to lateral extremities of ventral interarea.

Ventral interior having distinct median sub-pseudodeltidial groove and strong, anteriorly directed hinge teeth, supported by dental ridges. Dental ridges strong, supported posteriorly by thin dental plates; plates arising, keel-like, near anterior ends of teeth. Dental plates straight, converging but not meeting be-

fore contacting floor of valve; not modified, except anteroposteriorly striate toward anteroventral extremities in larger individuals. Surface smooth, anteriorly plicate, reflecting exterior ornament. Muscle attachment field smooth, indistinct, even in large specimens.

Dorsal interior having long cardinal process that arises normal to plane of valve. Bilobate myophore recurved sharply posteriorly; lobes slit posterodorsally; slits arising one-half way up vertical shaft, continuing to distal end of myophore. Myophore mesially cleft, lobes separate but closely appressed about one-half distance up myophore. Shaft supported dorsally by very thin erismata that diverge anteriorly at about 50° in plane defined by their anterior edges. Posterior face of myophore grooved dorsad to cleft; mesially cleft keel present in some specimens. Dentifers present as comparatively large alate extensions on sides of erismata, extending ventroposteriorly as slender, pointed brachiophores. Proximal ends of dentifers cleft, having fulcral plate fused to palintrope. Subcardinal cavity deep, commonly smooth, having low, rounded but distinct median ridge arising abruptly just anterior to umbo and terminating anterior to distal ends of erismata. Remainder of surface broadly plicate, mirroring exterior ornament.

Measurements (in mm).—

	Length	Hinge Width	Maximum Width	Height or Thickness	Material
LOCALITY 3					
USNM 221003	7.4	6.5	10.4	6.5	(articulated valves)
USNM 221004	11.8_b	6.5	12.6	7.7_e	(articulated valves)
USNM 221005	15.4	9.1	13.1	16.5	(articulated valves)
LOCALITY 4					
USNM 221006	26.3_e	27.6	33.5_e	7.5	(dorsal valve)
USNM 221007	30.3_b	20.9_b	32.4_b	10.7	(dorsal valve)

Occurrence.—*Meekella skenoides* is known in the West Texas area from the Road Canyon, Cherry Canyon, Word, Bell Canyon and Capitan Formations of Late Leonardian and Guadalupian age. In the Palmarito Formation it is recognized at localities 3, 4, 7, 8 and 11, while a single partial dorsal valve was recovered in float in the Quebrada de Portachuelo (Field No. PRH-71-VE-23). Specimens which may be referable to the species were described as *Meekella* sp. (Stehli and Grant, 1970 [p. 27, pl. 7, figs. 37–40]) from the Chochal Limestone (Leonardian) of Guatemala. The Late Leonardian or Guadalupian age of the West Texas specimens does not contradict the ages of the above Palmarito assemblages as based on other biostratigraphic indicators.

Diagnosis.—Medium-sized to large *Meekella* with strong angular plications averaging twelve in number.

Types.—Figured Specimens: USNM 221003–221005, USNM 221007–221011; Measured Specimens: USNM 221003–221007.

Comparison.—*Meekella skenoides* is characterized by its moderate size (rarely more than 50 mm wide), regular sharp plications arising near the beak, small ears, separate dental plates and proportionately high interarea. Of the species of *Meekella* which reach a comparable size, only a few are similar. *M. occidentalis* (Newberry, 1861) is distinguished by its larger size, more prominent auriculation, and more uniformly divergent costellae. *M. prionota* Cooper and Grant (1974) possesses a prominent dorsal sulcus, a feature that is rarely observed in *M. skenoides*, but is never so strongly expressed. *M. skenoides* attains a smaller maximum size than does *M. magnifica* Cooper and Grant (1974). Smaller individuals of *M. skenoides* might be mistaken for *M. attenuata* Girty (1909), but typical specimens of that species are less deep and have fewer costae. The auriculate cardinal extremities of *M. calathica* Cooper and Grant (1974) immediately distinguish it from *M. skenoides*.

Discussion.—The small maximum size attained by individuals recovered from Palmarito locality 3 may in part be the result of current sorting. The species is here commonly found firmly attached to sponges, and the largest specimens are commonly quite fragmented. Breakage of larger specimens of this fragile thin-shelled form would seem inevitable in a strong current regime.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
Field No. PRH-71-VE-23	—	1	—	fine silicification
3	9	24	24	fine silicification
4	1	5	—	fine silicification
7	1	—	—	calcite permineralization
8	—	2	3	fine silicification
11	—	1	—	coarse silicification

Superfamily **CHONETACEA** Muir-Wood, 1962
Family **RUGOSOCHONETIDAE** Muir-Wood, 1962

Diagnosis.—Small to large Chonetacea; shell rarely thickened; externally smooth, capillate, costellate or lamellose, rarely rugose. Median fold and sulcus variably developed; dorsal interarea may be reflexed. Spine row at variable angles to hinge, spinules usually developed. Median, lateral and commonly accessory septa developed in dorsal valve. Alveolus well-developed, deep; brachial ridges prominent. Adductor scars smooth or rarely dendritic; no accessory adductors.

Discussion.—The original diagnosis of the Rugosochonetinae, of the family Chonetidae Muir-Wood (1962), was far less comprehensive than the above. Cooper and Grant (1974) elevated the taxon to family rank, citing as justification the marked differences in internal structure between the rugosochonetids and earlier Paleozoic chonetaceans, especially in the nature of the cardinal process. That family diagnosis is here expanded to include forms like *Stauromata* new genus, which, except for certain internal details, are well within the range of variation of the Rugosochonetidae as previously recognized.

Subfamily **RUGOSOCHONETINAE** Muir-Wood, 1962

Diagnosis.—Small to moderately large, transverse, smooth to costellate, usually having ventral sulcus; spine row oblique; chilidium and pseudodeltidium usually present. Ventral interior having short posterior median septum and low, commonly anterospinose median ridge; surface strongly papillose. Dorsal interior having deep alveolus, usually well-developed; anderidia commonly protuberant; median septum long; adductors smooth; lateral regions usually strongly endospinose.

Discussion.—The subfamily includes the Late Paleozoic genera *Rugosochonetes* Sokolskaya (1950), *Dyoros* Stehli (1954), *Eolissochonetes* Hoare (1960), *Leurosina* Cooper and Grant (1975), *Lissochonetes* Dunbar and Condra (1932), *Mesolobus* Dunbar and Condra (1932), *Neochonetes* Muir-Wood (1962), *Quadrochonetes* Stehli (1954), *Stauromata* new genus and *Sulcataria* Cooper and Grant (1969). *Dyoros* and *Stauromata* are recognized in the present collections.

Genus **DYOROS** Stehli, 1954

Type Species.—*Chonetes consanguineus* Girty, 1929, p. 409, figs. 8, 9.

Diagnosis.—Wide-hinged smooth Chonetacea with sulcus varying from deep to barely visible, the pedicle valve and visceral region usually strongly fringed by spines on the anterolateral side.

Occurrence.—*Dyoros* to date has been recognized only in the western United States, where it occurs in units that range in age from Leonardian to Guadalupian, although the type species, *D. consanguineus* (Girty, 1929) has been reported from the Wolfcampian Skinner Ranch Formation. A single dorsal valve (USNM 163553) from the Chochal Limestone (Leonardian) of Guatemala, described as "*Neochonetes* sp." (Stehli and Grant, 1970), is more properly placed in *Dyoros,* on the basis of its distinct median sulcus and internal anterior spinose fringe in the dorsal valve.

Comparison.—*Dyoros* differs from *Leurosina* Cooper and Grant (1975) and *Neochonetes* Muir-Wood (1962) in its possession of a definite median deflection, and from *Lissochonetes* Dunbar and Condra (1932) in the stronger expression of its internal details, particularly endospines. It differs from *Eolissochonetes* Hoare (1960), *Mesolobus* Dunbar and Condra (1932), *Quadrochonetes* Stehli (1954), *Rugosochonetes* Sokolskaya (1950) and *Sulcataria* Cooper and Grant (1969) in its distinct anterior endospinose fringes in the dorsal valve. *Stauromata* new genus, though quite similar to *Dyoros,* is distinguished by its unique anteroventral endospinose palisades.

Discussion.—Cooper and Grant (1975) have recognized three groups of species of *Dyoros* in the West Texas area, to which they have assigned the rank of subgenera: *Dyoros* (*Dyoros*), distinguished by its strong ears and deep sulcus; *Dyoros* (*Lissosia*), distinguished by its strong ears and reduced sulcus; *Dyoros* (*Tetragonetes*), distinguished by its reduced ears,

nearly vertical sides and strong sulcus. Although the form of *Dyoros* here described is closest to *D.* (*Tetragonetes*), it is felt that an unequivocal assignment of the Venezuelan forms to a particular subgenus of *Dyoros* is unwarranted.

Dyoros acanthopelix new species
Plate 2, figures 17–26

Etymology of Name.—Gr. *akantha* = thorn; Gr. *pelyx* = bowl.

Description.—Small, rectangular to transverse auriculate shells having straight hingeline and small triangular ears. Commissure rounded rectangular to semicircular in outline; not straight anteriorly, commonly having very broad dorsal fold and ventral sulcus. Well-preserved surfaces smooth, some poorly preserved, slightly decorticated individuals having radially disposed taleolar traces. Concentric growth lines not conspicuous in early growth stages; overlapping lamellae often present in later shell accretions.

Ventral valve convex, having greatest height near midvalve. Three to five posterolaterally directed hinge spines, oriented at about 30° to hinge on either side of low beak. Interarea low, apsacline, slightly concave, faintly dorsoventrally striate. Narrow, crescentic, hood-like pseudodeltidium filling apex of small triangular delthyrium.

Dorsal valve concave to planar. Interarea very low, commonly one-half height of ventral interarea, anacline to hypercline. Chilidial plates disjunct, covering portions of exterior sides and base of myophore.

Ventral interior having short ventrolaterally directed hinge teeth, unsupported by dental plates. Rounded to subcircular boss-like thickening of posteriormost median septum bearing two or more vertical grooves corresponding in position to lobes of myophore. Median septum narrow, bladelike anteriorly, thicker and higher near midvalve, there bearing stout endospines or tubercles on crest. Septum commonly ending short of anterior margin. Diductor scars oval, longitudinally striate or smooth, anterolaterally bounded by large endospines; spines apparently set on low rounded ridge or platform, reflecting form of brachial ridges of opposite valve. Inner surfaces of anterior and lateral margins and ears covered by numerous small pustules, in radial rows nearer margins.

Dorsal interior having short, stout cardinal process, supported by thin outer socket ridges, broad inner socket ridges and broad anderidia. Anterior margins of outer socket ridges diverging slightly from hingeline. Inner socket ridges straight, widening anterolaterally. Cardinal process shaft short, thick; myophore bilobate, effectively quadrilobate, each lobe mesially striate on posteroventral surface. Median septum thin, arising from junction of anderidia just anterior to deep submyophoral alveolus, continuing anteriorly just beyond midvalve, there thickened and commonly bearing small tubercles on crest. Broad anderidia arising from beneath inner socket ridges, extending anterolaterally to near midvalve, terminating in cluster of distally oriented endospines. Smaller endospines covering area with low rounded brachial ridges that extend anteriorly and laterally to valve margins. Brachial ridges indistinct, some marked by narrow zone of endospines arising at deep hollow between inner socket ridge and anderidium, spines increasing in size as ridges curve around just anterolateral of anterior end of median septum.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Thickness
LOCALITY 2				
USNM 221012	3.5	5.1_b	4.4	1.0
USNM 221013	5.0	7.7	6.9	1.3
USNM 221014	5.0	8.2	7.6	1.1
USNM 221015	5.1	6.5	6.4_b	1.6
USNM 221016	5.2	7.4_h	6.6	1.4
USNM 221017	5.8	7.8_b	8.0_b	2.3
USNM 221018	5.9	10.8_h	8.4	1.2
USNM 221019	6.0	8.8_b	8.0	1.6
USNM 221020	6.2	8.8	8.5	1.6
USNM 221021	6.3_b	10.4_h	9.9	1.7
USNM 221022	6.9	10.2	9.3	1.7
USNM 221023	7.2	10.5	9.3	2.1
USNM 221024	7.7	10.8_h	10.0	2.9
USNM 221025 (holotype)	7.8	11.0_b	10.9	1.9
USNM 221026	9.1	11.7	12.5	3.3
USNM 221027	9.1_b	12.1_b	11.4_b	2.9
USNM 221028	9.2	11.3	11.2	3.0
USNM 221029	9.4	14.7_h	13.1	3.3
USNM 221030	9.5	14.3	12.9	2.3
USNM 221031	9.5	13.6_b	14.6	3.2
USNM 221032	10.5	17.8	15.7	3.7

Occurrence.—*Dyoros acanthopelix* appears in the present collections only at locality 2.

Diagnosis.—Medium-sized, thin, quadrate *Dyoros* having strongly endospinose ventral interior and strongly tuberculate anteriorly elevated ventral median septum.

Types.—Holotype: USNM 221025; Figured Specimens: USNM 221012, USNM 221019, USNM 221025, USNM 221026, USNM 221031, USNM 221033–221035; Measured Specimens: USNM 221011–221032.

Comparison.—*Dyoros acanthopelix* is easily distinguished from the other Palmarito chonetaceans: from *Stauromata esoterica* n. gen. and sp. on the basis of

its smaller size, less pronounced fold and sulcus development, and the striking interior details of the latter form, and from *Chonetinetes* cf. *C. varians* Cooper and Grant (1975) on the basis of the squarer outline, more globose form and more conservative ventral interior exhibited by that form.

D. acanthopelix may be distinguished from many of the other species of the genus on the basis of its auriculate, but not acuminate or alate outline. These include *D.* (*Dyoros*) *angulatus* Cooper and Grant (1975), *D.* (*Dyoros*) *attenuatus* Cooper and Grant (1975), *D.* (*Dyoros*) *endospinus* Cooper and Grant (1975). *D.* (*Dyoros*) *extensiformis* Cooper and Grant (1975), *D.* (*Dyoros*) *extensus* Cooper and Grant (1975), *D.* (*Dyoros*) *intrepidus* Cooper and Grant (1975), *D.* (*Dyoros*) *hillanus* (Girty, 1909), *D.* (*Dyoros*) *robustus* Cooper and Grant (1975), *D.* (*Dyoros*) *transversus* Cooper and Grant (1975) and *D.* (*Lissosia*) *vagabundus* Cooper and Grant (1975). It may be differentiated from all species of *Dyoros* except *D.* (*Dyoros*) *magnus* Stehli (1954), *D.* (*Dyoros*) *planiextensus* Cooper and Grant (1975), *D.* (*Dyoros*) *tenuis* Cooper and Grant (1975), *D.* (*Lissosia*) *parvus* Cooper and Grant (1975) and the species of *D.* (*Tetragonetes*) on the basis of its quadrate form, and from *D.* (*Dyoros*) *magnus* and *D.* (*Tetragonetes*) *giganteus* Cooper and Grant (1975) on the basis of its smaller size. It may be distinguished from *D.* (*Dyoros*) *consanguineus* (Girty, 1929), *D.* (*Dyoros*) *convexus* Cooper and Grant (1975), *D.* (*Dyoros*) *vulgaris* Cooper and Grant (1975), *D.* (*Lissosia*) *concavus* Cooper and Grant (1975), *D.* (*Tetragonetes*) *auriculatus* Cooper and Grant (1975), *D.* (*Tetragonetes*) *quadrangulatus* Cooper and Grant (1975), *D.* (*Tetragonetes*) *solidus* Cooper and Grant (1975), *D.* (*Dyoros*) *subliratus* (Girty, 1909) and *D.* (*Tetragonetes*) *subquadratus* Cooper and Grant (1975), on the basis of its profile: thinner than those deeper, more globose forms. It is distinguished from all other species of *Dyoros* in the extraordinary development of ventral endospines. These are arranged in dense patches anterior to the adductor muscle field and along the crest of the enlarged, anteriorly elevated median septum. *D.* (*Dyoros*) *endospinus* also has large ventral endospines, but in that form the spines are located more posteriorly, and are much longer and thinner than those in *D. acanthopelix*. *D.* (*Dyoros*) *transversus* also exhibits exaggerated endospinose development in its ventral valve, but the spines in that form are located along the boundary between the visceral cavity and the ears, instead of anterior to the muscle fields, as in *D. acanthopelix*. *D.* (*Tetragonetes*) *strigosus* Cooper and Grant (1975) exhibits random scatterings of endospines anterior to the ventral adductor field, but no distinct elevated or tuberculated ventral median septum.

Of the three subgenera of *Dyoros* proposed by Cooper and Grant, *D. acanthopelix* is probably most closely allied to species of *D.* (*Tetragonetes*). Two diagnostic characters of that group in the West Texas region are the lack of strong endospines and the development of a strong sulcus in the ventral valve. Since the first of these criteria clearly is not satisfied and since the second is difficult to ascertain, due to the dorsoventral crushing common in individuals from locality 2, I have placed the new form within the genus *Dyoros* (*sensu lato*).

Discussion.—Specimens of *D. acanthopelix* in several ways foreshadow individuals of *Stauromata esoterica* n. gen. and sp. The clusters of endospines on the ventral valve floor anterior to the adductor attachment scars in *D. acanthopelix* could, through the course of ontogeny, develop into the comparatively massive anteroventral endospinose palisades seen in *S. esoterica*. Since, however, there is no direct evidence to indicate the comparative immaturity of any of the forms herein assigned to *D. acanthopelix*, such suggestions cannot be formalized to the extent of including one form in the synonymy of the other.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
2	85	34	35	calcite permineralization (fluoritized in preparation)

Genus **STAUROMATA** new genus

Etymology of Name.—Gr. *stauromatos* = palisades.

Description.—Slightly to highly concavo-convex transverse shell having straight hingeline, strong ventral sulcus and broad dorsal fold. Outline symmetrically trapezoidal, sides tapering anteriorly. Commissure W-shaped in ventral aspect, straight in anterior aspect. Beak low; hinge spines at low angles to hinge. Shell smooth to faintly capillate; finely pitted if decorticated.

Ventral valve convex, greatest height at or just posterior to midvalve. Interarea low, wide, apsacline. Hood-like crescentic pseudodeltidium filling small triangular delthyrium.

Dorsal valve moderately concave, greatest depth near mid-valve. Lateral margins reflexed dorsally,

sloping to planar ears. Interarea anacline, reflexed; triangular secondary interarea present. Chilidial plates conjunct, smooth. Small, spinelike chilidial boss protruding dorsally beyond interarea.

Ventral interior having small anteriorly directed hinge teeth, triangular in section. Delthyrial apex filled by boss-like secondary shell material, median boss merging anteriorly into median septum. Septum continuing anteriorly, merging into median ridge. Smooth posterior adductors, dendritic anterior adductors. Deeply excavate apparent diductor attachment scars, fringed mesially and posteriorly by high anterodorsally directed palisades of coalesced endospines.

Dorsal interior having inner and outer socket ridges and strong anderidia. Anderidia anteroventrally free, terminally endospinose. Alveolus deep. Adductors smooth. Thin median septum arising anterior to alveolus, broadening anteriorly. Apparent marginal rim of coalesced endospines around visceral disk.

Type Species.—*Stauromata esoterica* new species.

Diagnosis.—Rugosochonetinae having deeply excavate apparent ventral diductor attachment scars, fringed by palisades of coalesced endospines.

Occurrence.—*Stauromata* new genus is known only from the Palmarito Formation, at localities 1, 4, 7 and 8.

Comparison.—*Stauromata* is externally homeomorphous with many species of the genera *Chonetinella* Ramsbottom (1952) and *Dyoros* Stehli (1954), but its exaggerated internal characters serve to clearly differentiate it from either of those genera. Of the two, it is probably more closely related to *Dyoros,* but the striking palisade-like development of coalesced endospines is thought sufficient to warrant a new generic designation.

Discussion.—Specimens of *Stauromata* from localities 1 and 7 were first erroneously assigned to *Chonetinella,* on the basis of external characters, although this assignment was not formalized through publication. Later preparation revealed the internal features that allowed recognition of the greater similarity to but clearcut difference from, the genus *Dyoros.*

Stauromata esoterica new species
Plate 2, figures 33–37; Plate 3, figures 1–25; Plate 4, figures 1, 2

Etymology of Name.—Gr. *esoterikos* = inside.

Description.—Small to medium-sized, average-sized for genus, slightly to highly concavo-convex, transverse shell having straight hingeline, strong ventral sulcus and dorsal fold. Outline symmetrically trapezoidal, sides tapering anteriorly. Commissure W-shaped in ventral aspect, straight in anterior aspect. Beak low, flanked by five to seven spines that lie at low angles to hingeline. Shell faintly capillate, finely pitted if decorticated. Pits rounded to radially elongate, randomly scattered, in radial rows, or in radial and concentric rows.

Ventral valve convex, greatest height at or just posterior to midvalve. Visceral lobes high, rounded, diverging anteriorly at about 30°, intervening sulcus arising just anterior to beak. Interarea low, wide, apsacline. Hood-like crescentic pseudodeltidium filling small triangular delthyrium.

Dorsal valve moderately concave, greatest depth near midvalve. Sharp median fold arising one-fourth shell length anterior to beak. Lateral margins reflexed dorsally, sloping to planar ears. Interarea anacline, reflexed; triangular secondary interarea present. Chilidial plates conjunct, smooth. Small spinelike chilidial boss protruding dorsally beyond interarea.

Ventral interior having small anteriorly directed hinge teeth, triangular in section; entire beak and interarea supported by low rounded swelling originating in delthyrial cavity and running below interarea toward lateral extremities. Delthyrial apex filled by boss-like secondary shell material; median boss merging anteriorly into broad median septum. Septum continuing to anterior margin of adductors, at about one-fourth shell length, there becoming thin, blade-like median ridge, extending almost to anterior margin. Posterior adductors small, ovate, smooth, covering lateral surfaces of posteriormost median septum on slightly thickened shell plate, lapping slightly onto valve floor. Anterior adductors ovate to triangular, dendritic to cuspate, on slightly raised portions of valve floor, lapping onto median septum. Apparent diductors deeply excavate, striate; fringed by palisade of coalesced endospines. Remainder of surface finely papillose, granulose to endospinose; endospines stouter anterior to end of median septum, on radial ridges nearer lateral margins.

Dorsal interior having narrow outer and broad inner socket ridges; long, strong, anteroventrally free and endospinose anderidia. Cardinal process myophore quadrilobate. Alveolus deep, steep-sided posteriorly, gradually sloping anteriorly. Dorsal adductors small, smooth. Thin median septum arising a short distance anterior to alveolus, broadening anteriorly, terminating short of anterior margin in cluster of endospines. Apparent marginal rims of coalesced endospines around visceral disk, gradually sloping mesially, abrupt distally.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Thickness	
LOCALITY 4					
USNM 221036	11.0	21.0	13.0	4.5	(ventral valve)
LOCALITY 1					
USNM 221037	11.6	21.5$_e$	17.7	4.7$_e$	
LOCALITY 7					
USNM 221038	11.3	20.0	17.6	4.8$_e$	
USNM 221039	11.4	20.8	16.4	4.8$_e$	
USNM 221040 (holotype)	11.8	20.0	16.5	5.0$_e$	
USNM 221041	12.6	19.0	16.7$_e$	5.6	
USNM 221042	14.1	20.5	17.6	7.4$_e$	

Occurrence.—as for genus.

Diagnosis.—as for genus.

Types.—Holotype: USNM 221040; Figured Specimens: USNM 221036, USNM 221039, USNM 221040, USNM 221043–221045; Measured Specimens: USNM 221036–221042.

Comparison.—*Stauromata esoterica* is the only known species of the genus. It may, however, be closely related to species of the genus *Dyoros,* especially *D. acanthopelix* n. sp., which resembles an hypothetical immature form of *S. esoterica.* No specimens of *S. esoterica* were recovered in which the endospinose development was not fully expressed. *D. acanthopelix,* with its ventral valve lined by endospines, would make a suitable precursor to *S. esoterica.* Since they do not occur together, however, no suggestion of more than chance resemblance can be made at this time.

Discussion.—Very few of the present specimens of *S. esoterica* were silicified. Ordinary mechanical preparation with a needle failed to delineate sufficiently the internal features of the new form. In order to clarify the relationships of internal structures in both valves, twenty serial acetate peels of a single set of articulated valves (USNM 221045) were made. Instead of being oriented in the usual fashion, normal to plane of commissure, the sections were made parallel to the commissural plane. This was done so that finished schematic reconstructions could simulate conventional interior views of the valves. An attempt, largely successful, was made to keep a 0.15 mm spacing between successive sections. The peels were projected, at 10× magnification, onto 1.5 mm thick sheets of Plexiglas, using a photographic enlarger, and pertinent details inked thereon. Using reference marks to ensure their proper juxtaposition, a stack of sections were bolted together and photographed in stereo, to give an illusion of depth to the reconstructions. The peels, magnified ×2, and the schematic reconstructions of both valve interiors, magnified ×4, are presented as Plate 3. Although not all interior details are clear, one may distinguish the endospinose anterolateral fringes and median septum of the dorsal valve, and the palisade development of the ventral valve. In addition, it is readily apparent that the laterally expanded distally endospinose anderidia of the dorsal interior extend posterior to the ventral palisades. Whether this juxtaposition is an artifact of taphonomic crushing, or represents an operational life relationship is unknown. It seems likely that the combination of dorsal and ventral endospines formed an impressive barrier across the posterior portion of the valve. The function of this barrier might be speculated upon a great length. One obvious possibility is that of a structure to control and direct incurrent and excurrent flow. Another possible function might be body wall and (or) lophophore support. Arguments in favor of one or another of these possibilities should probably wait until the study of additional sections clarifies the relationships of the various structures observed.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	4	—	5	calcite permineralization
4	—	—	1	medium silicification
7	14	—	2	calcite permineralization
8	1	—	2	medium silicification

Subfamily **CHONETINELLINAE** Muir-Wood, 1962

Genus **CHONETINETES** Cooper and Grant, 1969

Type Species.—*Chonetinetes reversus* Cooper and Grant, 1969, p. 4, pl. 3, figs. 1–7.

Diagnosis.—Small, wide-hinged Chonetacea having the fold and sulcus best developed in the umbonal region and with subconical mounds of taleolae on each side of the visceral region toward the anterolateral margins.

Occurrence.—Species assigned to the genus are known, to date, from the Road Canyon and Bell Canyon Formations (uppermost Leonardian and Upper Guadalupian) of the West Texas area.

Comparison.—*Chonetinetes* is easily distinguished from *Chonetina* Krotov (1888), by its smooth exterior and single median septum. It differs from *Chonetinella* Ramsbottom (1952) in its smaller size and its incom-

plete ventral sulcus, which becomes weaker anteriorly.

Discussion.—This report constitutes the first known occurrence of the genus in South America.

Chonetinetes cf. **C. varians** Cooper and Grant
Plate 2, figures 27–32

cf. *Chonetinetes varians* Cooper and Grant, 1975, p. 1285, pl. 477, figs. 54–58.

Description.—Small, medium-sized for genus, concavo-convex, auriculate rugosochonetids having semicircular to subquadrate outline; widest at hinge. Sides sloping, width slightly greater than length. Surface apparently smooth, pseudo-costellate when decorticated (pseudo-costellae numbering eight in 1 mm distance at about midvalve). Very slight dorsal fold and ventral sulcus. Commonly six hinge spines on either side of beak.

Ventral valve high to globose, greatest height at about midvalve. Lateral commissure having slight dorsad flexure just anterior to well-defined ears. Interarea low, wide, apsacline.

Dorsal valve concave, having dorsad flexure just anterior to ears; lowest point mesial. Interarea reflexed, anacline to hypercline.

Ventral interior having large, anteriorly directed hinge teeth, triangular in section, unsupported by dental plates. Boss of callus shell material, anteriorly rounded, filling delthyrial apex, merging ventrally and anteriorly into short median ridge. Ridge low, rather broad, notched where it meets valve floor, continuing anteriorly to about one-third valve length as low median myophragm, dividing well-defined, inset, ovate, smooth to striate muscle attachment scars. Remainder of surface finely papillose, papillae in radial rows nearer margins.

Dorsal interior having mesially slit, quadrilobate to hexalobate cardinal process myophore, subcircular in posterior aspect, lateral and ventral lobes posteriorly slightly cuspate. Slight chilidial boss as spinelike protrusion from dorsal extremity of myophore. Deep, well-defined submyophoral alveolus. Hinge sockets deep, well-defined by small, swollen outer socket ridges and large laterally widening inner socket ridges that diverge slightly from hingeline. Anderidia distinct, low, anteriorly bearing a few stout endospines. Median septum arising at alveolus, continuing anteriorly as low rounded ridge, becoming narrower and more marked opposite and anterior to ends of anderidia, ending at or slightly anterior to midvalve. Muscle attachment scars indistinct. Remainder of surface finely papillose, radially striate where decorticated.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height or Thickness	Material
LOCALITY 4					
USNM 221047	5.5	10.2	7.3	2.3	(articulated valves)
USNM 221049	6.0_e	10.8_{he}	9.0_h	2.1	(ventral valve)
USNM 221053	6.6	10.2_h	7.0_h	2.5	(ventral valve)
LOCALITY 8					
MMH DG-508	5.0_e	8.0_e	7.0	2.0	(articulated valves)
USNM 221048	6.0	10.0	8.0	2.2	(articulated valves)
USNM 221051	6.5	9.6	7.2	2.0	(ventral valve)
LOCALITY 13					
USNM 221046	2.5	5.0	3.5	0.8	(ventral valve)
USNM 221050	6.2_h	11.4	8.4_e	2.3_e	(ventral valve)
USNM 221052	6.5_e	10.2_h	7.5_h	2.7_e	(ventral valve)
USNM 221054	8.2	13.8_h	9.7	3.0	(dorsal valve)
USNM 221055	8.3_e	12.2_{he}	7.6_e	3.5_e	(ventral valve)

Occurrence.—*Chonetinetes* cf. *C. varians* has been recovered from localities 4, 8 and 13 in the present collections from the Palmarito Formation. In the West Texas area, *C. varians* is known only from the three lower members (Hegler, Rader and Lamar) of the Bell Canyon Formation (Late Guadalupian), though the individuals most similar to the Venezuelan specimens are limited to the Hegler Member. This age is younger than that obtained from other parts of the fauna at those localities.

Diagnosis.—Small, moderately convex *Chonetinetes*, resembling *C. varians* Cooper and Grant (1975) but lacking the strong ventral sulcus of that species.

Types.—Figured Specimens: USNM 221048, USNM 221051, USNM 221056; Measured Specimens: USNM 221046–221055, MMH DG-508.

Comparison.—*Chonetinetes* cf. *C. varians* is easily distinguished from all other Palmarito chonetaceans by its concavo-convex form, its smaller size and far more conservative interiors. *Stauromata esoterica* n. gen. and sp., is larger, less globose, and has a more endospinose interior. The same may be said for *Dyoros acanthopelix* n. sp., although the interior ornament of that form is not so striking as that of *S. esoterica*. It is more difficult to distinguish it from West Texas species of *Chonetinetes*.

C. varians may be distinguished from *C. angustisulcatus* Cooper and Grant (1975) on the basis of the very small size and narrow ventral sulcus of the latter. It may theoretically be distinguished from the type species of the genus, *Chonetinetes reversus* Cooper and Grant (1969), by having a strong ventral sulcus. Most of the West Texas specimens assigned to *C. varians* do have such a feature, but some, including a figured paratype of the species (USNM 153677b) do not. Specimens from locality 732a [Hegler Member of the (Capitanian) Bell Canyon Formation] consist in part of essentially asulcate forms, of which the cited paratype is one. In these asulcate forms the dorsal valve does not exhibit the subconical taleolar mounds flanking the median septum that are supposedly characteristic of the genus. It is these atypical forms that are here identified with the Palmarito specimens, not the majority of more typical West Texas *C. varians*.

Discussion.—Since the characters of minor sulcation and dorsal valve interior conservatism are best expressed in the earliest representatives of the species, it would be tempting to suggest that they represent a genetic variant, perhaps worthy of a new specific designation. *C. varians* is, however, such a rare form, that no such conclusions can confidently be drawn.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
4	1	—	2	fine silicification
8	2	1	1	fine silicification
13	—	2	4	fine silicification

Suborder **PRODUCTIDINA** Waagen, 1883
Superfamily **AULOSTEGACEA**
Muir-Wood and Cooper, 1960
Family **AULOSTEGIDAE** Muir-Wood and Cooper, 1960
Subfamily **ECHINOSTEGINAE**
Muir-Wood and Cooper, 1960

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

Type Species.—*Xenosteges adherens* Muir-Wood and Cooper, 1960, p. 112, pl. 10, figs. 1–13.

Diagnosis.—Nearly smooth Aulostegidae, generally of small size, having rhizoid spines only and prominent, commonly elevated brachial ridges and dorsal adductor scars.

Occurrence.—Several species of *Xenosteges* are known from the West Texas area in rocks ranging in age from Late Wolfcampian to Late Guadalupian (Capitanian). Two specimens questionably assigned to the genus have been reported from Thailand (Waterhouse and Piyasin, 1970) in rocks correlated to the Cathedral Mountain Formation of the West Texas area (Grant, *pers. comm.*, 1974).

Comparison.—*Xenosteges* is easily distinguished from other genera of the Echinosteginae by its total lack of ornament spines, all spines being of rhizoid habit and involved intimately in the attachment of the shell to the substrate. *Strophalosiella* Likharev (1935) lacks ornament spines as well, but it is finely costellate on both valves, while *Xenosteges* is lamellose to weakly rugose. *Xenosteges* may be distinguished from the similarly aspinose strophalosiid genus *Heteralosia* R. H. King (1938) by the presence of teeth and sockets in that form. It is distinguished from another small aulostegacean, *Atelestegastus* Cooper and Grant (1975), by the consistently narrower hinge and fine ornament spines of that form.

Discussion.—*Xenosteges,* by virtue of its total lack of ornament spines and its lamellose to weakly rugose ornament should be readily recognizable in Permian faunas. One obstacle to this recognition may be its small size. If the Thai specimens are indeed improperly assigned to the genus, its absence outside the Western Hemisphere Tethyan realm may indicate that the genus is longitudinally as well as latitudinally endemic.

Xenosteges minusculus new species
Plate 4, figures 3–18

Etymology of Name.—L. *minusculus* = diminutive.

Description.—Small to minute, very small for genus, unequally biconvex to concavo-convex, having wide straight hinge. Operculiform dorsal valve deeply inset into marginally flanged cup-like ventral valve. Outline subcircular to semicircular. Umbonally cemented to substrate; circlet of rhizoid attachment spines along ventral hinge and umbo. Few propping spines higher up anterolateral slopes of ventral valve. Surface smooth or concentrically wrinkled. Attachment plane at variable angles to plane of commissure,

commonly approaching or exceeding 90° in mature specimens.

Ventral valve deep, cuplike, with wide flange surrounding smaller dorsal valve. Flange commonly everted to approximate plane of commissure. Umbo commonly flattened, thinned or missing. Interarea very low, having tiny open delthyrium. Ears variably expressed, tapering gradually anteriorly into flanges. Commonly widest at midvalve, slightly less wide at hinge; deepest at midvalve. Flanks gradually sloping anteriorly and laterally, cut off abruptly posteriorly at attachment scar.

Dorsal valve commonly subcircular to semicircular in outline. Immature valves convex; mature valves commonly concavo-convex, having convex umbonal region, raised margin and intervening concentric furrow. Surface concentrically wrinkled and dimpled; no spines. Posteromesial projection of lophidium closing delthyrium of ventral valve. Ears small, very thin, triangular.

Ventral interior having triangular median umbonal rise, providing attachment for paired adductor muscles. Thickened marginal ridge extending from either side of delthyrium toward flanges, longitudinally grooved; groove articulating with corresponding ridge in dorsal valve. Hinge spines hollow, bases open, communicating to exterior.

Dorsal interior having prominent marginal ridges arising at base of cardinal process, slightly thickened posteriorly to form ridges that articulate with grooves in marginal ridges of ventral valve. Ridges continuing around entire valve in some specimens, anteriorly commonly expressed as abrupt dorsad deflection of valve surface. Cardinal process on stout, short shaft, bilobate or secondarily quadrilobate; myophore lobes closely appressed or splayed. Submyophoral alveolus present, produced anteriorly as shallow furrow; furrow healed anteriorly to produce narrow, anteriorly raised median septum. Septum terminating posterior to midvalve, often as pointed projection above valve floor. Septum flanked posteriorly by paired inset posterior adductor scars; surfaces of scars commonly tilted posteriorly from plane of valve floor. Brachial ridges of productoid type, given off horizontally, commonly elevated and strong, terminating in circular mounds at or posterior to midvalve. Interior surface otherwise smooth, except anteriorly endospinose in some specimens. Endospines small, apparently in a few concentric rows near margins.

Measurements (in mm).—

	Ventral Valve			Dorsal Valve				
	Length	Hinge Width	Maximum Width	Length	Hinge Width	Maximum Width	Thickness	Ventral Valve Height
USNM 221057	2.3	2.2	2.5	1.9	1.8	2.0	0.8	1.2
USNM 221058	2.7_b	2.5	3.0	2.7_b	2.0	2.5	1.0	1.7
USNM 221059	2.8	2.8	3.4	2.5	2.5	2.8	1.0	1.2
USNM 221060	3.5_r	3.2	4.1	2.5	2.5	2.8	1.7	3.0
USNM 221061	3.2	4.0_h	4.0	2.7	3.6_h	3.1	1.2	2.0
USNM 221062 (holotype)	3.5	4.4	5.1	2.9	3.2	3.5	2.3	3.7

Occurrence.—*Xenosteges minusculus* has been recovered only from locality 6. It is common in block A, rare in block B and abundant in block C.

Diagnosis.—Very small *Xenosteges* having reduced ears, strong dorsal interior marginal ridges and rounded, posteriorly set brachial ridges.

Types.—Holotype: USNM 221062; Figured Specimens: USNM 221057–221059, USNM 221062–221071; Measured Specimens: USNM 221057–221062.

Comparison.—*Xenosteges minusculus* is easily distinguished from all other known species of the genus by its smaller overall size, the largest specimen being slightly over five mm in its largest dimension. In addition, it is distinguished from *X. adherens* Muir-Wood and Cooper (1960), *X. anomalus* Cooper and Grant (1975) and *X. trivialis* Cooper and Grant (1975) by its relatively narrow hingeline, compared to those prominently auriculate forms. It lacks the ventral sulcus of *X. magnus* Cooper and Grant (1975), and is more equidimensional than the commonly elongate *X. umbonatus* Cooper and Grant (1975). Of the described species of *Xenosteges*, *X. minusculus* probably most closely resembles *X. quadratus* Cooper and Grant (1975), from which it differs in the smaller, more mesially appressed brachial ridges and the umbonally concave dorsal valve of that form.

Discussion.—*Xenosteges minusculus* is the first reported occurrence of the genus outside of the West Texas area, with the exception of two specimens from Thailand questionably assigned to the genus (Waterhouse and Piyasin, 1970).

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block A)	13	23	11	fine silicification
6 (block B)	3	2	1	fine silicification
6 (block C)	15	115	74	fine silicification

Family **COOPERINIDAE** Pajaud, 1968

Subfamily **COOPERININAE** Pajaud, 1968

Genus **COOPERINA**
Termier, Termier and Pajaud, 1966

Type Species.—*Cooperina inexpectata* Termier, Termier and Pajaud, 1966, pp. 332–335.

Diagnosis.—Cooperininae bearing spines on both valves, flangelike dorsal submarginal ridge, short but prominent dorsal anteromedian ridge and elevated, excavate adductor platforms.

Occurrence.—*Cooperina* is known in rocks of Pennsylvanian and Permian age, from every continent but Africa, Australia and Antarctica. Its occurrence appears to be limited to the Tethyan realm during the Permian. It first appears, reported as *Leptalosia spondyliformis* White and St. John (1867) [*in* Dunbar and Condra (1932)], in the Pawnee Formation (Laberdie Limestone Member) of Late Desmoinesian age, from Oklahoma. It is next seen in Thailand, in the Early Permian of Ko Muk, as *C. polytreta* Grant (1976). *C. triangulata* Cooper and Grant (1975), from the Lower Wolfcampian of the West Texas area is another Early Permian form. *C. parva* Cooper and Grant (1975) is found at various localities in the Leonardian of West Texas, while *C. subcuneata* Cooper and Grant (1975), is at present limited to the Upper Leonardian of that area. *C. inexpectata* has been recovered from various localities from the Guadalupian of West Texas, and from locality 6, blocks A, B and C in this study of the Palmarito Formation. A form recognized as belonging to the genus has been recovered from the Upper Permian Zechstein of Germany (Grant, 1976, p. 89).

Comparison.—*Cooperina* is with great difficulty distinguished from *Ansehia* Termier and Termier (1970), and indeed the two genera are probably closely related. Only the apparent absence of dorsal spines and the latest Permian (Dzhulfian) age of the Cambodian genus support the idea that they are distinct taxa. A definitive decision must await development of the internal details of *Ansehia*. *Atelestegastus* Cooper and Grant (1975), lacks any ornament spines or an anteromedian ridge in the ventral valve interior, and possesses a characteristic wide flange around the cup-like ventral valve, surrounding the inset dorsal valve. *Falafer* Grant (1972), is easily distinguished by its prominent muscle platform and its calcified ptycholophous brachidium in the dorsal valve.

Discussion.—*Cooperina* was originally suggested (Pajaud, 1968) as the ancestor to extant thecidian brachiopods (*e.g., Thecidellina*). Subsequent studies (Cooper and Grant, 1969; Grant, 1972; Cooper and Grant, 1975; Grant, 1976) have demonstrated its proper placement within the Productidina.

Cooperina inexpectata
Termier, Termier and Pajaud
Plate 4, figures 19–37

Cooperina inexpectata Termier, Termier and Pajaud, 1966, p. 332, fig. 1; Cooper and Grant, 1969, pl. 3, figs. 14–27; Cooper and Grant, 1975, p. 824, pl. 210, figs. 1–61; pl. 212, figs. 11–22.

Description.—Small to minute *Cooperina* having straight hingeline, deeply concave ventral valve and convex to concavo-convex dorsal valve. Rhizoid attachment spines in circlet around ventral umbo and on ears of ventral valve; crudely parallel rows of exterior ornament spines; common on ventral valve, rare on dorsal valve. Plane of commissure horizontal to vertical, with respect to substrate, becoming more vertical with growth.

Ventral valve outline ovate to subquadrate in dorsal aspect. Umbonal region commonly modified or missing, depending on form of substrate. Attachment spines densely packed, conforming to substrate; ornament spines straight or slightly curved, commonly at low angle to surface, inclined toward plane of commissure. Interarea moderately high, commonly 0.15 of shell length (Range: 0.11 to 0.21 in 12 specimens), commonly orthocline to apsacline, very thin, overhanging posterior margin of dorsal valve to form grooved hinge insertion. Broad ears gradually tapering anteriorly, in dorsal aspect producing egg-shaped outline of visceral cavity. Thickened lateral and anterior margins forming rim around inset dorsal valve margin. Anterior margin, rounded, straight or very slightly indented mesially.

Dorsal valve subquadrate, elongate rectangular or rounded in outline, with or without slight anteromesial indentation. Surface smooth to wrinkled, convex posteriorly, concave anteriorly in more mature individuals. Ears tiny, thin, delicate, acuminate triangular.

Ventral interior deeply concave, of variable form depending on attachment surface; umbonal region commonly flattened or missing. Muscle scars indistinct, on either side of low umbonal mound or broad ridge. Umbonal mound merging anteriorly and dorsally into low, variably expressed median ridge. Ridge broadening anteriorly, continuing to anterior margin,

effectively dividing valve into two lobes, and articulating with anteriorly divided anteromedian ridge of dorsal valve.

Dorsal interior having thin, flangelike submarginal ridges, arising laterally at base of cardinal process, running just inside valve margins to reach highest point at about midvalve, there turning anteromesially and becoming lower toward the anterior margin, there continued as a single row of small, low pustules. Ridges re-arising mesially, recurving posteriorly to conjoin near midvalve as high, anterodorsally grooved median ridge. Median ridge gradually sloping anteriorly, sharply cut off posteriorly, merging into distinct narrow median furrow nearer hingeline. Submarginal ridges commonly (49 of 59 specimens) highest posterior to highest point of anteromedian ridge; submarginal ridges commonly (in 52 of 59 specimens) lower than anteromedian ridge; neither relationship correlated to growth stage. Delicate bilobate cardinal process myophore set on short slender shaft, shaft at angle to valve plane, allowing insertion below ventral interarea. Myophoral lobes moderately splayed, dorsoposteriorly cleft, producing effective quadrilobation. Thin, obliquely-oriented adductor platforms set in posterolateral corners of valve, attached laterally to inside walls of submarginal ridges and posteriorly to valve floor, merging posteriomesially into broad, ridge-like bases of cardinal process shaft. Brachial ridges poorly defined, elongate.

Measurements (in mm).—

	Ventral Valve			Dorsal Valve			
	Total Length	Maximum Width	Interarea Height	Length	Hinge Width	Maximum Width	Thickness
Locality 6 (block C)							
USNM 221072	1.8	1.8	0.2	1.4	0.6	1.5	0.4
USNM 221073	2.3	1.9	0.3	2.0	1.0	1.7	0.8
USNM 221074	2.6	2.7	0.3	2.2	1.3	2.2	0.3
USNM 221075	2.9	2.8	0.4	2.6	1.2	2.3	1.2
USNM 221076	3.2	2.8	0.5	2.3	1.4	2.2	1.1
USNM 221077	3.3	3.4	0.5	2.5	1.7	2.6	1.1
USNM 221078	3.4	2.4	0.5	2.5	1.1	2.3	1.3
USNM 221079	3.4	3.1	0.7	2.4	1.6	2.3	1.6
USNM 221080	3.4	3.5	0.6	2.6	1.7	3.0$_p$	2.0
USNM 221081	3.5	3.0	0.5	2.5	1.8	2.2	1.6
USNM 221082	3.6	2.9	0.6	2.5	1.3	2.2	2.0
USNM 221083	3.6	3.0	0.6	2.6	1.4	2.3	1.6

Occurrence.—*Cooperina inexpectata* is known from rocks of Guadalupian age in the West Texas area. The specimens herein described constitute the other known occurrence of the species. Individuals have been recovered only from locality 6, blocks A, B, and C. They are common to abundant in blocks A and C, but are rare in block B.

Diagnosis.—

Rectangular to square *Cooperina* having long curved ornament spines, a broad attachment area on the pedicle valve and strongly elevated median ridge in the brachial valve. (Cooper and Grant, 1975, p. 825)

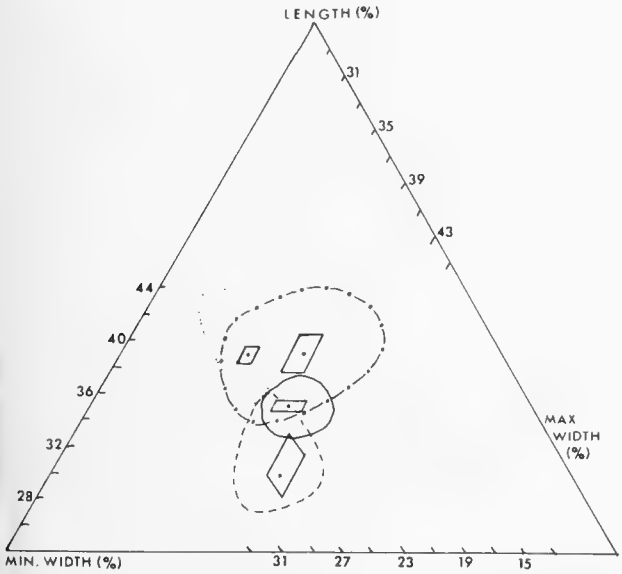
Types.—Figured Specimens: USNM 221075, USNM 221079, USNM 221084, USNM 221086, USNM 221092, USNM 221104, USNM 221112, USNM 221117, USNM 221118, USNM 221121, USNM 221132, USNM 221142–221146. Measured Specimens: USNM 221072–221142.

Comparison.—*Cooperina inexpectata* is easily distinguished from the only other Palmarito brachiopod of similar form and size, *Xenosteges minusculus* n. sp., by its more elongate form and its strikingly different interior details. It may be distinguished from other species of *Cooperina* with somewhat more difficulty. It is distinguished from *C. subcuneata* Cooper and Grant (1975) by the narrow hinge and conspicuous brachial pits in that form. It is generally larger and less triangular than *C. triangulata* Cooper and Grant (1975) and has ornamental spines, which that form lacks. It is similarly distinguished from *C. spondyliformis* (White and St. John, 1867). *C. parva* Cooper and Grant (1975) bears close resemblance to juvenile and apparently neotenous (large but with low dorsal median and submarginal ridges) individuals of *Cooperina inexpectata* from the Palmarito Formation, but is not placed in synonymy here because the two species do not overlap in many taxonomic characters in the West Texas area where they were defined.

Discussion.—The dorsal valve of *Cooperina*, probably less affected by local environmental variables

(substrate type, site of attachment, etc.) than the ventral may be defined in outline by three measurable variables: hinge, or minimum width, maximum width, and length. Some concept of the shape variability of the species can be gained through a plot, on a triangular diagram of these variables, normalized to 100% (Text-fig. 9). This diagram shows four variability fields. The point within each defines the position of the mean of the indicated variable: the polygon surrounding that point extends one standard deviation to each side of the mean, and the dotted line surrounding the polygon is a measure of the range of variation of the form described. The data on which the illustration is based are presented as Table 9. The numerical transformations employed are summarized in Table 10.

In terms of outline of the dorsal valve, the four forms are clearly related. There is considerable overlap between the Venezuelan forms (C & D), which are here considered as different ontogenetic stages of the same species. There is no overlap between the ranges of variation in shape of the two West Texas forms (A & B), but it is readily apparent that they are related in much the same manner as are the Venezuelan forms, though not so closely.



Text-figure 9.—Shape variation of dorsal valves of four samples of *Cooperina* from the Permian of West Texas and Venezuela. Field surrounded by ····· = *Cooperina inexpectata* from West Texas; field surrounded by ------ = *Cooperina parva* from West Texas; field surrounded by —·—·—·— = mature *Cooperina inexpectata* from Venezuela; field surrounded by —— = apparent immature *Cooperina inexpectata* from Venezuela. (Within each field, the coded line surrounds all data points; the polygon defines one standard deviation on each side of the mean for all three variables; the point within each polygon is the mean for all three variables. Data are summarized in Tables 9 and 10.)

One possible resolution of this situation might be to designate three species: *C. inexpectata,* as typified by the West Texas forms (field A), *C. parva,* again typified by West Texas specimens (field B), and a new Venezuelan species of *Cooperina*. This strategy is not employed because there is no obvious morphological difference between *C. inexpectata* of West Texas and the mature Venezuelan forms that cannot be explained in terms of normal infraspecific variation. Since forms transitional between juvenile and mature individuals are observed in the Venezuelan collections, it is reasonable to combine them as a single species. It cannot be determined whether the juvenile *ontogenetic stage* seen in Venezuela is genetically related to the apparently neotenous *species* of *C. parva* of West Texas. It is, however, reasonable to consider similar morphologies in fossils as representing ontogenetically distinct but genetically conspecific organisms in one place and time, while they represent genetically distinct species in another. Geographic and temporal separation are recognized factors in speciation.

Family **RHAMNARIIDAE** Muir-Wood and Cooper, 1960

RHAMNARIIDAE cf. **Ramavectus** sp.
Plate 4, figures 38, 39

cf. *Ramavectus* Stehli, 1954, p. 327 ff.

Types.—Figured Specimen: USNM 221147.

Discussion.—A single poorly preserved specimen recovered from locality 11 is questionably referred to *Ramavectus*. It is largely decorticated, the only remaining shell material being several pieces of ventral valve surface, the ventral beak and the proximal portion of the dorsal umbo. The umbonal region has been silicified as a unit, so that the form of the cardinal process is lost. Grinding the umbonal region did not reveal the presence of the large median septum characterisitc of *Tschernyschewia* Stoyanov (1910). The absence of a distinct cicatrix of attachment suggests that it does not belong in either *Rhamnaria* Muir-Wood and Cooper (1960), *Spuriosa* Cooper and Grant (1975) or *Juresania* Frederiks (1928), externally similar forms. In addition, most species of *Rhamnaria* are smaller, and none bears the distinctive regularly spaced elongate spine bases on the ventral valve that in *Ramavectus*, and the Palmarito specimen, suggest periodically interrupted costae. The specimen might be mistaken on casual inspection for a large species of *Bathymyonia* Muir-Wood and Cooper (1960), but the presence of a true interarea in the Palmarito form clearly removes it from the Echinoconchidae.

Table 9.—Measurements of dorsal valves of *Cooperina inexpectata* Termier, Termier and Pajaud (1966) from locality 6, Palmarito Formation.

SMRH = Submarginal Ridge Height
MRH = Median Ridge Height
SMRD = Distance from highest point on submarginal ridge to anteriormost point of shell, measured parallel to shell length.
MRD = Distance from highest point on median ridge to anteriormost point on shell, measured parallel to shell length.

	Length	Hinge Width	Minimum Width	Maximum Width	SMRH	MRH	SMRD	MRD
(block A)								
USNM 221084	2.4	1.0	1.0	2.6	0.6	1.0	1.3	1.1
USNM 221085	2.1	1.0	1.0	2.2	0.6	0.5	1.1	0.7
USNM 221086	2.1	1.4	1.3	2.0	0.7	1.1	1.6	1.1
USNM 221087	2.1	1.4_h	1.3_h	2.1	0.6	0.7	1.2	1.0
USNM 221088	2.1	1.5	1.3	2.0	0.7	1.0	1.4	1.0
USNM 221089	2.2	0.9	0.9	1.9	0.4	0.7	1.2	0.7
USNM 221090	2.2	1.4	1.2	2.0	0.6	0.8	0.9	0.7
USNM 221091	2.2	1.4_h	1.1_h	2.1	0.6	0.7	1.4	0.9
USNM 221092	2.2	1.3	1.2	2.2	0.7	0.9	1.2	0.8
USNM 221093	2.2	1.4	1.3	2.4	0.9	0.9	1.2	1.0
USNM 221094	2.3	1.7	1.6	2.3	0.6	1.0	1.3	1.0
USNM 221095	2.3	1.2	1.2	2.4	0.6	0.9	0.8	1.0
USNM 221096	2.3	1.3_b	1.3	2.4	0.8	1.3	1.6	1.1
USNM 221097	2.3	2.1_h	1.9_h	2.6	0.7	0.7	1.4	1.1
USNM 221098	2.4	1.6	1.5	2.2	0.7	1.0	1.5	1.0
USNM 221099	2.4	2.0	1.6	2.2	0.7	0.9	1.1	1.7
USNM 221100	2.4	0.9	0.9	2.3	0.6	0.9	1.3	1.3
USNM 221101	2.4	1.3	1.1	2.3	0.6	0.9	1.6	1.1
USNM 221102	2.4	1.3	1.3	2.3	0.6	1.1	1.3	1.0
USNM 221103	2.4	1.3	1.3	2.4	0.7	1.1	1.2	0.9
USNM 221104	2.4	1.3	1.3	2.4	0.8	1.1	1.6	1.4
USNM 221105	2.4	1.5	1.4	2.5	0.7	1.0	1.3	1.2
USNM 221106	2.4	1.6	1.5	2.5	0.9	1.1	1.9	1.4
USNM 221107	2.4	1.0	1.0	2.6	0.6	1.0	1.3	1.1
USNM 221108	2.5	1.8	1.4	2.0	0.6	0.9	1.8	0.9
USNM 221109	2.5	1.4_b	1.3	2.2	0.7	1.1	1.9	1.3
USNM 221110	2.5	1.0	1.0	2.4	1.0	1.2	1.3	1.1
USNM 221111	2.5	1.5	1.4	2.4	0.8	1.2	1.2	1.2
USNM 221112	2.5	1.4	1.3	2.5	0.9	1.5	1.3	1.2
USNM 221113	2.5	1.8	1.4	2.5	0.6	1.0	1.6	1.1
USNM 221114	2.5	1.9	1.8	2.6	0.7	1.0	1.9	1.2
USNM 221115	2.6	1.5	1.2	2.3	0.6	0.7	1.6	1.3
USNM 221116	2.6	1.8_h	1.8_h	2.7	0.8	1.0	1.2	1.5
(block C)								
USNM 221117	1.4	1.0	0.9	1.7	—	0.1	—	0.5
USNM 221118	1.6	1.3	1.3	1.9	0.4	0.3	0.9	0.3
USNM 221119	1.8	1.4	1.3	2.2	0.2	0.1	—	0.6
USNM 221120	1.9	1.3	1.1	2.0	0.3	0.7	1.1	0.7
USNM 221121	1.9	1.5	1.5	2.1	0.4	0.6	1.3	0.6
USNM 221122	2.0	1.4_h	1.2_h	2.3	1.1	0.9	1.4	0.8
USNM 221123	2.1	1.4_h	1.4_b	1.9	0.8	0.9	1.2	0.8
USNM 221124	2.2	1.5	1.3	1.9	0.6	0.7	1.0	0.6
USNM 221125	2.2	1.1	1.1	2.2	0.3	0.6	1.5	0.8
USNM 221126	2.2	1.5	1.4	2.2	0.6	0.7	1.5	1.1
USNM 221127	2.2	1.0_{bh}	1.0_{bh}	2.4	1.2	1.2	1.1	0.9
USNM 221128	2.2	1.8_h	1.7	2.4	0.6	0.6	1.3	1.1
USNM 221129	2.3	1.8_h	1.4_h	2.3	0.6	0.9	1.4	0.9
USNM 221130	2.3	1.3	1.3	2.3	0.7	0.9	1.2	0.8
USNM 221131	2.3	1.5	1.5	2.4	0.7	1.1	1.3	1.0
USNM 221132	2.3	1.9	1.8	2.6	0.4	0.7	1.4	0.8
USNM 221133	2.4	1.0	1.0	2.3	0.8	1.2	1.2	1.0
USNM 221134	2.4	1.6	1.6	2.4	0.8	1.2	1.6	1.1
USNM 221135	2.4	1.4	1.4	2.6	1.0	1.1	1.7	1.0

Table 9.—Continued.

SMRH = Submarginal Ridge Height
MRH = Median Ridge Height
SMRD = Distance from highest point on submarginal ridge to anteriormost point of shell, measured parallel to shell length.
MRD = Distance from highest point on median ridge to anteriormost point on shell, measured parallel to shell length.

	Length	Hinge Width	Minimum Width	Maximum Width	SMRH	MRH	SMRD	MRD
USNM 221136	2.4	1.7	1.7	2.6	1.0	1.4	1.1	1.2
USNM 221137	2.5	1.8_h	1.7_h	2.5	0.6	0.9	1.4	1.1
USNM 221138	2.5	1.8_h	1.4_h	2.6	0.6	0.9	1.5	1.0
USNM 221139	2.5	1.6	1.6	2.6	0.6	1.2	1.3	1.2
USNM 221140	2.6	1.1	1.1	2.9	0.9	1.2	1.0	1.2
USNM 221141	2.7	2.1	1.9	2.6	0.9	1.1	1.5	1.1
USNM 221142	2.8	2.1	1.9	2.3	0.6	1.0	1.7	1.0

Table 10.—Statistics calculated from measurements of dorsal valves of two species of *Cooperina* Termier, Termier and Pajaud (1966).

	Measured Parameter	Calculated Statistic	Value (in mm)
Cooperina inexpectata	Hinge Width	mean	2.30
Mature individuals from West Texas		standard deviation	0.59
9 specimens		range	1.3–3.0
[USNM 152637a–i]	Maximum Width	mean	3.14
		standard deviation	0.65
		range	2.0–4.2
	Length	mean	3.46
		standard deviation	0.71
		range	2.3–4.5
Cooperina parva	Hinge Width	mean	1.28
Mature individuals from West Texas		standard deviation	0.29
6 specimens		range	1.0–1.8
[USNM 152638a–c; USNM 152639d, e, g]	Maximum Width	mean	1.95
		standard deviation	0.35
		range	1.5–2.4
	Length	mean	1.40
		standard deviation	0.11
		range	1.2–1.5
Cooperina inexpectata	Hinge Width	mean	1.35
Mature individuals from Venezuela		standard deviation	0.27
53 specimens		range	0.8–2.1
[USNM 221084–221116; USNM 221122–221131; USNM 221133–221142]	Maximum Width	mean	2.34
		standard deviation	0.21
		range	1.9–2.9
	Length	mean	2.35
		standard deviation	0.17
		range	2.0–2.8
Cooperina inexpectata	Hinge Width	mean	1.32
Apparent juvenile individuals from Venezuela		standard deviation	0.31
6 specimens		range	0.9–1.8
[USNM 221117–221121, USNM 221132]	Maximum Width	mean	2.08
		standard deviation	0.31
		range	1.9–2.6
	Length	mean	1.82
		standard deviation	0.31
		range	1.4–2.3

The roughly triangular outline, small ears, bunch of fine spines along the hinge, short hingeline, distinct interarea and peculiar spine arrangement clearly suggest placement of this form within the Rhamnariidae, but do not permit more than tentative assignment to the genus *Ramavectus*.

Superfamily **PRODUCTACEA** Gray, 1840
Family **MARGINIFERIDAE** Stehli, 1954
Subfamily **COSTISPINIFERINAE**
Muir-Wood and Cooper, 1960

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

Type Species.—Echinauris lateralis Muir-Wood and Cooper, 1960, p. 222, pl. 68, figs. 1–13.

Diagnosis.—

Costispiniferinae ornamented by spines and spine ridges on pedicle valve and spines and dimples on brachial valve, lateral halteroid spines long and extended laterally. (Cooper and Grant, 1975, p. 1000)

Occurrence.—The various species assigned to the genus *Echinauris* have been recovered from rocks ranging in age from earliest Wolfcampian to Early Guadalupian equivalents. It has been reported from West Texas (Muir-Wood and Cooper, 1960; Cooper and Grant, 1975), Guatemala (Stehli and Grant, 1970), Greece (Grant, *pers. comm.*, 1974), Tunisia (Termier and Termier, 1957), Pakistan (Grant, 1968), Nepal? (Waterhouse, 1966), China (Chao, 1927), Thailand (Waterhouse and Piyasin, 1970; Grant, 1976) and Timor (Broili, 1916).

Comparison.—Echinauris is distinguished from *Elliottella* Stehli (1955) and *Oncosarina* Cooper and Grant (1969) by the lack of dorsal exterior spines in the latter forms; from the Asian genus *Haydenella* Reed (1944) by the paucispinose ventral valve of that form; from *Costispinifera* by the greater spine density and anterior ventral costation of that form; from *Bothrionia* Cooper and Grant (1975) by the fold-sulcus development and ventral marginal rim of that form. The most readily apparent diagnostic characters of *Echinauris* are the aspinose "denuded" ventral umbonal region, the centripetally-directed dorsal spines, and the absence of strong radial ornament on either valve.

Discussion.—Echinauris has not been reported from Australia, southern Africa, or either polar region. In the Permian, it appears to have had a Tethyan ("tropical" to "subtropical") distribution.

Echinauris bella Cooper and Grant
Plate 4, figures 40–55; Plate 5, figures 1–2

Echinauris bella Cooper and Grant, 1975, p. 1003, pl. 326, figs. 1–58; pl. 410, figs. 9–13.

Description.—Small, less than average-sized for genus, concavo-convex shells; ovate outline interrupted by ventral ears. Commonly widest at hinge, but ears delicate, commonly broken or missing. Umbo swollen, greatest height at hinge. Both valves spinose; spines long, slender, curving. Anterior margin commonly evenly rounded, rarely slightly sulcate, straight in anterior view. Surface smooth, having faint concentric wrinkles or faint low costae, produced anterior to spine bases and quickly becoming obsolete anteriorly.

Ventral valve convex, having small apical cicatrix of attachment; umbo commonly overhanging long straight hingeline. Umbonal slopes of mature specimens bearing spine bases but no spines; delicate umbonal spines present in attached (cemented) juveniles. Interarea missing, but weak, very low ginglymus sporadically developed. Single row of posteroventrally directed small spines along hinge; one to several irregular rows of spines ventral to hinge. Cluster of long, halteroid spines arising at break in slope of flanks, just ventral to, but not on ears; directed laterally, ventrolaterally, and posteroventrolaterally. Ears narrow, triangular, set at a sharp angle to body, not bearing spines. Ornament spines sheathing remainder of valve, arising in roughly concentric rows normal to shell surface, turning abruptly anterodorsally following shell surface; last few generations curving dorsoposteriorly over anterior margin. Weak low costae, arising at spine bases, becoming obsolete anteriorly.

Dorsal valve concave, semi-circular in outline, having sloping flanks; commonly auriculate, ears thin, delicate, rarely preserved; reflexed, lying in plane of commissure. Spinelike lophidium, anterodorsally directed, projecting slightly beyond hinge. Surface pitted or very rarely bearing numerous short, very fine erect spines, anteriormost spines centripetally directed. Paired tufts of more commonly preserved, long centripetally-directed straight or slightly curving spines arising on ears and arching over vault of valve.

Ventral interior having deep umbonal cavity with low apical longitudinal ridge; ridge in articulated valves lying between lateral lobes of cardinal process. Elongate, anteriorly broadened adductor scars faintly impressed in median valve floor, flanked posteriorly by small, more equidimensional diductor scars. Ears slightly concave, abruptly separated from body cavity by coarsely crenulate ridges.

Dorsal interior having characteristic W-shaped cardinal process myophore, each lobe U-shaped posteriorly. Lobes appressed dorsally, moderately splayed ventrally; posteroventral extremities somewhat angular. Myophore set on short stout shaft; shaft bearing median ventral furrow. Weakly crenulate low marginal

ridges arising at base of shaft, running laterally, rarely continuing to anterior margin. Thin, low breviseptum running anteriorly from furrow of cardinal process shaft, terminating about midvalve. Anterior extremity pointed, free of valve floor in mature specimens, in gerontic specimens having expanded, spatulate, ventrally directed tip. Anteriorly broad, triangular, apparently smooth anterior adductor muscle scars flanking median breviseptum, somewhat raised on platforms. Posterior adductor scars smooth, small, elongate oval, somewhat inset into valve floor. Brachial ridges given off horizontally, commonly faintly raised, rarely endospinose anteriorly, endospines low. Valve surface very finely pustulose, pustules in radial rows nearer anterior and lateral margins.

Measurements (in mm).—

	Length	Dorsal Valve Length	Hinge Width	Mid-Width	Height
LOCALITY 13					
USNM 221148	4.5	3.8$_e$	4.0$_b$	4.6	2.0
USNM 221149	5.5$_e$	4.7	5.0$_b$	6.5$_b$	2.3
USNM 221150	5.8	5.3	5.0$_b$	6.1	2.7
USNM 221151	6.8	5.8	7.0$_b$	8.0	3.6
USNM 221152	8.0	6.5	7.5$_b$	8.7	5.5
USNM 221153	8.2	7.0	7.4$_b$	9.2$_b$	5.0
USNM 221154	8.5	7.0	8.6$_b$	8.9	5.9
USNM 221155	8.6	6.1	6.7$_b$	8.6	5.0
USNM 221156	8.7	6.5	9.5$_e$	9.0	5.5
USNM 221157	8.9	7.0	9.4$_b$	8.7	5.6
USNM 221158	9.0	7.2$_e$	8.2$_b$	9.2	5.6
USNM 221159	9.0	7.0	7.0$_b$	9.6	5.6
USNM 221160	9.1	6.9	8.2$_b$	9.1	4.8
USNM 221161	9.2	6.6	8.9$_b$	8.6	6.7
USNM 221162	9.3	7.0	10.2$_b$	10.0	5.6
USNM 221163	9.6	7.0	8.5$_b$	8.2$_b$	6.0
USNM 221164	9.6	6.7	9.3$_b$	9.0	5.5
USNM 221165	9.6	7.5	10.0$_b$	9.7	5.7
USNM 221166	10.0	6.5	9.8$_b$	9.2$_b$	6.2
USNM 221167	10.0	7.7	10.0$_b$	10.5	6.0
USNM 221168	10.2	6.9	8.6$_b$	7.9	6.3
USNM 221169	10.3	8.0$_e$	10.6$_b$	9.4	6.9
USNM 221170	11.0	7.7	9.0$_b$	9.0	7.1
USNM 221171	11.3$_e$	7.5$_e$	10.9$_b$	11.7	7.0
USNM 221172	12.7	8.4	11.7$_b$	11.1$_b$	6.6

Occurrence.—*Echinauris bella* is found in the West Texas area in the Cibolo and Road Canyon Formations of Late Leonardian age. In the Palmarito Formation it has been recovered from locality 13, where it is by far the most abundant brachiopod. A single well-preserved dorsal valve of *E. bella* was recovered from locality 6, block C.

Diagnosis.—Small *Echinauris,* with length and width nearly equal, but hinge commonly greater than midwidth, and scattered spines.

Types.—Figured Specimens: USNM 221173–221183; Measured Specimens: USNM 221148–221172.

Comparison.—The diminutive size of *E. bella* effectively separates it from *E. boulei* (Kozlowski, 1914), *E. interrupta* Cooper and Grant (1975), *E. irregularis* Cooper and Grant (1975), *E. lappacea* Cooper and Grant (1975), *E. lateralis* Muir-Wood and Cooper (1960), *E. liumbona* Cooper and Grant (1975), *E. magna* Cooper and Grant (1975), *E. productelloides* Cooper and Grant (1975), *E. subhorrida* (Meek, 1877) and *E. subquadrata* Cooper and Grant (1975) of the West Texas area. The heavy and sparsely distributed spines of *E. crassa* clearly differentiate that form from *E. bella.* The spinose brachial ridges best developed in *E. venustula* Cooper and Grant (1975) are missing from *E. bella,* thus distinguishing that form. The Guatemalan species *E. huehuetenanguensis* Stehli and Grant (1970) is somewhat larger, and more transverse than *E. bella.* The Asian species *E. opuntia* (Waagen, 1884) and the Chinese species *E. jisuensis* (Chao, 1927) are both larger forms than *E. bella.* The three species *E. circularis* Cooper and Grant (1975), *E. parva* Cooper and Grant (1975) and *E. venustula* exhibit several characters in common: narrow ventral hinge, as compared to the midwidth; variable density and directional development of long thin endospines along the anterior portions of the brachial ridges. Although the latter character was mentioned in a discussion of *E. bella* (Cooper and Grant, 1975, pp. 1003, 1005), I was unable to discover it in specimens referred to the species in the National collections.

Discussion.—The Palmarito forms are assigned to the species *E. bella,* although there are important differences between them and populations of the species in the West Texas area where it was first described. Text-figure 10 shows variability in form of the ventral valve in samples of *E. bella* from West Texas and Venezuela, as described by their length, midwidth and height. Although there is considerable overlap of the variability fields of the two samples, the North American form has greater length and midwidth components, while the Venezuelan specimens are proportionally higher. This is in part due to the higher proportion of juvenile specimens in the West Texas sample, but even with this bias recognized, the West Texas forms are a bit more transverse than their Venezuelan counterparts. In addition the West Texas forms have finer, more slender spines on both valves and tend to be shallower than the Venezuelan specimens. Spine diameter may be a parameter which is covariant with the substrate encountered by the settling spat (Grant, *pers. comm.,* 1974). Judging from the development of the median breviseptum of the

dorsal valve and the muscle attachment impressions in both valves, none of the *E. bella* from West Texas appear to have reached the same ontogenetic age as that seen in many gerontic Venezuelan specimens.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block C)	—	1	—	fine silicification
13	83	50	294	fine silicification

Echinauris cf. **E. lappacea** Cooper and Grant
Plate 5, figures 3–12

cf. *Echinauris lappacea* Cooper and Grant, 1975, p. 1010, pl. 336, figs. 1–31; pl. 476, figs. 1–18.

Description.—Small to medium-sized, average-sized for genus, concavo-convex shells; outline transversely oval to transversely rectangular; commonly widest at hinge. Ears small, triangular, delicate, set off from visceral cavity. Umbo low, only slightly swollen, not incurved over hingeline, without apical cicatrix of attachment. Both valves bearing spines of various sizes. Anterior margin commonly rounded to slightly indented in dorsal aspect; straight in anterior aspect.

Ventral valve deeply convex; greatest height commonly at midvalve. Umbonal slopes bearing spine bases but no spines. Low ginglymus present. Several irregular rows of spines ventral to hinge and on ears. Spines irregularly scattered over remainder of surface; more densely packed on lateral than mesial slopes, quincunxially arranged or in roughly concentric rows. Spine bases anteriorly somewhat elongate, suggesting costae. Slight mesial sulcus developed in larger specimens.

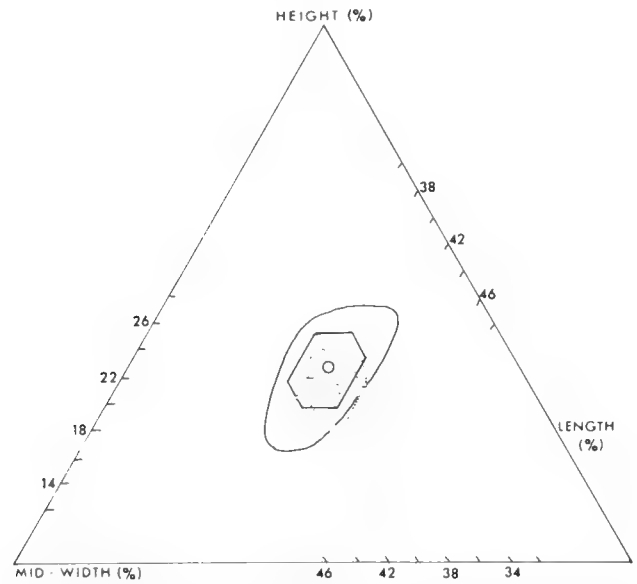
Dorsal valve concave; greatest depth anteriorly. Surface dimpled and spinose. Spines in dense wedge radiating anterolaterally from umbo, corresponding in position to break in slope between ears and visceral cavity; also on ears. Less densely packed, more slender, centripetally directed spines on remainder of valve exterior. Slight anteromesial fold developed in larger specimens.

Ventral interior unknown.

Dorsal interior having "ginglymus," perhaps articulating with negative structure in ventral valve, and pointed small lophidium. Cardinal process small, compact, broad-based, W-shaped in posterior aspect, having disjunct, vertically oriented bladelike lateral lobes and higher, broader ventromesial lobe. Lateral ridges diverging from hinge, continuing only to lateral margins. Alveolus not observed. Cardinal process merging anteriorly into broadened breviseptum; breviseptum separating two pairs of narrowly elongate muscle attachment scars. Muscle scars anteriorly raised on platforms; surfaces minutely crenulate, sloping posterolaterally. Breviseptum continued anterior to muscle scars as narrow, bladelike ridge, terminating in anteroventrally directed point just anterior to midvalve. Remainder of interior surface otherwise minutely pustulose.

Measurements (in mm).—

	Length	Dorsal Valve Length	Hinge Width	Mid-Width	Height
LOCALITY 11					
USNM 221184	9.6	8.0	10.2_{b}	11.6	6.2
USNM 221185	10.5	8.8	13.5	11.2	7.8
USNM 221186	10.5	8.7	12.1_{b}	11.5	7.9
USNM 221187	11.5_{c}	8.5	9.4_{bc}	11.8	7.0_{c}
USNM 221188	12.0	10.3	16.5_{b}	15.0	7.2
USNM 221189	12.9_{be}	10.6_{be}	17.0_{be}	15.5	8.9
USNM 221190	13.5	11.1	16.3_{be}	15.2	7.9



Text-figure 10.—Comparison of shell form of two population samples of *Echinauris bella* Cooper and Grant (1975). Dotted lines indicate statistics derived from measurements of a West Texas sample; solid lines indicate statistics derived from measurements of a Venezuelan sample; ○ indicates the mean of the distribution; the polygon surrounds one standard deviation on each side of the mean for all three variables; the ovoid form surrounds all pertinent data points.

Occurrence.—*E. lappacea* is known only from the Road Canyon Formation of the West Texas area. In the Palmarito fauna *E.* cf. *E. lappacea* has been recovered only from locality 11. A Late Leonardian age for this unit is not inconsistent with other faunal evidence.

Diagnosis.—Subrectangular *Echinauris* with low umbonal region, not overhanging hinge, coarse scattered ornament spines and thick mat of spines on dorsal valve.

Types.—Figured Specimens: USNM 221185, USNM 221188, USNM 221191–221193; Measured Specimens: USNM 221184–221190.

Comparison.—*Echinauris* cf. *E. lappacea* is easily distinguished from *E. bella* Cooper and Grant (1975), *E. circularis* Cooper and Grant (1975), *E. crassa* Cooper and Grant (1975), *E. huehuetenanguensis* Stehli and Grant (1970), *E. parva* Cooper and Grant (1975) and *E. venustula* Cooper and Grant (1975) by its larger size, and from *E. magna* Cooper and Grant (1975), *E. subhorrida* (Meek, 1877), *E. subquadrata* Cooper and Grant (1975) and *E.* sp. Stehli and Grant (1970) from the Chochal Limestone of Guatemala, by its smaller size. It is distinguished from *E. lateralis* Cooper and Grant (1975) by its wider hinge, from *E. boulei* (Kozlowski, 1914) by the pronounced ventral costation of that form, and from *E. huehuetenanguensis*, *E. interrupta* Cooper and Grant (1975), *E. liumbona* Cooper and Grant (1975) and *E. productelloides* Cooper and Grant (1975) by the more swollen, incurved umbo of those forms. Of the West Texas forms it most closely resembles *E. irregularis* Cooper and Grant (1975), from which it differs in its lower umbonal region and more transverse outline. It differs from *E. opuntia* (Waagen, 1884), from the Salt Range, in its lower umbo and less pronounced ventral costae.

Discussion.—The Palmarito specimens cannot definitely be assigned to the species *E. lappacea,* because they lack the dorsal endospines characteristic of the species in the West Texas area from which it was first described, because no ventral interiors are available for comparison, and because the suite of specimens is too small to give a fair representation of the range of variation that may be present.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
11	19	1	—	coarse silicification

Echinauris cf. **E. liumbona** Cooper and Grant
Plate 5, figures 13–19

cf. *Echinauris liumbona* Cooper and Grant, 1975, p. 1012, pl. 337, figs. 1–36.

Description.—Medium-sized, average-sized for genus, slightly to markedly transverse, concavo-convex shells; outline subpentagonal to sub-trigonal; commonly having greatest width anterior to hinge. Umbo commonly swollen, produced considerably posterior to hinge. Trail long; greatest height commonly anterior to midvalve. Ears small, delicate. Both valves sparsely spinose; dorsal spines very delicate, rarely preserved. Distinct broad ventral sulcus; indistinct dorsal fold. Commissure straight in anterior aspect.

Ventral valve deeply convex; tightly spiralled. Umbo high, apex slightly overhanging hinge; umbonal slopes steep; ears small, at sharp angle to body of shell. Median sulcus arising anterior to umbo, continuing to anterior margin. Broad band of spines running up break in slope between ears and umbonal slopes; scattered on flanks; in cluster just ventral to ears, and continuing around anterior margin. Umbo and posterior umbonal slopes non-spinose to sparsely spinose; spines rare in sulcus except anteriorly, low obsolete spine ridges there producing faint costation.

Dorsal valve broadly concave; greatest depth at midvalve, commonly markedly transverse. Ears small, delicate; set at sharp angle to body; rarely preserved. Ornament of concentric rugae and dimples; delicate spines present, but rarely preserved.

Ventral interior having two pairs of muscle scars in umbonal apex; mesial pair narrow, elongate, apparently smooth, set on slight callus platform. Smaller elongate lateral pair of smooth scars set slightly posteriorly, not on platforms. Ear baffles developed: slightly raised, interiorly striate; striae directed posteroventral-anterodorsal. Ears slightly concave. Remainder of surface finely pustulose.

Dorsal interior having large trilobate cardinal process myophore with short shaft. Two pairs of elongate triangular adductor scars flanking posterior portion of narrow breviseptum; breviseptum terminating near midvalve. Rough row of large endospines across anterior portion of the valve anterior to breviseptum, but indented posteriorly to meet end of breviseptum. Brachial ridges indistinct.

Measurements (in mm).—

	Length	Dorsal Valve Length	Mid-Width	Height
LOCALITY 4				
USNM 221211	11.6_{b}	9.1_{e}	14.1	7.4_{e}
USNM 221212	14.5	12.0_{e}	17.8_{be}	10.3_{be}
USNM 221213	19.9_{be}	12.8_{be}	21.4	12.9_{be}
LOCALITY 7				
USNM 221205	12.5	10.5	14.1	7.9_{be}
USNM 221206	13.9	11.1	16.2	9.9
USNM 221207	14.9	11.8	14.4	9.3
USNM 221208	15.0_{c}	11.4_{c}	15.8	10.9_{ce}
USNM 221209	16.0_{bc}	11.0_{e}	15.2	9.4_{c}
USNM 221210	17.5_{e}	12.9_{e}	17.8	11.4_{e}

Measurements (in mm).—Continued

	Length	Dorsal Valve Length	Mid-Width	Height
LOCALITY 8				
USNM 221194	11.6	10.3	15.4	7.6
USNM 221195	12.5	10.8	16.8	8.0
USNM 221196	13.5_{be}	11.3	16.5	9.1
USNM 221197	13.8	10.9	22.2_{b}	9.8_{be}
USNM 221198	14.5_{e}	12.4_{e}	18.0_{e}	9.0_{e}
USNM 221199	14.9	11.4	15.2	9.3
USNM 221200	15.4	11.5	18.4	9.8
USNM 221201	16.1_{be}	11.3	18.2	10.1_{be}
USNM 221202	16.4	12.2_{e}	21.0_{h}	10.1_{be}
USNM 221203	16.6_{be}	13.5_{be}	20.0	11.7_{e}
USNM 221204	16.8	12.5	17.1	10.9

Occurrence.—*Echinauris liumbona* occurs in the West Texas area only in the Road Canyon Formation, of Late Leonardian age. In the Palmarito fauna it has been recovered at localities 1, 4, 7 and 8. It is uncommon to rare at localities 1, 4 and 8 and common to abundant at locality 7. A Late Leonardian age for the Palmarito localities in which it occurs is consistent with biostratigraphic evidence provided by other faunal elements.

Diagnosis.—Subrectangular to transverse *Echinauris* with nearly naked umbonal regions, few spine ridges, emarginate anterior and swollen umbo.

Types.—Figured Specimens: USNM 221203, USNM 221204, USNM 221213; Measured Specimens: USNM 221194–221213.

Comparison.—*E. liumbona* may be distinguished from *E. bella* Cooper and Grant (1975), *E. circularis* Cooper and Grant (1975), *E. crassa* Cooper and Grant (1975), *E. irregularis* Cooper and Grant (1975), *E. parva* Cooper and Grant (1975), and *E. venustula* Cooper and Grant (1975) by the smaller average size of apparent mature individuals of those forms, and from *E. boulei* (Kozlowski, 1914), *E. magna* Cooper and Grant (1975), *E. subhorrida* (Meek, 1877) and *E. subquadrata* Cooper and Grant (1975) by the larger average size of apparent mature individuals of those forms. The comparatively wide hinge of *E. interrupta* Cooper and Grant (1975), *E. lateralis* Cooper and Grant (1975) and *E. productelloides* Cooper and Grant (1975) effectively distinguishes *E. liumbona* from those forms. *E.* cf. *E. liumbona* from the Palmarito Formation lacks the clusters of spine bases on the dorsal ears that are characteristic of *E. lappacea* Cooper and Grant (1975). On the Venezuelan form, the band of spines below the ventral ears that extends across the anterior margin, is one of its characteristic features. *E.* cf. *E. liumbona* is outwardly similar to forms described as *Echinauris* sp. (Stehli and Grant, 1970, p. 32, pl. 8, figs. 19–28) from the Chochal Limestone of Guatemala. There are, however, too few specimens of that form to allow a more definitive comparison. The specimens here referred to *E. liumbona* also bear external resemblance to an undescribed form (Wardlaw, *pers. comm.*, 1975) from the Gerster Formation (Wordian of Nevada). That form, assignable to the Paucispiniferidae, is generally more spinose, and possesses a complete marginal ridge and well-defined zygidium in the dorsal valve.

Discussion.—The Palmarito specimens tentatively referred to *Echinauris liumbona* have been recovered from four localities within the Palmarito Formation. At localities 1 and 7, the specimens are preserved by calcite permineralization. Consequently, while well-preserved, they are difficult to prepare in internal detail. The forms from localities 4 and 8 are silicified, and internal details may be seen somewhat more clearly. The silica replicas of locality 8 are quite coarsely silicified, and fine details are commonly obscured. No dorsal interiors were observed, but details were elucidated from partially decorticated shells in which the interior details were expressed in internal molds. At locality 4, however, preservation was fine. A single partial dorsal valve was recovered, which, although apparently incompletely silicified, showed a typical omega-shaped costispiniferine cardinal process myophore, without development of a zygidium.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	5	—	—	calcite permineralization casts, with some adherent silicified shell
4	4	1	9	
7	93	—	—	calcite permineralization casts, with considerable amounts of adherent silicified shell
8	10	—	1	

Family **PAUCISPINIFERIDAE** Muir-Wood and Cooper, 1960

Discussion.—The elevation of the Paucispiniferidae to family rank (Cooper and Grant, 1975) places it on equal footing with the Linoproductidae and the Marginiferidae, with each of which it shares many characteristics. The marginal ridge development of the Marginiferidae is commonly found in association with the zygidium, which feature is taken as the most salient diagnostic character of the family Paucispinifer-

idae (*e.g.*, in *Paucispinifera*). Which of the morphologic characters displayed by a shell shall be designated as "genetically controlled" and which "environmentally controlled" is, in consideration of forms with no living representatives, largely subjective. Internal characters are generally considered to be less affected by environmental variability than are external features, but this is not invariably so. In sum, the assignment of all small Productacea bearing a zygidium to the Paucispiniferidae is consciously subjective, and morphologically based. It is hoped that this provisional classification may be refined by more objective future work.

Genus **ANEMONARIA** Cooper and Grant, 1969

Type Species.—Marginifera sublaevis R. E. King, 1931, p. 89, pl. 23, figs. 15a–c (*non* figs. 13, 14, 17 = *Anemonaria inflata* Cooper and Grant, 1969, p. 8, pl. 5, figs. 28, 29)

Diagnosis.—

Outline subrectangular, widest at hinge, ears extended; profile deeply concavo-convex; trail with distinct sulcus. Surface nearly smooth except for numerous indistinct costellae on trail; spines few; 1 row on each lateral slope, scattered individual spines on trail and visceral disc. Pedicle valve interior with small sessile cardinal process with broad zygidium; breviseptum reduced. (Cooper and Grant, 1969, p. 8)

Occurrence.—Anemonaria is known from the Bone Spring, Cathedral Mountain and Road Canyon Formations of the West Texas region. In the present study it has been recovered from localities 1, 10 and 11. The ages represented by the occurrences of the West Texas forms are not inconsistent with the other biostratigraphic indicators for those Palmarito localities.

Comparison.—Anemonaria is externally similar to several genera of the Marginiferidae, but differs from all in its possession of a zygidium. Its regularity of form differentiates it from *Polymorpharia* Cooper and Grant (1975), while its more subdued radial ornament and distinctive spine pattern distinguish it from *Liosotella* Cooper (*in* Cooper *et al.*, 1953). In its fine, obsolescent ornament, *Anemonaria* Cooper and Grant (1969) resembles two species of *Paucispinifera, P. costellata* Cooper and Grant (1975), and *P. sulcata* Cooper and Grant (1975), in each of which the ornament is somewhat more strongly expressed than in *Anemonaria*. It may be that these forms are more closely related to *Anemonaria* than their generic assignment would indicate.

Discussion.—The genus *Anemonaria* was originally based on the type species *Anemonaria inflata* Cooper and Grant (1969). Various forms which R. E. King (1931) had named *Marginifera sublaevis,* but not the holotype of that species, were included in the synonymy of *A. inflata*. Later studies of King's material showed that the holotype of *M. sublaevis* was, after all, conspecific with *A. inflata*. Therefore, by the rules of nomenclature *A. inflata,* became a junior synonym to *A.* (*M.*) *sublaevis*. Cooper and Grant (1975), therefore so named the species when they described it: *Anemonaria sublaevis* (R. E. King, 1931).

Anemonaria sublaevis (R. E. King)
Plate 5, figures 20–27

Marginifera sublaevis R. E. King, 1931, p. 89, pl. 23, figs. 15a–c, ?16a, b, 19 (*non* figs. 13, 14, 17).
Anemonaria inflata Cooper and Grant, 1969, p. 8, pl. 5, figs. 28, 29.
Anemonaria sublaevis (R. E. King) Cooper and Grant, 1975, p. 1103, pl. 408, figs. 1–26.

Description.—Medium-sized, average sized for genus, having transverse rectangular to subpentagonal outline and prominent triangular ears; widest at hinge. Umbo small, low; posterior and anterior slopes steep; greatest height at midvalve. Surface ornament of low, obsolescent costellae; concentric rugae on ears.

Ventral valve deeply convex, with no delthyrium. Ginglymus low, poorly developed. Ears flat, in plane of commissure, separated from visceral slopes by single row of halteroid spines. Additional halteroid spines sparsely distributed over anterior and lateral slopes of valve. Spines very rare along hinge or on ears. Entire surface bearing very low obsolescent costellae; costellae about six in a five mm distance at midvalve, rarely increasing anteriorly by intercalation; becoming more apparent anteriorly. Commissure straight in anterior aspect. Anterior margin broadly sulcate, sulcus arising anterior to umbo and continuing to commissure.

Dorsal valve concave; greatest depth anterior to midvalve. Surface generally smooth, non-spinose, but anteriorly faintly costellate, costellae approximating in size those of opposite valve. Ears small, triangular, set at sharp angle to visceral slopes. Small rounded triangular lophidium surmounting low, variably developed zygidium. Margin anteromesially indented, anteriorly producing low broad fold.

Ventral interior having indistinct, apparently striate, paired diductor scars. Lateral walls of umbonal cavity slightly swollen, bearing shallow horizontal grooves; grooves articulating with zygidium of opposite valve. Distinct marginal ridge arising in umbo, continuing around shell near margin, evident anteriorly as low step on interior surface of trail; crenulate across ears on larger specimens. Inner surface smooth in smaller

specimens; in larger specimens bearing faint costellae which mirror external ornament.

Dorsal interior having small, stout cardinal process without shaft; myophore omega-shaped to triangular in posterior aspect, with small dorsally reflexed median lobe and broad lateral lobes. Mesial portions of lateral ridges at base of cardinal process produced posteriorly to form edge of zygidium, articulating with grooves in ventral umbo. Muscle scars indistinct, paired, narrowly elongate. Marginal ridges continuous, arising at base of cardinal process, surrounding visceral disc, distally geniculate across ears, distally gradually sloping anteriorly and laterally. Surface anteriorly and laterally faintly costellate; ornament more pronounced in larger specimens.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height	Material
LOCALITY 10					
USNM 221214	12.0	10.7_b	17.4_b	6.7_b	(ventral valve)
USNM 221215	12.1_b	13.3_b	18.0_b	5.2_b	(dorsal valve)
USNM 221216	13.7_b	16.3_b	20.1_b	7.0_b	(dorsal valve)
USNM 221217	13.8	16.8_b	18.7	8.9_b	(ventral valve)
USNM 221218	15.7	24.0_h	22.1_h	10.7_b	(ventral valve)

Occurrence.—*Anemonaria sublaevis* is known from the Bone Spring, Cathedral Mountain and Road Canyon Formations of the West Texas region. In the Palmarito Formation it has only been recovered from locality 10, where it is rare. An Early Permian age, based on its occurrence in North America, is not inconsistent with other biostratigraphic indicators in the assemblage at locality 10.

Diagnosis.—Medium-sized *Anemonaria* having slender halteroid spines and broad ventral sulcus.

Types.—Figured Specimens: USNM 221216–221220; Measured Specimens: USNM 221214–221218.

Comparison.—Since *A. sublaevis* is the only species of the genus, no infrageneric comparison is necessary. It may be distinguished from any of the species of *Hystriculina* Muir-Wood and Cooper (1960), which it resembles in exterior ornament, by its larger size and presence of a zygidium. It may be distinguished from species of *Liosotella* Cooper (*in* Cooper *et al.*, 1953) by the coarser ornament of those forms. It is probably very closely related to *Paucispinifera sulcata* Cooper and Grant (1975), from which it differs only in its more subdued radial ornament, and to *Paucispinifera costellata* Cooper and Grant (1975), which is distinguished by the high ridge bounding its ventral apical muscle scars. It is easily distinguished from other similar forms in the Palmarito: none of the Marginiferidae bear a zygidium. In addition, *Echinauris bella* Cooper and Grant (1975) is smaller, has more spines on the ventral valve, and bears dorsal spines as well, while *Echinauris* cf. *E. lappacea* Cooper and Grant (1975) bears on each dorsal ear a thick brush of centripetally-directed thin spines. The smaller umbo of *Echinauris* cf. *E. liumbona* Cooper and Grant (1975) in combination with other, less obvious characters, immediately distinguishes it from *A. sublaevis*.

Discussion.—As stated above, *Anemonaria sublaevis* appears most closely related to *Paucispinifera sulcata*. A slight suppression of the costellae of the latter would produce the appearance of the former. The Palmarito form is assigned to *A. sublaevis* with the decided reservation that the classification system is, with regard to these forms, beginning to reveal its arbitrary nature to a great extent. There appears to be a continuous range of variation in radial ornament between *A. sublaevis* and *P. sulcata*, though, with a single exception (in the Road Canyon Formation of West Texas), they do not co-occur in a single bed in any region. It is hoped that future studies of specimens from single localities, showing a more complete range of infrapopulation variation of these rare forms, will aid in clarification of their relationships.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
10	4	4	25	fine silicification

Anemonaria? cf. **A. sublaevis** (R. E. King)
Plate 5, figure 28

cf. *Anemonaria sublaevis* (R. E. King) Cooper and Grant, 1975, p. 1103, pl. 408, figs. 1–26.

Types.—Figured Specimen: USNM 221221.

Discussion.—Four fragmentary specimens from locality 11 and one ventral valve from locality 1 exhibit the characteristically subdued costellate exterior of *Anemonaria sublaevis* (R. E. King) and are of the proper size, shape and spine arrangement to warrant such specific assignment. No complete dorsal valve has been recovered, however, in the absence of which the presence or absence of a zygidium cannot be ascertained. Hence these specimens are only questionably assigned to the genus and species.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	1	—	—	calcite permineralization
11	3	—	1	internal casts, with considerable adherent silicified ventral valve shell material

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

Type Species.—*Paucispinifera auriculata* Muir-Wood and Cooper, 1960, p. 320, pl. 122, figs. 1–16.

Diagnosis.—Usually transversely rectangular, zygidium-bearing shells with poorly developed radial ornamentation.

Occurrence.—*Paucispinifera* is known from the West Texas area, in formations ranging in age from Late Wolfcampian (Bone Spring Fm.) to Late Guadalupian (Bell Canyon Fm.). A large species occurs in the Guadalupian (*Waagenoceras* zone) of Las Delicias, Coahuila, Mexico. In the Palmarito fauna it has been recovered only from locality 8.

Comparison.—*Paucispinifera* is distinguished from all genera outside the Paucispiniferidae by its having a zygidium in the dorsal valve. Of the Paucispiniferidae it is in general most closely related to *Liosotella* Cooper (*in* Cooper *et al.*, 1953), though certain species of *Paucispinifera* may bear closer resemblance to other paucispiniferids. *Liosotella* is commonly strongly costate on both trail and visceral disc, whereas *Paucispinifera* commonly is variably ornamented longitudinally along the shell surface.

Discussion.—Within the Paucispiniferidae, *Anemonaria* Cooper and Grant (1969), *Liosotella* and *Paucispinifera* appear to constitute a plexus of forms which exhibit an almost continuous range of variation in radial ornament. Future studies of large samples of these forms are likely to reveal even more extensive intergradation than is now evident. Two Palmarito forms, *Paucispinifera*? cf. *P. sulcata* Cooper and Grant (1975) and *Anemonaria sublaevis* (R. E. King, 1931) are here considered similar at the conspecific or subspecific level, a relationship which their present generic assignments do not indicate. The number of specimens available for comparison in the Palmarito fauna, however, is insufficient to warrant placement of *Anemonaria* in synonymy.

Paucispinifera? cf. **P. sulcata** Cooper and Grant
Plate 5, figures 29–32

cf. *Paucispinifera sulcata* Cooper and Grant, 1975, p. 1137, pl. 418, figs. 1–51; pl. 475, figs. 21, 22.

Description.—Medium-sized, small for genus, having transverse rectangular to subpentagonal outline and prominent triangular ears; widest at hinge. Umbo small, low; posterior and anterior slopes steep; greatest height at midvalve. Surface ornament of closely spaced costellae (commonly six in 5 mm at midvalve). Costellae weak on umbo, stronger anteriorly.

Ventral valve deeply convex, delthyrium obsolete. Ears flat, slightly concave; separated from visceral slopes by single row of halteroid spines. Additional halteroid spines sparsely distributed over anterior and lateral slopes. Spines very rare along hinge and on ears. Entire surface bearing closely spaced costellae; costellae increasing anteriorly by intercalation. Occasional stronger costellae arising abruptly at halteroid spine bases, continuing anteriorly to margin. Commissure straight in anterior aspect. Anterior margin distinctly sulcate; sulcus broad, commonly V-shaped, arising close to umbo and continuing to commissure.

Dorsal valve concave; greatest depth anterior to midvalve. Surface faintly costellate, costellae stronger anteriorly, spaced as on opposite valve. Ears large, triangular, set at obtuse angle to umbonal slopes. Small triangular spine surmounting apparent zygidium. Margin anteromesially indented, producing low broad fold anteriorly only.

Ventral interior unknown.

Dorsal interior having small trilobate cardinal process with short shaft. Elongate triangular muscle scars flanking slender breviseptum; breviseptum terminating at midvalve. Row of small endospines anterior to end of breviseptum, extending across valve. Brachial ridges given off horizontally, lightly impressed.

Measurements (in mm).—

	Length	Dorsal Valve Length	Hinge Width	Mid-Width	Height
LOCALITY 8					
USNM 221222	17.3	15.2	20.0_{e}	19.5_{e}	10.3_{c}
USNM 221223	17.9	13.5	29.4_{eh}	20.4	11.3
USNM 221224	18.3_{be}	15.6_{be}	25.2_{eh}	22.2_{be}	10.2

Occurrence.—*Paucispinifera sulcata*, in the West Texas region where it was defined, occurs only in the Road Canyon Formation (Leonardian). The form here questionably assigned to the species has been recovered in the Palmarito fauna from locality 8 where it is rare. A Leonardian age for this locality in the Palmarito is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Small *Paucispinifera*? with numerous costellae and a wide deep sulcus.

Types.—Figured Specimens: USNM 221222–221223; Measured Specimens: USNM 221222–221224.

Comparison.—Apparent mature individuals of *P. auriculata* Muir-Wood and Cooper (1960), *P. intermedia* Cooper and Grant (1975), *P. rara* Cooper and Grant (1975) and *P. tumida* Cooper and Grant (1975) are larger in size than are similar ontogenetic stages of *P. sulcata,* while "mature" specimens of *P. indentata* (Girty, 1909) are smaller. *P. costellata* Cooper and Grant (1975), which has radial ornament of the same scale and form as *P. sulcata,* bears a distinctive shelf surrounding the muscle attachment scars of the ventral apex. *P. latidorsata* (Girty, 1909), *P. quadrata* Cooper and Grant (1975), *P. spinosa* Cooper and Grant (1975) and *P. suspecta* Cooper and Grant (1975) have coarser radial ornament. *P. transversa* Cooper and Grant (1975) is far more transverse in outline. *P. rectangulata* Cooper and Grant (1975) is more square in outline, and more geniculate in lateral aspect. *P. magnispina* Cooper and Grant (1975) bears much larger halteroid spines. *P. parasulcata* Cooper and Grant (1975) has a very small ventral umbo, which projects little beyond the hingeline. *Anemonaria sublaevis* (R. E. King, 1931) is very similar to *P. sulcata,* yet may be distinguished by its less well-defined radial ornament. The presence of a zygidium in the dorsal valve effectively distinguishes *P.? sulcata* from other Palmarito productaceans, except *Anemonaria sublaevis.*

Discussion.—see discussion of *Anemonaria sublaevis.*

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
8	4	—	—	internal casts [dorsal valves]; medium-grained silicification [ventral valves]

Family **LINOPRODUCTIDAE** Stehli, 1954
Subfamily **LINOPRODUCTINAE** Stehli, 1954

Genus **HOLOTRICHARINA** Cooper and Grant, 1975

Type Species.—*Holotricharina hirsuta* Cooper and Grant, 1975, p. 1175, pl. 444, figs. 1–49; pl. 445, figs. 9–15; pl. 446, figs. 42–45.

Diagnosis.—

> Linoproductidae related to *Grandaurispina* but having two sizes of spines on the pedicle valve, non-costellate pedicle valve, but a capillate brachial valve. (Cooper and Grant, 1975, p. 1175)

Occurrence.—*Holotricharina* occurs in the Cathedral Mountain and Road Canyon Formations (Leonardian) of the West Texas area. In the Palmarito Formation it has been recovered from localities 4, 8 and 13. A Leonardian age for these localities is not inconsistent with biostratigraphic evidence from other faunal elements in the Palmarito.

Comparison.—*Holotricharina* may be distinguished from most Overtoniidae by its distinctively linoproductid cardinal process, and by the presence of fine capillae on the dorsal valve. The linoproductid *Grandaurispina* Muir-Wood and Cooper (1960) has a more regular spine arrangement, and lacks the dorsal radial ornament of *Holotricharina.* Both *Holotricharina* and *Grandaurispina* have laterally directed clusters of halteroid spines arising below the ventral ears, but those of *Grandaurispina* are distinctly coarser than the larger body spines, whereas those of *Holotricharina* are of about the same size. *Holotricharina* may be distinguished from all Linoproductidae except *Grandaurispina* by the presence of two distinct kinds of spines, and by the absence of any radial ornament on the ventral valve. The regularity of spine arrangement sets apart the overtoniid *Krotovia* Frederiks (1928), as well as the Asian Permian overtoniids *Comuquia* Grant (1976) and *Stictozoster* Grant (1976). The Asian Permian genus *Dyschrestia* Grant (1976) is externally probably closest to *Holotricharina,* but its less transverse outline, a cardinal process of more marginiferid than linoproductid aspect and the lack of a dorsal breviseptum clearly distinguish it from *Holotricharina.*

Discussion.—The two characters diagnostic of the genus, dorsal radial capillae and a linoproductid cardinal process are present only in the dorsal valve. There is only a single fragmentary, apparently immature dorsal valve in the entire Palmarito suite of *Holotricharina.* Nevertheless, the presence of two kinds of ornament spines, as well as their irregular distribution suggests assignment of the Venezuelan forms to the genus *Holotricharina.*

Holotricharina hirsuta Cooper and Grant
Plate 5, figures 33–42

Holotricharina hirsuta Cooper and Grant, 1975, p. 1175, pl. 444, figs. 1–49; pl. 445, figs. 9–15; pl. 446, figs. 42–45.

Description.—Medium-sized, average for genus, concavo-convex thin shells; outline transversely subrectangular to subtrigonal, interrupted by ears. Sides nearly straight to gently rounded in anterior aspect; anterior slope broadly rounded in lateral aspect. Anterior commissure unfolded. Hinge narrower than

midwidth; ears small, set at slight angle to body of shell. Dense cluster of slender halteroid spines along hinge, on and below ventral ears. Hinge spines directed posteriorly and posteroventrally, others directed posterodorsolaterally, groups of spines commonly crossing near ears. Additional suberect, anterodorsally directed halteroid spines scattered on anterior and ventrolateral slopes. Finer anteriorly directed recumbent ornament spines on slopes and flanks of ventral valve.

Ventral valve strongly and evenly convex in lateral profile, flat-topped and steep-sided in anterior profile. Beak small, pointed, umbo terminating above hingeline; umbo moderately swollen posteriorly, protruding back beyond hingeline. Sulcus rarely developed.

Dorsal valve moderately to deeply concave; greatest depth at or anterior to midvalve; steeper anteriorly than laterally. Ears only slightly set off from body of valve. Surface ornament of closely spaced concentric rugae; rugae weak mesially and anteriorly, very strong laterally and posterolaterally. Spines not observed; surface otherwise apparently smooth.

Ventral interior having large, subcircular, paired diductor scars developed subapically, bearing relatively widely spaced narrow radial ridges. Surface otherwise smooth.

Dorsal interior having small, slender bilobate cardinal process with minute median lobe, only slightly deflected dorsally, and small shallow alveolus. Muscle scars paired, apparently elongate suboval, separated by slender breviseptum; breviseptum extending to midvalve. Anterior half of valve finely endospinose.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Hinge Width	Mid-Width	Height
LOCALITY 4					
USNM 221225	12.7	11.3	10.8	16.7_{be}	6.4
USNM 221226	14.8	12.3	11.0	17.2_{be}	8.2
USNM 221227	16.5_{be}	14.1_{be}	19.2_{be}	21.1_{be}	10.3_{be}
USNM 221228	16.7_{be}	13.1_{be}	19.2_{eh}	21.2_{eh}	11.1_{e}
USNM 221229	17.7_{be}	14.1_{be}	24.8_{eh}	26.6_{eh}	10.7_{be}
LOCALITY 8					
USNM 221230	14.5	11.2	13.2_{be}	18.2	7.8
USNM 221231	16.0_{b}	12.4_{b}	14.0_{h}	20.8_{h}	9.8

Occurrence.—*Holotricharina hirsuta* is known from the Cathedral Mountain and Road Canyon Formations of the West Texas region. This species was recovered in the Palmarito Formation at localities 4 and 8. A Leonardian age for these localities is not inconsistent with the other faunal evidence available.

Diagnosis.—Medium-sized *Holotricharina*, somewhat transverse in outline, with numerous spines on the body.

Types.—Figured Specimens: USNM 221225, USNM 221227, USNM 221228, USNM 221230, USNM 221232; Measured Specimens: USNM 221225–221231.

Comparison.—*Holotricharina hirsuta* is one of three known species of the genus, all originally described from the West Texas area. It is distinguished from *H. sparsa* Cooper and Grant (1975) by the lesser numbers of spines on that form, and from *H.*? sp. 1 of Cooper and Grant (1975), by its smaller size. The Palmarito specimens assigned to *H. hirsuta* are somewhat larger than most of the West Texas individuals, but are here considered to be within the range of variation in size of the species. In addition, the Venezuelan examples are commonly more transverse than are their West Texas counterparts. This in itself might seem a basis for separation of the Palmarito specimens as a separate species, but it is considered that a larger suite of Venezuelan specimens should be studied before such distinctions are attempted.

A second Venezuelan form, *Holotricharina*? sp. A, is much larger than *H. hirsuta*. Its relationship to *H.*? sp. 1 is uncertain, however, since only a single relatively complete specimen of each is known.

Discussion.—Only a single fragmentary dorsal valve of *H. hirsuta* was recovered in the present collections. Small in size, the undifferentiated cardinal process and presence of a shallow submyophoral alveolus indicate it to be that of an immature individual. In all other characters, however, the Palmarito specimens can be assigned confidently to *H. hirsuta*.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
4	4	—	4	fine silicification
8	3	1	—	fine silicification; internal cast of a single dorsal valve

Holotricharina? sp. A
Plate 5, figures 43–45

Description.—Medium-sized, large for genus, thin, convex ventral valve; in general form, outline and spine arrangement as in *H. hirsuta*, except umbo greatly swollen, produced further posterior to hingeline.

Ventral interior having slight ginglymus developed mesially; surface otherwise smooth.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Hinge Width	Mid-Width	Height
LOCALITY 13					
USNM 221233	26.5	16.4_{e}	13.2	25.1	16.2_{bce}

Occurrence.—Holotricharina? sp. A is known from a single ventral valve recovered from locality 13. The age of the assemblage at that locality, based on other faunal evidence is latest Leonardian to Early Guadalupian.

Diagnosis.—Large *Holotricharina*? with swollen, posteriorly produced umbo and two sizes of spines.

Types.—Figured and Measured Specimen: USNM 221233.

Comparison.—Only *Holotricharina*? sp. 1 Cooper and Grant (1975) is of sufficiently large size to be confused with *H.*? sp. A. It may be distinguished by the presence of three distinct sizes of spines on the ventral valve, as contrasted to the two sizes seen in *H.*? sp. A. It may be that these two species are related more closely than their designations would indicate. The difference in type of spinose development would appear, however, to make this unlikely.

Discussion.—More formal designation of a species name for this form should await study of additional specimens of both it and related forms. Although fragments of ventral valve apparently belonging to this form were recovered at several localities, no recognizable piece of dorsal valve was found. In the absence of this, an unequivocal generic assignment cannot be made.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
8	—	—	1	fine silicification
10	—	—	1	fine silicification
11	—	-?-	—	fine silicification
13	—	—	1	fine silicification

Family **RETARIIDAE** Muir-Wood and Cooper, 1960

Genus **KUTORGINELLA** Ivanova, 1951

Type Species.—Kutorginella mosquensis E. A. Ivanova, 1951, p. 329.

Occurrence.—Kutorginella is known from latest Mississippian and Pennsylvanian and Permian strata. In the Mississippian it has been recognized only in Europe, while in the Pennsylvanian it is reported from both Europe and the North American midcontinent. In the Permian its range extends to include the South American continent as well (Samtleben, 1971).

Comparison.—Kutorginella may be distinguished from *Tubaria* Muir-Wood and Cooper (1960) by the wider hinge and distinctive long tubiform trail of that genus; from *Thamnosia* Cooper and Grant (1969) by the greater number of spines on species of that genus, these especially concentrated on the anterior portions of the trail and on the ears.

Discussion.—Antiquatonia Miloradovich (1945) is externally quite similar to *Kutorginella*: indeed, they differ only in the tubiform trail that may form a diagnostic character in the latter genus, but which all too often is not preserved. Internally, however, the shorter dorsal lateral ridges and the massive, sessile cardinal process clearly distinguish *Antiquatonia*. Variation in these very internal characters, however, in the Venezuelan specimens, indicates the close relationship existing between the two genera, notwithstanding their classification in two distinct families. Indeed, Sarytcheva (1971, p. 452) suggests that *Kutorginella* was derived in Early Pennsylvanian time from an *Antiquatonia*-like ancestor, if not *Antiquatonia* itself.

Kutorginella cf. **K. umbonata** (Muir-Wood and Cooper) Plate 6, figures 1–10

cf. *Retaria umbonata* Muir-Wood and Cooper, 1960, p. 231, pl. 70, figs. 1–15.

cf. *Kutorginella umbonata* (Muir-Wood and Cooper) Cooper and Grant, 1975, p. 1030, pl. 343, figs. 18–33; pl. 344, figs. 1–30.

Description.—Medium-sized, average for genus, subplanoconvex to concavo-convex thin shells with large body cavity; subtrigonal in outline; hinge equal to or slightly less than midwidth; distinctly bilobate in anterior aspect, with gently rounded flanks and distinct ventral sulcus; broadly domed in lateral aspect, having steep anterior and posterior slopes. Both valves geniculate. Umbonal regions strongly reticulate; anterior regions distinctly costellate. Valves sparsely spinose.

Ventral valve having low umbo, produced a small distance beyond hingeline. Ears thin, triangular, planar to somewhat convex exteriorly, set at acute angle to body. Umbo finely reticulate, having rugae stronger than costellae; rugae increasing in strength laterally to bases of ears, diminishing in strength anteriorly, obsolescent at margin of visceral disc. Costellae fine, commonly seven to eight in a 5 mm distance at mid-

valve; rarely increasing anteriorly by splitting or intercalation. Spines in single row roughly following hinge; in more distinct row up flanks, not on spine ridge, definitely mesial to break in slope between body and ears; scattered over flanks, sulcus and trail, increasing in size anteriorly; arising from crests of costellae. Distinct sulcus arising just anterior to umbo, continuing to anterior commissure. Delthyrium tiny, nearly obsolete.

Dorsal valve without spines, having planar to slightly concave visceral disc margin. Low obscure fold developed on visceral disc, becoming more distinct on trail, continuing to anterior commissure. Visceral disc finely, strongly reticulate; trail evenly, finely costellate. Tiny pointed lophidium closing ventral delthyrium.

Ventral interior having low, wide ginglymus extending laterally onto ears. Submarginal ridges non-crenulate, arising in umbo and continuing across bases of ears as ear baffles; not internally striate. Umbonal apex having sharp median ridge, separating paired, striate, anteriorly expanded, rounded triangular diductor scars; median ridge succeeded anteriorly by raised callus platform bearing paired elongate dendritic adductor scars. Diductors large, extending anterior of ends of adductors. Remainder of surface broadly reflecting exterior ornament.

Dorsal interior having variable cardinal process, with or without short shaft; commonly trilobed, with expanded median lobe, lobe dorsally deflected and mesially sulcate. Strong lateral ridges running along hingeline and across bases of ears as ear baffles; ridges sharply crested, but not crenulate or internally striate. Broad base of cardinal process narrowing anteriorly to form slender breviseptum; breviseptum continuing to visceral disc margin, posteriorly separating posteriorly broad, elongate oval, dendritic adductor scars, scars raised on callus platforms. Reniform, mesially concave, lightly impressed, finely pitted areas posterior and lateral to adductors. Remainder of surface reflecting exterior ornament.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height	Material
LOCALITY 4					
USNM 221234	19.1_{be}	30.0_{eh}	—	11.4_{e}	(dorsal valve)
USNM 221235	22.5_{be}	—	30.0_{eh}	16.3	(articulated valves)
LOCALITY 8					
USNM 221236	18.8	31.0_{h}	—	6.3	(dorsal valve)
USNM 221237	23.0	—	28.8	13.8_{b}	(articulated valves)

Occurrence.—*Kutorginella umbonata* has been recovered, in the West Texas region where it was first described, from the Cathedral Mountain and Road Canyon Formations. In the Palmarito the form here referred to the species appears at localities 1, 4, 7, 8 and 11. It is not abundant at any of these localities, but is commonest at localities 4 and 8. The Leonardian age of the West Texas forms is not inconsistent with biostratigraphic evidence available as a guide to the age of the Palmarito beds in which the related form occurs.

Diagnosis.—Large *Kutorginella* with anterior margin thrown into a broad plication.

Types.—Figured Specimens: USNM 221234–221239; Measured Specimens: USNM 221234–221237.

Comparison.—*Kutorginella umbonata* may be distinguished from *K. robusta* Cooper and Grant (1975) by the larger size and more subtle sulcation of the latter form; from *K. sullivanensis* (R. E. King, 1931) by the distinctive spine distribution of that form; from *K. uddeni* Cooper and Grant (1975) by the smaller lateral spines of that form and its less well-defined ventral sulcus. *K. lasallensis* (Worthen *in* Meek and Worthen, 1873) is somewhat more strongly costellate and has stronger, more numerous body spines; *K. parvispinosa* (Stehli, 1954) is a very similar form, but it is not so distinctly sulcate ventrally. *K. subquadrata* (Cooper *in* Cooper *et al.*, 1953) and *K. occidentalis* (Cooper *in* Cooper *et al.*, 1953) also lack this distinct character. *K. meridionalis* (McKee, 1938) also is less sulcate and has coarser costellation.

Discussion.—None of the Palmarito specimens shows the distinctive trail development that is characteristic of the Retariinae. No dorsal valve is preserved in its entirety, but the various pieces recovered allow the formulation of a composite description. The distinct deep ventral sulcus of the Palmarito form sets it apart from most other species of the genus, except *K. umbonata*. It does not appear to have as great a development of the anterior marginal ring of dorsal endospines as is common in *K. umbonata* in West Texas. The distinctive row of spines across the flanks, above the ventral ears, and across the anterior margin is clearly seen only on a single Palmarito specimen,

from locality 1. This specimen is unfortunately severely crushed, and none but exterior details can be discerned. For the above reasons, in addition to the comparative rarity of the form in the Palmarito Formation, no definite species assignment can be made.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	1	—	—	calcite permineralization
4	2	1	12	fine silicification; some internal casts
7	—	—	1	calcite permineralization
8	6	7	10	fine silicification; some internal casts
11	2	1	3	medium-grained silicification

Family **ECHINOCONCHIDAE** Stehli, 1954

ECHINOCONCHIDAE genus indeterminate
Plate 5, figure 46

Types.—Figured and Measured Specimen: USNM 221240.

Discussion.—A single specimen, comprised of the partial interior of a dorsal valve and the adjacent apical portion of the ventral valve of an unsilicified, apparent echinoconchid brachiopod was recovered from an horizon high in the Palmarito Formation. It was not collected during the present study, but forms part of the Arnold Collection, now housed in the collections of the National Museum of Natural History in Washington, D.C. This collection was assembled in the course of a chiefly stratigraphically-oriented study undertaken by H. C. Arnold in 1960 and later formally reported (Arnold, 1966). The specimen, designated as Ar. 981-R, was identified for that publication as "?*Bathymyonia* cf. *nevadensis* (Meek)," by Helen M. Muir-Wood. It has not, however, been formally described.

The myophore and shaft of the cardinal process have unfortunately been lost. Some diagnostic features, however, remain in the dorsal interior. The thin lateral ridges diverge slightly from the hingeline. The muscle attachment area appears small and poorly impressed. A thin median septum, flanked on either side by a broader, low submedian ridge, extends to about midvalve. Endospines, arranged in distinct concentric rows beyond the septum, are assumed to reflect an exterior ornament of concentric bands. The valve itself is only slightly concave and appears somewhat geniculate anteriorly.

The ventral umbo appears to extend considerably beyond the hinge.

The flattened dorsal valve, protruding ventral umbo, obscure brachial ridges and most of all the apparent concentrically banded ornament indicate proper assignment of this productacean to the Echinoconchidae.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Hinge Width	Maximum Width
USNM 221240 (Arnold Coll. Field No. Ar. 981-R)	37.4_e	31.5_e	29.6_b	32.6_e

Family **DICTYOCLOSTIDAE** Stehli, 1954

Subfamily **DICTYOCLOSTINAE** Stehli, 1954

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

Type Species.—*Peniculauris mckeei* Muir-Wood and Cooper, 1960, p. 280, pl. 100, figs. 1–7; pl. 101, figs. 1–3 = *Aulosteges subcostatus* R. E. King, 1931, p. 94, pl. 25, figs. 5–7.

Diagnosis.—Large semireticulate dictyoclostids having an irregularly semireticulate visceral disc region, numerous small body spines on the visceral disc and trail, and a brush of fairly slender but long halteroid spines on the ears. Numerous spines on the dorsal valve. Cardinal process commonly large, spreading, strongly trilobed.

Occurrence.—*Peniculauris* occurs in the West Texas region in beds of from Late Wolfcampian (Skinner Ranch Formation) to Late Leonardian (Road Canyon Formation) age. It appears in the Chochal Limestone (Leonardian) of Guatemala (Stehli and Grant, 1970), identified as *Kochiproductus*? sp. (p. 32, pl. 11, fig. 11; pl. 13, figs. 1–7) and as *Peniculauris mckeei* Muir-Wood and Cooper (1960) (Stehli and Grant, 1970, p. 32, pl. 11, figs. 7–10). In the Palmarito fauna it has been recovered from localities 1 and 5. A Late Wolfcampian to Late Leonardian age is consistent with other biostratigraphic indicators for these localities.

Comparison.—*Peniculauris* closely resembles *Kochiproductus* Dunbar (1955) externally, but may be

distinguished from that genus by its lack of an antron in the base of the dorsal breviseptum, a diagnostic feature of that buxtoniid genus. *Peniculauris* somewhat resembles *Squamaria* Muir-Wood and Cooper (1960), but lacks the auricular cluster of dorsal spines diagnostic of that genus. *Dasysaria* Cooper and Grant (1969), although similar in exterior ornament, lacks the dorsal spines characteristic of *Peniculauris*.

Peniculauris subcostata latinamericana
new subspecies
Plate 6, figures 11–20

Peniculauris mckeei Muir-Wood and Cooper, Stehli and Grant, 1970, p. 32, pl. 11, figs. 7–10.
Kochiproductus? sp. Stehli and Grant, 1970, p. 32, pl. 11, fig. 11; pl. 13, figs. 1–7.

Etymology of Name.—Engl. *latin american* + *a*.

Description.—Large, small to average for genus, subrectangular to transverse in outline, concavo-convex shells; widest at hinge, moderately to highly domed in anterior aspect, with narrow sulcus and steeply sloping flanks; anterior and posterior slopes rounded in lateral aspect; geniculation pronounced. Ears small, triangular to rounded, concave. Both valves spinose, ventral valve considerably so.

Ventral valve deeply convex, elongate to transverse; greatest height at venter; ovate to trapezoidal in outline, quite variable. Beak small, low, raised only slightly dorsal to hingeline; umbo comparatively small, projecting short distance posterior to hingeline. Ornament of (1) concentric rugae, very strong along hinge, weaker mesially, weakening anteriorly and becoming obsolete at venter, and (2) fine costellae, six to eight in a 10 mm distance posterior to venter, eight or more in a 10 mm distance on trail, becoming higher, wider, more prominent from umbo to venter; at venter abruptly splitting and thinning, becoming less prominent toward anterior margin; increasing anteriorly in each region by intercalation or splitting. Spines (1) in ray originating at beak, diverging slightly from hinge, spreading onto ears, there expressed as dense tuft of slender halteroid spines, (2) dispersed over surface of valve posterior to venter on locally raised intersections of costellae and rugae, increasing in size from umbo to venter, decreasing in size from venter anteriorly, very fine on trail, staggered on alternating costellae. Interspine portions of costellae distinctly lower, each spine concentrically adjacent to saddle between spines in next radial row. Trail repeatedly broken some distance anterior to venter, commonly exhibiting ten or more overlapping lamellar trails. Ears rounded or triangular, sides anterior to ears indented or not, quite variable. Distinct narrow sulcus, arising at umbo and continuing to anterior margin, somewhat obscured anteriorly by overlapping trails. Anterior commissure broadly rounded, slightly indented mesially.

Dorsal valve concave, greatest depth at about midvalve, surface finely costellate umbonally, more coarsely so anteriorly; finely rugose posteriorly, rugae becoming obsolete anteriorly. Both radial and concentric ornament less pronounced than on opposite valve. Maximum degree of reticulation at midvalve. Fine spines apparently present, rarely preserved, located on intersections of costellae and rugae, as on opposite valve. Ears gently rounded, concave; valve distinctly geniculate. Low broad fold, originating in umbonal hollow, broadening anteriorly, slightly indenting anterior commissure.

Ventral interior finely granulose, otherwise unknown.

Dorsal interior having small, short-shafted, typically dictyoclostid cardinal process; trilobate, median lobe of myophore dorsally deflected, mesially sulcate, all lobes crenulate. Lateral ridges arising at base of cardinal process, thinner and flatter laterally, diverging slightly from hinge, crossing bases of ears as distinct, somewhat raised, granulose to pustulose ridges, there expressed as low step in shell surface, step continuing around visceral disc. Broad base of cardinal process thinning anteriorly, replaced by narrow, bladelike breviseptum; breviseptum continuing beyond midvalve, terminating in slightly raised, slightly broadened keel. Breviseptum flanked posteriorly by two pairs of adductor muscle scars. Anterior pair coarsely dendritic, elongate triangular, broadening anteriorly, terminating short of brachial ridges; posterior pair elongate triangular, coarsely dendritic, broadening anteriorly, adjoining anterior pair posterolaterally, the two making a larger, more equilaterally triangular composite muscle scar. Both marks raised on low callus platforms. Brachial ridges given off horizontally, narrowly looped anteriorly. Remainder of surface (1) irregularly pustulose posterior to brachial ridges, (2) smooth to obliquely broadly ridged within brachial ridge field, and (3) covered by low, conical, striate, anteriorly directed, prostrate endospines mesial, anterior and anterolateral to brachial ridges. Endospines smaller anteriorly, raised on low ridges mirroring external costellae. Exterior fold internally reflected as anteriorly broadening mesial furrow, containing breviseptum.

Measurements (in mm).—

	Length	Surface Length	Hinge Width	Mid-Width	Height	Costae in 10 mm on trail
LOCALITY 1						
USNM 221241	39.9_c	77	59.2_h	46.3_c	30.0_c	9
USNM 221242	42.5	80	60.0_h	50.4_{eh}	28.3_b	8
USNM 221243	44.5_c	76	71.6_{eh}	57.5_c	26.2_c	8
USNM 221244 (holotype)	47.0	82	52.6_h	46.2	26.2	8
USNM 221245	48.0	95	50.0_e	45.1	33.3	9

Occurrence.—Peniculauris subcostata latinamericana n. ssp. is known at present only from Central and South America. Stehli and Grant (1970) reported it as *P. mckeei* Muir-Wood and Cooper (1960) and as *Kochiproductus*? sp., from the Chochal Limestone (Leonardian) of Guatemala. In the Palmarito fauna it has been recovered only from locality 1. A single set of extremely poorly preserved articulated valves, questionably referred to the subspecies, was recovered from locality 5.

Diagnosis.—Medium-sized, variably shaped *Peniculauris subcostata* having fine costae; costae increasing dramatically in number anterior to venter.

Types.—Holotype: USNM 221244; Figured Specimens: USNM 221242, USNM 221244–221248. Measured Specimens: USNM 221241–221245.

Comparison.—Peniculauris subcostata latinamericana n. ssp. is distinguished from *P. bassi* McKee (1938), *P. costata* Cooper and Grant (1975), *P. imitata* Cooper and Grant (1975) and *P. subcostata subcostata* (R. E. King, 1931) by the larger mean size of the costae in those forms; from *P. peniculifera* Cooper and Grant (1975) by the smaller size of the mature individuals of that species; from *P. ivesi* (Newberry, 1861) by the larger size and wider costae of that form; from *P. transversa* Cooper and Grant (1975) by the more transverse outline, larger ears, generally larger size and coarser costae of that form.

Some of the West Texas specimens referred by Cooper and Grant (1975) to *P. subcostata* (R. E. King, 1931) show the anterior proliferation of small costae peculiar to *P. s. latinamericana,* but not to the extent or degree exhibited by the majority of the Palmarito specimens. In addition the sample of the Venezuelan population shows a far greater degree of variation in form and outline than do the West Texas samples. Although there is some overlap in size between the two samples, it is readily apparent that the mean size of mature individuals is greater in the West Texas forms. Due to the extreme crushing suffered by most of the Venezuelan specimens, comparative measurements are not as impressive or consistent as they might be. *P. s. latinamericana* n. ssp. is easily distinguished from other Palmarito Dictyoclostinae: from *Spinifrons grandicosta* n. sp. by the broader costae and large anteroventral halteroid spines of that form; from *Rugatia intermedia* n. sp. and *R. occidentalis* (Newberry, 1861) by the smaller size, coarser ornament and aspinose dorsal valve of those forms.

Discussion.—Peniculauris subcostata, as clearly elucidated by Cooper and Grant (1975), is in a peculiar position. The type specimens, a holotype and three paratypes, all fragmental valves, were mistaken by R. E. King (1931) for *Aulosteges,* and were so considered until additional preparation by Cooper revealed their dictyoclostid affinities. The type specimens of *Peniculauris mckeei,* now in synonymy with *A. subcostatus,* constitute a much larger, more representative suite, yet the rules of taxonomic procedure determine that comparisons should formally be made with the primary types, not synonymous forms. The assignment of the Venezuelan forms to *P. subcostata latinamericana,* however, is entirely on the basis of comparisons made to Muir-Wood and Cooper's now-ineligible types and topotypic material, rather than to King's primary types.

The Guatemalan specimens here referred to *P. s. latinamericana* represent extremes of the range of variation of the Palmarito representatives. The two specimens described (Stehli and Grant, 1970, p. 32) as *Kochiproductus*? sp. (USNM 163587 and USNM 163588) are of a large form compared to most Palmarito specimens, with comparatively coarse costae, yet they show the anterior proliferation of costae well. The form and size of the larger specimen (USNM 163587) is similar to Palmarito specimen USNM 221243. The single shell (USNM 163575) described as *Peniculauris mckeei* (Stehli and Grant, 1970, p. 32) is more similar in size and form to a Palmarito specimen USNM 221245. In the presence of the Venezuelan material, it is not difficult to consider the Guatemalan specimens as individuals deriving from the same species population.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	3	4	26	calcite permineralization
5	1	—	—	coarse silicification

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

Type Species.—*Productus (Dictyoclostus) paraindicus* McKee, 1938, p. 241, pl. 46, figs. 5a–b.

Diagnosis.—Crudely reticulate and irregularly costate Dictyoclostidae, commonly with a cluster of large thick halteroid spines on the ears and a few scattered on the trail slope.

Occurrence.—*Rugatia* has been recovered from Permian rocks in the Western United States, Central America and, with this report, South America. In the West Texas area where it has been most extensively studied, it has been recovered from the Neal Ranch, Skinner Ranch and Bone Spring Formations (Wolfcampian) and the Cathedral Mountain and Road Canyon Formations (Leonardian). One species, *R. occidentalis* (Newberry, 1861) is known from the Kaibab Formation (Leonardian) of Arizona, and another, *R. andersoni* Stehli and Grant (1970) from the Chochal Limestone (Leonardian) of Guatemala. Two species, one of them new, are here reported from the Palmarito Formation of Venezuela. An Early Permian age for the localities in which these species were found is not inconsistent with other biostratigraphic indicators.

Comparison.—*Rugatia* may be distinguished easily from *Antiquatonia* Miloradovich (1945), *Spinarella* Cooper and Grant (1975) and *Dasysaria* Cooper and Grant (1969) by the finer radial ornament of those forms; from *Peniculauris, Spinifrons* Stehli (1954) and *Squamaria* Muir-Wood and Cooper (1960) by the presence of dorsal spines in those genera; from *Costiferina* Muir-Wood and Cooper (1960), *Liosotella* Cooper (*in* Cooper *et al.*, 1953) and *Antiquatonia*, which also have a single row of halteroid spines arising at the ventral umbo, but in none of which does the row pass over the surface of the ears themselves, but rather follows the break in slope between ears and body; from *Reticulatia* Muir-Wood and Cooper (1960), *Peniculauris* Muir-Wood and Cooper (1960) and *Stereochia* Grant (1976) by the stronger reticulation of those forms; from *Peniculauris, Reticulatia, Xestosia* Cooper and Grant (1975) and *Dasysaria* by their having a thick brush of spines on the ears, although one species of *Rugatia, R. paraindica* (McKee 1938) does approach this condition. *Nudauris* Stehli (1954) has a distinctive ornament of mixed costellae and costae, not seen in *Rugatia*. *Chaoiella* Frederiks (1933), unlike *Rugatia*, bears very weak radial ornament.

Discussion.—It is in one sense unfortunate that the type species of the genus *Rugatia* should be *R. paraindica*. In making this form representative of the genus, it follows that a trait like the tuft of spines on the ventral ears will be taken as pervasive in, rather than indicative of the genus. In actuality however, most species of the genus do not share this trait, but rather have a single well-defined row of halteroid spines arising on the ventral umbo and running out onto the ears.

Rugatia intermedia new species
Plate 6, figures 21–28

Etymology of Name.—L. *intermedia* = intermediate.

Description.—Medium to large, large for genus, concavo-convex transverse shells, trapezoidal in outline, widest at hinge, Highly domed, steep-sided in anterior aspect; steeply sloping anteriorly and posteriorly in lateral aspect; both valves strongly geniculate. Surface sparsely spinose. Umbonal regions and visceral discs semi-reticulate, having rugae stronger than radial ornament; anterior and lateral regions strongly costate. Distinct ventral sulcus; subtle dorsal fold.

Ventral valve deeply convex, having long acuminate concave ears set at sharp angle to body of shell. Single row of spines arising at umbo, increasing in size laterally and posteriorly, diverging from hinge at low angle; eight spines on each side of ventral umbo of specimen having hinge width = 46.4 mm. Additional very fine halteroid spines scattered on flanks and in sulcus; spines quite large near anterior margin. Costae increasing in size and strength anteriorly.

Dorsal valve concave, geniculate; triangular concave ears set off from excavate visceral disc by low oblique ridge. Surface dimpled, semireticulate on visceral disc, faintly rugose laterally and on ears; costae more evident anterolateral of visceral disc.

Ventral interior having low, wide ginglymus and open delthyrium. Bases of ear spines open to interior below ginglymus. Narrow, elongate, dendritic adductor muscle scars, posteriorly striate, on high platform; platform median in shell, narrowing anteriorly. Adductors separating large, anteriorly expanded, striate

diductor scars. Adductor platform extending to opposite margin of dorsal visceral disc. Surface anteriorly and laterally faintly granulose, bearing low furrows reflecting exterior ornament.

Dorsal interior having typical sessile dictyoclostid cardinal process with broadly trilobate myophore; median lobe mesially sulcate. Spinelike lophidium, serving to close ventral delthyrium, produced dorsally. Lateral ridges serving mesially as articulatory processes, following along hinge, becoming low, obsolete on ears. Broad base of cardinal process narrow anteriorly, forming slender bladelike breviseptum; breviseptum anteriorly raised, terminating at anterior margin of visceral disc. Breviseptum flanked posteriorly by large elongate triangular dendritic adductor scars, set on callus platforms. Brachial ridges given off horizontally, faintly impressed. Remainder of surface semireticulate, rugose or costate, mirroring external ornament.

Measurements (in mm).—

	Length	Surface Length	Hinge Width	Mid-Width	Height	Thickness
LOCALITY 10						
USNM 221249 (holotype)	26.3	50_e	46.4	32.6	21.6	12.0_e

Occurrence.—*Rugatia intermedia* occurs in the Palmarito Formation at localities 4, 8, 10 and 11. It is a rare element at localities 4, 10 and 11, but common at 8. Similar forms, *R. mckeei* Cooper and Grant (1975) of the West Texas region and *R. andersoni* Stehli and Grant (1970) from the Chochal Limestone of Guatemala, are of Leonardian age. A Leonardian age for the above localities is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Strongly costate, transverse *Rugatia* with a single row of spines on the ventral ears and distinctly reticulate visceral disc regions.

Types.—Holotype: USNM 221249; Figured Specimens: USNM 221249–221252; Measured Specimen: USNM 221249.

Comparison.—*Rugatia intermedia* is easily distinguished from *R. incurvata* (R. E. King, 1931) by its larger adult size, and from *R. paraindica* (McKee, 1938) by the larger size and greater number of ear spines of that form. It is more transverse in outline and somewhat larger than *R. convexa* Cooper and Grant (1975), and both larger and more strongly ornamented than the other Palmarito species, *R. occidentalis* (Newberry, 1861). It is probably most closely related to *R. mckeei,* which is larger, has fewer spines on the ears, and bears slightly less marked reticulation on the umbonal regions, and to *R. andersoni,* which is slightly smaller, less transverse, and bears weaker costae that are less closely packed than on *R. intermedia.* It is easily distinguished from other Palmarito Dictyoclostinae: from *Peniculauris subcostata latinamericana* n. ssp. by the larger size, more distinct ornament and greater spine density of that form; from *Spinifrons grandicosta* n. sp. by the dorsal fine and anteroventral coarse spines of that form.

Discussion.—*R. andersoni, R. intermedia* and *R. mckeei* evidently form a plexus within which specific distinctions are cloudy. Since the gradation is chiefly in shape and form, and because the Palmarito specimens are largely fragmented, no "quantitative" estimate of comparative similarity of *R. intermedia* to one of the other two species is here attempted.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
4	1	1	—	fine silicification; some casts
8	5	3	25	fine to medium silicification; some casts
10	1	—	—	fine silicification
11	1	1	3	fine silicification

Rugatia occidentalis (Newberry)
Plate 6, figures 29–35

Productus costatus Marcou (*non* Sowerby, 1827), 1858, p. 46, pl. 5, fig. 5.

Productus occidentalis Newberry, *in* Ives, 1861, p. 122, pl. 2, figs. 9, 10; R. E. King, 1931, p. 72, pl. 14, figs. 11, 12, 14 (*non* fig. 13 = *Rugatia paraindica* McKee, 1938, p. 239, pl. 46, figs. 1–4).

Productus (*Dictyoclostus*) *meridionalis* McKee *in* Stoyanov, 1936, p. 523.

Rugatia occidentalis (Newberry), Cooper and Grant, 1975, p. 1082, pl. 378, figs. 9–13.

non Productus occidentalis Newberry, Girty, 1909, p. 262, pl. 12, figs. 4a–c [=*Liosotella* Cooper (*in* Cooper *et al.,* 1953)].

Description.—Medium to large, average-sized for genus, concavo-convex shells, subquadrate to elongate rectangular in outline. Hinge width variable; slightly less than to slightly more than midwidth. Steep-sided, flat-bottomed, subrectangular in anterior aspect; spiral, somewhat geniculate in lateral aspect, having steep posterior slope and gently rounded anterior slope. Surface sparsely spinose. Umbonal regions having faint concentric lirae and faint reticulation; anterior regions broadly costate; costae low, obsolescent. Variable ventral sulcus developed. Commissure straight in anterior aspect, gently rounded in dorsal aspect. Delthyrium obsolete; low ginglymus present.

Ventral valve deep, having small, compact, distinctly concave ears. Single row of spines arising at umbo, increasing in size laterally and posteriorly, diverging from hinge at low angle; 11 spines on each side of beak on specimen with hinge width = 39.0 mm. Additional slender halteroid spines arising on crests of obsolescent costae, scattered on slopes and in sulcus, becoming more robust anteriorly. Costae arising and dying out anteriorly by intercalation.

Dorsal valve gently concave, with small concave ears, valve very sparsely spinose, spines rarely preserved. Ornament of faint concentric lirae.

Ventral interior faintly granulose near anterior and lateral margins, otherwise not observed.

Dorsal interior having typical sessile dictyoclostid cardinal process; trilobed myophore, with large, dorsally reflexed, mesially sulcate median lobe. All lobes corrugate. Lateral ridges short, low, dying out mesial to ears. Basal boss of cardinal process merging anteriorly into long slender breviseptum; breviseptum terminating at anterior end of visceral disc. Anterior adductor scars elongate, dendritic, diverging anteriorly from breviseptum; dendritic posterior adductor scars reniform, concave mesially, located posterolateral of anterior adductors. Both sets of scars set on slightly raised callus platforms. Anterior and lateral portions of valve not seen.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height
LOCALITY 1				
USNM 221253	21.5_c	39.0_{ch}	20.8_{ce}	17.8_c
USNM 221254	25.0_b	30.0_c	27.6_b	15.0_c
USNM 221255	28.3_b	32.2_c	30.0_b	16.5_c
USNM 221256	32.8_b	34.0_{ch}	30.0_b	19.7_c

Occurrence.—R. E. King (1931) reported *R. occidentalis* from various localities in the West Texas area, in beds ranging in age from Late Wolfcampian to Early Guadalupian. A subspecies, *R. occidentalis parvauris* Cooper and Grant (1975), came from the Cathedral Mountain Formation (Leonardian) in the same area. Newberry (1861) collected the type *Productus occidentalis* from the Kaibab Formation of the Grand Canyon region, Arizona, the age of which is Late Leonardian. In the Palmarito Formation this form has been recovered only from locality 1, for which an Early Permian age is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Elongate rectangular, steep-sided *Rugatia,* with small concave ears and subdued ornament.

Types.—Figured Specimens: USNM 221253, USNM 221254, USNM 221256, USNM 221257; Measured Specimens: USNM 221253–221256.

Comparison.—On the average, mature specimens of *Rugatia occidentalis* are larger than similar ontogenetic stages of *R. incurvata* (R. E. King, 1931), and smaller than like stages of *R. andersoni* Stehli and Grant (1970), *R. mckeei* Cooper and Grant (1975) or *R. paraindica* (McKee, 1938). A similar form, *R. convexa* Cooper and Grant (1975), is more tightly spiralled than *R. occidentalis*. Although some of the Palmarito specimens have the very small ears and short hinge of *R. occidentalis parvauris,* these appear in the Venezuelan specimens to intergrade with more typical *R. occidentalis,* so that assignment to that subspecies is not there justified. *R. occidentalis* may be distinguished from the other Palmarito species of the genus, *R. intermedia* n. sp., by its smaller size, less prominent, smaller ears, and the less pronounced reticulation of the visceral disc regions of both valves. It may as easily be distinguished from other Palmarito Dictyoclostinae: from *Peniculauris subcostata latinamericana* n. ssp. by the larger size, more distinct ornament and greater spine density of that form; from *Spinifrons grandicosta* n. sp. by the presence of dorsal fine and anteroventral coarse spines in that form.

Discussion.—The range of variation of topotypic specimens of *R. occidentalis* is not well-known. Because the Palmarito material is scanty and not well-defined stratigraphically, it is better to assign the form to an existing if incompletely understood species, than to erect another incompletely known species in order to justify real or imagined differences between the two.

The Palmarito specimens were all recovered from a limy shale, and in the process of compaction of that rock had been extensively crushed. They were not silicified and were removed mechanically from the enclosing matrix. Thus it is difficult to ascertain the original form of the shell with certainty.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	1	1	32	calcite permineralization
7	—	—	1?	calcite permineralization

Genus **SPINIFRONS** Stehli, 1954

Type Species.—*Spinifrons quadratus* Stehli, 1954, p. 318, pl. 20, figs. 6–10.

Diagnosis.—Large Dictyoclostidae with a tuft of large spines on the ears, large halteroid spines on the anterior median part of the trail and slender hair-like spines on the dorsal valve.

Occurrence.—*Spinifrons* is known from the Pennsylvania and Permian of the United States, though only a single species of Pennsylvanian age is referred to the genus (Stehli, 1954, p. 318). In the West Texas region it appears to be largely limited to Late Wolfcampian strata, although specimens questionably referred to *Spinifrons* spp. have been recovered from strata as young as Guadalupian. Other biostratigraphic indicators in the Palmarito Formation suggest that the age of the Venezuelan representatives of the genus lies in the Leonardian, if not Guadalupian.

Comparison.—*Spinifrons* is easily distinguished from other genera within the Dictyoclostinae: from *Antiquatonia* Miloradovich (1945), *Spinarella* Cooper and Grant (1975) and *Dasysaria* Cooper and Grant (1969) by the finer radial ornament of those genera; from *Squamaria* Muir-Wood and Cooper (1960) by the presence of a brush of dorsal ear spines in that genus; from *Reticulatia* Muir-Wood and Cooper (1960) and *Rugatia* Muir-Wood and Cooper (1960) by the absence of dorsal spines of any form in those genera; from all others by the presence of large halteroid spines, not only in a dense brush on the ears, but also in a conspicuous group anteromesially on the ventral sulcus and near the ventral anterior margin.

Discussion.—*Spinifrons* is easily identified if well preserved: if the dorsal spines and anteroventral halteroid spines are poorly preserved and (or) not observed, recognition of the genus can be very difficult. The specimens here questionably assigned to *Spinifrons grandicosta* n. sp., all poorly or incompletely preserved, had been initially assigned to the genus *Peniculauris* Muir-Wood and Cooper (1960), on the basis of the preserved spine arrangement. Later recognition of similarity of form and other diagnostic characters permitted assignment to *Spinifrons*.

Spinifrons grandicosta new species
Plate 7, figures 1–10

Etymology of Name.—L. *grandis* = grand, large + L. *costa* = rib.

Description.—Large, larger than average for genus, concavo-convex transverse shells; subpentagonal in outline, having small, rounded triangular ears. Anterior commissure gently rounded, not appreciably indented mesially. In anterior aspect moderately domed, with steep flanks; in lateral aspect tightly spiralled, geniculate, having steep anterior and posterior flanks and subparallel visceral disc and trail surfaces. Ornament of rugae and costae producing faintly reticulate surface posteriorly. Ventral valve spinose; dorsal valve apparently so, but spines not preserved. Umbo small, low, not protruding appreciably posterior or dorsad to hingeline. Slight fold and sulcus development.

Ventral valve deeply convex; greatest height at about midvalve. Ears curving smoothly into flanks. Surface ornamented by (1) irregular concentric rugae, arising at umbo, becoming obsolete ventral of hinge, posterior to venter, (2) irregular costae, weak at umbo, but increasing in strength anteriorly, increasing in number by irregular bifurcation and intercalation, or arising abruptly anterior of spine bases, continuing to anterior margin; four to five in a 10 mm distance on trail. Spines (1) in ray divergent from hinge, terminating laterally in sparse tuft of robust halteroid spines on ears, (2) as smaller ornament spines scattered over flanks and sulcus, on crests of costae at intersections with rugae or not, (3) as large, heavy erect halteroid spines on crests of costae near anterior margin, concentrated in sulcus and anteromesial portions of shell. Anterior commissure gently rounded, slightly indented in dorsal aspect. Minute open triangular delthyrium present.

Dorsal valve deeply concave; greatest depth at or slightly anterior to midvalve. Ears slightly set off from visceral disc by low rounded oblique ridge. Low obsolescent rugae, originating at umbo, covering visceral disc. Obsolescent costae, arising as fine costellae at umbo, appearing distinctly only on trail, there as broad folds separated by narrower furrows. Apparent spine bases scattered over visceral disc and trail, increasing in size distally. Anterior margin gently rounded, very slightly mesially indented. Low fold arising at umbo, continuing across visceral disc and trail to anterior margin.

Ventral interior having flattened ears, set off from visceral cavity by diductor-bounding ridges; ridges extending about one-half distance across bases of ears. Diductor muscle scars large, elongate triangular,

striate and flabellate, anteriorly broadening, inset into valve floor. Diductors separated posteromesially by narrowly elongate, paired, dendritic adductor muscle scars, raised on slight callus platforms. Interior of ears faintly granulose, remainder of surface minutely endospinose, having furrows on trail reflecting exterior costation.

Dorsal interior having typical dictyoclostid cardinal process: trilobed, with dorsally deflected mesially sulcate median lobe; lateral lobes considerably reduced. Lateral ridges diverging slightly from hinge; appearing to continue across ears as low, distinct ridges; continued at geniculation to about midvalve as low rounded step in shell surface. Base of cardinal process narrowing anteriorly to form long slender breviseptum; breviseptum continuing to point of geniculation, there terminating in high, very thin blade. Paired, broadly triangular, dendritic adductor muscle scars posteriorly flanking breviseptum, slightly raised on thin callus platforms. Brachial ridges given off horizontally; narrowly looped anteriorly. Surface granulose posterior to brachial ridges, smoother within brachial ridge loops; remainder minutely endospinose; endospines semierect, anteriorly directed, on trail arising from costae; costae reflecting exterior ornament.

Measurements (in mm).—

	Length	Surface Length	Dorsal Valve Length	Hinge Width	Mid-Width	Height	Thickness
LOCALITY 13							
USNM 221258	42.9_{eh}	—	—	60.6_{eh}	46_{eh}	25_{e}	—
USNM 221259 (holotype)	43.8	90_{e}	33.4	63.6_{b}	48.4	32.6_{e}	15.6_{e}

Occurrence.—*Spinifrons grandicosta* n. sp. occurs at locality 13 in the Palmarito Formation. A single ventral valve questionably referred to the species has been recovered from locality 8. The West Texas form probably most closely related to *S. grandicosta, S. quadrata* Stehli (1954), is largely limited to the lower Bone Spring Formation, of Late Wolfcampian age. This age is older than that inferred for the localities in the Palmarito in which *S. grandicosta* has been identified.

Diagnosis.—Larger than average subquadrate *Spinifrons* having coarse, extremely irregular ornament, robust halteroid spines and relatively low profile in anterior aspect.

Types.—Holotype: USNM 221259; Figured Specimens: USNM 221258–221260; Measured Specimens: USNM 221258, USNM 221259.

Comparison.—*Spinifrons grandicosta* is distinguished from *S. portlockianus* (Norwood and Pratten, 1855) and *S. delicatula* Cooper and Grant (1975) by the smaller size of the mature specimens of those species. *S. magna* Cooper and Grant (1975) is larger, more quadrate, and has relatively finer halteroid spines on the ears. The most similar form, *S. quadratus* is smaller, more finely and regularly ornamented, more steeply domed, and has lateral ridges that do not extend across the bases of the ears in the dorsal interior.

It is easily distinguished from other Palmarito Dictyoclostinae: from *Peniculauris subcostata latinamericana* n. ssp. and *R. occidentalis* (Newberry, 1861) by the smaller spines on the trail of those forms; from *Rugatia intermedia* n. sp. and *R. occidentalis* by the smaller size, less quadrate outline, and lack of tufts of ear spines in those forms.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
8	1	—	3	medium to coarse silicification
13	1	—	1	fine silicification

Spinifrons? cf. **S. grandicosta** new species
Plate 7, figures 11–15

Description.—Large, average-sized for genus, concavo-convex transverse shells; subpentagonal in outline. Lateral slopes gently rounded, venter slightly indented in anterior view; anterior and posterior slopes rounded in lateral view. Ears large, rounded, merging smoothly into visceral mass. Umbo low, small, protruding only slightly dorsal and posterior to hingeline. Distinct costae arising as costellae at umbo, increasing anteriorly in size, and in number, by intercalation and bifurcation; anteriorly of venter quite strong, coarse. Rugae, distinct posteriorly, becoming somewhat weaker anteriorly, rather abruptly dying out at venter. Both valves spinose.

Ventral valve broadly convex, geniculate; greatest height at or anterior to midvalve; coarsely reticulate from umbo to venter; rugae abruptly disappearing at

venter; costae anterior to venter coarse, four to five in a 10 mm distance on trail, separated by furrows about equal in width to costae. Ears broad, slightly flattened; body not appreciably indented anterior to ears. Small triangular open delthyrium. Spines (1) in ray from umbo to ears, (2) as dense tuft of coarse halteroid spines on ears, (3) as fine spines scattered over surface of visceral disc on intersections of rugae and costae. Spines on locally raised portions of costae, staggered so that no spine is concentrically adjacent to one on neighboring costa. Spines apparently rare to absent on trail. Distinct broad mesial sulcus arising at umbo, continuing to indent anterior commissure. Broken-off trails common anteriorly, there forming distinct overlapping lamellae.

Dorsal valve slightly to deeply concave, visceral disc planar to slightly concave, junction with trail distinctly geniculate. Ears flattened. Visceral disc finely reticulate; rugae fine, rather uniform; costae fine umbonally, increasing anteriorly in size; in number by intercalation. Trail broadly costate, there commonly bearing four to six rounded costae in a 10 mm distance, costae separated by considerably narrower furrows. Narrow fold arising anterior to shallow umbonal hollow, continuing to, and indenting anterior margin. Fine, delicate, erect spines scattered over visceral disc in rough quincunx pattern; absent or not preserved on trail. Minute lophidium, aiding in closure of ventral delthyrium.

Ventral interior having raised elongate median callus platform bearing paired dendritic adductor muscle scars; platform flanked by larger, anteriorly broadened, radially striate, triangular diductor muscle scars inset onto valve floor and lateral umbonal walls. Distinct muscle-bounding ridges, non-crenulate, arising in umbo, running along posterolateral margins of diductor scars, extending about one-half way across bases of ears, overhanging visceral cavity. Distinct curved ginglymus present. Ears slightly concave, smooth. Surface otherwise minutely pustulose to finely pitted.

Dorsal interior having typical sessile to semi-erect, posterior- to posterodorsal-facing cardinal process myophore; myophore trilobate, with larger median lobe dorsally deflected, mesially sulcate. Shaft short to obsolete. Lateral ridges running along hinge, diverging from hinge to bend across bases of ears; anterior extent or continuation not observed. Broad base of cardinal process narrowed anteriorly to form slender low breviseptum; breviseptum terminating nearly opposite anterior margin of dorsal visceral disc in broadened, raised blade. Paired, dendritic, broadly triangular adductor scars posteriorly flanking breviseptum; scars bounded posterolaterally by low, incipient secondary septum, this arising from broad base of cardinal process. Coarse, raised brachial ridges given off horizontally from anterior end of adductor scars, narrowly looped anteriorly.

Measurements (in mm).—

	Length	Hinge Width	Mid-Width	Height	Thickness
LOCALITY 11					
USNM 221261	40_{be}	30.5_{b}	47.6_{b}	—	13.1_{e}
USNM 221262	—	67.2_{b}	46.5_{e}	34_{e}	19.0_{b}

Occurrence.—*Spinifrons*? cf. *S. grandicosta* n. sp. occurs in the Palmarito fauna at localities 3, 4 and 11. It is rather rare at localities 3 and 4 and common at locality 11.

Diagnosis.—Like *Spinifrons grandicosta,* but aspinose or rarely spinose on the trails.

Types.—Figured Specimens: USNM 221262–221266; Measured Specimens: USNM 221261, 221262.

Discussion.—Because it lacked the anteroventral trail spines diagnostic of *Spinifrons,* I first assigned this form to *Peniculauris* Muir-Wood and Cooper (1960). Later comparison with specimens assigned to *S. grandicosta,* showed great similarities, but no exact correspondence. In the absence of any traces of ventral trail spines, these forms can only questionably be assigned to *Spinifrons,* although they share many of the specific characters of *S. grandicosta.*

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	1	—	—	fine silicification
4	1	—	—	medium to coarse silicification
11	7	—	—	fine to coarse silicification

Suborder **OLDHAMINIDINA** Williams, 1953
Superfamily **LYTTONIACEA** Waagen, 1883
Family **LYTTONIIDAE** Waagen, 1883

Discussion.—Worldwide distribution of lyttoniid brachiopods made possible prediction of their presence in rocks of proper age and lithotype in Venezuela. Their previous absence from reports and faunal lists was probably due, among many other factors, to the search for fossils chiefly in rocks that preserved soft-bottom assemblages. The environments represented by such rocks lacked the hard substrate necessary for the cemented attachment of the lyttoniids (Hoover, 1975).

Genus **COLLEMATARIA** Cooper and Grant, 1974

Type Species.—*Collemataria elongata* Cooper and Grant, 1974, p. 137, pl. 139, figs. 11, 17–20; pl. 170,

figs. 1–16; pl. 171, figs. 1–18; pl. 172, figs. 1–16; pl. 173, figs. 1–40; pl. 181, figs. 12–15; pl. 183, figs. 22–23; pl. 191, fig. 10.

Diagnosis.—Usually large Lyttoniidae having progressive lateral septa, posterior callus flap for attachment, and hinge at margin of cowl.

Occurrence.—Specimens referable to *Collemataria* have been reported to date only from the West Texas area, in rocks of from Wolfcampian (Skinner Ranch Formation) to Guadalupian (Bell Canyon and Capitan Formations) age.

Comparison.—*Collemataria* might best be called the "North American *Leptodus,*" since it includes many of the Western United States species formerly assigned to that genus. Many of these species were removed from *Leptodus* Kayser (*in* Richthofen, 1882) upon recent study of type specimens of the genus that revealed the presence of a ventral diductor muscle attachment area in that form. This attachment, bounded by shell plates, is a feature not seen in many of the American forms. The genus *Collemataria* was therefore erected to house these *Leptodus*-like forms which had no well-defined muscle attachment areas.

Collemataria may be distinguished from all Lyttoniidae except *Leptodus* and *Petasmaia* Cooper and Grant (1969) by the manner of attachment to the substrate. In these three genera, the callus shell growth above the ventral valve hinge is posterior, forming a flap, which is reflexed ventrally and joins with the apex as a secondary site of shell attachment. The other genera of the Lyttoniidae have a similar shell structure, but it grows anteriorly, forming a cowl, and giving the entire shell a more conical aspect. Both *Leptodus* and *Petasmaia* have so-called "dental plates" (muscle field bounding ridges), located at either side of the midline in the ventral interior apex. While those of *Petasmaia* are quite strong and well-defined, those of *Leptodus* are less so. *Collemataria* rarely exhibits any indication of the scope of its diductor musculature, beyond the shape and form of its cardinal process.

Collemataria venezuelensis new species
Plate 7, figures 16–23

Lyttoniid specimen of Hoover, 1975, p. 152, text-fig. 2.

Etymology of Name.—Venezuela + L. *-ensis* = at the place of.

Description.—Small, commonly low, relatively broad, ostreiform shells having irregular, concentrically wrinkled exterior. Attached at apex and by everted posterior callus flap, cicatrix commonly at considerable angle to plane of shell. Valve floor flat or concave, with margins commonly flexed dorsally.

Ventral interior having narrow, straight hinge, inset at junction of valve and relatively large posterior flap; ventrally bearing small symmetrical articulatory processes. No apparent muscle scars or plates defining muscle field. Seven to twelve, commonly eight to nine longitudinally compressed, angustilobate to solidiseptate septa of subuniform height, having posteriorly fluted or beaded faces. Posteriormost two to three lateral septa approaching anguliseptate condition. Well-defined median ridge extending from just anterior to hingeline as sharp solidiseptate form, commonly mesially grooved; narrowly bifurcate anteriorly.

Dorsal valve small, thin, having narrow straight hinge; commonly bent at high (nearly 90°) angle near bifurcation to conform to similar deflection in ventral valve. Surface smooth, rounded, having low median depression extending anteriorly from hinge to bifurcation. Bifurcation persistent, not narrowed or healed anteriorly. Lateral lobes separate, distinct, not healed laterally.

Dorsal interior having small, commonly eccentrically positioned, bilobate to quadrilobate cardinal process, set on very short shaft. Narrow median ridge arising at base of cardinal process, doubled or longitudinally grooved and broadening anteriorly up to bifurcation. Lobes concave, commonly having inner linear or beaded marginal rim.

Measurements (in mm).—

	Length	Maximum Width	Height
LOCALITY 6 (block A)			
USNM 221267	16.3_b	20.8_b	6.8_b
USNM 221268	20.1_b	20.6_b	5.7_b
USNM 221269 (holotype)	26.6_b	20.7_b	14.0_b
USNM 221270	32.4_b	24.4_b	5.8_b

Occurrence.—*Collemataria venezuelensis* n. sp. has only been recovered from locality 6, block A. Blocks B and C from the same locality contain no traces of the form, indicating its patchy distribution. The most similar previously described species of the genus, *C. spatulata* Cooper and Grant (1974) is known from the Bell Canyon and Capitan Formations (Guadalupian) of West Texas. Such an age assignment is not inconsistent with that provided by other biostratigraphic indicators for this Palmarito locality.

Diagnosis.—Small *Collemataria,* having discrete low lateral lobes and narrow, uniform lateral septa. Ventral valve cemented to substrate near beak only; remainder of valve commonly at a high angle to substrate.

Types.—Holotype: USNM 221269; Figured Speci-

mens: USNM 221269–221274; Measured Specimens: USNM 221267–221270.

Comparison.—The Palmarito specimens are easily differentiated from other species of *Collemataria*. *C. americana* (Girty, 1909) is similar in overall appearance but tends to be larger and to have a more granulose interseptal area in the ventral interior than does *C. venezuelensis*. *C. batilliformis* Cooper and Grant (1974) is typically anteriorly constricted, in some cases to such a degree that the anterior margin is tubiliform. *C. elongata* Cooper and Grant (1974) and *C. gregaria* Cooper and Grant (1974) are much larger than *C. venezuelensis*: the former also differs in its higher lateral septa, while the lateral lobes of the dorsal valve are commonly merged in the latter. *C. irregularis* Cooper and Grant (1974) in general has a deeper shell, with greater development of the cowl. *C. marshalli* (Stehli, 1954) has thick, high lateral septa, quite unlike the narrow, more uniform ones of *C. venezuelensis*. *C. platys* Cooper and Grant (1974) is commonly cemented to the substrate over much of its ventral surface, unlike *C. venezuelensis*, in which attachment is limited to the apex and posterior flap, while the remainder of the shell lies at a considerable angle to that plane. *C. spatulata* is commonly somewhat larger and flatter than *C. venezuelensis*, though of the West Texas forms it is the most similar to *C. venezuelensis*.

Discussion.—The present collection of *C. venezuelensis* consists of just over forty specimens, many of them fragmentary. Only two sets of articulated valves were recovered, and only a single set is separable so that the interior may be examined. Most specimens are missing much of the lateral and anterior margins.

The remainder of the brachiopod assemblage collected from locality 6, blocks A, B and C consists of small forms. Some of these may be immature, though in some cases distinct evidence of maturity is present (*e.g.*, loop development in Terebratulida). *C. venezuelensis* is by far the largest brachiopod present, although it is smaller than many previously described lyttoniids. Although some of the specimens bear juvenile characters (predominance of angustilobate, as opposed to solidiseptate septa; small, commonly bilobate, rather than quadrilobate cardinal process myophore), sufficient numbers of specimens are present to demonstrate that mature individuals are also represented.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block A)	1	10	44	fine silicification

Order **RHYNCHONELLIDA** Kuhn, 1949
Superfamily **RHYNCHONELLACEA** Gray, 1848
Family **PONTISIIDAE** Cooper and Grant, 1976a

Discussion.—This family, created from part of Wellerellidae (*sensu lato*) includes forms which externally resemble *Wellerella* Dunbar and Condra (1932) (*sensu stricto*) but lack the dorsal median septum characteristic of wellerellids. In *Wellerella* (*sensu stricto*) however, this septum is limited to the apical portion of the valve. In the National collections, some specimens identified as *W. girtyi* Cooper and Grant (1976a) have such a small dorsal median septum that it cannot readily be discerned; in the same collection, specimens of *Pontisia stehlii* Cooper and Grant (1969), an external homeomorph of *W. girtyi*, have a "median ridge" that rises apically to join the underside of the hinge plate in the dorsal valve, a condition most atypical for that genus. Cooper and Grant (1976a, p. 2019) state

> In old specimens [of *Pontisia*] the low [median] ridge often swells to a boss posteriorly under the hinge plate. This simulates *Wellerella* but the boss is never a septum although it may help to support the hinge plate.

While the Pontisiidae and Wellerellidae appear to intergrade in terms of development of the median septum, they include too diverse a group of forms to be considered as a single family. Hence the somewhat artificial distinction is necessary, to allow recognition of workable, if not strictly valid family groupings. The spatio-temporal continuum of organic life may provide a more-or-less continuous gradation of phenotypes. When such a data set is incomplete, distinctions appear clearcut; as sampling becomes more comprehensive however, the sharp edges of differentiation become somewhat more rounded.

Genus **PONTISIA** Cooper and Grant, 1969

Type Species.—*Pontisia stehlii* Cooper and Grant, 1969, p. 13, pl. 4, figs. 7–10.

Diagnosis.—Pontisiids with hinge plate similar to that of *Wellerella* but not supported by a median septum.

Occurrence.—*Pontisia* is known from North, Central and South America, and has been reported in Thailand (Grant, 1976). Its range almost certainly is greater than this, but since familial and generic distinctions are based upon internal characters, many previously described forms [*e.g.*, *Wellerella* (*sensu lato*)] cannot properly be reassigned until extensive additional preparation has been undertaken.

Comparison.—*Pontisia* may be distinguished with ease from other genera of the Pontisiidae: *Lirellaria* Cooper and Grant (1976a) is costellate, while *Divari-*

costa Cooper and Grant (1969) has bifurcating costae; a number of the median costae of the dorsal fold of *Antronaria* Cooper and Grant (1976a) are characteristically depressed; *Aphaurosia* Cooper and Grant (1976a) has irregular radial ornament and a more rounded outline; species of *Acolosia* Cooper and Grant (1976a) are commonly smaller and smoother than those of *Pontisia*; *Anteridocus* Cooper and Grant (1976a) has only rudimentary dental plates, in contrast to the strong ones seen in species of *Pontisia*. As stated above, *Pontisia* may be distinguished from most species of *Wellerella,* by the presence of a dorsal median septum in those forms. Some species of *Pontisia* may resemble *Allorhynchus* Weller (1910), in that the radial ornament arises at or just anterior to the beaks, but the presence of an undivided hinge plate clearly permits their assignment to *Pontisia*.

Pontisia stehlii Cooper and Grant
Plate 7, figures 39–48

Pugnoides texanus R. E. King (*non* Shumard, 1860), 1931, p. 108, pl. 34, figs. 5–9.

Pugnoides elegans R. E. King (*non* Girty, 1909) part, 1931, p. 106, pl. 33, figs. 12, 13; pl. 34, fig. 4 (*non* figs. 2, 3).

Pontisia stehlii Cooper and Grant, 1969, p. 13, pl. 4, figs. 7–10.

Pontisia stehlii stehlii Cooper and Grant, 1976a, p. 2027, pl. 517, figs. 21–25, 38–47; pl. 533, figs. 40–61; pl. 534, figs. 1–49; pl. 552, fig. 14.

Description.—Small to medium sized, average to large for genus, unequally biconvex, in mature examples somewhat bulbous, having rounded trigonal to subpentagonal outline; dorsal valve much deeper than ventral. Lateral profile subtrigonal; anterior commissure uniplicate; fold low to moderately high, commonly beginning about 5 mm anterior to dorsal beak; profile flattened near beak, abruptly convex anteriorly; sulcus shallow to moderately deep, commonly beginning about 9 mm anterior to ventral beak. Anterior face commonly rounded in lateral view, rarely slightly facetted in mature to gerontic individuals. Costae strong, broad, crowded, commonly angular, less commonly rounded in section, separated by angular troughs of width equal to costae; commonly arising 5 to 7 mm from ventral beak, numbering three to five on dorsal fold, three to five on each flank; costae on flanks less pronounced than mesially. Concentric ornament absent; growth lines faint, rare.

Ventral valve low, but strongly convex through sulcus, slightly convex on flanks; beak sharp, attenuate, commonly parallel to hingeline; lateral pseudointerareas narrow, partly covered by overlap of dorsal valve. Delthyrium narrow, open, basically closed by disjunct trapezoidal deltidial plates; pedicle foramen elongate, oval.

Dorsal valve moderately to strongly convex transversely and longitudinally, more so in mature individuals; non-costate umbo may be slightly indented.

Ventral interior having sides of delthyrium widely diverging anterior to deltidial plates; teeth elongate, supported by strong vertical dental plates reaching floor of valve. Muscle field poorly impressed.

Dorsal interior having undivided but anteriorly notched triangular hinge plate, bounded laterally by deep, anteriorly more massive sockets; apparent falcifer crura projecting anteriorly; extremities not observed. Low median ridge on valve floor separating elongate oval, apparently striate adductor scars.

Measurements (in mm).—

	Length	Dorsal Valve Length	Maximum Width	Maximum Thickness	Number of Costae on Fold	Number of Ventral Costae	Costal Origin Distance from Ventral Beak
LOCALITY 8							
USNM 221282	11.3	9.6	10.7	7.1	3	11	6_e
USNM 221283	12.1	10.7	12.5	10.6	4	11	5_e
LOCALITY 10							
USNM 221280	13.5_c	11.9_c	16.0_c	12.4_{ce}	3	12	7_e
USNM 221281	14.5_b	12.1_c	16.2_c	12.5_c	3	12	7_e
LOCALITY 11							
USNM 221275	8.5	—	8.6	—	—	14	6
USNM 221276	8.9_b	8.0	8.6	5.0	3	11	6
USNM 221277	9.8	8.6	9.2	3.8	3	11	6
USNM 221278	12.4	10.7	11.1	8.7	5	13	7
USNM 221279	16.1_c	14.1_c	15.5_c	12.4_c	3	14	7

Occurrence.—*Pontisia stehlii* has been recovered in the West Texas region from rocks ranging in age from Leonardian (Cathedral Mountain and Road Canyon Formations) to Early Guadalupian (middle Word Formation). In the Palmarito Formation it has been recovered from localities 8, 10 and 11. It is not a common faunal element at any of these localities. A Leonardian to Early Guadalupian age is consistent with other biostratigraphic indicators.

Diagnosis.—Large *Pontisia* having deep dorsal valve and closely crowded angular costae, but smooth beaks and umbonal areas.

Types.—Figured Specimens: USNM 221277–221280, USNM 221283, USNM 221284; Measured Specimens: USNM 221275–221283.

Comparison.—Mature individuals of *P. franklinensis* Cooper and Grant (1976a), *P. nanas* (Stehli, 1954), *P. parva* Cooper and Grant (1976a) and *P. wolfcampensis* Cooper and Grant (1976a) are markedly smaller than similar growth stages in *P. stehlii*. The low dorsal valve of *P. kingi* Cooper and Grant (1976a) easily distinguishes that species from *P. stehlii*, and the larger, coarser and sparser costae of *P. costata* Cooper and Grant (1976a), *P. magnicostata* Cooper and Grant (1976a) and *P. truncata* Cooper and Grant (1976a) effectively distinguish those species. The costae of *P. longicosta* (Stehli, 1954) arise much closer to the beaks than do those of *P. stehlii*. *P. ventricola* Cooper and Grant (1976a) presents a much smoother exterior than does *P. stehlii*. *P. robusta* Cooper and Grant (1976a) is less globose and more transverse than most specimens of *P. stehlii*.

P. stehlii is similar to *Pontisia* sp. Stehli and Grant (1970) from the Chochal Limestone (Leonardian) of Guatemala, but differs from that poorly known species in its more globose form, broader and higher fold and sulcus, and its somewhat more pronounced ornament.

P. stehlii may easily be differentiated from a smaller, paucicostate, less globose *Pontisia* from the Copacabana Formation (Wolfcampian) of the Lake Titicaca region, Peru and Bolivia.

Discussion.—It may be considered by some unwarranted to assign the same species name to forms from such presently distant areas as Venezuela and West Texas. In this case however, the morphology of individuals and the variation in samples of populations are so strikingly similar that such a conclusion is inescapable.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
8	6	—	—	fine silicification
10	3	1	—	fine silicification
11	11	5	6	fine silicification

Pontisia cf. **P. stehlii tumidosa**
Cooper and Grant
Plate 7, figures 24–36

cf. *Pontisia stehlii tumidosa* Cooper and Grant, 1976a, p. 2028, pl. 510, figs. 56–62; pl. 535, figs. 52–66.

Description.—Small- to medium-sized, average for genus, subtrigonal to subpentagonal in outline, dorsal valve deeper than ventral. Sides rounded, greatest width at or anterior to midvalve; anterior margin moderately rounded to subtruncate; anterior commissure uniplicate. Beak short, sharply angular, having elongate pedicle foramen and elevated, short, disjunct deltidial plates. Surface variably costate, having from three to six, commonly three, rounded to subangular costae on the dorsal fold, and four on each flank. Intercostal furrows narrower than costae.

Ventral valve moderately convex in lateral profile; broadly and gently convex in anterior profile. Sulcus originating near midvalve; broad, shallow, poorly to moderately defined. Tongue moderately strongly geniculated, convex in lateral aspect. Costae commonly arising about 4 mm anterior to ventral beak.

Dorsal valve moderately convex in lateral view, but strongly domed in anterior view, having nearly vertical flanks. Umbonal region gently convex; fold originating near midvalve, moderately wide, only slightly elevated above flanks through entire length, flat-crested in mature specimens.

Interior as for *Pontisia stehlii*.

Measurements (in mm).—

	Length	Dorsal Valve Length	Maximum Width	Maximum Thickness	Number of Costae of Fold	Number of Ventral Costae	Costal Origin Distance from Ventral Beak
LOCALITY 3							
USNM 221285	4.9	4.4	4.2	3.2	3	9_e	4_e
USNM 221286	6.0	5.5	5.7	4.1	4	13_e	4_e
USNM 221287	6.7	6.1	7.2	5.5	3	13	4
USNM 221288	7.0	6.5	7.3	4.6	3	13	4_e
USNM 221289	7.3	6.4	7.4	5.0	4	15	4
USNM 221290	7.3	6.5	7.1	5.1	3	14	4
USNM 221291	7.5	6.5	7.7	5.9	4	13	4
USNM 221292	7.6	6.4	7.9	5.8	3	13	4
USNM 221293	7.6	7.0	7.6	6.0	3	13	4
USNM 221294	8.1_b	7.4_b	8.5_c	6.8_c	4	11_e	4
USNM 221295	8.6	7.5	8.2	7.7	4	14	4
USNM 221296	8.6_b	7.6	9.6	6.8	5	16	3_e
USNM 221297	10.5_e	9.3_e	13.3	9.3	6	14	4_e

Occurrence.—*Pontisia stehlii tumidosa* occurs in the Cathedral Mountain and Road Canyon Formations (Leonardian) of West Texas. In the Palmarito Formation the form tentatively referred to this subspecies has been recovered only from locality 3, where it is common. A Leonardian age for that assemblage is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Rotund and bulbous *Pontisia* having costae extended to but not onto the beaks.

Types.—Figured Specimens: USNM 221285, USNM 221286, USNM 221289, USNM 221292, USNM 221295, USNM 221298; Measured Specimens: USNM 221285–221297.

Comparison.—*Pontisia stehlii tumidosa* is distinguished from other West Texas *Pontisia* species by its more dense costation and more globular profile. It is distinguished from *P. stehlii stehlii* Cooper and Grant (1969) by its smaller average size, lower fold, shallower sulcus, more convex ventral valve and more extensive costation. The Venezuelan form here referred tentatively to the subspecies differs from that West Texas form in having apparent disjunct rather than conjunct deltidial plates, and by having a slightly more transverse outline, although this latter feature may in part be due to crushing.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	21	12	12	fine silicification

RHYNCHONELLACEA family uncertain
Plate 7, figures 49–55

Discussion.—A number of small shells, trigonal in outline and bearing characteristic rhynchonellacean costation were recovered from Palmarito locality 6, blocks B & C, and locality 10. The latter differ from *Pontisia stehlii* Cooper and Grant (1969), in their smaller size, more extensive, finer costation, and less globose profile, and from *Pontisia* cf. *P. stehlii tumidosa* Cooper and Grant (1976a) in their more elongate, more distinctly trigonal outline, and their less globose profile. Their profile suggests they may be juveniles. No apical interiors were sufficiently well preserved to permit determination of familial affinities. The material

from locality 6 is so fragmentary (a single ventral valve is the only unbroken specimen) that taxonomic conformity with those from locality 10 cannot be assured.

Types.—Figured Specimens: USNM 221300–221302; Measured Specimens: USNM 221299–221303.

Measurements (in mm)—

	Length	Dorsal Valve Length	Maximum Width	Maximum Thickness	Number of Costae		Costal Origin Distance from Ventral Beak
					Ventral	On Fold	
LOCALITY 10							
USNM 221299	5.9$_e$	5.4	5.7	3.1	16	4	4
USNM 221300	6.0	5.0	5.0	3.1	14$_e$	3	4$_e$
USNM 221301	6.6	5.8	7.0	4.5	16	4	4$_e$
USNM 221302	6.9	5.9	5.9	3.6	16	4	4
USNM 221303	6.9	6.2	6.1	4.0	14	3	4

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block B)	—	2	2	fine silicification
6 (block C)	—	—	4	fine silicification
10	5	—	—	fine silicification

Order **SPIRIFERIDA** Waagen, 1883
Suborder **RETZIIDINA**
Boucot, Johnson and Staton, 1964
Superfamily **RETZIACEA** Waagen, 1883
Family **RETZIIDAE** Waagen, 1883

Genus **HUSTEDIA** Hall and Clarke, 1893

Types Species.—Terebratula mormoni Marcou, 1858, p. 51, pl. 6, figs. 11a–c.

Diagnosis.—

> Small, strongly costate . . . [Retziidae] with a rostrate pedicle beak and a flat symphytium. (Stehli, 1954, p. 350)

Occurrence.—Hustedia is known from rocks varying in age from Mississippian through Permian, in Europe, Asia, and the Western Hemisphere. In the Permian its distribution appears to have been tropical to subtropical: it does not appear in truly Boreal assemblages. It is probably the most common brachiopod in the Palmarito fauna, occurring at localities 1, 3, 6, 8, 10, 11 and 13, and being the dominant faunal element in assemblage 10.

Comparison.—The family Retziidae is rather poorly represented in the Upper Paleozoic, only two of nine genera assigned to it in the *Treatise* (Williams *et al.*, 1965) falling within that time range. Only *Hustedia* and *Thedusia* Cooper and Grant (1976b), represent the family in the Permian. *Thedusia* is easily distinguished from *Hustedia* by its generally smaller size, elongate beak, bisulcate valves and emarginated anterior.

Hustedia hyporhachis new species
Plate 8, figures 1–18

Etymology of Name.—Gr. *hypo* = smaller; Gr. *rhachis* = backbone, midrib.

Description.—Small to medium-sized, average for genus, strongly biconvex; outline elongate suboval, normally widest at or slightly anterior to midlength; commissure serrate, anteriorly bearing low fold and sulcus; costae commonly rounded to square-topped, from 11 to 16, commonly 13 on dorsal valve; median costa of dorsal valve depressed near beak in juveniles, anteriorly somewhat broader, more flat-topped than lateral costae; median trough of ventral valve slightly wider than lateral troughs, most mature specimens bearing a very weak median ridge anteriorly; fold and sulcus development encompassing mesial three to four costae; growth lines fine, rarely visible, growth laminae weak, normally observed only near anterior margins.

Ventral valve deepest near midvalve, anterior to dorsal umbo; beak somewhat long, blunt, suberect to erect; foramen round, of normal size, permesothyridid; symphytium longitudinally concave.

Dorsal valve deepest just anterior to umbo, commonly posterior to greatest width of shell, commonly slightly less convex than ventral valve; beak blunt, curving only slightly posterior to hinge.

Ventral interior having blunt, transverse teeth; pedicle collar rarely preserved; crests of internal costae flat to slightly concave, flanks of internal costae of anterior third to half of valve bearing one to several short lirae that may crenulate anterior margin.

Dorsal interior having moderately deep sockets; hinge plate short, only slightly recurved, projecting anteroventrally, median portion near base extended as short curved ligulate process projecting anteroven-

trally; median septum very short, low, thin, apically confined, extending at most 1–2 mm along valve floor; crura short, projecting ventrally; mesial portions of spiralium not preserved intact, up to ten loops on each side, axis of spire at right angles to shell length across widest part; costae and intercostal lirae as in ventral valve.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Total Width	Hinge Width	Thick-ness	Number of Dorsal Costae
LOCALITY 10						
USNM 221304	3.6	2.9	2.5	1.0	1.7	13
USNM 221305	3.9	3.0	3.1	1.4	2.2	15
USNM 221306	5.0	4.0	4.0	1.5	3.2	15
USNM 221307	5.1	4.0	4.4	1.7	3.0	13
USNM 221308	5.3	4.2	4.2	1.6	2.8	13
USNM 221309	5.4	4.2	4.7	1.7	3.4	13
USNM 221310	5.5	4.4	4.8	1.8	3.2	13
USNM 221311	5.7	4.7	5.3	1.7	3.6	13
USNM 221312	6.3_e	5.2	4.8	1.5	3.8	13
USNM 221313	6.7	5.0	5.0	1.8	3.7	13
USNM 221314	6.8	6.0	5.3	2.2	4.0	15
USNM 221315	7.0	6.0	5.5	2.0	4.4	15
USNM 221316	7.0	5.9	6.2	2.0	4.1	15
USNM 221317	7.1	5.8	5.5	1.8	4.2	13
USNM 221318	7.1	5.9	5.5	1.7	4.5	13
USNM 221319	7.3	6.0	6.3	2.5	4.8	13
USNM 221320	7.4	6.3	6.3	1.7	4.5	13
USNM 221321	7.4	6.5	6.3	1.8	4.6	13
USNM 221322	7.5	6.0	4.5	1.8	4.0	13
USNM 221323	7.5	6.0	6.6	2.2	5.2	13
USNM 221324	7.5	6.4	5.6	1.8	4.2	13
USNM 221325	7.6	6.1	6.8	2.0	4.8	11
USNM 221326	7.8	6.1	6.2	2.1	4.9	13
USNM 221327	8.3	6.6	7.1	2.4	5.0	13
USNM 221328	8.5_e	7.0	6.4	1.7	4.8	13
USNM 221329	8.5	7.0	7.3	2.4	5.1	15
USNM 221330	8.7	6.8	7.1	2.2	5.5	13
USNM 221331	8.8	7.0	7.1	2.4	5.7	13
USNM 221332	8.8	7.5	7.1	2.2	5.2	13
USNM 221333	9.0	7.5	7.8	2.0	5.5	13
USNM 221334	9.2_e	7.5_e	7.8	2.5_e	5.7	13
USNM 221335	9.2	7.8	7.8	2.2	5.5	13
USNM 221336	9.3	7.6	7.2	2.2	5.5	13
USNM 221337	9.5	7.5	8.2	2.5	6.0	15
USNM 221338	9.5	7.8	7.7	1.8	5.8	13
USNM 221339	9.6	8.0	8.2	2.2	5.7	13
USNM 221340	9.7	7.8	7.7	2.0_e	5.8	13
USNM 221341	9.7	8.0	8.3	2.8	6.4	15
USNM 221342	9.7	8.1	8.4	3.0	6.3	13
USNM 221343	9.7	8.3	7.8	2.0	5.8	13
USNM 221344	9.8	7.8	8.2	2.3	6.0	13
USNM 221345	10.0	8.0	9.5	2.2	6.2	13
USNM 221346	10.0	8.2	7.2	2.3	6.5	13
USNM 221347	10.3	8.8	9.7	3.0	6.9	15
USNM 221348	10.5	8.7	8.7	2.7	7.1	13
USNM 221349	10.5	8.7	9.1	2.9	5.7	13
USNM 221350	11.0	9.5	9.1	2.6	7.5	13
USNM 221351	11.3	9.6	9.1	3.2	6.4	13
USNM 221352	11.3	9.8	7.9	2.8	7.8	13
USNM 221353	11.3	9.8	9.1	3.2	7.5	13
USNM 221354	11.4	9.9	10.0	3.1	7.6	13
USNM 221355	11.7	10.1	8.9	3.1	7.5	13
USNM 221356	12.0	10.3	9.5	3.0	7.8	13

	Total Length	Dorsal Valve Length	Total Width	Hinge Width	Thick-ness	Number of Dorsal Costae
USNM 221357	12.1	9.8	9.1	3.4	7.2	17
USNM 221358	12.2	10.3	9.6	3.0	7.8	15
USNM 221359	12.4	10.5	9.8	3.4	8.0	13
USNM 221360	12.5	10.5	10.1	3.3	8.1	13
USNM 221361	12.5	10.8	10.6	3.5	7.9	13
USNM 221362	12.7	11.0	10.5	3.3	8.8	13
USNM 221363	12.9	10.8	11.0	3.2	9.2	13
USNM 221364	12.9	11.1	10.6	3.5	8.1	13
USNM 221365	13.1	11.1	10.6	3.3	8.5	13
USNM 221366	13.2	11.2	10.1	3.5	8.6	13
USNM 221367	13.3	11.1	10.8	3.4	8.4	13
USNM 221368	13.3	11.6	11.2	3.3	8.9	13
USNM 221369	13.3	11.8	11.3	2.8	8.9	11
USNM 221370	13.4	11.3	10.8	3.5	9.8	13
USNM 221371	13.5	11.7	11.3	3.7	8.6	13
USNM 221372	13.5	11.8	11.7	3.4	9.2	13
USNM 221373	13.5	11.4	10.9	3.6	8.4	13
USNM 221374	13.6	11.7	11.5	3.8	9.6	16
USNM 221375	13.8	11.7	11.0	3.6	8.2	14
USNM 221376	13.8	11.8	10.5	3.1	10.0	13
USNM 221377	13.8	12.0	11.5	3.4	10.0	13
USNM 221378	14.0	12.0	12.1	3.7	9.8	15
USNM 221379	14.2	11.9	11.8	3.5	9.7	13
USNM 221380	14.2	12.1	12.6	3.7	9.8	13
USNM 221381	14.3	12.1	10.8	3.0	9.0	13
USNM 221382	14.3	12.2	10.6	3.2	10.4	15
USNM 221383	14.4	12.1	11.1	3.5	8.4	13
USNM 221384	14.6	12.6	11.1	3.2	9.3	13
USNM 221385	14.6	12.7	11.2	3.4	9.8	13
USNM 221386	14.8	12.7	11.7	3.6	10.4	15
USNM 221387	15.0	12.7	11.7	3.6	10.1	15
USNM 221388	15.0	12.7	13.4	4.5	11.0	13
USNM 221389	15.0	12.9	12.4	4.1	10.6	15
USNM 221390	15.0	13.0	12.9	3.8	9.6	13
USNM 221391	15.0	13.1	10.8	2.6	11.2	13
USNM 221392	15.2	12.5	11.5	4.3	10.5	13
USNM 221393	15.2	13.0	12.2	3.4	10.2	13
USNM 221394	15.2	13.2	12.3	3.5	10.7	13
USNM 221395	15.3	12.9	13.2	3.8	12.1	13
USNM 221396	15.5	13.3	12.8	4.4	11.1	15
USNM 221397	15.6	13.5	11.3	4.0	12.3	13
USNM 221398	15.6	13.5	11.7	2.6	10.3	13
USNM 221399	16.0	13.4	12.2	4.1	10.7	15
USNM 221400	16.1	13.7	11.9	3.5	12.1	13
USNM 221401 (holotype)	16.3	14.0	12.8	3.6	11.0	13
USNM 221402	16.4	13.7	13.3	4.3	11.2	15
USNM 221403	16.7	14.7	12.9	4.1	10.9	13

Occurrence.—Hustedia hyporhachis has been recovered from localities 3, 10, 11 and 13 in the Palmarito Formation. Juvenile specimens questionably referable to the species, resembling juveniles from localities 10 and 13, were recovered from locality 6, blocks A and C. *H. hyporhachis* is uncommon in the assemblages at localities 3, 6 and 11, and common to abundant in those of localities 10 and 13. At locality 10 it dominates the fauna.

The most closely related West Texas form, *H. consuta* Cooper and Grant (1976b) has been recovered from the upper portion of the Cathedral Mountain Formation, and from the Road Canyon and Cibolo Formations, all of Leonardian age. Such an age assign-

ment is not inconsistent with other biostratigraphic indicators in the Palmarito faunal assemblages.

Diagnosis.—Average-sized, strongly convex *Hustedia,* having low, rounded costae and a thin median ridge in the median trough of the ventral exterior.

Types.—Holotype: USNM 221401; Figured Specimens: USNM 221308, USNM 221324, USNM 221335, USNM 221339, USNM 221352, USNM 221354, USNM 221358, USNM 221370, USNM 221386, USNM 221399, USNM 221401, USNM 221404–221406; Measured Specimens: USNM 221304–221403.

Comparison.—*H. hyporhachis* may be distinguished from *H. crepax* Cooper and Grant (1976b), *H. culcitula* Cooper and Grant (1976b) and *H. trita* Cooper and Grant (1976b) by the absence of striae on the internal costal flanks in those forms. The smaller size of mature individuals of *H. bipartita* Girty (1909, *H. catella* Cooper and Grant (1976b), *H. hapala* Cooper and Grant (1976b), *H. inconspicua* Cooper and Grant (1976b), *H. lusca* Cooper and Grant (1976b), *H. narinosa* Cooper and Grant (1976b), and *H. trisecta* Cooper and Grant (1976b), and the larger size of mature individuals of *H. citeria* Cooper and Grant (1976b) and *H. rupinata* Cooper and Grant (1976b) effectively distinguish those species from *H. hyporhachis*. The smaller average number of costae in *H. cepacea* Cooper and Grant (1976b), *H. citeria, H. compressa* Cooper and Grant (1976b), *H. consuta* Cooper and Grant (1976b), *H. decollatensis* Cooper and Grant (1976b), *H. opsia* Cooper and Grant (1976b), *H. samiata* Cooper and Grant (1976b), *H. spicata* Cooper and Grant (1976b), and *H. tomea* Cooper and Grant (1976b) and greater average number of costae of *H. cuneata* Cooper and Grant (1976b), *H. huecoensis* R. E. King (1931) and *H. stataria* Cooper and Grant (1976b) distinguish those forms from *H. hyporhachis*. The lamellose anterior and short median costa of *H. demissa* Cooper and Grant (1976b) effectively distinguishes that form, while the thickened shell of *H. connorsi* Cooper and Grant (1976b) distinguishes that form. The presence of obvious growth lines on *H. ampullacea* Cooper and Grant (1976b), *H. glomerosa* Cooper and Grant (1976b), *H. hessensis* R. E. King (1931), *H. pugilla* Cooper and Grant (1976b) and *H. sculptilis* Cooper and Grant (1976b) distinguishes those species from *H. hyporhachis*. *H. hyporhachis* differs from all West Texas species but *H. consuta* in bearing the thin median lira in the ventral median exterior trough, and differs from that species in its lower, more rounded, and somewhat more numerous costae.

H. hyporhachis generally resembles *H. grandicosta* (Davidson, 1862) from the Upper Productus Limestone of the Salt Range, but differs, bearing a mesial ridge in the median ventral exterior trough. It is similar to *H. sicuaniensis* Chronic (1949) from the Copacabana Formation of Peru, which appears to have a weak median ventral mesial lira (Newell, Chronic *et al.*, 1953, pl. 17, fig. 7b), but differs from that species in its posteriorly indented dorsal valve, larger mature individuals, and the presence of striations on the flanks of the internal costae, which *H. sicuaniensis* does not appear to have (Cooper and Grant, 1976b, p. 2763).

Discussion.—The taxonomically significant features of the species of *Hustedia* are commonly quite subtle. Assignment to species is a difficult task requiring examination of large population samples, in order to determine the size, form and characteristics of juvenile and mature individuals, and the ranges of variation of taxonomically significant characters at various growth stages and throughout ontogeny. Without such a large suite, proper placement of isolated specimens within an ontogenetic framework, and consequently specific identification, can be seriously hampered. In *H. hyporhachis,* three such characters (length, width, thickness) are related in a systematic manner. Text-figure 11 shows the relationships of these parameters for two population samples of *H. hyporhachis* (locs. 10 and 13) and a single sample of *H. consuta*. It may easily be seen that there is a linear relationship between length and width during ontogeny, while the relationship between length and thickness is non-allometric, thickness increasing little during early as compared to later stages of ontogeny. The latter relation is subtle, but can be seen in all three plots, and is a common ontogenetic strategy in many groups of brachiopods, indicating that there is some threshold size which must be attained before substantial increase in the internal volume of the shell can be initiated.

The difference in dispersion of the plots from localities 10 and 13 may possibly be explained by examination of the overall character of those assemblages. At locality 10, *H. hyporhachis* is the dominant brachiopod present: large numbers of individuals competed for the available living space, and were often closely crowded together. Such close proximity may influence the shape of mature shells by randomly limiting directional growth. At locality 13 however, no such crowding appears to have occurred, although the assemblage is unquestionably autochthonous. Shells in such an uncrowded environment would be free to follow an "ideal" growth plan, and there would be less deviation from their standard mode of ontogenetic development.

The appearance of internal striations on the intercostal flanks may be of considerable stratigraphic sig-

Text-figure 11.—Scattergrams of dimensions of two population samples of *Hustedia hyporhachis* n. sp. from Venezuela and one population sample of *Hustedia consuta* Cooper and Grant (1976b) from West Texas. In all diagrams, the upper vertical axis represents maximum width; the middle, horizontal axis represents shell length; and the lower vertical axis represents the maximum thickness. All measurements are in mm. The dashed lines indicate equidimensionality.

nificance. Stehli (1954, p. 351) hypothesized that they might represent an interlocking straining device, operational at the anterior margin. Cooper and Grant (1976b, p. 2761), following an informal suggestion by Stehli, demonstrated that such valve margin crenulations do not interlock in articulated silicified specimens, and in many cases leave large gaps along the commissure which would not serve well as incurrent strainers. They suggest that these internal ridges may have served as seats for attachment of marginal setae which appear to have been present in many groups of brachiopods.

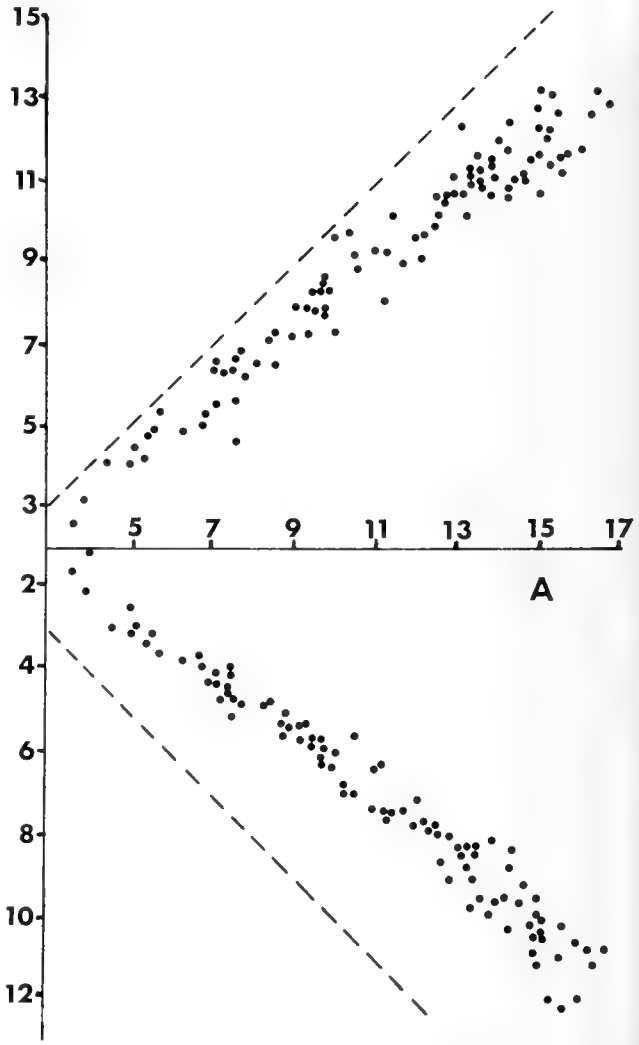
These striae appear to have been a rather late development in the Retziidae, appearing only in the Permian forms, and were not well-expressed until the Leonardian. Those of *H. hyporhachis* appear to arise at about midvalve in most cases, and to continue distinctly to the anterior margin, indicating that they arose early in ontogeny. This morphological-stratigraphic relationship tends to support the Leonardian age indicated by other Palmarito biostratigraphic indicators.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	19	—	1	fine silicification
6 (block A)	11	2	—	fine silicification
6 (block B)	2	2	—	fine silicification
6 (block C)	14	1	6	fine silicification
10	297	33	38	fine silicification
11	30	13	11	medium-grained silicification
13	81	8	7	fine silicification

Hustedia sp.
Plate 7, figures 37, 38

Discussion.—A single poorly preserved specimen referable to the genus *Hustedia* was recovered from each of localities 1 and 8. No internal details can be seen, and the surface is insufficiently preserved to allow even a count of number of costae. The specimens are, however, of the same general size and shape as



A. Plot for *Hustedia hyporhachis* from locality 10, Palmarito Formation (100 specimens).

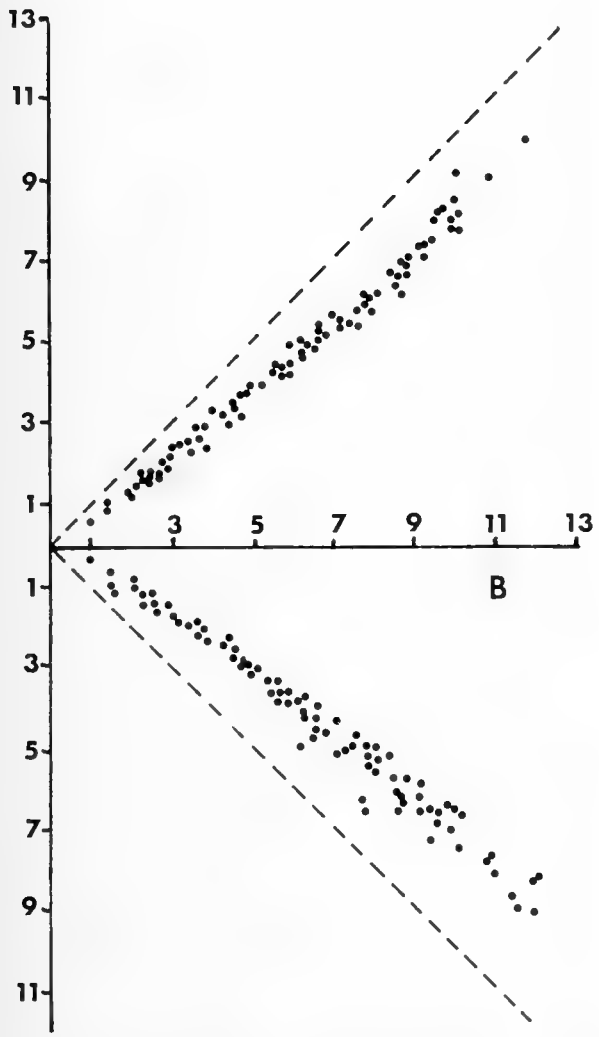
mature individuals of *Hustedia hyporhachis* n. sp., although they cannot confidently be assigned to that or any other species of the genus.

Types.—Figured Specimens: USNM 221407, USNM 221408.

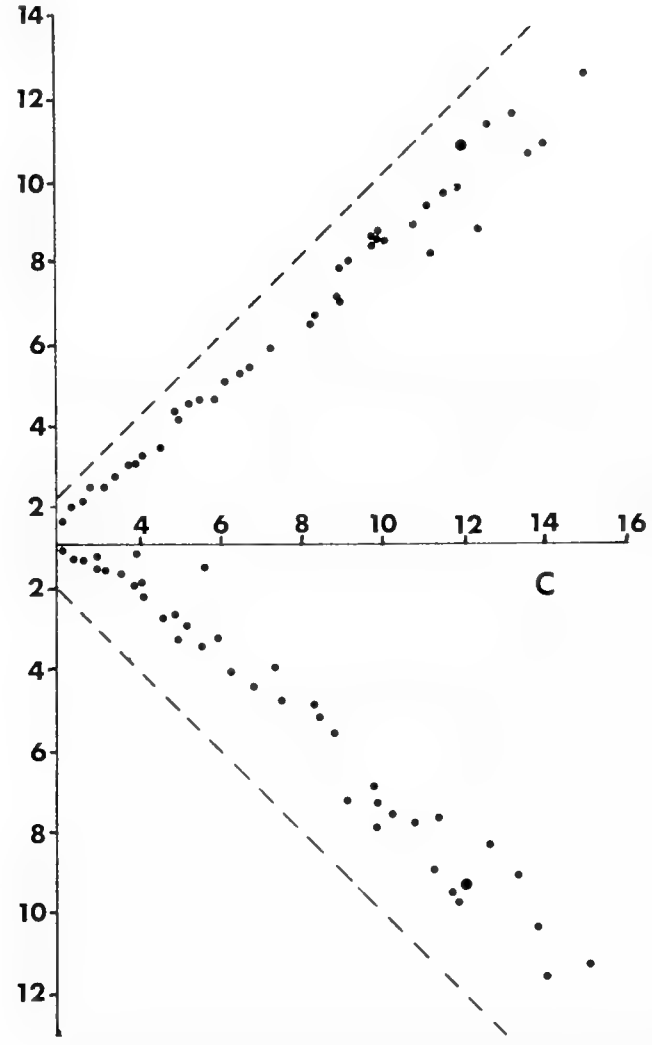
Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	1	—	—	calcite permineralization
8	1	—	—	coarse silicification

Suborder **ATHYRIDIDINA**
Boucot, Johnson and Staton, 1964
Superfamily **ATHYRIDACEA** McCoy, 1844



B. Plot for *Hustedia hyporhachis* from locality 13, Palmarito Formations (100 specimens).



C. Plot for *Hustedia consuta* Cooper and Grant (1976b), locality 707e, Road Canyon Formation, West Texas (42 specimens; larger dot represents the dimensions of the holotype).

Family **ATHYRIDIDAE** McCoy, 1844

Subfamily **ATHYRIDINAE** McCoy, 1844

Genus **CLEIOTHYRIDINA** Buckman, 1906

Type Species.—*Spirifer deroysii* Leveille, 1835, p. 39 = *Athyris roysii* Davidson, 1860, p. 84, pl. 18, fig. 8 (by original designation of Buckman, 1906, p. 324).

Diagnosis.—Athyridinae having concentric lamellae that bear short spines, ventral beak without interarea, subcircular pedicle foramen that penetrates the apex of the beak, small dental plates in the ventral interior and an apically perforate hinge plate in the dorsal interior.

Occurrence.—*Cleiothyridina* occurs in rocks ranging in age from Late Devonian through the Permian, and its distribution is cosmopolitan. In the Permian it occurs in both Austral and Boreal regions, and is common in Europe and Asia. It is a rare element in Western Hemisphere Permian faunas, where the species are generally small and easily overlooked. Two fragmentary specimens referable to the genus have been recovered from locality 3 in the Palmarito Formation.

Comparison.—The Palmarito Formation forms of *Cleiothyridina* may easily be distinguished from *Composita* Brown (1849), the only other co-occurring athyridine genus, by its characteristic broad lamellar extensions, arising at the concentric growth lines, and extending anteriorly as fine solid spines.

Discussion.—*Cleiothyridina* demonstrates one of the difficulties inherent in recognizing many of the cosmopolitan forms in their Tethyan realm occurrences:

genera which are relatively abundant and possess shells of moderate size in Boreal and Temperate realms, appear to exist at a competitive disadvantage at lower latitudes, where they are rare, small and patchily distributed.

Cleiothyridina cf. **C. nana** Cooper and Grant
Plate 8, figures 19–25

cf. *Cleiothyridina nana* Cooper and Grant, 1976a, p. 2136, pl. 650, figs. 36–49, 84–99.

Description.—Small, small for genus, suboval to subpentagonal in outline, moderately globose in lateral aspect, biconvex; greatest width at or anterior to mid-length, commissure weakly uniplicate; fold low and rounded, sulcus shallow, limited to anterior portion of shell; concentric lamellae closely spaced, spinose, spines better preserved nearer margins, short, closely spaced; posteriorly bearing fewer and lower spines and numerous spine bases; growth laminae few and weak.

Ventral valve moderately convex; beak thick, nearly straight; foramen small, round, poorly preserved, piercing beak at apex; dorsal valve somewhat more convex, especially posteriorly, bearing small spines as on ventral valve.

Interiors unknown.

Measurements (in mm).—

	Length	Dorsal Valve Length	Maximum Width	Maximum Thickness	Height of Fold at Commissure
LOCALITY 3					
USNM 221409	7.0	6.0	6.5$_e$	5.0	1.5

Occurrence.—*Cleiothyridina nana* has previously been recovered only from the Road Canyon Formation (Leonardian of West Texas), where it is rare. In the Palmarito Formation it is also rare. Only a single juvenile and a single adult specimen were recovered from locality 3. A Late Leonardian age for that locality in the Palmarito is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Very small *Cleiothyridina* with slightly folded anterior commissure.

Types.—Figured Specimens: USNM 221409–221410; Measured Specimen: USNM 221409.

Comparison.—*C. nana* is effectively distinguished from *C. ciriacksi* Cooper and Grant (1976a), *C. rara* Cooper and Grant (1976a), *C. rectimarginata* Cooper and Grant (1976a) and several undescribed species from the West Texas region by the slight uniplication of its anterior commissure. Its commissure is, however, less strongly uniplicate than that of another West Texas species, *C. pilularis* Cooper and Grant (1976a). *C. mulsa* Cooper and Grant (1976a) is very weakly uniplicate, and has vestigial dental plates, compared to the robustness of those features in *C. nana*. The Bolivian species *C. intonsa* Chronic (1949) is rectimarginate.

Discussion.—*Cleiothyridina* cf. *C. nana* is rare in the Palmarito Formation. The small size of this form agrees well with other Western Hemisphere Tethyan species of the genus. Its rarity in apparently autochthonous collections of silicified material may indicate that its life distribution was extremely discontinuous, rather than that the sampling was poor.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	2	—	—	fine silicification

Genus **COMPOSITA** Brown, 1849

Type Species.—*Spirifer ambiguus* Sowerby, 1823, p. 105, Tab. 376, 4 figs. (by original designation of Brown, 1849, p. 131).

Diagnosis.—Biconvex, streamlined narrow-hinged Athyridinae lacking interarea or beak ridges, having uniplicate commissure and proportionately large oval, epithyridid or permesothyridid pedicle foramen.

Occurrence.—*Composita* has been reported from rocks of Devonian through Permian age. In the Permian it appears to have had a world-wide Tethyan distribution. Although it occurs sparingly in intermediate ("temperate") paleoclimatic zones, it has never been reported from Boreal assemblages. In the Western Hemisphere it is known from southern and central North America, northern Central America and northern and central South America.

Comparison.—Its longer, more erect beak, larger pedicle foramen, generally more elongate outline and lack of surface spines distinguish *Composita* from the other co-occurring athyridine genus *Cleiothyridina* Buckman (1906). The lack of beak ridges or deltidial plates, and the type and position of the pedicle foramen distinguish *Composita* from *Dielasma* W. King (1859). *Neophricadothyris* Likharev (1934) or *Martinia* McCoy (1844) have the same sort of outline, but may be distinguished by their trigonal delthyria and unperforated beak apices.

Discussion.—*Composita,* originally separated from the genus *Spirifer* Sowerby (1816), is still of relatively

hoary antiquity. Although it now houses probably less than half the species originally assigned to it, due to refinement of the genus over the last hundred or more years, the number of species within the genus taxes the credulity of the average investigator. Various investigators (*e.g.*, Grinnell and Andrews, 1964; Lutz-Garihan, 1974) have demonstrated that a continuum of intergrading forms exists between several of the better-known species of *Composita* in North America. The artificiality of paleospecies assignment is rarely better exhibited than in *Composita*.

The brachiopod fauna of the Palmarito Formation appears to show greatest overall similarity to forms from the Permian basins of West Texas: therefore it is among these well-studied and thoroughly investigated faunas that similar species of *Composita* are chiefly sought.

Composita cf. **C. pilula** Cooper and Grant
Plate 8, figures 26–38

cf. *Composita pilula* Cooper and Grant, 1976a, p. 2159, pl. 657, figs. 1–39.

Description.—Small, small for genus, subtrigonal, subovate or subpentagonal in outline, commonly somewhat elongate, widest anterior to midlength; anterior commissure weakly parasulcate; fold standing only slightly higher than flanks anteriorly, sulcus expressed anteriorly only; growth laminae weak, widely spaced over most of shell; stronger, more crowded nearer margins; latest growth increments of largest specimens imbricate, forming somewhat inset, corrugate face oriented normal to plane of commissure.

Ventral valve strongly convex, radius of curvature smallest posteriorly; beak short, thick, suberect or erect; foramen small, periphery narrowly incomplete; edge of valve flanged or bearing shallow groove in most mature specimens.

Dorsal valve less strongly convex, greatest height at or slightly anterior to umbo, but posterior to midvalve; valve margins fitting flange or groove of opposite valve.

Ventral interior having slender, sharp, posterodorsally recurved pair of hinge teeth; dental plates thin, subparallel, free of apical walls anteriorly; muscle area shallowly impressed, pattern normal for genus.

Dorsal interior having small hinge plate, with deep median notch in many specimens; cardinal process bilobate, lobes bearing small muscle attachment mark on anterodorsal faces; adductor muscle attachment area elongate, narrow, having low median dividing ridge posteriorly; crura, descending lamellae and spiralia not seen.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Maximum Width	Maximum Thickness
LOCALITY 3				
USNM 221411	17.7_{e}	15.3_{e}	—	11.2_{e}
LOCALITY 4				
USNM 221412	11.8	10.2	10.5	8.3
USNM 221413	13.0_{e}	11.5_{e}	10.0_{e}	8.7_{e}
LOCALITY 7				
USNM 221414	15.0	12.7	12.5	10.9
USNM 221415	17.2	14.8	14.3_{e}	11.8_{e}
USNM 221416	17.5	15.0	16.9	12.0
USNM 221417	18.4	15.2_{e}	16.1	13.6
USNM 221418	21.8	18.5_{e}	18.6	14.6_{e}
USNM 221419	22.7	18.8_{e}	19.3	16.1
LOCALITY 8				
USNM 221420	5.4	4.6	5.2	3.0
USNM 221421	6.7	6.2	6.1	4.4
USNM 221422	7.8	6.9	7.1	5.0
USNM 221423	8.5_{b}	7.5	7.4	5.3
USNM 221424	10.0_{be}	9.0_{be}	8.1_{b}	6.5_{b}
USNM 221425	11.9	10.5	10.0	7.9
USNM 221426	12.4_{be}	11.7	10.4	7.6
USNM 221427	12.5_{be}	11.7	10.1	8.2
USNM 221428	12.9	11.1	11.9	8.4
USNM 221429	12.9	11.2	10.6	8.2
USNM 221430	13.1	11.4	11.6	8.1
USNM 221431	13.3	11.3	10.8	8.6
USNM 221432	13.3	11.3	11.5	9.0
USNM 221433	13.5	11.9	12.4	8.4
USNM 221434	14.3_{be}	13.1_{be}	11.5	9.3
USNM 221435	15.8	13.6	13.0	9.7
LOCALITY 11				
USNM 221436	16.2	13.5	13.8	10.9_{be}
USNM 221437	17.8	15.2	17.1_{be}	12.2
LOCALITY 13				
USNM 221438	—	—	12.5	9.5
USNM 221439	14.9	13.0	11.4	9.7

Occurrence.—*Composita pilula,* in the West Texas region where it was first described, has been recovered only from the Road Canyon Formation (Leonardian). In the Palmarito Formation it is one of the more ubiquitous articulate brachiopods, occurring sparingly in assemblages 1, 3, 4, 7, 10, 11 and 13 and abundantly in assemblage 8. A Late Leonardian age for all of these assemblages is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Shell small, outline elongate, beak short, growth laminae strong near margins, margins commonly flanged or grooved, fold and sulcus very weak, commissure weakly parasulcate.

Types.—Figured Specimens: USNM 221420, USNM 221421, USNM 221423, USNM 221425, USNM

221431, USNM 221433, USNM 221435, USNM 221437, USNM 221440, USNM 221441; Measured Specimens: USNM 221411–221439.

Comparison.—*Composita* cf. *C. pilula* includes mature individuals of a smaller size than *C. affinis* Girty (1909), *C. apheles* Cooper and Grant (1976a), *C. apsidata* Cooper and Grant (1976a), *C. cracens* Cooper and Grant (1976a), *C. crassa* Cooper and Grant (1976a), *C. emarginata* Girty (1909), *C. enormis* Cooper and Grant (1976a), *C. grandis* Cooper (1957), *C. hapsida* Stehli and Grant (1970), *C. imbricata* Cooper and Grant (1976a), *C. prospera* Cooper and Grant (1976a), *C. stalagmium* Cooper and Grant (1976a), *C. strongyle* Cooper and Grant (1976a), *C. subtilita* (Hall, 1852) and *C. subtilita peruviana* Chronic (1949), and of a larger size than those of *C. bucculenta* Cooper and Grant (1976a), *C. costata* Cooper and Grant (1976a), *C. mexicana* (Hall, 1857), *C. miniscula* Chronic (1949) and *C. nucella* Cooper and Grant (1976a). *C.* cf. *C. pilula* is generally more parasulcate than *C. minuscula, C. subtilita* or *C. subtilita peruviana,* and less parasulcate than *C. bucculenta* and *C. parasulcata* Cooper and Grant (1976a). *C. pyriformis* Cooper and Grant (1976a), of the same mature size as *C.* cf. *C. pilula,* has a more distinctly trigonal outline, while *C. emarginata* is distinguished by its markedly emarginate anterior commissure. *C. parasulcata,* which occurs in the Road Canyon and younger units in the West Texas region, is very similar to *C.* cf. *C. pilula,* but, in addition to its greater degree of parasulcation, is more distinctly transverse in outline. *C. pilula* of the West Texas region tends to be somewhat more globose than the Palmarito specimens tentatively referred to the species, and contains dental plates that are fused to the apical walls along their entire length, in contrast to their free-standing situation in the Venezuelan specimens.

Discussion.—*Composita* is an extremely conservative genus that contains variable and intergrading species. A single specimen of *Composita* could rarely be identified to species: large samples of populations are required to determine such taxonomically significant parameters as size of mature individuals, modal shape, outline, and variations in the development of fold and sulcus. The numerous species erected by Cooper and Grant (1976a) contain some stratigraphic input: the Wolfcampian species *C. bucculenta* contains many individuals which would be indistinguishable from those of *C. parasulcata* or *C. pilula.* Certainly in these taxa we are dealing with distinct populations of closely related brachiopods: whether or not these populations truly represent distinct biological species has not been demonstrated to my satisfaction. It is for this reason that the Palmarito *Composita* is only tentatively assigned to *C. pilula* Cooper and Grant.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	1	—	—	calcite permineralization
3	2	1	1	fine silicification
4	10	1	1	fine silicification
7	6	—	—	calcite permineralization
8	54	16	22	fine silicification
10	4	1	1	fine silicification
11	6	—	—	coarse silicification
13	4	4	4	fine silicification

Suborder **SPIRIFERIDINA** Waagen, 1883

Superfamily **CYRTIACEA** Frederiks, 1924

Family **AMBOCOELIIDAE** George, 1931

Genus **COSTICRURA** new genus

Etymology of Name.—L. *costa* = rib; L. *crura* = legs, shanks [used to connote affinity to *Crurithyris* George (1931)].

Description.—Unequally biconvex, commonly transverse, having ventral valve deeper than dorsal; hingeline straight, anterior and lateral margins gently rounded, cardinal extremities acute to obtuse, anterior commissure rectimarginate; ventral valve slightly flattened anteromesially, dorsal valve gently rounded in anterior aspect; valves costate; costae low, rounded, straight, extending from beaks to margins.

Ventral valve hemipyramidal, considerably inflated, having high, ventral to apsacline interarea, high, open delthyrium, and straight hingeline.

Dorsal valve more flatly convex, low beak rarely produced posterior to hingeline. Interarea very low, dorsal to anacline, having small open notothyrium.

Ventral interior without dental plates, median septum or recognizable muscle attachment scars. Short simple teeth at anterior edges of delthyrium.

Dorsal interior having simple paired sockets, unsupported by socket plates; cardinal process inset, bilobate, divided by relatively coarse simple median ridge. Crural plates long, delicate, arising from posterior valve floor anterodorsal of sockets, curving gently anteroventrally and mesially to about midvalve, there turning ventrally, closely appressed; a short distance anteriorly becoming flattened, broadened, recurving laterally toward opposite valve walls, then mesially recurved, initiating first whorl of spiralium.

Type Species.—*Costicrura minuta* new species.

Diagnosis.—Costate Ambocoeliidae, lacking fold or sulcus.

Occurrence.—*Costicrura* has to date been recovered only from locality 6, blocks A, B and C, in the Palmarito Formation of Venezuela. A very small "ribbed *Crurithyris*" was noticed in acid etch residues from Permian rocks of Thailand (Grant, 1975, *pers. comm.*), but since this was not recovered, its relationship to *Costicrura* cannot be ascertained.

Comparison.—*Costicrura* is easily distinguished from the other Permian ambocoeliid genera *Crurithyris* George (1931) and *Attenuatella* Stehli (1954), by its costate ornament and lack of fold or sulcus. It is distinguished from the finely costellate genus *Wilberrya* Yancey (1978), by its less globose anterior profile, its acuminate cardinal extremities, and its coarser radial ornament.

Discussion.—It is likely that further occurrences of *Costicrura* will be reported from the Permian Tethyan realm, as more studies of silicified faunas are undertaken. The extremely small size of the Palmarito species may be typical of the genus. If so, only picking of fine size fractions of acid etch residues could yield specimens of this elusive genus. The small size would, in addition, preclude recovery of these forms from faunas preserved by other modes than silicification.

Costicrura minuta new species
Plate 8, figures 39–44

Etymology of Name.—L. *minuta* = small.

Description.—Minute, unequally biconvex, transverse, having straight hingeline; hinge width varying from slightly less than to slightly more than midwidth, commonly about one and one-half times as wide as long. Anterior commissure rectimarginate, lacking distinct fold or sulcus; ventral valve straight-sided, flat-crested in anterior aspect, high triangular in lateral aspect; dorsal valve low, gently and broadly rounded in anterior and lateral aspects. Both valves costate; costae extending from beaks to margins.

Ventral valve hemipyramidal, considerably inflated, having high, ventral to apsacline interarea, high, open triangular delthyrium, and straight hingeline.

Dorsal valve shallowly convex, low beak produced slightly posterior to hingeline. Very low, dorsal to anacline interarea having small open triangular notothyrium.

Ventral interior without dental plates, median septum or recognizable muscle attachment scars. Short simple teeth at anterior edges of delthyrium.

Dorsal interior having simple paired sockets, unsupported by socket plates; cardinal process inset, bilobate, divided by relatively broad simple median ridge. Crural plates long, delicate, arising from posterior valve floor anterodorsal of sockets, curving gently anteroventrally and mesially to about midvalve, there closely appressed, turning ventrally, a short distance anteriorly becoming flattened, broadened, recurving laterally toward opposite valve walls, then mesially recurved, initiating first whorl of spiralium.

Measurements (in mm).—

	Total Length	Hinge Width	Mid-Width	Thickness
LOCALITY 6 (block A)				
USNM 221442	1.1	1.3_b	1.6	0.9
USNM 221443	1.2	1.2_b	1.7	1.2
USNM 221444	1.2	1.4	1.6	1.0
USNM 221445	1.3	1.5_b	1.8	1.1
USNM 221446	1.3	1.7	1.8	1.2
USNM 221447	1.4	1.6	1.8	1.3
USNM 221448	1.4	1.7	1.9	1.2
USNM 221449	1.4	1.8	1.8	1.2
USNM 221450	1.4	1.8	1.9	1.3
USNM 221451	1.4	1.9	1.8	1.2
LOCALITY 6 (block B)				
USNM 221452	0.9	1.0_b	1.3	0.8
USNM 221453 (holotype)	1.5	2.3	2.1	1.4
LOCALITY 6 (block C)				
USNM 221454	0.7	0.7	1.0	0.5
USNM 221455	0.7	0.9	1.0	0.5
USNM 221456	0.8	1.1	1.2	0.6
USNM 221457	0.9	0.9	1.1	0.5_b
USNM 221458	1.0	1.2	1.3	0.8
USNM 221459	1.1	1.4	1.6	0.9
USNM 221460	1.1	1.5	1.6	1.0
USNM 221461	1.2	1.5	1.7	1.0
USNM 221462	1.2	1.6	1.7	1.1
USNM 221463	1.2	1.4_b	1.8	1.0
USNM 221464	1.2_b	1.6_c	2.1_c	1.2_c
USNM 221465	1.4	1.9	1.8	1.3
USNM 221466	1.4_b	2.1	2.0	1.2_b

Occurrence.—as for genus.

Diagnosis.—Minute *Costicrura*.

Types.—Holotype: USNM 221453; Figured Specimens: USNM 221453, USNM 221467, USNM 221468; Measured Specimens: USNM 221442–221466.

Comparison.—*C. minuta* is the only species of the genus.

Discussion.—The small "ribbed *Crurithyris*" mentioned above, from the Permian of Thailand, if related to *Costicrura minuta*, probably represents a different species. It is hoped that examination of fine size fractions of Permian acid etch residues will yield comparative material.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block A)	13	5	7	fine silicification
6 (block B)	3	3	—	fine silicification
6 (block C)	16	14	7	fine silicification

Superfamily **RETICULARIACEA** Waagen, 1883

Family **ELYTHIDAE** Frederiks, 1924

Genus **NEOPHRICADOTHYRIS** Likharev, 1934

Type Species.—*Squamularia asiatica* Chao, 1929, p. 91, pl. 11, figs. 12–14, by original designation of Likharev, 1934, pp. 211, 213.

Diagnosis.—Spiriferacea having biramous spines in concentric rows and the spiral axes coiled posterolaterally.

Occurrence.—*Neophricadothyris* is a Permian representative of a stock of elythids that range from the Lower Carboniferous through the highest stage of the Permian. In the Permian its geographic range is truly cosmopolitan. In the Palmarito Formation it has been recovered from localities 1, 7 and 8. It is rare at locality 1, common at locality 8 and abundant at locality 7.

Comparison.—*Neophricadothyris* differs from *Squamularia* Gemmellaro (1899) in its biramous spines, narrower, posteriorly directed and more numerous coils of spiralia, and its apparent more evenly concentric ornament. It differs from *Phricadothyris* George (1932), in its posterolaterally, rather than laterally directed spiralia. *Martinothyris* Minato (1953) and *Nebenothyris* Minato (1953) differ in having dental plates or strong median septa internally, but Maxwell (1961) has noted that both are invalid on nomenclatural grounds as well. *Condrathyris* Minato (1953) is apparently (*fide* Cooper and Grant, 1976a, p. 2247) a junior synonym of *Phricadothyris*.

Pavlova (1965) studied the type species of the genus, *Squamularia asiatica* Chao (1929), and determined that it is not distinct from species of *Phricadothyris*. *Permophricodothyris* Pavlova (1965) was introduced to accommodate those forms, such as the Palmarito species, in which the spiral axes are directed posterolaterally. I concur with Cooper and Grant (1976a, p. 2248) in supporting the validity of *Permophricodothyris*, but have retained the name *Neophricadothyris*, in order that the Venezuelan and West Texas species may be less ambiguously comparable.

Neophricadothyris cf. **N. crassibecca**
Cooper and Grant
Plate 8, figures 45–57

cf. *Neophricadothyris crassibecca* Cooper and Grant, 1976a, p. 2253, pl. 638, figs. 1–33.

Description.—Small to medium-sized, average sized for genus, strongly biconvex; outline variable, subpentagonal to subelliptical, juveniles commonly transverse, mature individuals commonly more elongate; greatest width near midlength of shell; commissure rectimarginate in juveniles, becoming weakly uniplicate in more mature individuals; fold very low, not normally expressed posterior to commissure, sulcus more prominent, shallow, arising about 10–15 mm anterior to ventral beak; concentric lamellae moderately strong, variable in density, from four to 14 in a 5 mm distance at about midlength of mature individuals; each lamella bearing one or two rows of double-barrelled spines; growth lamellae unevenly spaced, locally crowded.

Ventral valve strongly convex, greatest height posterior to midvalve; beak commonly thickened, blunt, strongly curved, erect to slightly incurved; interarea curved, narrow, outlined by poorly defined beak ridges; delthyrium nearly equilaterally triangular, laterally bounded by low deltidial flanges, leaving delthyrium entirely open.

Dorsal valve less strongly convex; low beak in some mature specimens partially blocking delthyrium; interarea flat to slightly concave, of moderate height, broken by low, broad notothyrium; low flanges bounding margins of notothyrium.

Ventral interior having very short, pointed, slightly hooked teeth; dental ridges weak to moderately strong, united below delthyrial apex, not obstructing delthyrium; muscle area weakly to strongly impressed, elongate subelliptical to heart-shaped (in latter case bisected by very low narrow median ridge), commonly longitudinally striate, migrating anteriorly during ontogeny; earlier, posterior traces covered by secondary callus shell material. Adductor marks commonly present, diductor marks rarely preserved.

Dorsal interior having comparatively large hinge sockets, socket ridges having tooth-like swellings anteriorly; cardinal process small, poorly defined; helicophores and spiralia not preserved in silicified specimens, but axes of coiling generally divergent toward posterior, trending from lateral toward posterior orientation during course of ontogeny; muscle area narrow, elongate, weakly striate, sides slightly divergent anteriorly, bisected by very low, narrow median ridge.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Hinge Width	Maximum Width	Maximum Thickness
LOCALITY 7					
USNM 221469	10.3	8.8	8.4_e	11.8	11.7
USNM 221470	11.8	10.8	9.6_e	13.1	9.5
USNM 221471	13.5	11.8	8.6_e	14.0	9.8
USNM 221472	15.0	13.5	10.7_e	16.1	11.3
USNM 221473	15.3	13.8	10.3_e	16.1	12.2
USNM 221474	16.8	15.5	10.9_e	17.8	13.0
USNM 221475	16.9_c	15.5_c	11.1_e	18.6_c	11.9_c
USNM 221476	17.5	15.4	9.6_e	18.2	17.5
USNM 221477	18.7	15.8	11.8_e	19.5	13.7
USNM 221478	18.8	15.2	10.7_e	15.5	13.0
USNM 221479	20.7	18.5	14.6_e	20.8	14.6
USNM 221480	21.5	19.4	14.2_e	21.0	14.8
USNM 221481	21.8	18.8	15.5	21.0	16.1
USNM 221482	22.0	17.5	16.0_e	21.9	15.8
USNM 221483	23.1_c	19.6_c	14.1_e	21.0_c	17.4_c
USNM 221484	23.1	20.0	15.3_e	24.0	17.1
USNM 221485	24.5	19.3	11.9_e	22.4	18.8
USNM 221486	26.2	21.9	16.1_e	25.2	18.9
USNM 221487	26.4	22.5	16.8_e	24.6	19.5
LOCALITY 8					
USNM 221488	—	—	14.8	21.8	17.4
USNM 221489	25.2	21.5	14.1	20.1	20.2_e

Occurrence.—In the West Texas region where it was first described *N. crassibecca* occurs only in the Road Canyon Formation (Late Leonardian). A very closely related species, *N. bullata* Cooper and Grant (1976a), has been recovered from the Bone Spring, Hess, Cathedral Mountain and Road Canyon Formations, of from Late Wolfcampian to Late Leonardian age. In the Palmarito Formation individuals here tentatively referred to *N. crassibecca* but also similar to *N. bullata* have been recovered from localities 1, 7 and 8. An Early Permian age for the assemblages recovered from these localities is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Strongly biconvex, apically thickened *Neophricadothyris* having variable outline and ornament.

Types.—Figured Specimens: USNM 221469, USNM 221472, USNM 221479, USNM 221485, USNM 221487, USNM 221488–221493; Measured Specimens: USNM 221469–221489.

Comparison.—*Neophricadothyris* cf. *N. crassibecca* in the Palmarito Formation is an extremely variable species. It is easily distinguished from some of the West Texas species of the genus. *N. catatona* Cooper and Grant (1976a) is much larger and more transverse, while *N. transversa* Cooper and Grant (1976a) is more uniformly transverse throughout its ontogenetic development. Mature individuals of *N. conara* Cooper and Grant (1976a) are smaller than those of *N.* cf. *N. crassibecca* while similar ontogenetic stages of *N. guadalupensis* (Shumard, 1859) are larger, more commonly elongate, and have a flatter dorsal valve and higher deltidial flanges and dental ridges. *Squamularia guadalupensis* R. E. King (1931) included individuals assignable to two distinct species, *N. bullata* and *N. conara,* and cannot thus be directly compared to *N.* cf. *N. crassibecca.* In the West Texas area, several characters serve to distinguish suites of *N. bullata, N. cordata* and *N. crassibecca.* The Venezuelan specimens are most similar to the West Texas *N. crassibecca,* but, because they are more variable than known individuals of that species, they intergrade more extensively with other similar species. In the West Texas region, *N. crassibecca* is distinguished from closely related species by its small size, pentagonal or elliptical outline, crowded concentric lamellae, each bearing but a single row of double-barrelled spines, its great biconvexity, and its thickened ventral umbonal region. In the Venezuelan specimens only the last of these characters appears to be consistently different from other known species, except *N. crassibecca.* This single feature alone is clearly insufficient for erection of a new species. *N.* cf. *N. crassibecca* differs from the Bolivian Permian *Phricodothyris septata* Chronic (1949) in lacking a median septum in the ventral valve, and from *Phricodothyris guadalupensis peruensis* Chronic (1949) in the larger size of its mature individuals.

Discussion.—Cooper and Grant (1976a, p. 2254) have suggested that *N. crassibecca* may indeed be considered a subspecies of *N. bullata.* It does seem very difficult to differentiate in an objective manner between the various species of *Neophricadothyris* that have been erected. Perhaps the feeling that organisms must evolve through time has led to the expression of specific differences where only population variation exists. If, as has been suggested (*e.g.,* Eldredge and Gould, 1972, pp. 82 ff.) speciation does take place near the extremes of the geographic range of a species, it becomes more realistic to consider that the species *bullata, crassibecca* and *cordata* may be separable in the West Texas region, yet occur within a single population in Venezuela. A similar situation apparently occurs in the relationship of Texan and Venezuelan species of *Cooperina* Termier, Termier and Pajaud (1966).

Several of the Venezuelan specimens from locality 7 do not follow the common ontogenetic pattern in

form development. These more elongate individuals may be responding to the same sort of crowding pressures noted in population samples of *Hustedia hyporhachis* n. sp. from locality 10, Palmarito Formation. Certainly, equivalent positions of faunal dominance are attained by *Hustedia* Hall and Clarke (1893) at locality 10 and *Neophricadothyris* at locality 7, and to a lesser degree, at locality 8.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	2	—	5	calcite permineralization
7	110	11	40	calcite permineralization
8	6	7	36	fine silicification

Superfamily **SPIRIFERACEA** W. King, 1846

Family **SPIRIFERIDAE** W. King, 1846

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968

Genus **NEOSPIRIFER** Frederiks, 1924

Type Species.—*Spirifer fasciger* Keyserling, 1846, *in* Keyserling and Krozenstern, p. 231, pl. 8, figs. 3–3b (by original designation of Frederiks, 1924, p. 311). Lectotype = *Spirifer fasciger* Keyserling, 1846, pl. 8, fig. 3b (*non* figs. 3, 3a = species unknown) (by designation of Cooper and Grant 1976a, p. 2173).

Diagnosis.—Spiriferidae with fasciculate costae, without scaly, raised growth laminae, and with fine radial ornamentation weak or absent.

Occurrence.—*Neospirifer* ranges through Pennsylvanian and Permian strata, and in the Permian has a cosmopolitan distribution. In the Palmarito Formation, it has been recovered from localities 1 and 7, where it is common, and localities 4 and 8 where it is rare.

Comparison.—*Neospirifer* is distinguished from *Aperispirifer* Waterhouse (1968), an Asian and Australian genus, by the absence of any delthyrial plate in juvenile or early mature stages of that form. *Cartorhium* Cooper and Grant (1976a) is distinguished by its more rounded flanks, consistently triangular ventral interarea, subelliptical or rarely transverse outline, and limitation of its costal bifurcations to the posterior part of the valves. *Fusispirifer* Waterhouse (1966) is generally far more transverse, and has much fainter, lower radial ornament, and a more massive delthyrial plate. *Grantonia* Brown (1953), from the Permian of Southeast Asia and Australia, is generally similar to *Neospirifer* but has stronger, less numerous fascicles, and greatly thickened shells. *Gypospirifer* Cooper and Grant (1976a) has more numerous, finer, not distinctly fasciculate costae, and no real plications of the commissure except the median fold itself. *Lepidospirifer* Cooper and Grant (1969) differs in having weaker fasciculation, finer costae, scaly ornamentation and a straighter beak, with the apical plate small, low, and normally fused to the floor of the valve. *Spiriferinaella* Frederiks (1926) differs in having non-fasciculate costae. *Trigonotreta* Koenig (1825) bears costae which bifurcate only once, in an extremely regular fashion, in contrast to the condition of *Neospirifer*.

Neospirifer venezuelensis (Gerth)
Plate 9, figures 1–13

Spirifer cameratus Morton var. *venezuelensis* Gerth *in* Gerth and Kräusel, 1931, p. 525, pl. 22, figs. 3–4 (non *Spirifer venezuelensis* Weisbord, 1926, p. 19, 20, pl. 4, fig. 6).

Neospirifer thescelus Cooper and Grant, 1976a, p. 2189, pl. 609, figs. 30–48; pl. 610, figs. 1–38; pl. 611, figs. 1–12; pl. 612, figs. 1–12.

Description.—Large, strongly biconvex; outline irregularly semi-elliptical to subpentagonal or trapezoidal, normally widest at hinge but only slightly alate; commissure uniplicate medially, slightly undulating laterally; fastigium narrow, high anteriorly on larger shells; sulcus deep, broadly V-shaped in cross section, well-defined laterally by sharp costae. Costae strongly fasciculate, fascicles forming four to five plications on either flank of shell, progressively weaker laterally, commonly with prominent mesial costa arising at beak, subsidiary costae arising anteriorly by bifurcation, up to eight per fascicle, most on mesial fascicles; median costa of fastigium bifurcating near beak, continuing anteriorly as dual crest, bifurcating laterally only anteriorly. Median costa of sulcus narrowly bifurcated near beak, continuing to commissure, other costa in sulcus produced by lateral bifurcations of sulcus-bounding costae. Fine radial ornament absent; concentric ornament of fine, closely spaced growth lines, interrupted by stronger, irregularly spaced growth laminae, laminae becoming more frequent toward margins.

Ventral valve strongly convex transversely and longitudinally, greatest convexity posteriorly, shell thickened along hinge in large individuals; beak strongly hooked, overhanging open, triangular delthyrium; pseudodeltidium apical or absent, rarely preserved; interarea concave, commonly faintly striate longitudinally, extending to cardinal extremities; edge of hinge bearing numerous short denticles, apparently serving as articulatory processes.

Dorsal valve less strongly convex, produced only

slightly posterior to hinge; interarea low, slightly concave, but equal in width to ventral counterpart; notothyrium wide, low, apex bearing low, longitudinally finely striate cardinal process.

Ventral interior bearing strong, but very short, knob-like, anteriorly diverging teeth, supported by thick, deep dental ridges; ridges commonly converging toward valve floor; dental plates continuous with dental ridges apically, diverging to intersect floor on either side of muscle attachment area, in larger shells partly obscured laterally by secondary shell growth, callus material also commonly filling apical cones. Muscle area elongate oval, commonly excavate apically, slightly elevated anteriorly in larger shells; adductor marks elongate, narrow, lightly striate longitudinally, lying along each side of low, thin median ridge; diductor marks large, lateral to adductors. Floor of valve along hinge pitted and pustulose in irregularly radiating pattern. Pattern fading anteriorly.

Dorsal interior having widely divergent, thick-walled hinge sockets, non-functional posteromesial portions roofed by thin plates. Helicophores, spiralia not observed. Muscle attachment area elongate, bisected by low, sharp median ridge; exterior plications strongly reflected on remainder of surface. Median sulcus (reflection of external fold) bearing narrow shallow parallel furrows, running anteroventrally from midline toward sulcal margins.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Hinge Width	Mid-Width	Thickness
USNM 221494	52_c	46_c	69_{be}	62_c	21_c
USNM 221495	58	45	67_{be}	60	40_c
USNM 221499 (plastolectotype)	48	37	52	55	33
USNM 221500 (plastoparalectotype)	40	36	60_h	60_h	30

Occurrence.—In his discussion of the Palmarito Formation Gerth (*in* Gerth and Kräusel, 1931, p. 524) stated:

> . . . Der Fusulinenkalk geht in kalkig-mergelige Lagen über, die die folgenden Fossilien geliefert haben:
> *Spirifer cameratus* Mort. var. *venezuelensis* Gerth
> *Seminula argentea* Shep.

A fusulinid-bearing limestone occurs high in the Palmarito Formation and has been noted both in the type section and in the reference section established by Arnold (1966). Specimens of *Neospirifer venezuelensis* from localities 1, 4, 7 and 8 in the present study cover most of the stratigraphic extent of the formation. The form described as *N. thescelus* Cooper and Grant (1976a), has been recovered only from the (Late Leonardian) Road Canyon Formation of West Texas. A latest Leonardian age for the cited localities in the Palmarito Formation is not inconsistent with other biostratigraphic indicators.

Diagnosis.—Large, thick *Neospirifer* having strong costae and prominent fascicles producing plications, wide hinge but short or absent alae, and a moderately deep sulcus.

Types.—Lectotype: NHB L4453; Paralectotype: NHB L4452; Figured Specimens: USNM 221494–221500; Measured Specimens: USNM 221494–221495, USNM 221499–221500.

Comparison.—*N. venezuelensis* is easily differentiated from *N. cameratus* (Morton *in* Hildreth, 1836), as a variety of which it was first described, by its much stronger ornament of both costae and fasciculate plicae. The average size of mature individuals of *N. venezuelensis* is greater than that of the West Texas species *N. apothescelus* Cooper and Grant (1976a) and *N. formulosus* Cooper and Grant (1976a). It is less alate, or mucronate, than the West Texas species *N. amphigyus* Cooper and Grant (1976a), *N. bakeri bakeri* R. E. King (1931), and *N. bakeri columbiarus* Cooper and Grant (1976a). *N. huecoensis* R. E. King (1931) is less strongly uniplicate. *N. mansuetus* Cooper and Grant (1976a), *N. notialis* Cooper and Grant (1976a), and *N. placidus* Cooper and Grant (1976a) share the lower, less marked radial ornament that is more characteristic of *N. cameratus* than of *N. venezuelensis*. *N. neali* Cooper and Grant (1976a) is seldom as long-hinged as is *N. venezuelensis*, and has a longer, more strongly apsacline interarea. The characteristic dual crest of the fold distinguishes *N. venezuelensis* from the North American mid-Continent species *N. triplicatus* (Hall, 1852) and *N. latus* Dunbar and Condra (1932). It is effectively distinguished from *Spiriferella pseudocameratus* (Girty, 1920), commonly considered a species of *Neospirifer*, by the pustulose surface ornament which places that form within the Brachythyrididae.

Discussion.—Cooper and Grant (1976a) described the species *N. thescelus*, understandably having overlooked Gerth's (*in* Gerth and Kräusel, 1931) comparatively obscure publication of *S. cameratus* var. *venezuelensis*. Although the Palmarito suite of *N. venezuelensis* is small, such diagnostic characters as the very strong fasciculate plicae and the dual crest of the fold demonstrate the synonymy of *N. venezuelensis* and *N. thescelus*.

N. venezuelensis was first described on the basis of specimens provided to Gerth by the collector, Peter

Christ, who published the first account (Christ, 1927) of the Palmarito Formation. The specimens (two syntypes) are part of the collections of the Basle Naturhistorisches Museum. A holotype was not designated, possibly because Gerth described the form as a new variety of an existing species, rather than as a new species. To clarify future comparisons, I have here designated these as lectotype (NMB L4453) and paralectotype (NMB L4452). The International Code of Zoological Nomenclature (ICZN, 1961, Art. 45, sect. d, part ii) clearly states that a *variety* or *form* erected before 1961, if it has inherent geographic significance, may be considered of *infraspecific*, rather than *infrasubspecific* status, and therefore available for elevation to specific status when the generic designation is changed. Casts of the Swiss type specimens have been included with the present topotypic material as bases for the descriptions, and are figured here (Pl. 9, figs. 8, 9).

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
1	2	—	1	calcite permineralization
1	—	1	—	internal cast
1	—	—	1	external mold
4	—	—	1	coarse silicification
7	4	5	12	calcite permineralization
8	1	—	—	fine silicification
unknown*	2	—	—	calcite permineralization

* purchased from child at type locality of Palmarito Formation

Superfamily **SPIRIFERINACEA** Davidson, 1884

Discussion.—According to the *Treatise* (Boucot *et al., in* Williams *et al.*, 1965, p. H711) the Spiriferinacea consists of a single family including 19 genera ranging in age from Early Carboniferous to Early Jurassic. Only seven of these occur in the Permian. In the revision of the superfamily (Cooper and Grant, 1976b, p. 2666), the impunctate forms *Odontospirifer* Dunbar (1955) and *Spiriferinaella* Frederiks (1926) were removed on that basis. In addition, *Paraspiriferina* Reed (1944) was removed from synonymy with *Callispirina* Cooper and Muir-Wood (1951), and redesignated a valid genus. Three new genera, *Metriolepis* Cooper and Grant 1976b), *Arionthia* Cooper and Grant (1976b) and *Scenesia* Cooper and Grant (1976b), plus two others, *Sarganostega* Cooper and Grant (1969) and *Xestotrema* Cooper and Grant (1969), thus brought the total number of Permian spiriferinacean genera to 11, which were distributed in six new families: Reticulariinidae, Crenispiriferidae, Paraspiriferinidae, Sarganostegidae, Xestotrematidae and an un-named family containing the single genus *Scenesia*. While this arrangement has some drawbacks (non-spinose *Spiriferellina* [*sensu* Frederiks, 1924] are included in the Reticulariinidae, of which a diagnostic character is that genera included in it bear large hollow spines on the exterior), it is followed here, since it results from study of faunas very similar to the Venezuelan ones, and because it is the most recent comprehensive study of its kind.

Family **RETICULARIINIDAE** Cooper and Grant, 1976b

Genus **SPIRIFERELLINA** Frederiks, 1924

Type Species.—*Terebratulites cristatus* Schlotheim, 1816, p. 16, pl. 1, figs. 1a–c, by original designation of Frederiks, 1924, p. 299.

Diagnosis.—Typically small, transversely rounded, having flat-crested, low fastigium, few lateral plications, irregularly spaced growth lines; surface smooth or having many small low pustules; cardinal process narrow, crural plate broad, forming small apical platform.

Occurrence.—*Spiriferellina* is a nearly cosmopolitan Permian genus, having been recovered from both the Tethyan and Boreal realms. It has not to date been recognized in Australia or New Zealand.

Comparison.—*Spiriferellina* is easily distinguished from the other two Permian Reticulariinidae, *Reticulariina* Frederiks (1916) and *Altiplecus* Stehli (1954), by the conspicuous hollow ornament spines of these genera, which are never present in species of *Spiriferellina*.

Discussion.—Due to an initial oversight by Frederiks (1924), who named *Terebratulites cristatus* Schlotheim (1816) as the type of the genus *Spiriferellina*, none of Schlotheim's specimens was cited, and reference was instead made to descriptions and illustrations by Tschernyschev (1902). Frederiks also cited a Bolivian Permian species, *S. campestris* (White, 1874) Kozlowski (1914), since demonstrated (Chronic, *in* Newell *et al.*, 1953; Cooper and Grant, 1976b) to belong in *Reticulariina*.

With this confusion, *Spiriferellina* easily became a catch-all genus for punctate spiriferoids, often without regard to comparison with its type species *S. cristata*. Campbell (1959) clarified the relationships of some spiriferinaceans by redescribing type materials of *Punctospirifer* North (1920), *Reticulariina* and *Spiriferellina*. Cooper and Grant's (1976b, p. 2666 ff.) separation of the former family Spiriferinidae into six

new families, each distinguished on clear morphological grounds, is clearly a step towards a more systematic, if not more realistic treatment of these punctate forms.

Spiriferellina cf. **S. hilli** (Girty)
Plate 8, figures 58–71; Plate 9, figures 28–29

cf. *Spiriferina hilli* Girty, 1909, p. 379, pl. 30, figs. 15–15b.
cf. *Spiriferellina hilli* (Girty), Cooper and Grant, 1976b, p. 2703, pl. 704, figs. 18–25; pl. 709, figs. 18–71.

Description.—Small, average sized for genus, unequally biconvex; subovate to transversely subelliptical in outline; hinge wide, cardinal extremities commonly rectangular or slightly extended; commissure plicated by median fold and three to four, most commonly three lower plications on each flank; plications separated by nearly equally wide troughs, all arising at beaks or along hingeline; median plication widening anteriorly, in lateral aspect rising slightly above more tightly curved lateral plications; crest of plication flattened at beak, remaining flattened toward anterior; sulcus shallow, somewhat quadrate in cross section, median trough flattened or slightly swollen to form low ridge. Surface bearing low, rarely preserved pustules between punctae; spines absent; growth laminae strong, widely and irregularly spaced, somewhat more crowded near margins.

Ventral valve moderately deep; beak prominent, elongate or attenuate, apex bluntly pointed, moderately to strongly curved; interarea broadly triangular, apsacline, radius of curvature lessening towards apex; delthyrium triangular, apically bearing short bridge across median septum; deltidial plates not preserved.

Dorsal valve less strongly convex, fastigium in lateral view nearly straight; beak bluntly pointed, interarea low, wide, slightly concave; notothyrium broadly triangular, apex bearing narrow, ventrally striate cardinal process.

Ventral interior having short, knob-like teeth; dental ridges moderately strong, tapering anteriorly, converging slightly toward midline of valve; dental plates short, apical in adults, meeting dental ridges at about one-half their length; median septum high, very thin, abruptly sloping anteriorly, extending about one-third to one-fourth valve length from apex. Muscle marks on floor of valve and sides of septum insufficiently well-preserved to distinguish adductors or diductors.

Dorsal interior having wide, open sockets, partially roofed posteriorly by anterior edge of interarea; socket ridges thick, slightly elevated anteriorly; hinge plates attached to socket ridges, strongly deflected dorsally, converging and fusing along midline to form concave hinge plate, bisected by cardinal process ventroposteriorly, markedly notched anterodorsally; crura extending anteriorly from hinge plates, bowed outward, then converging; jugal processes and spiralia not observed. Muscle area elongate, mesial, undifferentiated.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Hinge Width	Mid-Width	Maximum Width	Thickness
LOCALITY 3						
USNM 221501	2.4	2.0	2.2	2.4	2.4	1.8
USNM 221502	3.2	3.2	4.2	4.5	4.7	3.0
USNM 221503	3.5	3.2	3.8_h	4.8_h	4.8_h	3.0
USNM 221504	4.0	3.8	4.6_b	5.4_b	5.4_b	3.2
USNM 221505	4.5	3.9	5.0	4.9	5.4_b	3.6
USNM 221506	5.3	4.7	7.0_h	5.6_h	7.0_h	4.8
USNM 221507	6.1	5.3	—	6.0	—	4.8
USNM 221508	7.8	6.0	7.9	7.5	8.5	5.3
USNM 221509	8.1	6.7	10.4_{bh}	7.5_b	10.4_{bh}	6.0
USNM 221510	8.0	6.3	10.3_b	9.5	10.3_b	7.2

Occurrence.—*Spiriferellina* cf. *S. hilli* has been recovered from locality 3 of the Palmarito Formation. *S. hilli* is known in the West Texas region from various localities within the Word Formation (Guadalupian). Such an age assignment is a bit younger than that indicated by other biostratigraphic indicators for the Palmarito locality, but is not beyond the realm of reasonable possibility.

Diagnosis.—Transverse to nearly equidimensional wide-hinged *Spiriferellina* with moderately flat dorsal valve.

Types.—Figured Specimens: USNM 221501, USNM 221505, USNM 221506, USNM 221508, USNM 221510–221515; Measured Specimens: USNM 221501–221510.

Comparison.—*S. hilli* may easily be distinguished

from *S. paucicostata* Cooper and Grant (1976b) by the larger size of mature individuals of that species, and from *S. nuda* Cooper and Grant (1976b) and *S. cristata* (Schlotheim, 1816) by the smaller size of mature individuals of those species. *S. nasuta* Cooper and Grant (1976b) is characterized by a markedly elongate interarea and ventral beak, while *S. vescula* Cooper and Grant (1976b) is much more strongly biconvex. The Late Leonardian species *S. tricosa* Cooper and Grant (1976b) is very similar to *S. hilli,* but differs in the slightly larger size of mature individuals, its wider hinge and its more abundant pustules. The Venezuelan form here tentatively assigned to *S. hilli* differs from that form in West Texas in its slightly more transverse outline and its slightly higher fastigium. The outline of *S.* cf. *S. hilli* from the Palmarito is quite variable, with the hinge equal to or slightly less than the greatest width of the shell. West Texas species seem less variable, but whether this is ecologically caused or due to over-splitting of taxa cannot be determined.

Discussion.—As in the Chonetacea, surface ornament is used here as an important diagnostic character at the generic level. Within any genus, specific differentiation is not unduly difficult. Differences at the generic level however, are made less concise by the vagaries of preservation: a hollow spine, if broken off, may produce either a pustule-like prominence, a recognizable hollow-spine base, or no trace; differing degrees of decortication may produce surface punctae of differing patterns or sizes. In taxonomic determinations, presence of a morphologic feature is far more significant than absence.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	18	11	10	fine silicification

Order **TEREBRATULIDA** Waagen, 1883

Suborder **TEREBRATULIDINA** Waagen, 1883

Superfamily **DIELASMATACEA** Schuchert, 1913

Family **DIELASMATIDAE** Schuchert, 1913

Subfamily **DIELASMATINAE** Schuchert, 1913

Genus **ANEUTHELASMA** Cooper and Grant, 1976b

Type Species.—*Aneuthelasma amygdalinum* Cooper and Grant, 1976b, p. 2906, pl. 762, figs. 26–61.

Diagnosis.—Dielasmatinae without dental plates and with inner hinge plates widely separated where they meet the valve floor.

Occurrence.—The genus *Aneuthelasma* has been reported from the West Texas region, where it occurs in the Capitan and Bell Canyon Formations (Guadalupian). The Venezuelan form assigned to the genus is probably from a somewhat lower level.

Comparison.—*Aneuthelasma* differs from *Dielasma* W. King (1859), *Dielasmina* Waagen (1882), *Ectoposia* Cooper and Grant (1976b), *Fletcherithyris* Campbell (1965), *Hoskingia* Campbell (1965), *Plectelasma* Cooper and Grant (1969), *Whitspakia* Stehli (1964) and *Yochelsonia* Stehli (1961a) by its total lack of dental plates in the ventral interior. *Hemiptychina* Waagen (1882) has an anteriorly plicate commissure, and *Camarelasma* Cooper and Grant (1976b) and *Lowenstamia* Stehli (1961b) both have inner hinge plates in the dorsal valve, features that *Aneuthelasma* lacks. Three genera known from the Permian of the Australia–New Zealand area [*Gilledia* Stehli (1961a), *Maorielasma* Waterhouse (1964) and *Marinurnula* Waterhouse (1964)], are *Dielasma*-like terebratuloids that also lack dental plates. These three have been combined to form the Gillediidae (Campbell, 1965), chiefly on that basis. Although *Aneuthelasma* and some other Dielasmatidae would logically fit in that family, I have considered it premature to relocate these genera without knowing whether hinge structure or presence/absence of dental plates is more significant at the generic level. Of the three genera mentioned above, *Gilledia* may be distinguished from *Aneuthelasma* by its commonly uniplicate anterior commissure; *Maorielasma,* like most of the Dielasmatidae, has inner hinge plates that combine to form a septalium, and *Marinurnula* is a much larger shell, with a distinct tendency toward folding of the anterior commissure. Internally the genera of the Labaiidae [*Labaia* Likharev (1956), *Pseudodielasma* Brill (1940), *Oligothyrina* Cooper (1956)] closely resemble *Aneuthelasma*. The anterior commissures of the latter two genera however are distinctly folded. The loop in those genera, as it arises from the crural bases, is more robust, and the two parallel elements are more closely appressed than is the case with *Aneuthelasma*. In addition, the outer hinge plates of the Labaiidae are secondary, while in *Aneuthelasma* they are not. *Labaia* itself is poorly known: though it does not appear (Likharev, 1956, pl. 72, fig. 3) to be folded, the interior is not shown and has only been very broadly defined (Stehli, 1965, p. H755).

Aneuthelasma globosum new species
Plate 9, figures 14–27

Etymology of Name.—L. *globosus* = rotund, globose.

Description.—Small, small for genus, subtriangular to suboval to subpentagonal in outline, maximum width about midvalve. Anterior commissure rounded, straight. Valves nearly equal in depth. Surface smooth.

Ventral valve evenly and moderately convex in lateral view; broadly and evenly convex in anterior view, with somewhat flattened flanks in older specimens. Beak short, suberect to erect; umbonal region somewhat swollen, swelling absent at midvalve. Sulcus absent. Foramen small, slightly labiate; beak ridges strong, rounded. Deltidial plates thin, disjunct, well-defined.

Dorsal valve broadly convex in lateral and anterior views. Beak small; umbonal region narrowly swollen, anterior portion somewhat flattened.

Ventral interior without dental plates, but having a well-defined, thick pedicle collar; muscle area ovate, poorly defined. Teeth short, strong, hooked slightly dorsoposteriorly.

Dorsal interior having strong socket ridges and posterolaterally recurved fulcral plates; outer hinge plates obsolete; crural bases broad; inner hinge plates very short to absent, if present widely separated, contacting valve floor vertically. Descending branches of loop long, subparallel; transverse ribbon not observed.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Maximum Width	Thickness
LOCALITY 6 (block A)				
USNM 221516	2.3	2.0	2.0	1.4
USNM 221517	3.4_b	3.1	2.7	1.8
USNM 221518	3.9_b	3.5	3.4_{be}	—
USNM 221519	5.5_b	4.7	4.5	3.1
USNM 221520 (holotype)	6.1	5.5	5.4	3.4
LOCALITY 6 (block B)				
USNM 221521	2.9	2.5	2.3	1.5
USNM 221522	4.7	4.0	3.6	2.9
USNM 221523	5.1	4.3	3.8	3.5_{be}
LOCALITY 6 (block C)				
USNM 221524	3.0	2.6	2.5	1.6
USNM 221525	3.1_b	2.7_b	2.9_b	1.7
USNM 221526	3.3	2.8	2.7	1.8
USNM 221527	3.7	3.3	2.9	1.9_b
USNM 221528	3.8	3.3	3.1	2.1
USNM 221529	4.0	3.5	3.4	2.2
USNM 221530	4.5	4.0	3.7	2.7
USNM 221531	4.5	3.9	3.7_b	3.0
USNM 221532	4.8	4.2	4.2	3.1_e

Occurrence.—*Aneuthelasma globosum* n. sp. has been recovered only from locality 6, blocks A, B and C, in the Palmarito Formation. The other known species of the genus, *A. amygdalinum* Cooper and Grant (1976b), is known from the Capitan and Bell Canyon Formations in the West Texas Permian.

Diagnosis.—Small, globose *Aneuthelasma.*

Types.—Holotype: USNM 221520; Figured Specimens: USNM 221516, USNM 221520, USNM 221522, USNM 221523, USNM 221526, USNM 221529, USNM 221530, USNM 221533; Measured Specimens: USNM 221516–221532.

Comparison.—*Aneuthelasma globosum* is distinguished from the other known species of the genus, *A. amygdalinum,* by its more rotund form and smaller size of mature individuals. It may be distinguished from the superficially similar form *Pseudodielasma brilli* Cooper and Grant (1976b) by the slight tendency of that form toward a uniplicate anterior commissure, as well as its more narrowly appressed, more robust crural bases. It differs from internally similar species of *Marinurnula* Waterhouse (1964) and *Gilledia* Stehli (1961a) in its decidedly equivalved condition and absence of anterior commissural plication or folding.

Discussion.—*A. amgygdalinum* is known only from the Early Guadalupian of the West Texas region. Although possible, it is unlikely, on the bases of other Palmarito biostratigraphic indicators, that *A. globosum* is this young.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block A)	12	3	3	fine silicification
6 (block B)	15	9	5	fine silicification
6 (block C)	25	9	13	fine silicification

Family **PSEUDODIELASMATIDAE** Cooper and Grant, 1976b

Genus **OLIGOTHYRINA** Cooper 1956

Type Species.—*Oligothyrina alleni* Cooper, 1956, p. 526, pl. 61, figs. 33–41.

Diagnosis.—Small, with a weakly to strongly intraplicate anterior commissure; folds arising anterior to midlength; transverse band not projecting anteriorly.

Occurrence.—*Oligothyrina* is known from rocks ranging in age from Middle Pennsylvanian to Early Permian, in North America. The genus has tentatively

been identified from the Chochal Limestone (Leonardian) of Guatemala. It is also tentatively identified at localities 3 and 13 of the Palmarito Formation, Venezuela.

Comparison.—*Oligothyrina* is easily distinguished from *Pseudodielasma* Brill (1940) by the paraplicate anterior commissure of that genus, and from *Pleurelasma* Cooper and Grant (1976b) by the costate anterior commissure of that genus, as compared to the intraplicate commissure characteristic of *Oligothyrina*.

Discussion.—*Oligothyrina* has not been recognized in the West Texas region. This is peculiar as few genera present in the Palmarito Formation are neither "West Texas" genera nor new. Its absence there may in some manner be facies-related, though no hard data either support or negate that suggestion.

Oligothyrina? sp.
Plate 10, figures 1–4

cf. *Oligothyrina*? sp. Stehli and Grant, 1970, p. 34, pl. 12, figs. 1–12; pl. 13, figs. 8–16.

Description.—Small, slightly small for genus, strongly biconvex, teardrop-shaped in outline; beak erect to slightly incurved; foramen somewhat telate; anterior commissure intraplicate to antiplicate; anterior face somewhat truncate. Surface smooth.

Ventral valve evenly convex, greatest depth about midvalve; median portion of shell somewhat flattened from about midvalve anteriorly.

Dorsal valve unevenly convex, greatest depth umbonal; beak small, narrow, not protruding much beyond outline of remainder of valve.

Interiors unknown.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Maximum Width	Thickness
LOCALITY 3				
USNM 221534	3.0	2.5	2.1	1.8
USNM 221535	3.8	3.2	2.8	2.4
USNM 221536	4.1	3.6	3.0	3.1
USNM 221537	4.2	3.4	3.3	3.0
USNM 221538	4.4	3.6	3.0	2.9
LOCALITY 13				
USNM 221539	4.4	3.4	3.2	3.2
USNM 221540	4.6	3.5	3.5	3.5

Occurrence.—*Oligothyrina*? sp. is here reported from localities 3 and 13, of the Palmarito Formation, Venezuela. Another terebratulid, larger than the Palmarito specimens, but also assigned tentatively to the genus *Oligothyrina* was reported from the Chochal Limestone, of Leonardian-equivalent age, of Guatemala (Stehli and Grant, 1970, p. 34). The type species of the genus, *O. alleni* Cooper (1956), is known only from North America, where it occurs in Pennsylvanian strata.

Diagnosis.—Small, strongly biconvex *Oligothyrina*?, with width commonly equal to thickness.

Types.—Figured Specimen: USNM 221539; Measured Specimens: USNM 221534–221540.

Comparison.—Since the interior of the Venezuelan form is entirely unknown, it cannot be directly compared to such details in known species of *Oligothyrina*. It is, however, more strongly convex than either *O. alleni* or *O.*? sp. Stehli and Grant (1970), and is smaller than the latter form.

Discussion.—While the interior details of the Terebratulida are of great recognized importance in taxonomic differentiation of that group, some distinctions can nevertheless be made on the basis of external characteristics, especially in the case of the distinctive commissural folding of *Oligothyrina*.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
3	34	—	—	coarse silicification
13	2	—	—	coarse silicification

Suborder **TEREBRATELLIDINA**
Muir-Wood, 1955

Superfamily **CRYPTONELLACEA** Thomson, 1926

Family **CRYPTONELLIDAE** Thomson, 1926

Subfamily **CRYPTACANTHIINAE** Stehli, 1965

ANAPTYCHIUS new genus

Etymology of Name.—Gr. *ana* = not; Gr. *ptychios* = folded.

Description.—Small, subtriangular to subovate to subpentagonal in outline, having broadly convex ventral and dorsal valves; anterior commissure rectimarginate, unfolded; shell gently rounded in lateral and

anterior views; beak suberect; umbonal region flattened, broad in dorsal view, thin in lateral view; beak ridges distinct, strong, rounded; foramen commonly open, not labiate, rarely closed by thin disjunct deltidial plates anteriorly in larger shells; surface smooth.

Ventral valve evenly convex, teardrop-shaped in dorsal view; greatest depth commonly at midvalve; greatest width commonly anterior thereto; foramen submesothyridid; umbonal region distinctly swollen in dorsal aspect; flattened in lateral view.

Dorsal valve evenly but more flatly convex than ventral, without fold or commissural flexure; valve subcircular in outline; outline broken by narrow, short beak, beak protruding short distance into delthyrium; greatest width and depth about midvalve.

Ventral interior having pair of small, blunt hinge teeth; edges of delthyrium supported by strong dental plates; muscle attachment areas posterior, elongate, poorly differentiated, divided by low broad median rise; valve floor in larger specimens thickened between dental plates.

Dorsal interior having low outer hinge plates; inner hinge plates apparently disjunct in immature specimens, in mature specimens conjunct, slightly raised mesially and anteriorly, with small elongate apical perforation; outer socket ridges obsolete; inner socket ridges high, thin, flared distally; hinge plate free of valve floor; median septum absent; muscle attachment areas elongate, poorly differentiated, separated by low, indistinct median rise; loop long, cryptacanthiform, anteriorly spinose, with descending lamellae joined distally by mesially recurved jugum in immature specimens, but free in mature specimens; ascending lamellae bearing broad bands.

Type Species.—*Anaptychius minutus* n. sp.

Diagnosis.—Small, rectimarginate, unfolded Cryptacanthiinae.

Occurrence.—*Anaptychius* is known only from locality 6, blocks A, B and C, of the Palmarito Formation.

Comparison.—*Anaptychius* is distinguished from *Cryptacanthia* White and St. John (1867) and *Gacina* Stehli (1961b) by its rectimarginate, unfolded shell, and from *Glossothyropsis* Girty (1934) by that feature and its lack of a dorsal median septum.

Discussion.—The loop and hinge of *Anaptychius* unequivocally link it with the Cryptacanthiinae. I decided to expand the bounds of that subfamily to receive unfolded shells, rather than to erect a new subfamily. The small size of this shell may in part account for its previous obscurity.

Anaptychius minutus new species
Plate 10, figures 5–17

Etymology of Name.—L. *minutus* = minute.

Description.—Minute to small, small for genus, subtriangular to subovate to subpentagonal in outline, having broadly convex ventral and dorsal valves; anterior commissure rectimarginate, unfolded; shell gently rounded in lateral and anterior views; beak suberect; umbonal region flattened, broad in dorsal view, thin in lateral view; beak ridges distinct, strong, rounded; foramen commonly open, but partially closed by thin, disjunct deltidial plates in larger specimens; surface smooth.

Ventral valve evenly convex, teardrop-shaped in dorsal view; greatest depth commonly at midvalve; greatest width commonly anterior thereto; foramen submesothyridid; umbonal region distinctly swollen in dorsal aspect; flattened in lateral view.

Dorsal valve evenly but more flatly convex than ventral, without fold or commissural flexure; valve subcircular in outline; outline broken by narrow, short beak, beak protruding short distance into delthyrium; greatest width and depth about midvalve.

Ventral interior having pair of small, blunt hinge teeth; edges of delthyrium supported by strong, ventrally slightly convergent dental plates; muscle attachment areas posterior, elongate, poorly differentiated, divided by low, broad median rise; valve floor between dental plates thickened secondarily in larger specimens.

Dorsal interior having low outer hinge plates; inner hinge plates apparently disjunct in immature specimens, in mature specimens conjunct, slightly raised mesially and anteriorly, with small elongate apical perforation; outer socket ridges obsolete; inner socket ridges high, thin, flared distally; hinge plate free of valve floor; median septum absent; muscle attachment areas elongate, poorly differentiated, separated by low, indistinct median rise; loop long, cryptacanthiform, anteriorly bearing two or three sharp narrow anteriorly-directed spines on each bout of junction between descending and ascending lamellae; descending lamellae diverging slightly from bases, bearing dorsal cuspate points, joined in young mature specimens by posteromesially cuspate jugum, jugum apparently resorbed in mature individuals; descending lamellae closely appressed anteriorly near junction with ascending lamellae; ascending lamellae diverging dorsoposteriorly, broadening, curving around to join as slightly inclined broad transverse band at midline.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Maximum Width	Thickness
LOCALITY 6 (block A)				
USNM 221541	1.8	1.5	1.7	0.9
USNM 221542	2.0	1.6	1.8	0.8
USNM 221543	2.3_b	1.9	2.1	1.0
USNM 221544	2.3_b	2.0	2.0	1.0
USNM 221545	2.7_b	2.3	2.5	1.4
USNM 221546	2.8	2.3	2.6	1.5
USNM 221547	2.8_b	2.4	2.6	1.5
USNM 221548	4.8	3.1	4.3	2.4
LOCALITY 6 (block C)				
USNM 221549	4.1_b	3.5	3.1	2.1
USNM 221550	4.8	4.1	4.0	2.5
USNM 221551	4.9	4.1	4.0	2.5
USNM 221552 (holotype)	6.5	5.6	5.7	3.4

Occurrence.—*Anaptychius minutus* n. sp. is known only from locality 6, blocks A, B and C of the Palmarito Formation. Based on other biostratigraphic indicators, this horizon contains a fauna of latest Leonardian to Early Guadalupian equivalent age.

Diagnosis.—Small *Anaptychius*.

Types.—Holotype: USNM 221552; Figured Specimens: USNM 221550–221554; Measured Specimens: USNM 221541–221552.

Comparison.—*Anaptychius minutus* is the only species of the genus. It is differentiated from other Cryptacanthiinae chiefly by its rectimarginate, unfolded commissure and secondarily by its lack of a median septum. Its small to minute size suggests that it may be a small species of the genus.

Discussion.—Externally *Anaptychius minutus* is very similar to such forms as *Dielasmella* Weller (1911), a Mississippian cryptonellid. Internally, however, its hinge and loop clearly demonstrate its cryptacanthine affiliation.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
6 (block A)	18	6	5	fine silicification
6 (block B)	2	4	4	fine silicification
6 (block C)	17	4	3	fine silicification

Subfamily **CRYPTONELLINAE** Thomson, 1926

Genus **TEXARINA** Cooper and Grant, 1970

Type Species.—*Texasia oblongata* Cooper and Grant, 1969, p. 17, pl. 5, figs. 7–9.

Diagnosis.—Elongate, slender sulciplicate Cryptonellacea.

Occurrence.—*Texarina* has to date been reported only from the West Texas region, in rocks ranging in age from Leonardian (Cathedral Mountain and Road Canyon Formations) to Guadalupian (Cherry Canyon and Word Formations). An exact external homeomorph, *Mimaria* Cooper and Grant (1976b) (Heterelasminidae) is known from the Sosio Formation of Sicily. It differs from *Texarina* in having a short loop, no dental plates and no hinge plate.

Comparison.—*Texarina* may be distinguished from *Cryptonella* Hall (1861), in anterior view, by its more broadly triangular outline, which is somewhat concave ventrally, in contrast to the narrow transverse-elliptical outline characteristic of *Cryptonella*. The ventral valve of *Cryptonella* is rarely so strongly sulcate as that of *Texarina*. *Heterelasma* Girty (1909) and *Texarina* are very similar. The beak of *Heterelasma* tends to be more incurved, and the anterior folding is commonly better expressed in *Texarina*, though it is present as well in *Heterelasma*.

Discussion.—The rare Palmarito specimens are assigned tentatively to the genus *Texarina* not so much on the basis of their generic characters, but rather because they are most similar to a *species* of *Texarina*.

Texarina? cf. **T. wordensis** (R. E. King)
Plate 10, figures 18–29

cf. *Dielasma problematicum wordense* R. E. King, 1931, p. 131, pl. 44, figs. 16a–e.

cf. *Texarina wordensis* (R. E. King), Cooper and Grant, 1976b, p. 2836, pl. 771, figs. 1, 2; pl. 773, figs. 21–42; pl. 774, figs. 1–56; pl. 775, figs. 55–60.

Description.—Medium-sized, about average-sized for genus, longer than wide; subtrigonal to elongate rhomboid in outline, becoming more elongate through ontogeny; greatest width variable, but commonly in anterior third of shell in young, near midlength in mature individuals; sides broadly rounded at maximum width; anterior margin narrow, only slightly truncated in lateral view. Anterior commissure broadly uniplicate in young, sharply sulciplicate in adult shells. Surface smooth except for anterior shell flexures.

Ventral valve broadly convex in lateral view, greatest convexity posterior; anterior profile moderately to deeply concave, with sides elevated and narrowly rounded, forming short, steep slopes. Beak suberect to erect, beak ridges sharp; foramen small. Umbonal region moderately convex. Sulcus very low, arising on anterior slope of umbonal region, broadening anteriorly. Anterior commissure emarginate, sulcus there bearing low costa in adults.

Dorsal valve of adults evenly, gently convex in lateral view, more convex posteriorly in immature specimens; in anterior view narrowly domed and with a subcarinate keel; lateral slopes steep. Median region broadly keeled from umbo nearly to anterior margin, where shallow median sulcus developed, sulcus bounded by strong rounded costae.

Interiors unknown.

Measurements (in mm).—

	Total Length	Dorsal Valve Length	Maximum Width	Thickness
LOCALITY 11				
USNM 221555	9.6_b	8.6	7.0	4.6
USNM 221556	20.0	18.5	10.8	9.5

Occurrence.—*Texarina wordensis* occurs in the Cathedral Mountain and Road Canyon Formations of West Texas. In the Palmarito Formation the specimens tentatively referred to the species have been recovered only from locality 11, where they are a rare faunal element. A Late Leonardian age, based on this occurrence, is not inconsistent with other biostratigraphic indicators in assemblage 11.

Diagnosis.—Narrow, moderately thick *Texarina* having subtruncate anterior margin and subcarinate dorsal valve.

Types.—Figured and Measured Specimens: USNM 221555–221556.

Comparison.—*Texarina wordensis* may easily be distinguished from *T. oblongata* (Cooper and Grant, 1969) by the larger size of mature individuals of that species, and from *T. paucula* Cooper and Grant (1976b) and *T. solita* Cooper and Grant (1976b) by the smaller size of mature individuals of those species. *T. elongata* Cooper and Grant (1976b) is much deeper and in lateral view has a distinctly truncate anterior margin. *T. parallela* Cooper and Grant (1976b) shares these characteristics with *T. elongata,* but has nearly parallel sides that do not narrow appreciably anteriorly. In anterior view, the Palmarito specimens differ from *T. wordensis* in their somewhat narrower outline and less marked ventral sulcus.

Discussion.—The Palmarito specimens are tentatively assigned to *Texarina* since they more closely resemble a species of that genus than species of other elongate sulciplicate terebratulid genera. Comparisons are made to the West Texas form *Texarina,* rather than its external homeomorph *Mimaria* Cooper and Grant (1976b), since the latter is geographically far distant from Venezuela, lessening the probability that it and the Palmarito specimens could be closely related.

Material.—

Locality	Articulated Valves	Dorsal Valves	Ventral Valves	Type of Preservation
11	4	1	—	fine silicification

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PLATES

EXPLANATION OF PLATE 1

Figure — Page

1–6. **Petrocrania teretis** Cooper and Grant 39

1–5. Dorsal valve, USNM 220975; 1. exterior view, ×1; 2. interior view, ×1; 3. exterior view showing smooth exterior surface, ×5; 4. interior view, showing well-impressed muscle scars, ×5; 5. lateral view, showing asymmetrical profile, ×4; locality 6 (block A).

6. Articulated valves, USNM 220979. ventral view, showing valve overlap, ×4; locality 6 (block A).

7–9. **Acosarina**? sp. 40

Ventral valve, USNM 220981; 7. interior view, showing development of dental plates and median septum, ×1; 8. same view, showing disposition of teeth, ×2; 9. posterior view, showing narrow delthyrium and small triangular teeth, ×2; locality 7.

10–16. **Derbyia** cf. **D. complicata** Cooper and Grant 43

10–12. Articulated valves, USNM 220988; 10. posterior view, showing low dorsal interarea and well-developed chilidium, ×1; 11. dorsal view, showing distinct sulcus and characteristic surface ornament of alternating crenulate costae and costellae, ×1; 12. ventral view, showing low fold and characteristic surface ornament, ×1; locality 8.

13–15. Single dorsal valve, USNM 220986; 13. ventral (interior) view, showing broadly divergent erismata, shallowly bifurcate cardinal process myophore and internal reflection of exterior surface ornament, ×1; 14. posteroventral (interior) view, showing relation of cardinal process to hingeline and development of hinge sockets, ×1; 15. posterior view, showing development of chilidium, ×2; locality 4.

16. Fragment of ventral valve, USNM 220987; interior view, showing short median septum, faintly impressed muscle attachment scars, and interior reflection of exterior surface ornament, ×2; locality 8.

17–28. **Derbyia deltauriculata** n. sp. 44

17–19. Single dorsal valve, USNM 220991; 17. ventral (interior) view, showing moderately well-impressed adductor muscle attachment scars, distally sinuous erismata, and large deltoid ears, ×1; 18. posteroventral (interior) view, showing relation of cardinal process to hingeline, and development of hinge sockets, ×1; 19. posterior view, showing swollen valve and development of chilidium, ×1; locality 10.

20. Dorsal valve, USNM 220990; dorsal view, showing large deltoid ears, characteristic subdued surface ornament and low cardinal process, ×1; locality 10.

21–22. Articulated valves, USNM 220994; 21. posterodorsolateral view, showing relation between the two valves, ×1; 22. ventral view, showing horn coral (possible symbiont) attached to ventral valve, in position to intercept inferred incurrent flow (lateral portion obscured by photographic mounting medium), ×1; locality 10.

23. Ventral valve, USNM 220995; dorsal (interior) view, showing deflection of anterior margin and asymmetric interarea, produced by growth in crowded conditions, ×1; locality 10.

24. Ventral valve, USNM 220996; posterior view, showing asymmetry produced by growth in crowded conditions, ×1; locality 10.

25–26. Ventral valve, USNM 220989; 25. posterior view, showing actual size, ×1; 26. posterior view, showing low interarea and mesially grooved pseudodeltidium, ×2; locality 10.

27–28. Single ventral valve, USNM 220993 (holotype); 27. dorsal (interior) view, showing long median septum and well-impressed adductor muscle attachment scars, ×1; 28. ventral view, showing large deltoid ears and characteristic subdued surface ornament, ×1; locality 10.

29. **Derbyia** sp. 46

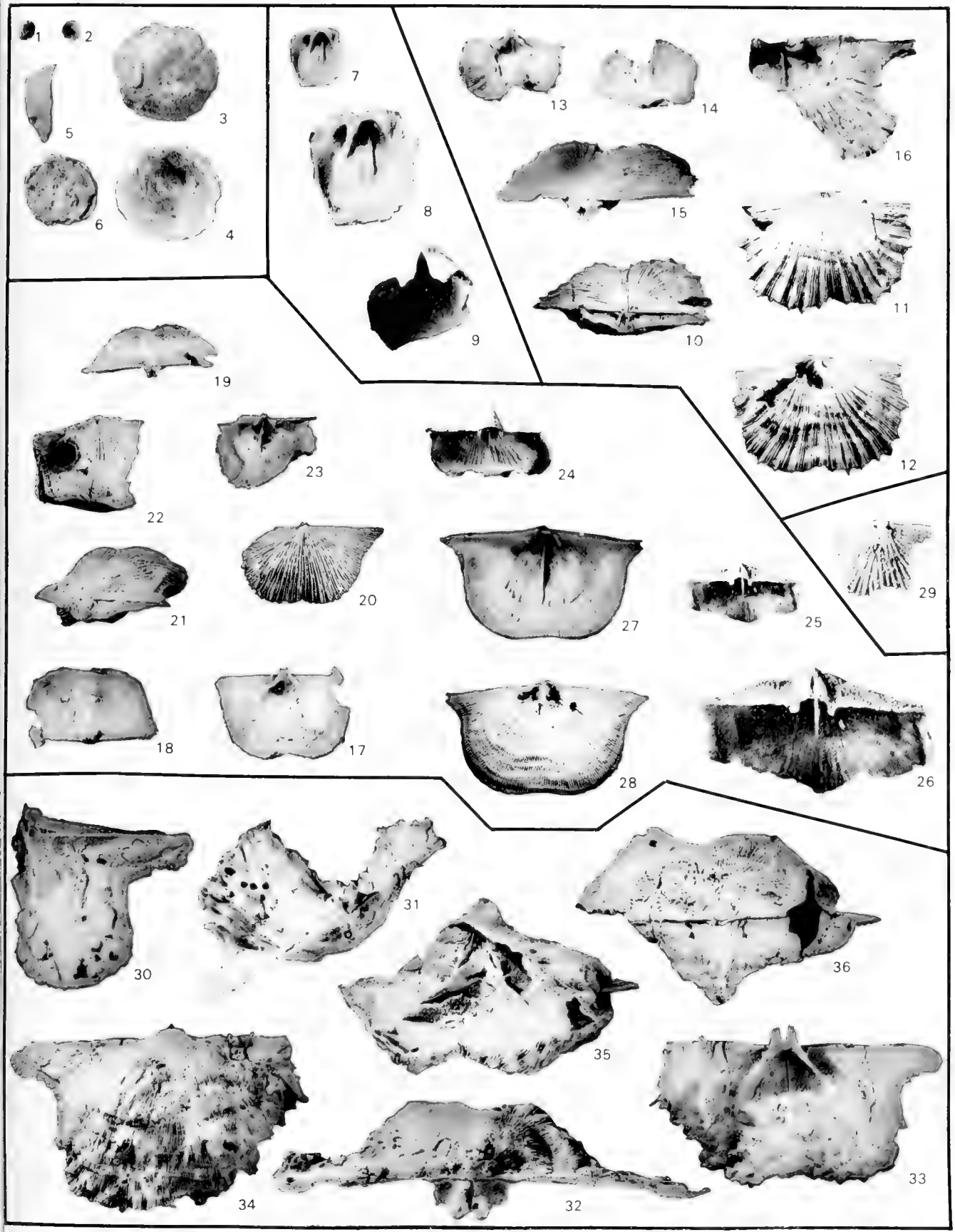
Portion of ventral valve, USNM 221002; ventral (exterior) view, showing characteristic surface ornament, ×3; locality 6 (block C)

30–36. **Derbyia auriplexa** n. sp. 42

30. Fragmentary ventral valve, USNM 220984; interior view, showing internal reflection of exterior ornament, adductor muscle scars and marginal setal grooves, ×1; locality 13.

31–34. Single dorsal valve, USNM 220983; 31. posteroventrolateral view, showing cardinal process, socket development and auriculation of hinge (anterolateral portion of valve obscured by photographic mounting medium), ×1; 32. posterior view, showing valve profile and relation of cardinal process myophore to erismata, ×1; 33. ventral view, showing adductor muscle marks, erismata, dentifers, and strongly cleft cardinal process myophore, ×1; 34. exterior view, showing irregular surface ornament and auriculation of hinge, ×1; locality 13.

35–36. Articulated valves, USNM 220982 (holotype); 35. anterior (interior) view, showing juxtaposition of cardinal process and dental ridges (dorsal side down), ×1.5; 36. posterior view, showing ungrooved pseudodeltidium and distinct dorsal sulcus, ×1.5; locality 13.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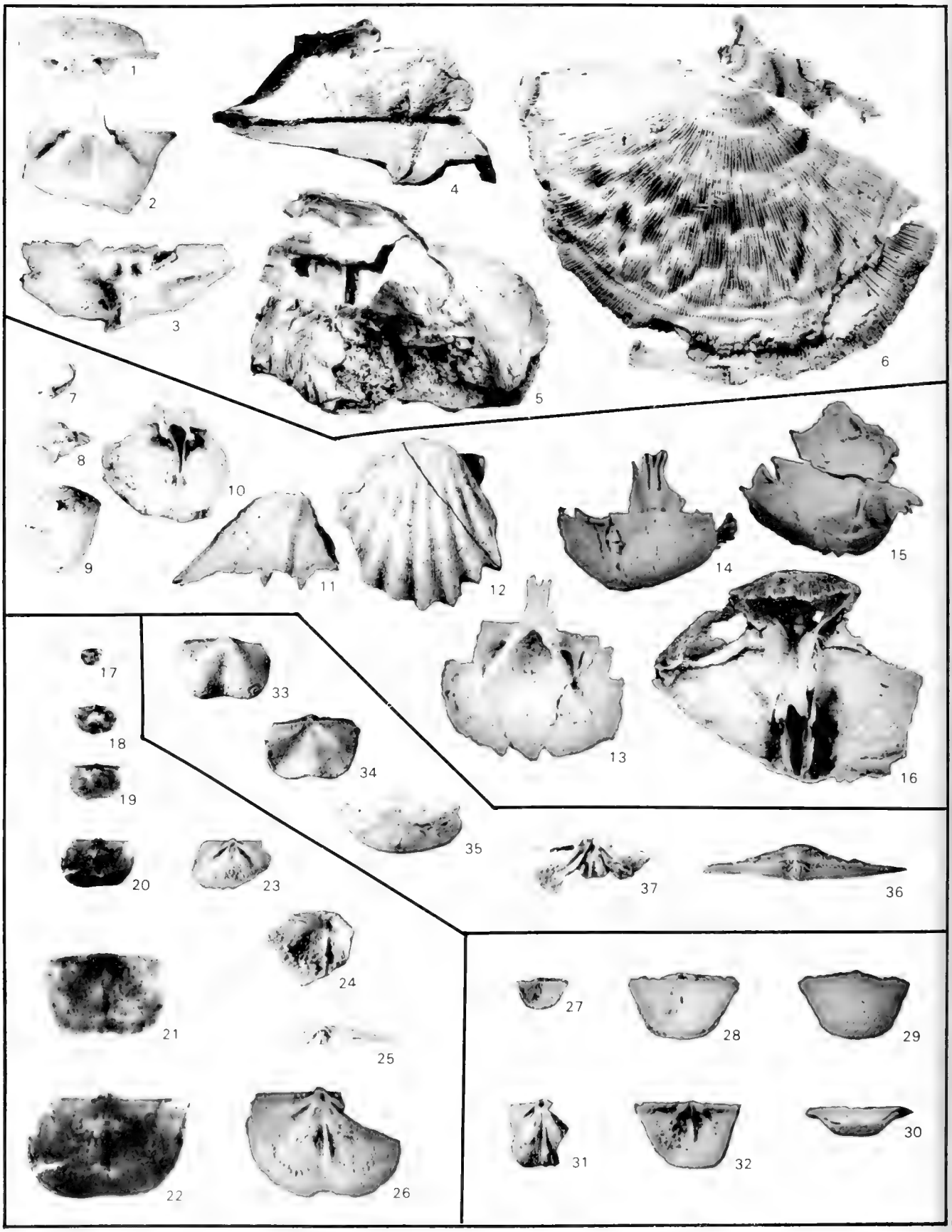
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EXPLANATION OF PLATE 2

Figure — Page

1–6. **Derbyia** cf. **D. filosa** Cooper and Grant 45

1–2. Apical fragment of large dorsal valve, USNM 221001; 1. posterior view, showing development of hinge sockets and relationship of cardinal process to hinge, ×1; 2. ventral (interior) view, showing development of erismata and dentifers, deeply cleft cardinal process myophore, and faintly striate adductor muscle attachment scars, ×1; locality 11.

3. Apical portion of ventral valve, USNM 220999; anteroventral view, showing the paired fossae located at the junction of median septum and dental ridges, ×1.5; locality 11.

4–5. Articulated valves, USNM 221000; 4. posterior view, showing relationship between dorsal valve and ventral interarea, ×1; 5. anterior (interior) view, showing relationship of juxtaposed cardinal process and dental ridges, ×1; locality 11.

6. Partial ventral valve, USNM 220998; ventral view, showing large size, fine ornament of costellae, and the irregular bumpy texture characteristic of larger valves, ×1; locality 11.

7–16. **Meekella skenoides** Girty 47

7–9. Three sets of articulated valves, USNM 221003, USNM 221004, and USNM 221005; posterodorsolateral views of simulated partial ontogenetic series, showing differential growth of the two valves, all ×1; locality 3.

10. Ventral valve, USNM 221011; dorsal (interior) view, showing relationship of teeth, dental ridges and dental plates, and internal fold corresponding to pseudodeltidial monticulus, ×1.5; locality 3.

11. Partial ventral valve, USNM 221008; posterior view, showing pseudodeltidium bearing monticulus, and sharp teeth, ×2; locality 3.

12. Dorsal valve, USNM 221007; dorsal (exterior) view, showing costae superposed on fine costellae, ×1; locality 4.

13–15. Single dorsal valve, USNM 221010; 13. ventral (interior) view, showing long cardinal process and dentifers, and comparatively short erismata, ×2; 14. posterior view, dorsal side down, showing broad dentifers, elongate, longitudinally-slit myophore with shallow median cleft and apparent lack of chilidium, ×2; 15. posteroventrolateral view, showing development of cardinal process and dentifers, and relationship of hinge socket to hinge, ×2; locality 3.

16. Articulated valves, USNM 221009; anterior (interior) view, showing juxtaposition of cardinal process and dental plates, ×2; locality 3.

17–26. **Dyoros acanthopelix** n. sp. 50

17–20. Four sets of articulated valves, USNM 221012, USNM 221019, USNM 221025 (holotype), and USNM 221031; ventral views, showing range of variation in size and outline of a simulated partial ontogenetic series, all ×1 (photographed in transmitted light, immersed in glycerine); locality 2.

21–22. Two sets of articulated valves, USNM 221025 (holotype) and USNM 221031; 21. ventral (exterior) view, showing smaller, somewhat inset dorsal valve and oblique spine bases along hingeline; 22. ventral (exterior) view, showing shadows of endospines on tips of anderidia and anterior end of median septum, as well as anterior endospinose fringe, both ×2; locality 2.

23. Dorsal valve, USNM 221035; ventral (interior) view, showing comparatively insignificant development of anderidia and anterior endospinose fringes in an inferred early ontogenetic stage, ×2; locality 2.

24. Fragmental ventral valve, USNM 221034; dorsal (interior) view, showing anteriorly endospinose median septum and large endospines fringing the adductor muscle attachment areas, ×2; locality 2.

25. Articulated valves, USNM 221026; posterior (exterior) view, showing hood-like crescentic pseudodeltidium and multilobate cardinal process, ×2; locality 2.

26. Partial dorsal valve, USNM 221033; ventral (interior) view, showing long median septum, short lateral septa, strong, anteriorly endospinose anderidia and anterolateral endospinose fringes, ×2; locality 2.

27–32. **Chonetinetes** cf. **C. varians** Cooper and Grant 54

27–30. Articulated valves, USNM 221048; 27. dorsal (exterior) view, showing size and outline of typical shell, ×1; 28. same view, showing radial ornament, hinge spine bases and surficial pits, ×2; 29. ventral (exterior) view, showing radial ornament, surficial pits and lack of a distinct median sulcus, ×2; 30. anterior view, showing lack of a distinct median fold or sulcus, ×2; locality 8.

31. Dorsal valve, USNM 221056; ventral (interior) view, showing long, anteriorly endospinose median septum, anteriorly endospinose anderidia and radial rows of minute endospines, ×2; locality 8.

32. Ventral valve, USNM 221051; dorsal (interior) view, showing comparatively large teeth, long median septum and interior endospines, ×2; locality 8.

33–37. **Stauromata esoterica** n. gen. and sp. 52

33–34. Articulated valves, USNM 221040 (holotype); 33. ventral view, showing valve outline and surface ornament, ×1; 34. dorsal view, showing size and outline of shell, ×1; locality 7.

35–36. Articulated valves, USNM 221039. 35. lateral view, showing sinuous curvature of commissure; 36. posterior view, showing interareas with hood-like crescentic pseudodeltidium and multilobate cardinal process myophore; both ×2; locality 7.

37. Apical portion of dorsal valve, USNM 221043; ventral (interior) view, showing bases of lateral septa, anderidia and median septum, and apparent dendritic adductor muscle attachment scars, ×2; locality 7.

EXPLANATION OF PLATE 3

Figure — Page

1–25. **Stauromata esoterica** n. gen. and sp. 52

1–20. Serial peels of a single set of articulated valves, USNM 221045; sections parallel to plane of commissure, ×2; locality 7.

Distance between successive peels as follows:

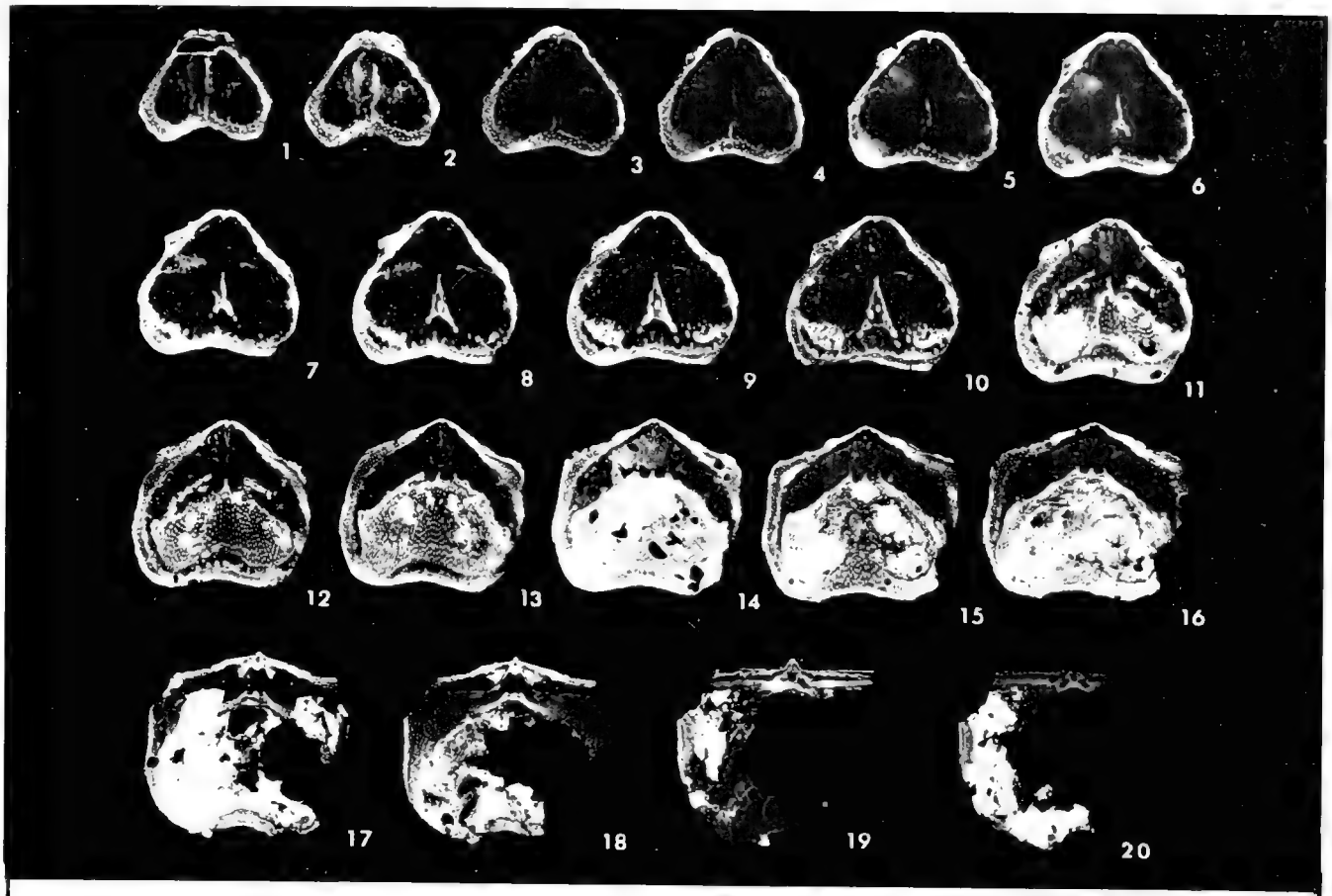
1–2	0.10 mm	10–11	0.20 mm
2–3	0.20 mm	11–12	0.15 mm
3–4	0.15 mm	12–13	0.15 mm
4–5	0.15 mm	13–14	0.15 mm
5–6	0.15 mm	14–15	0.15 mm
6–7	0.15 mm	15–16	0.15 mm
7–8	0.15 mm	16–17	0.45 mm
8–9	0.15 mm	17–18	0.15 mm
9–10	0.10 mm	18–19	0.45 mm
		19–20	0.15 mm

21–25. Schematic reconstructions (as stereopairs) of separated valves of USNM 221045, based on projections of the peels; all ×4.

21–22. Dorsal valve interior, seen from within, showing the prominent endospinose median ridge, anterior endospinose fringes and distally spinose anderidia.

22–23. Dorsal valve interior, seen through the [transparent] valve from the exterior, showing the relationship of the distal ends of the anderidia and the anteriorly placed ventral valve endospinose palisades (arrow).

24–25. Ventral valve interior, showing the position of the endospinose palisades (cf. Pl. 4, figs. 1, 2).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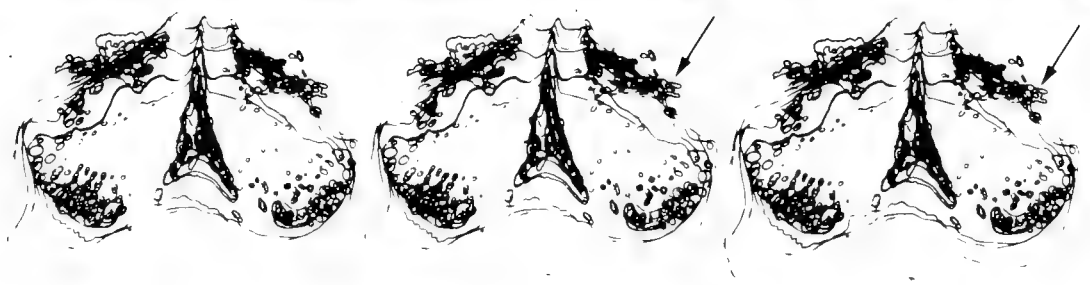
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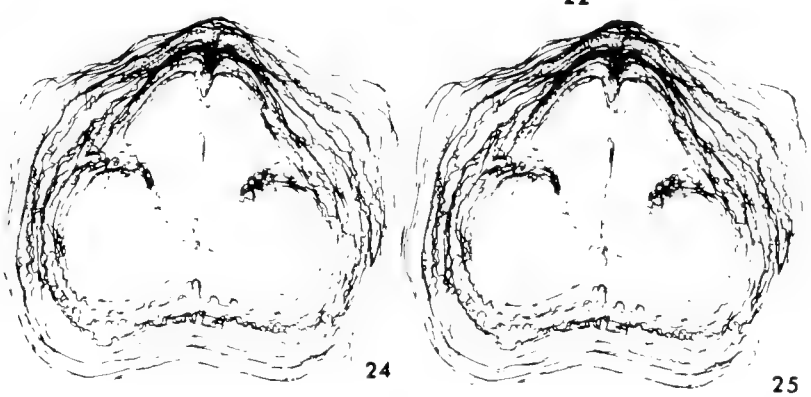
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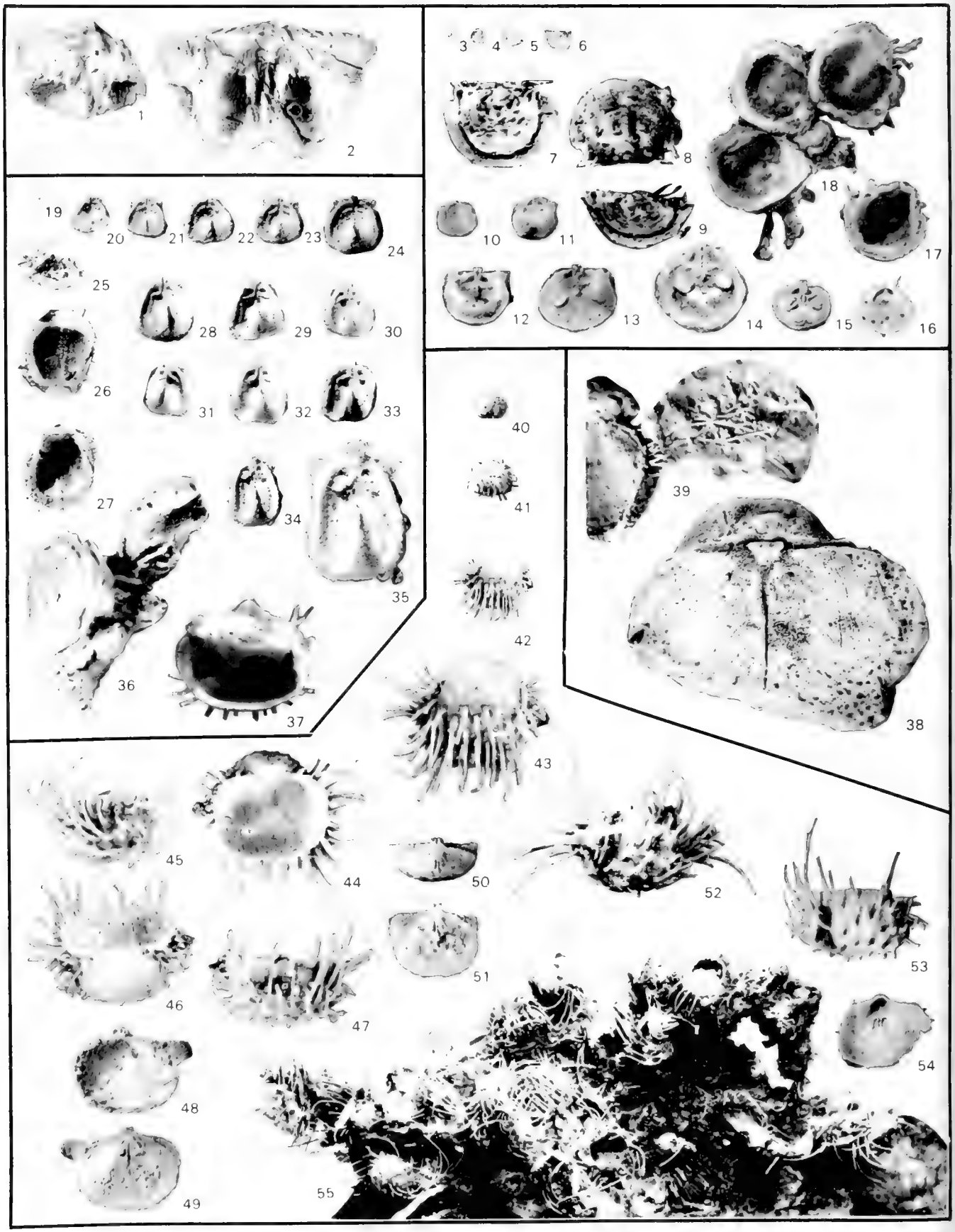
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EXPLANATION OF PLATE 4

Figure — Page

1–2. **Stauromata esoterica** n. gen. and sp. 52

1. Ventral valve fragment, USNM 221044; dorsal view, showing low ventral median septum, apparently dendritic adductor muscle attachment scars and coarse endospinose palisades, ×2; locality 8.
2. Ventral valve, USNM 221036; dorsal view, showing bases of hinge spines, narrow median ridge and prominent, internally striate endospinose palisades, ×2; locality 4.

3–18. **Xenosteges minusculus** n. sp. 55

3–6. Four sets of articulated valves, USNM 221057, USNM 221058, USNM 221059, and USNM 221062 (holotype); dorsal views, showing the size range of a simulated partial ontogenetic series, all ×1; locality 6.

7–9. Articulated valves, USNM 221062 (holotype); 7. dorsal view, showing smaller dorsal valve inset into larger, distally flanged ventral valve; 8. ventral view, showing lamellose ornament and lack of ornament spines; 9. anterodorsal view, showing smoothly curved commissure; all ×4; locality 6.

10–14. Five dorsal valves, USNM 221063, USNM 221064, USNM 221065, USNM 221066, and USNM 221067; ventral (interior) views, showing progressive development, in simulated partial ontogenetic series, of cardinal process, median septum, brachial ridges, adductor muscle scars, submarginal ridges, and endospines, all ×4; locality 6.

15. Dorsal valve, USNM 221068; ventral (interior) view, showing presence of ontogenetically "mature" characters (expression of muscle scars, brachial ridges) in small specimen, ×4; locality 6.

16. Ventral valve, USNM 221069; dorsal view, showing interarea and lightly impressed diductor scars, ×4; locality 6.

17. Ventral valve, USNM 221070; dorsal view, showing asymmetric form, marginal flange and interarea, ×4; locality 6.

18. Three ventral valves (cemented together), USNM 221071; dorsal view, showing commonly observed apparent life habit, attached to sponge, ×4; locality 6.

19–37. **Cooperina inexpectata** Termier, Termier and Pajaud 57

19. Dorsal valve, USNM 221117; ventral view, showing size of small individual of the species, ×1; locality 6.

20–24. Five dorsal valves, USNM 221117, USNM 221118, USNM 221084, USNM 221121, and USNM 221132; ventral (interior) views, showing progressive development of median and submarginal ridges in forms similar to *C. parva* Cooper and Grant (1975), ×4; locality 6.

25. Ventral valve, USNM 221144; dorsal (interior) view, showing a small apparent juvenile ontogenetic stage, ×4; locality 6.

26–27. Ventral valve, USNM 221143; 26. dorsal (interior) view, umbo down, showing distal flange and median ridge; 27. dorsal view, umbo up, showing flat interarea, anterior portion of median ridge, and some ornament spines; both ×4; locality 6.

28. Dorsal valve, USNM 221145; ventral (interior) view, showing the low median ridge and comparatively flat valve of an apparent young individual, ×4; locality 6.

29. Dorsal valve, USNM 221146; ventral (interior) view, showing the high median ridge and curved valve of an apparently mature individual, ×4; locality 6.

30–35. Five dorsal valves, USNM 221092, USNM 221086, USNM 221112, USNM 221104, and USNM 221142; 30–34. ventral views, showing the range of shape variation observed in Palmarito specimens, all ×4; (negative reversed on fig. 31, USNM 221086); 35. USNM 221142, ventral (interior) view, showing massive quadrilobate cardinal process, deeply set adductor muscle platforms, strong median and submarginal ridges, and the distally serrate brachial ridges, all indicative of a gerontic ontogenetic stage, ×8; all from locality 6.

36. Articulated valves, USNM 221075; posterodorsolateral view, showing attachment to bryozoan by basal circlet of rhizoid spines, ×8; locality 6.

37. Articulated valves, USNM 221079; anterodorsal view, showing the juxtaposition of dorsal and ventral valves when the shell is gaping, ×8; locality 6.

38–39. **Rhamnariidae** cf. **Ramavectus** sp. 59

38. Fragmental articulated valves, USNM 221147; dorsal view, showing low apparent interarea, impression of long narrow median septum and impressions of numerous endospines, ×1; locality 11.

39. Dorsolateral view of specimen shown in Plate 4, figure 38, taken during acid etching (spines later lost); dorsolateral view, showing the slender ear spines, approx. ×0.6; locality 11.

40–45. **Echinauris bella** Cooper and Grant 62

40–42. Three ventral valves, USNM 221175, USNM 221176, and USNM 221177; ventral views, showing simulated partial ontogenetic series, ×1; locality 13.

43–47. Single ventral valve, USNM 221177; 43. ventral view, showing brush of anterior ornament spines and comparatively bald umbo; 44. dorsal view, showing low, non-swollen umbo and equidimensional shape of the shell; 45. lateral view, showing the differing orientation of ear spines from those on the anterior slopes of the shell; 46. posterior view, showing the low umbo, and differing orientation of ear and anterior slope spines; 47. anterior view, showing the extension of the anterior slope spines well beyond the commissure; all ×2; locality 13.

48–49. Single dorsal valve, USNM 221179; 48. dorsal (exterior) view, showing small cardinal process, centripetally directed spines and dimpled ornament; 49. ventral (interior) view, showing marginal ridges, fragile ear, short median septum, muscle scars, and development of endospines, ×2; locality 13.

50–51. Dorsal valve, USNM 221178; 50. posterior (interior) view, showing quadrilobate cardinal process, muscle attachment scars and low bladelike median septum; 51. ventral (interior) view, showing cardinal process, muscle scars, marginal ridges, median septum and brachial ridges; both ×2; locality 13.

52. Partial ventral valve, USNM 221182; anteroventrolateral view, showing differing orientation of lateral (ear) and anterior slope spines, ×2; locality 13.

53. Ventral valve fragment, USNM 221173; anterolateral view, showing the great extent to which the anteriormost ventral spines overreach the commissure, ×2; locality 13.

54. Partial ventral valve, USNM 221183; dorsal (interior) view, showing paired, elongate, inset adductor scars, ×2; locality 13.

55. Group of articulated and disarticulated specimens, USNM 221174; photograph taken during acid etching process, showing the fine preservation that indicates this to have been a living position, despite the apparent random orientation of the shells, ×1; locality 13.

EXPLANATION OF PLATE 5

Figure — Page

1–2. **Echinauris bella** Cooper and Grant — 62

1. Dorsal valve, USNM 221180; ventrolateral view, showing a slightly more robust development of the median septum than that shown in Plate 4, figure 49, ×2; locality 13.
2. Dorsal valve, USNM 221181; posteroventral (interior) view, showing the heavy marginal ridges, muscle scars on platforms, and distally expanded median septum of an apparent gerontic specimen, ×2; locality 13.

3–12. **Echinauris** cf. **E. lappacea** Cooper and Grant — 64

3. Articulated valves, USNM 221185; dorsal (exterior) view, showing thick, centripetally-directed dorsal ear spines, small, protruding umbo, and transverse profile, ×1.5; locality 11.
4. Articulated valves, USNM 221192; posterodorsolateral view, showing extremely transverse individual, ×1.5; locality 11.
5. Articulated valves, USNM 221193; posterodorsolateral view, showing globose individual, ×1.5; locality 11.

6–8. Dorsal valve, USNM 221191; 6. dorsal (exterior) view, showing dimpled surface, fragile ear, and quadrilobate cardinal process; 7. ventral (interior) view, showing prominent muscle scars and long median septum; 8. posterior view, showing omega-shaped cardinal process myophore and elevated muscle scar platforms; all ×1.5; locality 11.

9–12. Articulated valves, USNM 221188; 9. dorsal view, showing bases of dense brush of centripetally-directed ear spines, low umbo and transverse outline; 10. posterodorsolateral view, showing shape of shell; 11. anterior view, showing slight ventral sulcus, extremely faint radial ornament, and bases of scattered spines; 12. ventral view, showing low umbo, transverse outline, and arrangement of sparsely scattered spines; all ×1.5; locality 11.

13–19. **Echinauris** cf. **E. liumbona** Cooper and Grant — 65

13–17. Associated valves, USNM 221213; 13–15. ventral valve; 13. lateral view, showing arrangement of lateral spines, low umbo and lateral outline, ×1; 14. anterior view, showing anterior profile and apical interior, ×1.5; 15. posterior view, showing low, denuded umbo and hinge spine disposition, ×1; 16–17. dorsal valve; 16. dorsal (exterior) view, showing partially silicified omega-shaped cardinal process, and lack of zygidium, ×1; 17. posterior view, showing form of cardinal process, ×4; locality 4.

18. Articulated valves, USNM 221203; dorsal view of negative impression (internal cast) of decorticated dorsal valve, showing bipartite muscle scars, omega-shaped cardinal process myophore, extent of narrow median septum and development of strong anterior endospines, ×1.5; locality 8.
19. Articulated valves, USNM 221204; posterior view, showing length of trail, posterior profile, low umbo and a few remaining dorsal exterior ornament spines, ×1.5; locality 8.

20–27. **Anemonaria sublaevis** (R. E. King) — 67

20. Ventral valve, USNM 221217; anterodorsal view, showing slight ginglymus in ventral apex, which accommodates dorsal zygidium, ×1; locality 10.

21–23. Ventral valve (broken and repaired), USNM 221218; 21. ventral view, showing faint low radial ornament and single row of spines along break in slope between body of shell and ears, ×1; 22. dorsal (interior) view, showing crenulate ear baffle, smooth interior and slight sulcus, ×1; 23. ventrolateral view, showing disposition of spine row, ×1.5; locality 10.

24–25. Fragmental dorsal valve, USNM 221216; 24. dorsal (exterior) view, showing fine radial ornament, dorsally-facing cardinal process myophore, and small, but prominent zygidium, ×1; 25. ventral (interior) view, showing complete submarginal ridge, crenulate across ears, muscle scars, and small, prominent zygidium, ×1; locality 10.

26–27. Two fragmental dorsal valves, USNM 221219 and USNM 221220; posterior views, showing forms of cardinal process myophore, both ×2; locality 10.

28. **Anemonaria**? cf. **A. sublaevis** (R. E. King) — 68

Ventral valve, USNM 221221; ventral view, showing subdued radial ornament, disposition of spine row and mesial sulcus, ×1; locality 1.

29–32. **Paucispinifera**? cf. **P. sulcata** Cooper and Grant — 69

29. Articulated valves, USNM 221222; dorsal view, showing partially decorticated dorsal valve and form and disposition of cardinal process myophore, muscle scars, median septum, brachial ridges and endospines, and suggesting the presence of a strong zygidium filling the ventral apex, ×1; locality 8.

30–32. Articulated valves, USNM 221223; 30. anterior view, showing prominent radial ornament bordering prominent sulcus, and anterior profile, ×1; 31. posterolateral view, showing disposition of spine row, ×1; 32. dorsal view, showing aspinose, radially ornamented dorsal valve, moderately deep umbo, and recurved ears, ×1; locality 8.

33–42. **Holotricharina hirsuta** Cooper and Grant — 70

33–35. Three ventral valves, USNM 221225, USNM 221228 and USNM 221227; ventral views, showing form and disposition of ventral spines, concentric ornament, and range of form and shape encountered; all ×1; locality 4.

36–37. Ventral valve, USNM 221228; 36. anterodorsal (interior) view, showing radiating ridged muscle attachment scars, ×1.5; 37. dorsal (interior) view, showing arrangement of spines on hinge and ears, and muscle scars, ×1.5; locality 4.

38–39. Articulated valves, USNM 221232; 38. ventral view, umbonally excavated, showing apical portion of partially silicified dorsal valve interior, ×1.5; 39. dorsal view of largely decorticated dorsal valve, showing long, slender median septum, ×1.5; locality 8.

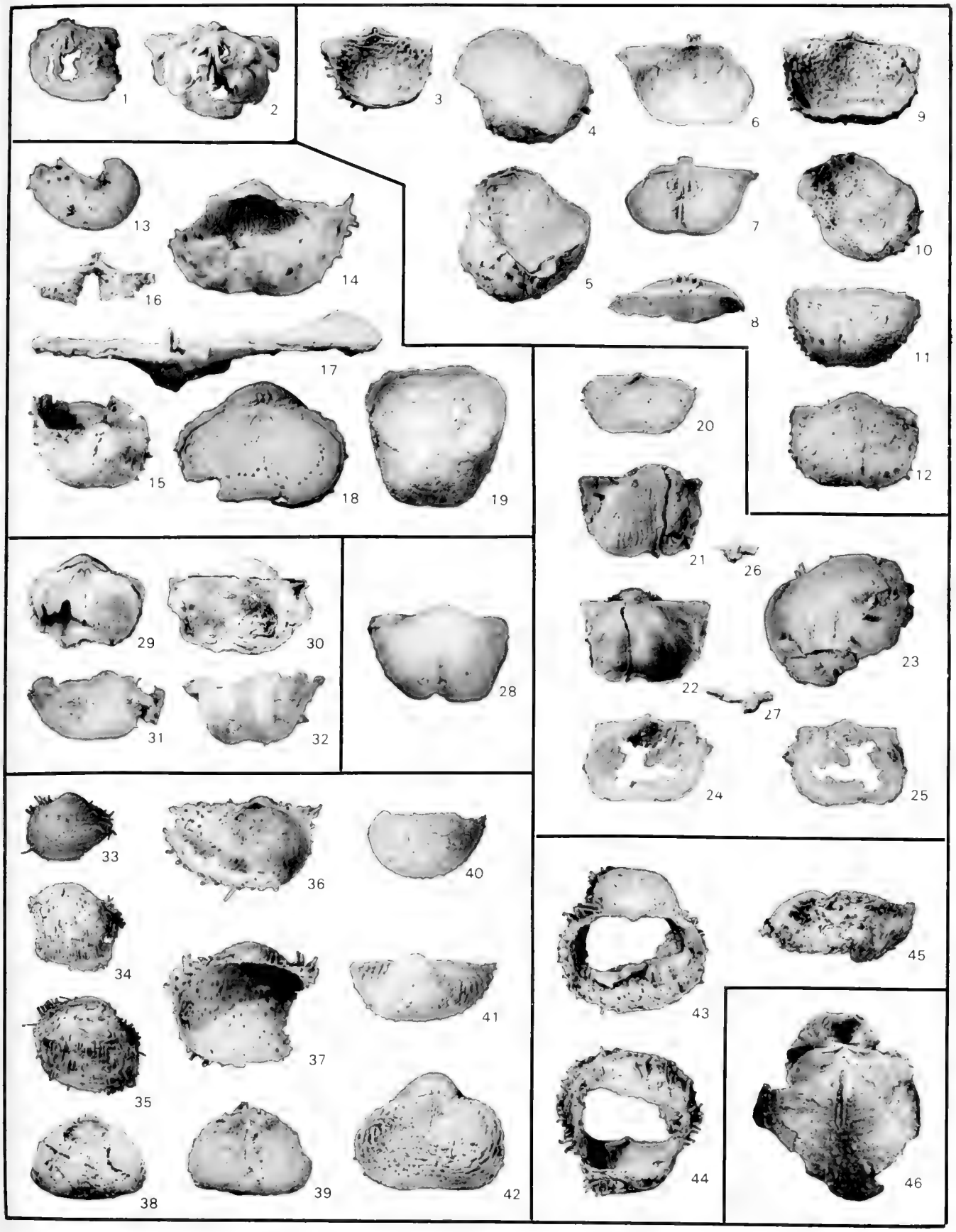
40–42. Articulated valves, USNM 221230; 40. dorsal view, showing concave dorsal valve and characteristic irregular concentric ornament, ×1.5; 41. lateral view, showing outline, ×1.5; 42. posterior view, showing low umbo, wrinkled ears, and lack of prominent ventral sulcus, ×1.5; locality 8.

43–45. **Holotricharina**? sp. A — 71

Single, fragmental, dorsoventrally-crushed ventral valve, USNM 221233; 43. dorsal view, showing swollen umbo, spine arrangement and somewhat flanged margin; 44. ventral view, showing spine arrangement and apical interior; 45. lateral view, showing profile and form and disposition of ornament spines; all ×1; locality 13.

46. **Echinoconchidae,** genus indeterminate — 74

Fragmental interior of articulated valves, USNM 221240; ventral (interior) view, showing impression of pointed ventral umbo and most of dorsal interior, with impression of lateral ridges, apparently bipartite median septum and endospines in rough concentric pattern apparently mirroring inferred external concentric banding, ×1; Field No. Ar-981 (Arnold coll.).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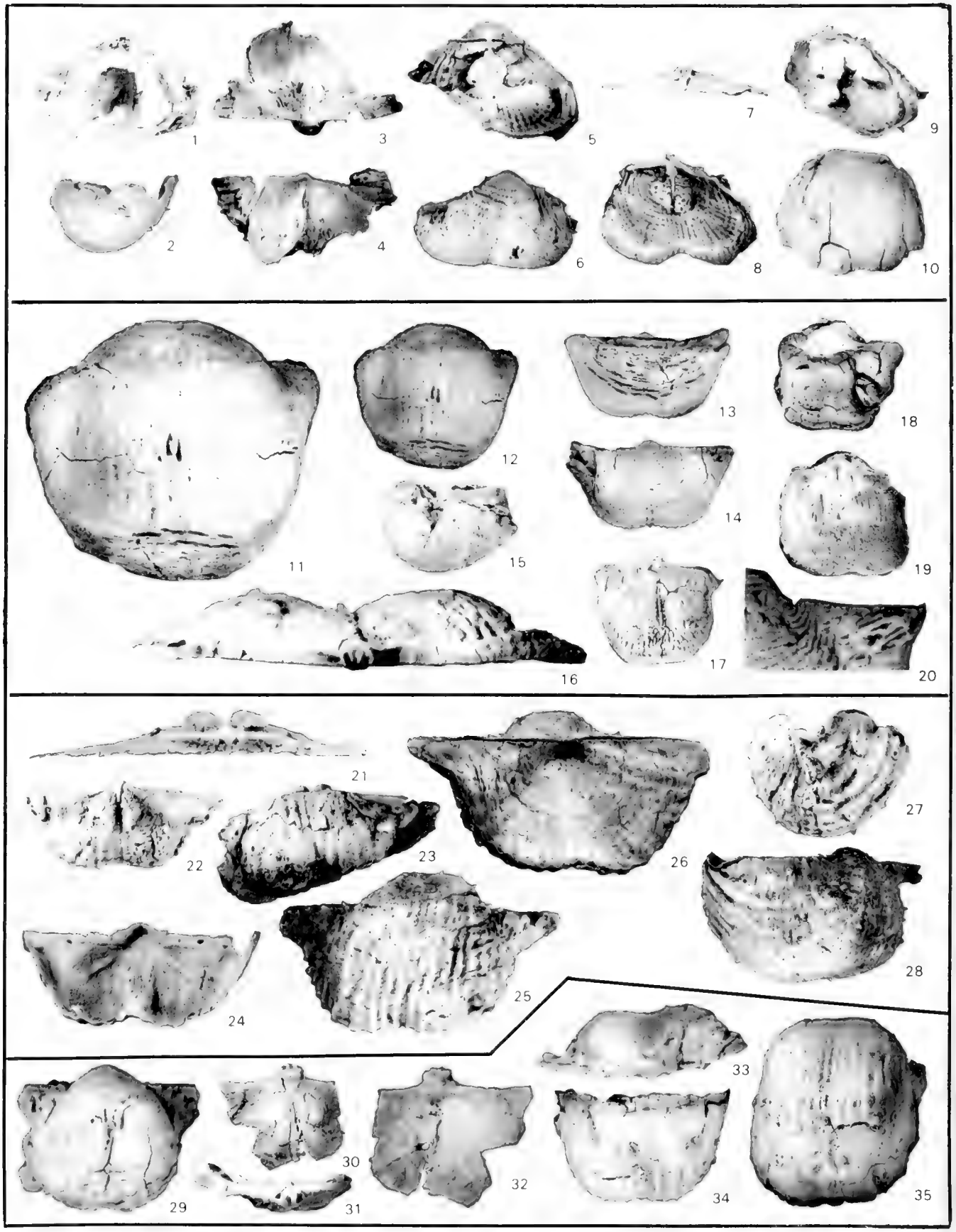
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EXPLANATION OF PLATE 6

Figure — Page

1–10. **Kutorginella** cf. **K. umbonata** (Muir-Wood and Cooper) 72

1–2. Fragmental articulated valves, USNM 221237; 1. dorsal view, showing shell outline and geniculation, development of fold and sulcus, thin trail, dorsal exterior ornament and dorsal aspect of cardinal process myophore; 2. lateral view, showing lateral profile; both ×1; locality 8.

3–4. Fragmental ventral valve, USNM 221234; 3. posterodorsal (interior) view, showing distinct ventral sulcus, muscle scars and sharply recurved ear; 4. anterior (interior) view, showing apically constricted median ridge flanked by diductor scars, and anteromesial dendritic muscle scars on slight platform, as well as sharply demarcated ears; both ×1; locality 4.

5–6. Fragmental articulated valves, USNM 221235; 5. dorsal view, showing dorsal exterior reticulate ornament; 6. posterior view, showing ventral exterior reticulation; both ×1; locality 4.

7–8. Fragmental dorsal valve and associated external mold, USNM 221236; 7. posterior view, ventral side up, showing form of myophore of cardinal process, ×2; 8. anteroventrolateral (interior) view, showing anteriorly constricted median septum, dendritic adductor muscle scars, strongly reticulate visceral disc, strong ridge across ears, and abrupt submarginal geniculation, ×1; locality 8.

9. Fragmental articulated valves, USNM 221239; dorsal view, showing form of cardinal process myophore; ×1, locality 8.

10. Dorsoventrally crushed ventral valve, USNM 221238; ventral view, showing sparsely spinose radial ornament, ×1; locality 1.

11–20. **Peniculauris subcostata latinamericana** n. ssp. 75

11–14. Ventral valve, USNM 221244 (holotype); 11. ventral view, showing anteriorly narrowing costae and size and outline of shell, ×1; 12. ventral view, included for size comparison to following figures, ×0.5; 13. anterior view, showing repeated trails, low umbo and anterior profile, ×0.5; 14. posterior view, showing prominent reticulation and brushes of spines on ears, ×0.5; locality 1.

15. Ventral valve, USNM 221245; lateral view, showing anteroposterior variation in surface ornamentation and lateral profile, ×0.5; locality 1.

16–17. Dorsal valve, USNM 221246; 16. posterior view, ventral side up, showing low median septum, prominent lateral ridges and massive mesially recurved cardinal process myophore, ×2; 17. ventral (interior) view, showing short-shafted cardinal process, strong lateral ridges crossing ears and continuous around visceral disc as low step in shell surface, long slender median septum, muscle scars, and concentric and endospinose ornament, ×0.5; locality 1.

18. Crushed articulated valves, USNM 221247; dorsal view, showing poorly preserved reticulation of dorsal visceral disc, ×0.5; locality 1.

19. Partial ventral valve, USNM 221248; dorsal (interior) view, showing raised, dendritic adductor scars flanked by inset, rounded, striate diductors, ×0.5; locality 5.

20. Portion of ventral valve, USNM 221242; ventral view, showing concentric wrinkling on ear and form and disposition of ornament spines, ×1; locality 1.

21–28. **Rugatia intermedia** n. sp. 77

21–23. Fragmental dorsal valve and external mold, USNM 221250; 21. posterior view, dorsal side down, showing relationship of cardinal process myophore to adductor muscle scars, ×2; 22. ventral (interior) view, showing short lateral ridges, raised dendritic adductor scars, subdued reticulation and moderate geniculation of the visceral disc, ×1; 23. anterior view, showing raised adductor scars, ×1; locality 8.

24. Portion of ventral valve, USNM 221252; anterior (interior) view, showing poorly impressed diductor scars, adductor scars on mesial platform, and slight apical ginglymus, ×1.5; locality 8.

25–28. Articulated valves, USNM 221249 (holotype); 25. ventral view, showing coarse radial ornament and sparsely spinose exterior of ventral valve; 26. dorsal view, showing form and ornament of dorsal valve and ventral umbo; 27. lateral view, showing apparently secondarily compressed profile and coarse ornament; 28. posterolateral view, showing disposition and form of spines running along ears and variation in radial ornament; all ×1; locality 11.

29–35. **Rugatia occidentalis** (Newberry) 78

29. Crushed ventral valve, USNM 221254; ventral view, showing subdued coarse radial ornament and small spinose ears, ×1; locality 1.

30–32. Fragmental (repaired) dorsal valve, USNM 221257; 30. ventral (interior) view, showing shaft of cardinal process and muscle scars, ×1.5; 31. posterior view, showing mesially reflexed dictyoclostid cardinal process, ×2; 32. dorsal view, showing apparent trilobate aspect and rough surface of cardinal process and nearly smooth exterior surface, ×2; locality 1.

33. Portion of ventral valve, USNM 221253; posterior view, ventral side up, showing disposition of spines from umbo toward lateral extremities, ×1; locality 1.

34–35. Portion of ventral valve, USNM 221256; 34. anterior view, showing anterior profile, repeated trails, radial ornament and spine disposition; 35. anteroventral view, ventral side up, showing subdued radial ornament and form and disposition of spines; both ×1; locality 1.

EXPLANATION OF PLATE 7

Figure — Page

1–10. **Spinifrons grandicosta** n. sp. 80

1–8. Articulated valves, USNM 221259 (holotype); 1. dorsal view, showing form, outline and size of the shell and the dorsal exterior ornament, ×1; 2. dorsal view, included for size comparison to following figures, ×0.5; 3. lateral view, showing anteroposterior change in surface ornament and lateral profile, ×0.5; 4. ventral view, showing somewhat irregular costation and sparsely distributed spines, ×0.5; 5. anteroventrolateral view, ventral valve down, showing relative valve forms, raised mesial dendritic ventral adductors and larger distal ventral diductor muscle scars, ×0.5; 6. anteroventrolateral view, dorsal valve down, showing cardinal process, lateral ridges and median septum of dorsal valve, ×0.5; 7. posterior view, showing form and disposition of spines along hinge and on ears, and reticulate ornament of ventral umbonal area, ×0.5; 8. anterior view, showing low, small umbo, raised trail margins, recumbent ears and repeated trails, ×0.5; locality 13.

9. Portion of ventral valve, USNM 221258; ventral view, showing somewhat irregular broad costae and clusters of spines laterally and anteromesially, ×0.5; locality 13.

10. Fragmental ventral valve and external mold, USNM 221260; dorsal (interior) view, showing disposition of muscle scars, ×0.5; locality 8.

11–15. **Spinifrons**? cf. **S. grandicosta** n. sp. 81

11–13. Three fragmental, partially silicified dorsal valves, USNM 221266, USNM 221264, and USNM 221265; posterior views, showing range of variation in form of the cardinal process myophore, all ×2; locality 11.

14. Fragmental dorsal valve, USNM 221263; ventral (interior) view, showing accessory septa, ×1; locality 4.

15. Fragmental articulated valves, USNM 221262; dorsal view, showing dorsal exterior ornament, ×0.5; locality 11.

16–23. **Collemataria venezuelensis** n. sp. 83

16–17. Ventral valve, USNM 221269 (holotype); 16. dorsal view, showing reflexed posterior attachment flap, beaded septa and encrusting bryozoan; 17. ventral view, showing smooth to lamellose ventral exterior, and attachment cicatrix; both ×1; locality 6.

18–19. Dorsal valve, USNM 221272; 18. ventral (interior) view, showing truncated hinge margin, median ridge and endospinose submarginal ridge; 19. dorsal (exterior) view, showing smooth rounded surface and median groove; both ×2; locality 6.

20. Dorsal valve, USNM 221274; ventral (interior) view, showing obliquely oriented bilobate cardinal process, ×2; locality 6.

21. Dorsal valve, USNM 221273; ventral (interior) view, showing submarginal ridge and anteromesial cleft, ×2; locality 6.

22. Two fragmental ventral valves, USNM 221271; anterodorsal views, showing inset triangular hinge area and reflexed attachment flap, ×2; locality 6.

23. Incompletely etched block with two ventral valves, USNM 221270; oblique view, showing concavity of valves, ×1; locality 6.

24–36. **Pontisia** cf. **P. stehlii tumidosa** Cooper and Grant 86

24–28. Simulated partial ontogenetic series of articulated valves, USNM 221285, USNM 221286, USNM 221289, USNM 221292, and USNM 221295; dorsal views, showing range of variation in outline and ornament, ×1; locality 3.

29–33. Articulated valves, USNM 221295; 29. dorsal view, showing beak, open delthyrium, sharp costae and distinct fold and sulcus; 30. ventral view, showing distinct flat-bottomed, inset ventral sulcus; 31. anterior view, showing high ventral tongue and rounded triangular outline; 32. posterior view, showing shallow ventral and deep dorsal valves, and smooth umbonal regions; 33. lateral view, showing short, flat ventral beak and truncated lateral profile; all ×2; locality 3.

34–36. Apical fragment of dorsal valve, USNM 221298; 34. anterior (interior) view, showing attitude of crura and their relationship to the cardinal process; 35. ventral view, showing attitude and angle of divergence of crura; 36. lateral view, showing angular relationship of valve surface, plane of commissure and plane of crura; all ×4; locality 3.

37–38. **Hustedia** sp. 92

Poorly preserved articulated valves, USNM 221407 and USNM 221408; dorsal views, showing outline and ornament indicative of the genus, ×1; 37. locality 8; 38. locality 1.

39–48. **Pontisia stehlii** Cooper and Grant 85

39–43. Five sets of articulated valves, USNM 221277, USNM 221283, USNM 221278, USNM 221280 and USNM 221279; dorsal views of simulated partial ontogenetic series, showing range of variation in shape, form and ornament, ×1; 39, 41, 43. locality 11; 40. locality 8; 42. locality 10.

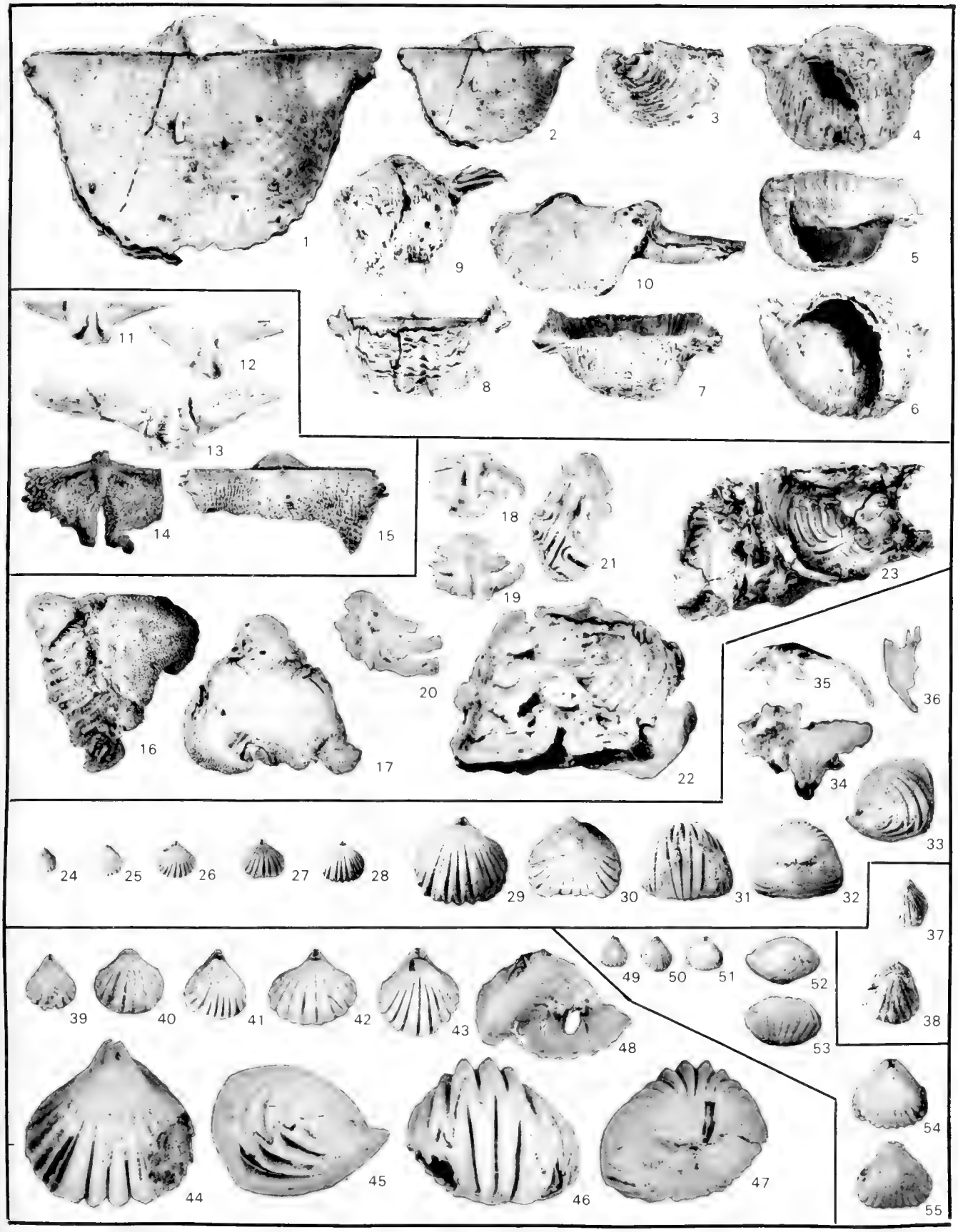
44–47. Articulated valves, USNM 221279; 44. ventral view, showing shell outline and form of beak and sulcus; 45. lateral view, showing truncated lateral profile; 46. anterior view, showing triangular outline, long ventral tongue, low fold and deep sulcus; 47. posterior view, showing somewhat distorted outline and smooth umbonal regions; all ×2; locality 11.

48. Apical fragment of articulated valves, USNM 221284; anterior (interior) view, showing disposition of dental plates and crura and lack of apical median septum, ×2; locality 10.

49–55. **Rhynchonellacea,** family uncertain 87

49–51. Three sets of articulated valves, USNM 221300, USNM 221302 and USNM 221301; dorsal views of simulated partial ontogenetic series, showing development of shape, form, and ornament, ×1; locality 10.

52–55. Articulated valves, USNM 221301; 52. lateral view, showing profile that is less globose than that of other Venezuelan Permian rhynchonellaceans; 53. anterior view, showing low fold and broad shallow sulcus; 54. dorsal view, showing open (?broken) delthyrium and characteristic rhynchonellacean form and ornament; 55. ventral view, showing triangular outline and wide beak; all ×2; locality 10.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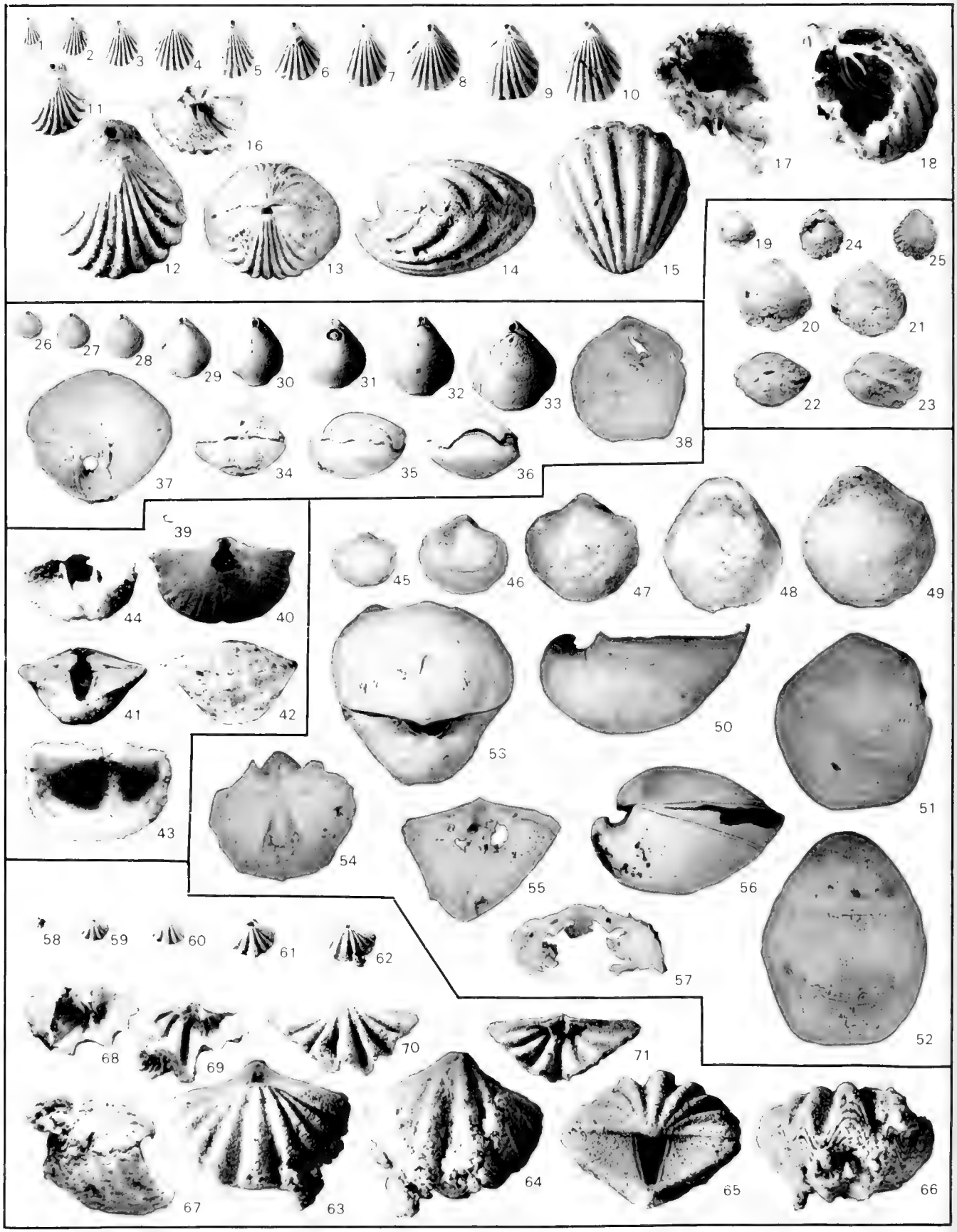
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EXPLANATION OF PLATE 8

Figure — Page

1–18. **Hustedia hyporhachis** n. sp. 88

1–10. Ten sets of articulated valves, USNM 221308, USNM 221324, USNM 221335, USNM 221339, USNM 221352, USNM 221354, USNM 221358, USNM 221370, USNM 221386, and USNM 221399; dorsal views of simulated partial ontogenetic series, showing range of variation in size and form, ×1; locality 10.

11–15. Articulated valves, USNM 221401 (holotype); 11. posterodorsal view, dorsal valve down, for comparison with simulated partial ontogenetic series shown above, ×1; 12. posterodorsal view, dorsal valve down, showing small triangular interarea, ×2; 13. posterior view, showing regular outline and origin of costae at pedicle foramen, ×2; 14. lateral view, showing short ventral beak, equally convex valves, and serrate and anteriorly subtruncate commissure, ×2; 15. anteroventral view, commissure up, showing low median ridge in ventral valve median trough, ×2; locality 10.

16. Apical fragment of articulated valves, USNM 221404; anterior view, dorsal side down, showing dorsal articulatory apparatus, including apical median septum, ×2; locality 10.

17. Apical fragment of articulated valves, USNM 221405; anterior view, dorsal side down, showing detail of articulatory apparatus, ×3; locality 10.

18. Portion of articulated valves, USNM 221406; posterodorsolateral view, showing portion of preserved spire and ascending and descending lamellae, ×2; locality 10.

19–25. **Cleiothyridina** cf. **C. nana** Cooper and Grant 94

19–23. Articulated valves, USNM 221409; 19. dorsal view, showing size and outline, ×1; 20. dorsal view, showing form and poorly preserved spinose concentric ornament, ×2; 21. ventral view, showing outline, ×2; 22. anterior view, showing truncated commissure and development of fold and sulcus, ×2; 23. lateral view, showing comparatively globose dorsal valve and truncate commissure, ×2; locality 3.

24–25. Articulated valves of fragmental apparent juvenile specimen, USNM 221410; 24. dorsal view, showing characteristic anterior spinose ornament; 25. ventral view, showing tear-drop form and spinose ornament; both ×4; locality 3.

26–38. **Composita** cf. **C. pilula** Cooper and Grant 95

26–32. Seven sets of articulated valves, USNM 221420, USNM 221421, USNM 221423, USNM 221425, USNM 221431, USNM 221433 and USNM 221435; dorsal views of simulated partial ontogenetic series, showing range of variation in outline and fold and sulcus development, ×1; locality 8.

33–36. Articulated valves, USNM 221437; 33. dorsal view, showing smooth surface with faint concentric ornament; 34. posterior view, showing regular profile and low, not incurved beak; 35. lateral view, showing lateral profile and subtruncate anterior commissure; 36. anterior view, showing development of fold and sulcus, and close spacing of last commissural growth increments; all ×1; locality 11.

37. Apical fragment of articulated valves, USNM 221440; anterior view, showing pedicle foramen, dental plates, and articulatory apparatus, ×2; locality 4.

38. Dorsal valve, USNM 221441; ventral (interior) view, showing hinge plate, ×2; locality 4.

39–44. **Costicrura minuta** n. gen. and sp. 97

39–42. Articulated valves, USNM 221453 (holotype); 39. ventral view, showing size of a large individual, ×1; 40. dorsal view, showing transverse profile and distinct ornament of costae, ×10; 41. posterior view, showing open delthyrium and notothyrium and distinct interareas of unequal height, ×10; 42. anterior view, showing characteristic surface ornament, deep ventral and shallow dorsal valves and rectimarginate commissure, ×10; locality 6.

43. Ventral valve, USNM 221467; dorsal (interior) view, showing straight hingeline and comparatively smooth interior surface, ×10; locality 6.

44. Partially broken articulated valves, USNM 221468; ventral view, showing position and form of crura, sockets and cardinal process, ×10; locality 6.

45–57. **Neophricadothyris** cf. **N. crassibecca** Cooper and Grant 98

45–49. Five sets of articulated valves, USNM 221469, USNM 221472, USNM 221479, USNM 221485, and USNM 221487; dorsal views of simulated partial ontogenetic series, showing commonly encountered changes in outline during growth, ×1; locality 7.

50–52. Associated valves, USNM 221489; 50. lateral view of ventral valve, showing tightly incurved beak of apparent mature to gerontic ontogenetic stage; 51. dorsal view of dorsal valve, showing subpentagonal shape, form and characteristic ornament; 52. ventral view of ventral valve, showing more elongate outline and characteristic ornament, all ×1.5; locality 8.

53. Articulated valves, USNM 221488; posterior view, showing open, rimmed delthyrium and healed commissural injury of dorsal valve, ×1.5; locality 8.

54. Apical portion of ventral valve, USNM 221492; dorsal view, showing pointed teeth and dental ridges, secondarily thickened umbonal area, inset muscle scars and flange bordering the delthyrium, ×2; locality 8.

55. Apical portion of dorsal valve, USNM 221493; ventral view, showing blade-like bases of helicophores, ×2; locality 8.

56. Articulated valves, USNM 221490; lateral view, showing profile of typical specimen, ×2; locality 8.

57. Fragmental dorsal valve, USNM 221491; ventral (interior) view, showing proximally roofed hinge sockets, ×2; locality 8.

58–71. **Spiriferellina** cf. **S. hilli** (Girty) 103

58–62. Five sets of articulated valves, USNM 221501, USNM 221505, USNM 221506, USNM 221508 and USNM 221510; dorsal views of simulated partial ontogenetic series, showing range of variation in size, outline and ornament, ×1; locality 3.

63–67. Articulated valves, USNM 221510; 63. dorsal view, showing narrow beak and open delthyrium bordered by flange; 64. ventral view, showing shell form and outline; 65. posterior view, showing high, smooth interarea, flange-bordered open delthyrium and small, low dorsal beak; 66. anterior view, showing characteristic ornament, subtruncate commissure, final growth lamellae oriented normal to plane of commissure, and subequally biconvex profile; 67. lateral view, showing comparative length of dorsal and ventral beaks, and subtruncate anterior commissure; all ×3; locality 3.

68. Portion of articulated valves, USNM 221515; anterodorsal view, with most of dorsal valve removed, showing ventral valve apical median septum, ×2; locality 3.

69. Portion of dorsal valve, USNM 221514; ventral (interior) view, showing hinge sockets and small cardinal process, ×2; locality 3.

70–71. Dorsal valve, USNM 221511; 70. dorsal (exterior) view, showing punctate shell and paucicostate ornament of somewhat alate individual; 71. ventral (interior) view, showing hinge sockets and socket plates; both ×3; locality 3.

EXPLANATION OF PLATE 9

Figure — Page

1–13. **Neospirifer venezuelensis** (Gerth) 100

1–7. Articulated valves, USNM 221495; 1. dorsal view, showing size of a large specimen, ×1; 2. dorsal view, showing curved ventral interarea with open delthyrium, incurved beak, prominent mesial fold and fasciculate costae, ×0.5; 3. ventral view, showing persistent ventral sulcus and lateral fasciculate costae, ×0.5; 4. anterior view, showing strong mesial dorsal deflection of commissure, ×0.5; 5. posterior view, showing very low dorsal interarea, ×0.5; 6. lateral view, showing typical profile with incurved ventral beak, posteriorly protruding dorsal umbo and truncate anterior margin, ×0.5; 7. posterodorsal view, showing conjoined interareas, ×0.5; locality unknown (purchased from child in type section of Palmarito Formation).

8. Artificial cast (USNM 221499) of articulated valves (NMB L4453, lectotype); dorsal view, showing size and form of a type specimen, ×1; type section of the Palmarito Formation. (Small black spots are air bubbles in plaster cast and do not represent shell ornament.)

9. Artificial cast (USNM 221500) of articulated valves (NMB L4452; paralectotype); ventral view, showing broad sulcus and pointed ear of a type specimen, ×1; type section of the Palmarito Formation. (Small black spots are air bubbles in plaster cast and do not represent shell ornament.)

10. Crushed articulated valves, USNM 221494; ventral view, showing conservative lamellose growth lines near valve margin, ×1; locality 7.

11. Apical portion of ventral valve, USNM 221497; anterior (interior) view, showing open delthyrium, strong triangular teeth, deeply inset, mesially separated muscle scars, and secondarily thickened shell apex, ×0.5; locality 7.

12. Portion of dorsal valve, USNM 221498; anteroventral view, showing small striate cardinal process, large proximally filled sockets (distally broken), diagonally striate apparent adductor muscle scars on apical flanks of mesial trough, and internal reflection of external fasciculate costae, ×0.5; locality 7.

13. Articulated valves, USNM 221496; ventral view of an apparent juvenile ontogenetic stage, ×1; locality 8.

14–27. **Aneuthelasma globosum** n. sp. 104

14–20. Seven sets of articulated valves, USNM 221516, USNM 221522, USNM 221526, USNM 221529, USNM 221530, USNM 221523, and USNM 221520 (holotype); dorsal views of simulated partial ontogenetic series, showing range of variation in size and outline, ×1; locality 6.

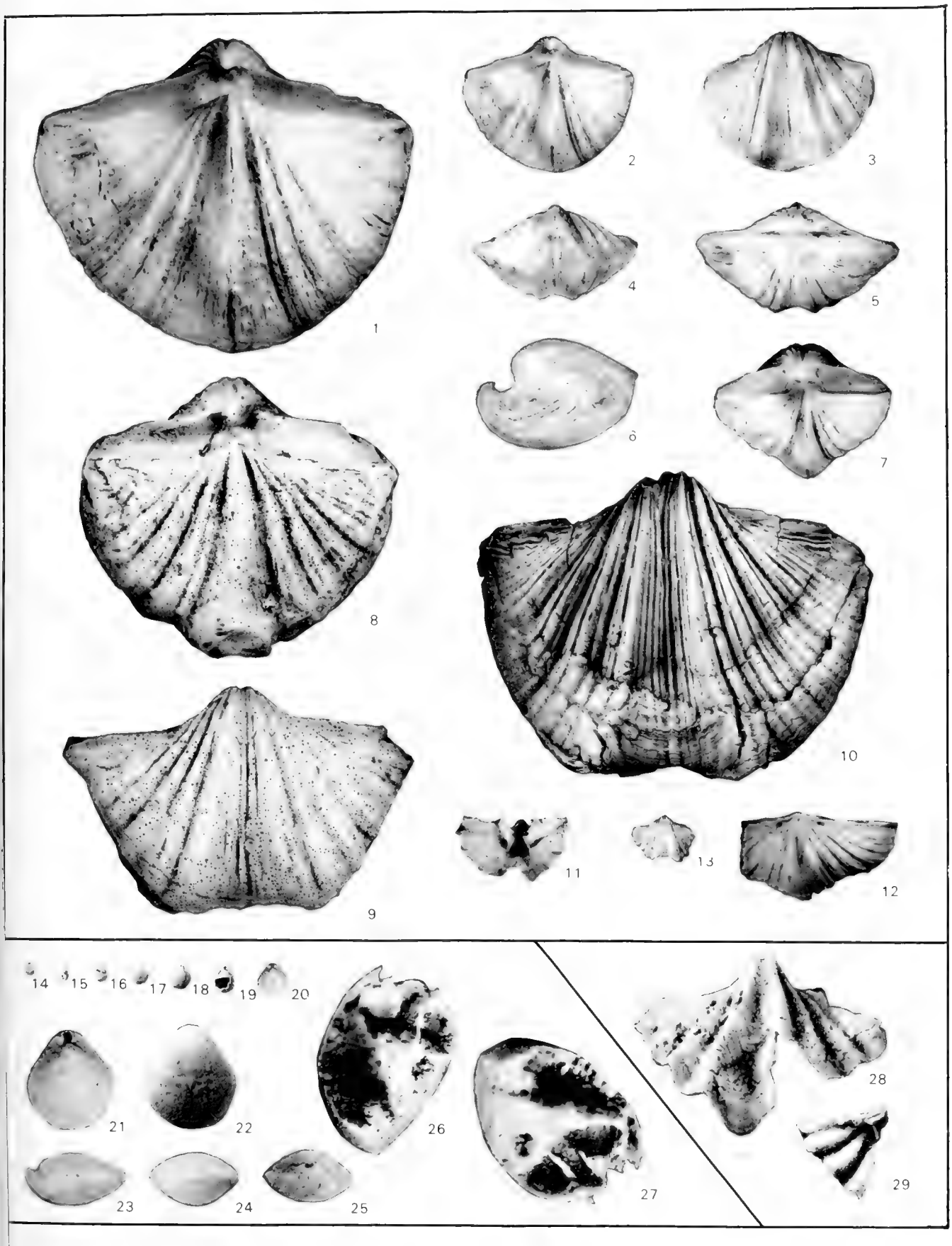
21–25. Articulated valves, USNM 221520 (holotype); 21. dorsal view, showing broad ventral beak and subpentagonal shell outline; 22. ventral view, showing shell outline; 23. lateral view, showing straight commissure and shell profile; 24. anterior view, showing equally biconvex profile and non-folded commissure; 25. posterior view, showing somewhat labiate pedicle foramen and broad flat ventral beak; all ×3; locality 6.

26–27. Portion of articulated valves, USNM 221533; 26. ventral view, showing lack of inner hinge plates and remnants of short loop arising just below hinge sockets; 27. posteroventrolateral view, showing position of origin of loop in dorsal valve apex; both ×8; locality 6.

28–29. **Spiriferellina** cf. **S. hilli** (Girty) 103

28. Fragmental ventral valve, USNM 221512; ventral view, showing ornament of overlapping lamellae, seen in some larger individuals, ×4; locality 3.

29. Portion of dorsal valve, USNM 221513; ventral (interior) view, showing hinge socket and socket plate, ×3; locality 3.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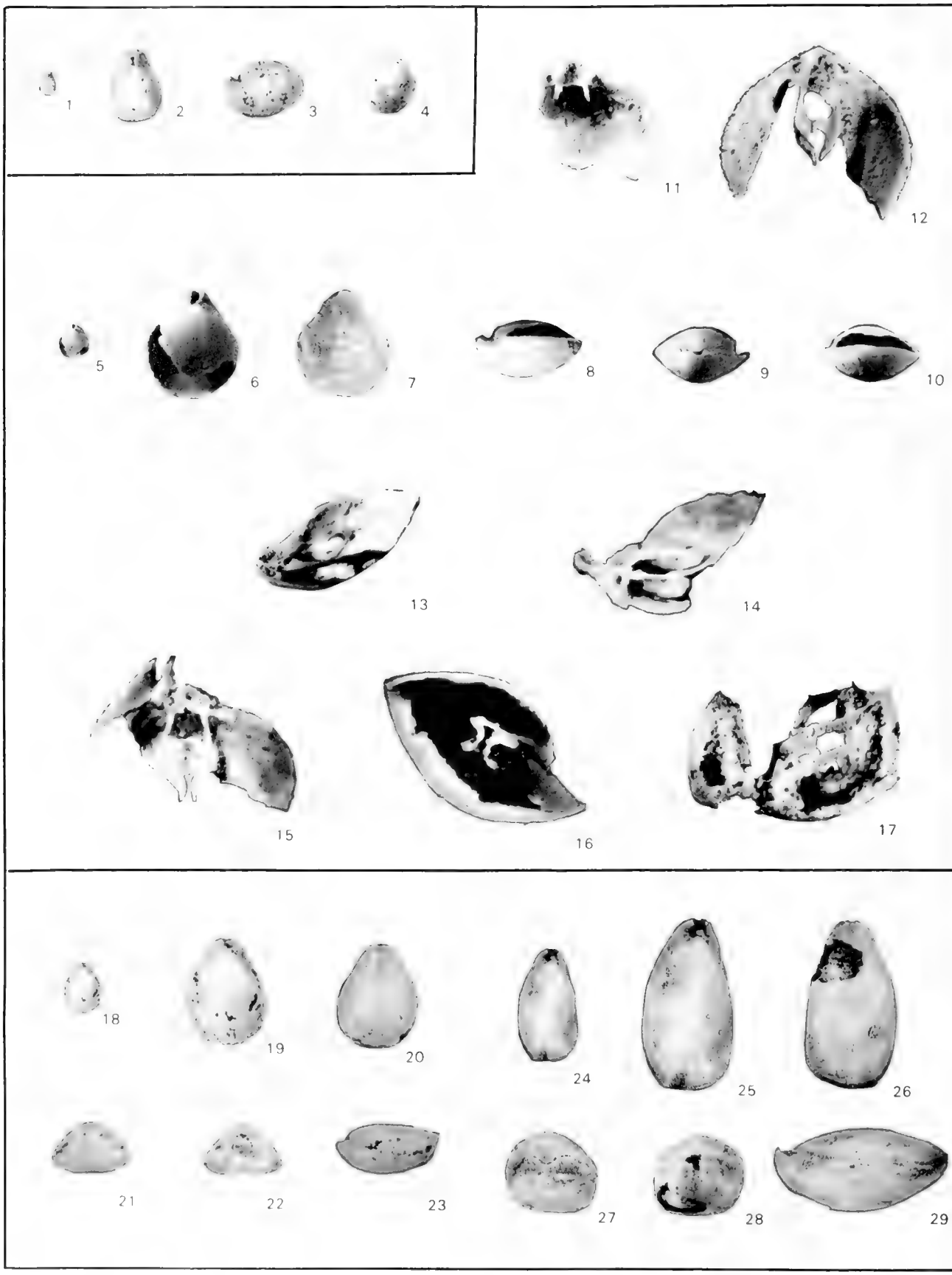
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EXPLANATION OF PLATE 10

Figure — Page

1–4. **Oligothyrina**? sp. 106
Articulated valves, USNM 221539; 1. dorsal view, showing size of a large specimen, ×1; 2. dorsal view, showing broad ventral beak and narrow outline, ×3; 3. lateral view, showing short beak and globose profile, ×3; 4. anterior view, showing globose profile and intraplicate commissure, ×3; locality 13.

5–17. **Anaptychius minutus** n. gen. and sp. 107

5–10. Portion of articulated valves, USNM 221552 (holotype); 5. dorsal view, showing size and form of a large specimen, ×1; 6. dorsal view, showing subtrigonal outline, rounded commissure and telate foramen, ×3; 7. ventral view, showing subtrigonal outline, ×3; 8. lateral view, showing unequally biconvex lateral profile and short, incurved beak, ×3; 9. posterior view, showing telate foramen located in plane of commissure, ×3; 10. anterior view, showing rectimarginate commissure, ×3; locality 6.

11. Portion of dorsal valve, USNM 221553; ventral (interior) view, showing complete, apically perforate hinge plate and origins of loop, ×6; locality 6.

12–13. Portion of dorsal valve, USNM 221551; 12. ventral view, showing hinge sockets and distally broken long loop; 13. ventrolateral view, showing long loop of apparent early ontogenetic stage, with posteroventral flanges, anterior spinose projections and anteromedian dorsal transverse band (see shadow); both ×8; locality 6.

14–16. Fragment of articulated valves, USNM 221550; 14. posteroventrolateral view, showing virtually complete long loop of apparent mature ontogenetic stage; 15. ventral view, showing relationship between hinge plate and loop; 16. oblique anterior view, showing relationship between loop and ventral valve articulatory structures, including dental plates; all ×8; locality 6.

17. Fragment of articulated valves, USNM 221554; lateral view, showing apparent late ontogenetic stage, and long loop without transverse band, ×8; locality 6.

18–29. **Texarina**? cf. **T. wordensis** (R. E. King) 108

18–23. Articulated valves, USNM 221555; 18. dorsal view, showing size and outline of apparent juvenile ontogenetic stage, ×1; 19. dorsal view, showing smoothly rounded fold of dorsal valve, ×2; 20. ventral view, showing pronounced ventral sulcus, ×2; 21. anterior view, showing trigonal profile and pronounced ventral sulcus, ×2; 22. posterior view, showing short (?broken) beak and striking trigonal outline, ×2; 23. lateral view, showing curved commissure and characteristic unequally biconvex profile, ×2; locality 11.

24–29. Articulated valves, USNM 221556; 24. dorsal view, showing size and outline of apparent mature ontogenetic stage, ×1; 25. dorsal view, showing strikingly elongate, narrow outline and anterior asymmetric folding of commissure, ×1.5; 26. ventral view, showing asymmetrically folded commissure and elongate outline, ×1.5; 27. anterior view, showing asymmetric folding of commissure, ×1.5; 28. posterior view, showing low, short (?broken) beak and unequally biconvex profile, ×1.5; 29. lateral view, showing elongate, unequally biconvex profile, ×1.5; locality 11.

INDEX

Note: Page numbers are in light face, plate numbers are in **bold face** type; numbers in *italics* indicate principal discussions.

aages, Lophophyllidium ... 20
?Acaciapora sp. ... 25,28
Acanthocrania Williams ... 39
Acanthopecten ... 25
  sp. ... 25
acanthopelys, Dyoros ... **2** ... 5,21,*50*,*51*,53,55,119
Acolosia Cooper and Grant ... 85
Acosarina Cooper and Grant ... 14,*40*,41
  dorsisulcata Cooper and Grant ... 40
Acosarina? ... 33,35
  sp. ... **1** ... 26,*40*,*41*,118
Acratia? sp. ... 21
adherens, Xenosteges ... 55,56
aduncoglossa (cf.), *Haplistion* ... 29
aequisulcatus, Euphemites ... 28
affinis, Composita ... 96
Africa ... 47,57,62
Ager (1974) ... 23,32
Aguardiente Formation ... 11
Alberding (1956) ... 11
alleni, Oligothyrina ... 105,106
Allorhynchus Weller ... 85
Altiplecus Stehli ... 102
Altube, R. ... 5
Alveolites ... 11
ambiguus, Spurifer ... 94
americana, Collemataria ... 84
American Museum of Natural History (New York City, NY, U.S.A.) ... 6
amphigyus, Neospirifer ... 101
ampullacea, Hustedia ... 91
amygdalinum, Aneuthelasma ... 104,105
?Ananas sp. indet. ... 28
Anaptychius n. gen. ... 5,14,25,33,35,*106*,*107*,108
  minutus n. sp. ... **10** ... 5,24,25,*107*,*108*,127
Andean geosynclinal belt ... 8,10
andersoni, Rugatia ... 77–79
Anemonaria Cooper and Grant ... 14,17,28,33,35,*67*,68,69
  inflata Cooper and Grant ... 67
  sublaevis (King) ... **5** ... 27,*67*,*68*,69,70,122
Anemonaria? cf. *A. sublaevis* (King) ... **5** ... 20,29,*68*,*69*,122
Aneuthelasma Cooper and Grant ... 14,33,35,*104*,105
  amygdalinum Cooper and Grant ... 104,105
  globosum n. sp. ... **9** ... 5,24,25,*104*,*105*,126
angulatus, Dyoros (*Dyoros*) ... 51
angustisulcatus, Chonetinetes ... 55
Anisopyge ... 16
  ?inornata Girty ... 30
  perannulata (Shumard) ... 28
anomalus, Xenosteges ... 56
Anomphalus
  n. sp. ... 21
  sp. indet. ... 29,30
Anychia Termier and Termier ... 57
Antarctica ... 57
Antiquatonia Miloradovich ... 17,72,77,80
Antronaria Cooper and Grant ... 85
Apachella
  aff. *A. francisana* (Chronic) ... 21,29
  sp. ... 23,29,30
  sp. indet. ... 21,28
Aperispurifer Waterhouse ... 100
Aphanosia Cooper and Grant ... 85
aphelus, Composita ... 96
apotheca, Xenosteges ... 101
Appalachian geosyncline ... 8
apsidata, Composita ... 96
arcuata, Neomanda ... 101
Argentina ... 10
Arionthia Cooper and Grant ... 102
Arizona ... 77
  Grand Canyon ... 79
Arnold, H. C. ... 74
Arnold (1966) ... 8,10,12,13,16,19,21,31,33,34,36,74,101
Artinskian strata ... 16
asiatica, Squamularia ... 98
Astartella sp. ... 29
Atelestegastus Cooper and Grant ... 55,57
Athyris roysii Davidson ... 93
attenuata, Meekella ... 48
Attenuatella Stehli ... 97
attenuatus, Dyoros (*Dyoros*) ... 51
Aulosteges ... 76
  subcostatus King ... 74,76
auriculata, Paucispinifera ... 69,70
auriculatus, Dyoros (*Tetragonetes*) ... 51
auripleva, Derbyia ... **1** ... 5,22,27,30,*42*,*43*,44,45,118
Australia ... 37,47,57,62,100,102,104
Aviculopecten sp. ... 29
Avonia ... 17

Baigendzhinian stage ... 17
Bairdia (*sensu lato*) spp. ... 21
bakeri bakeri, Neospirifer ... 101
bakeri columbiarus, Neospirifer ... 101
Banks, P. O. ... 6
basiculcata (cf.), *Discotomaria* ... 22
bassi, Peniculauris ... 76
Bathymyonia Muir-Wood and Cooper ... 17,59
?Bathymyonia cf. *nevadensis* (Meek) ... 74
batilliformis, Collemataria ... 84
Beattie Limestone, Florena Shale Member ... 45
Belize [*see* British Honduras]
Bell (1950) ... 38
bella, Echinauris ... **4,5** ... 25,30,*62*–*64*,65,66,68,121,122
Bell Canyon Formation ... 14,48,53,69,83,104,105
  Hegler Member ... 54,55
  Lamar Member ... 54
  Rader Member ... 54
Bellerophon (*?Pharkidonotus*) sp. ... 23
?Bellerophon sp. indet. ... 28
Bellizzia, A. ... 5
bipartita, Hustedia ... 91
Bolivia ... 10,13,45,94,102
  Lake Titicaca ... 6,86
Bone Spring Formation ... 41,67–69,77,81,99
Bonham-Carter (1967) ... 15
Bothrioma Cooper and Grant ... 62
Boucot, A. J. ... 33
Boucot, Johnson, and Staton (1964) ... 88,92
boulei, Echinauris ... 63,65,66
Bowen, Rhoads, and McAlester (1974) ... 23,32
Boyd and Newell (1972) ... 18,19,21
Brazil ... 10
Bretsky and Bretsky (1975) ... 23,32
Brigham Young University (Provo, UT, U.S.A.) ... 6
Brill (1940) ... 104,106
brilli, Pseudodielasma ... 105
British Honduras ... 9,13
Broili (1916) ... 62
Brown (1849) ... 93,94
Brown (1953) ... 100
bucculenta, Composita ... 96
buchi, Derbyia ... 45
Buckman (1906) ... 93

Bullard *et al.* (1965) ... 8
bullata, Neophricadothyris ... 99
Burgl (1973) ... 9
Burke, J. J. [JJB] ... 6,20
Burkley, L. ... 6

calathica, Meekella ... 48
California Academy of Sciences (San Francisco, CA, U.S.A.) ... 6
Callispirina Cooper and Muir-Wood ... 102
Camarelasma Cooper and Grant ... 104
Cambodia ... 57
cameratus, Neospirifer ... 101
cameratus venezuelensis, Spirifer ... 100
Campbell (1959) ... 102
Campbell (1965) ... 104
campestris, Spiriferellina ... 102
canalis, Schizodus ... 16,20,27
Cancrinella ... 17
Caparo Formation ... 12
Capitan Formation ... 14,48,83,104,105
Carey (1958) ... 8
Caribbean Sea ... 8,9
Cartorhium Cooper and Grant ... 100
Case-Western Reserve University (Cleveland, OH, U.S.A.) ... 6
catatona, Neophricadothyris ... 99
catella, Hustedia ... 91
Cathedral Mountain Formation ... 14,16,31,43,44,55,67, 68,70,71,73,77,79,86,87,90,99,108,109
Cavellina sp. ... 21
Cavellina? sp. ... 25
Cecioni (1956) ... 10
cepacea, Hustedia ... 91
Ceratobairdia? sp. ... 21
Chamberlain, C. K. ... 6,16,28,30
Chao (1927) ... 62,63
Chao (1929) ... 98
Chaoiella Frederiks ... 77
Chave (1964) ... 18
Cheetham and Hazel (1969) ... 14
Cherry Canyon Formation ... 14,40,46,48,108
Chile, Madre de Dios Archipelago ... 10
China ... 62,63
Chochal Limestone ... 9,13,16,48,49,65,66,74,76–78,86,106
Chonetes consanguineus Girty ... 49
Chonetina Krotov ... 53
Chonetinella Ramsbottom ... 52,53
Chonetinetes Cooper and Grant ... 14,33,35,*53*,*54*,55
angustisulcatus Cooper and Grant ... 55
reversus Cooper and Grant ... 53,55
varians Cooper and Grant ... 54,55
cf. *C. varians* Cooper and Grant ... **2** ... 22,27,30,51,*54*,*55*,119
Christ, P. ... 101,102
Christ (1927) ... 10,11,26,102
?Cibecuia sp. indet. ... 21
Cibolo Formation ... 63,90
cincinnata, Derbyia ... 43
circularis, Echinauris ... 63,65,66
ciriacksi, Cleiothyridina ... 94
citeria, Hustedia ... 91
Cities Service Company (Denver, CO, U.S.A.) ... 6
Cleiothyridina Buckman ... 14,22,33,35,*93*,*94*
ciriacksi Cooper and Grant ... 94
intonsa Chronic ... 94
mulsa Cooper and Grant ... 94
nana Cooper and Grant ... 94
cf. *C. nana* Cooper and Grant ... **8** ... 21,*94*,125
pilularis Cooper and Grant ... 94
rara Cooper and Grant ... 94
rectimarginata Cooper and Grant ... 94
Clemons *et al.* (1974) ... 9
Cleveland Museum of Natural History (Cleveland, OH, U.S.A.) ... 6

Collemataria Cooper and Grant ... 14,25,33,35,*82*,*83*,84
americana (Girty) ... 84
batilliformis Cooper and Grant ... 84
elongata Cooper and Grant ... 82,84
gregaria Cooper and Grant ... 84
irregularis Cooper and Grant ... 84
marshalli (Stehli) ... 84
platys Cooper and Grant ... 84
spatulata Cooper and Grant ... 83,84
venezuelensis n. sp. ... **7** ... 5,24,*83*,*84*,124
Colombia ... 9,12,13
Sierra de Perija ... 9,16
Colospongia sp. ... 22,29
"Colpites" sp. indet. ... 29
complex, Dichostasia ... 22
complicata, Derbyia ... 43,44
complicata (cf.), *Derbyia* ... **1** ... 22,27,*43*,*44*,45,118
Composita Brown ... 14,17,19,22,27,29,31,33,35,93,*94*,*95*,96
affinis Girty ... 96
apheles Cooper and Grant ... 96
apsidata Cooper and Grant ... 96
bucculenta Cooper and Grant ... 96
costata Cooper and Grant ... 96
cracens Cooper and Grant ... 96
crassa Cooper and Grant ... 96
emarginata Girty ... 96
enormis Cooper and Grant ... 96
grandis Cooper ... 96
hapsida Stehli and Grant ... 96
imbricata Cooper and Grant ... 96
mexicana (Hall) ... 96
minuscula Chronic ... 96
nucella Cooper and Grant ... 96
parasulcata Cooper and Grant ... 96
pilula Cooper and Grant ... 95,96
cf. *C. pilula* Cooper and Grant ... **8** ... 20–22,26,27,29,30,*95*,*96*,125
prospera Cooper and Grant ... 96
pyriformis Cooper and Grant ... 96
stalagmium Cooper and Grant ... 96
strongyle Cooper and Grant ... 96
subtilita (Hall) ... 96
peruviana Chronic ... 96
compressa, Hustedia ... 91
Comuquia Grant ... 70
conara, Neophricadothyris ... 99
concavus, Dyoros (*Lissosia*) ... 51
Condrathyris Minato ... 98
connorsi, Hustedia ... 91
consanguineus,
Chonetes ... 49
Dyoros (*Dyoros*) ... 51
consuta, Hustedia ... 90–93
convexa, Rugatia ... 78,79
convexus, Dyoros (*Dyoros*) ... 51
Cooper, G. A. ... 6,37,45
Cooper (1956) ... 104–106
Cooper (1957) ... 96
Cooper (1975) ... 41
Cooper and Grant (1969) ... 40,49,53,55,57,62,67,69,72,75, 83–85,87,100,102,104,108,109
Cooper and Grant (1970) ... 108
Cooper and Grant (1972) ... 9,13,34,38,39
Cooper and Grant (1974) ... 9,13,34,38–41,43–49,82–84
Cooper and Grant (1975) ... 9,13,34,38,39,49,51,54–58,62–73,76–81
Cooper and Grant (1976a) ... 9,13,34,38,39,84–87,94–96,98–101
Cooper and Grant (1976b) ... 9,13,34,38,39,88,90–93,102–106,108,109
Cooper and Grant (1977) ... 9,13,34,38,39
Cooper and Muir-Wood (1951) ... 102
Cooper *et al.* (1953) ... 9,36,67–69,73,77,78
Cooperina Termier, Termier, and Pajaud ... 14,33,35,*57*,58,59,61,99
inexpectata Termier, Termier, and Pajaud ... **4** ... 24,25,*57*–*61*,121

Cooperina parva Cooper and Grant 57–59,61,121
polytreta Grant 57
spondyliformis (White and St. John) 58
subcuneata Cooper and Grant 57,58
triangulata Cooper and Grant 57,58
Copacabana Formation 86,91
Copacabana Group 10,13
cordata, Neophricadothyris 99
corrugata (cf.), "*Worthenia*" 23
costata,
Composita 96
Peniculauris 76
Pontisia 86
costatus, Productus 78
costellata, Paucispinifera 67,68,70
Costicrura n. gen. 5,14,25,33,35,96,97
minuta n. sp. ..... **8** 5,24,25,37,96,*97*,*98*,125
Costiferina Muir-Wood and Cooper 77
Costispinifera Muir-Wood and Cooper 62
cracens, Composita 96
Crania Retzius 39
Cranella meduanensis Oehlert 39
crassa,
Composita 96
Derbyia 45
Echinauris 63,65,66
crassibecca, Neophricadothyris 98,99
crassibecca (cf.), *Neophricadothyris* ..... **8** 20,26,27,*98–100*,125
crenulata, Derbyia 44
crepax, Hustedia 91
cristata, Spiriferellina 104
cristatus, Terebratulites 102
Cruricella Grant 25
Crurithyris George 96,97
Cryptacanthia White and St. John 107
Cryptonella Hall 108
culcitula, Hustedia 91
cuneata, Hustedia 91
Cylicioscapha 16
sp. 29
Cystothalamia sp. (nov.?) 22,29

Dasysaria Cooper and Grant 75,77,80
Davidson (1860) 93
Davidson (1862) 91
Davidson (1884) 102
decollatensis, Hustedia 91
Defordia 22,25
cf. *densa* Finks 22,24,25,29
sp. 32
delicatula, Spinifrons 81
deltauriculata, Derbyia ..... **1** 5,27,*44*,*45*,118
demissa, Hustedia 91
Dengo and Bohnenberger (1969) 9
densa (cf.), *Defordia* 22,24,25,29
Derbyia Waagen 14,27,28,32,33,35,*41*,*42*,44–46
auriplexa n. sp. ..... **1** 5,22,27,30,*42*,*43*,44,45,118
buchi (d'Orbigny) 45
cincinnata Cooper and Grant 43
complicata Cooper and Grant 43,44
cf. *D. complicata* Cooper and Grant ..... **1** 22,27,*43*,*44*,45,118
crassa (Meek and Hayden) 45
crenulata Girty 44
deltauriculata n. sp. ..... **1** 5,27,*44*,*45*,118
filosa Cooper and Grant 45,46
cf. *D. filosa* Cooper and Grant ..... 2 ..... 29,44,*45*,*46*,119
informis Cooper and Grant 46
laqueata Cooper and Grant 41,44
nasuta Girty 46
pannucia Cooper and Grant 46
regularis Waagen 41
texta Cooper and Grant 44
sp. ..... **1** 21,22,25,30,*46*,*47*,118
Derbyia (*Plicatoderbyia*) Thomas 41
De Rivero (1956) 11
derovsii, Spirifer 93
diabloensis, Petrocrania 40
Dichostasia complex Yochelson 22
Dictyoclostus liddlei Harris 12
Dielasma King 17,94,104
problematicum wordense King 108
Dielasmella Weller 108
Dielasmina Waagen 104
difficilis, Meekella 47
Discotomaria cf. *D. basisulcata* Batten 22
Discotropis sp. 30
Divaricosta Cooper and Grant 84,85
Doescher, R. 5
cf. *Donaldina* sp. indet. 30
dorsisulcata, Acosarina 40
Douglass, R. C. [RCD] 6,16,23,24
Douglass and Nestell (1976) 10
Dumeril (1806) 39
Dunbar (1955) 74,102
Dunbar (1973) 10
Dunbar and Condra (1932) 45,49,57,84,101
dunbari (cf.), *Girtyocoelia* 22
Dunham (1962) 17
durhami, Parafusulina 16
Dutro, J. T., Jr. 6
Dyoros Stehli 14,17,33,35,*49*,*50*,51–53
acanthopelix n. sp. ..... **2** 5,21,*50*,*51*,53,55,119
Dyoros (*Dyoros*) Cooper and Grant 49
angulatus Cooper and Grant 51
attenuatus Cooper and Grant 51
consanguineus (Girty) 51
convexus Cooper and Grant 51
endospinus Cooper and Grant 51
extensiformis Cooper and Grant 51
extensus Cooper and Grant 51
hillanus (Girty) 51
intrepidus Cooper and Grant 51
magnus Stehli 51
planiextensus Cooper and Grant 51
robustus Cooper and Grant 51
subliratus (Girty) 51
tenuis Cooper and Grant 51
transversus Cooper and Grant 51
vulgaris Cooper and Grant 51
Dyoros (*Lissosia*) Cooper and Grant 49
concavus Cooper and Grant 51
parvus Cooper and Grant 51
vagabundus Cooper and Grant 51
Dyoros (*Tetragonetes*) Cooper and Grant 49–51
auriculatus Cooper and Grant 51
giganteus Cooper and Grant 51
quadrangulatus Cooper and Grant 51
solidus Cooper and Grant 51
strigosus Cooper and Grant 51
subquadratus Cooper and Grant 51
Dyschrestia Grant 70

Echinauris Muir-Wood and Cooper 14,17,30,33,35,*62*,63,66
bella Cooper and Grant ..... **4,5** 25,30,*62–64*,65,66,68,121,122
boulei (Kozlowski) 63,65,66
circularis Cooper and Grant 63,65,66
crassa Cooper and Grant 63,65,66
huehuetenanguensis Stehli and Grant 63,65
interrupta Cooper and Grant 63,65,66
irregularis Cooper and Grant 63,65,66
jisuensis (Chao) 63
lappacea Cooper and Grant 63–66
cf. *E. lappacea* Cooper and Grant ..... **5** 18,29,*64*,*65*,68,122

lateralis Muir-Wood and Cooper 62,63,65,66
liumbona Cooper and Grant 63,65,66
cf. *E. liumbona* Cooper and Grant ..... **5** 20,22,26,27,*65*,*66*,68,122
magna Cooper and Grant 63,65,66
opuntia (Waagen) 63,65
parva Cooper and Grant 63,65,66
productelloides Cooper and Grant 63,65,66
subhorrida (Meek) 63,65,66
subquadrata Cooper and Grant 63,65,66
venustula Cooper and Grant 63,65,66
sp. 65,66
Echinoconchidae, genus indeterminate ..... **5** *74*,122
Ectoposia Cooper and Grant 104
Ecuador 10
Cutucu Mountains 9
Quito 9
Eldredge and Gould (1972) 99
elegans, Pugnoides 85
El Horno Formation 12
Eliva 36
Elivina 36
Elliottella Stehli 62
elongata,
Collemataria 82,84
Texarina 109
emarginata, Composita 96
Emery and Rittenberg (1952) 18
endospinus, Dyoros (Dyoros) 51
England, Newcastle-upon-Tyne 6
Englemann (1935) 10
enormis, Composita 96
Eolissochonetes Hoare 49
Erdtmann and Prezbindowski (1974) 18
Eridmatus 36
esoterica, Stauromata **2,3,4** 5,20,22,26,27,50,51,*52*,*53*,55,119–121
Euphemites
aequisulcatus H. Chronic 28
cf. *E. exquisitus* Yochelson 28
exasperata, Petrocrania 40
exquisitus (cf.), *Euphemites* 28
extensiformis, Dyoros (Dyoros) 51
extensus, Dyoros (Dyoros) 51

Falafer Grant 57
fasciger, Spirifer 100
filosa, Derbyia 45,46
filosa (cf.), *Derbyia* ..... **2** 29,44,*45*,*46*,119
Fischer (1960) 6
Fletcherithyris Campbell 104
Folk (1962) 17
Fordiceras 20
formulosus, Neospirifer 101
Frakes *et al.* (1969) 10
franciscana (aff.), *Apachella* 21,29
franklinensis, Pontisia 86
Franks, S. 6
Frederiks (1916) 102
Frederiks (1924) 96,98,100,102
Frederiks (1926) 100,102
Frederiks (1928) 59,70
Frederiks (1933) 77
Freeland and Dietz (1971) 8
Furnish, W. M. [WMF] 6,16,20,23,27,29
Fusispirifer Waterhouse 100
Fusulina 10

Gacina Stehli 107
Gaptank Formation 40
García, C. 5
García-Jarpa, R. 5
Geinitzina sp. 23
Gemmellaro (1899) 98
Geological Society of America 5
George (1931) 96,97
George (1932) 98
Germany 57
Gerster Formation 66
Gerth and Kräusel (1931) 10,13,100
Getaway Formation 14
giganteus, Dyoros (Tetragonetes) 51
Gilledia Stehli 104,105
Giron Series 11
Girty (1909) 9,44,46–48,51,70,78,84,91,96,103,108
Girty (1920) 101
Girty (1929) 49,51
Girty (1934) 107
girtyi, Wellerella 84
Girtyocoelia
cf. *dunbari* King 22
n. sp. 22,29
Girtypecten 25
sp. 25
Glabrocingulum sp. indet. 36
Glenister, B. F. [BFG] 6,9,16,20,23,27,29
Globivalvulina 12
sp. 23
globosum, Aneuthelasma ..... **9** 5,24,25,*104*,*105*,126
glomerosa, Hustedia 91
Glossothyropsis Girty 107
gloveri, Pegmavalvula 24
gloveri (cf.), *Pegmavalvula* 25,29
Glyptotomaria sp. indet. 29
Glyptospira sp. indet. 28–30
Goniasma
sp. one 30
sp. two 30
sp. indet. 23,30
Gonzales de Juana (1951) 11,12
Gordon, M. 6
Grandaurispina Muir-Wood and Cooper 70
grandicosta,
Hustedia 91
Spinifrons ..... **7** 5,27,30,76,78,79,*80*,*81*,82,124
grandicosta (cf.), *Spinifrons?* ..... **7** 21,22,29,*81*,*82*,124
grandis, Composita 96
Grant, R. E. 6,37,55,62,63,97
Grant (1968) 62
Grant (1971) 37
Grant (1972) 57
Grant (1976) 25,36,57,62,70,77,84
Grant and Cooper (1973) 8,13,14,17
Grantonia Brown 100
Gray (1840) 62
Gray (1848) 84
Greece 62
gregaria, Collemataria 84
Grinnell and Andrews (1964) 95
gryphoides (cf.), *Megadesmus* 20
guadalupensis,
Neophricadothyris 99
Squamularia 99
Guadalupia cf. *williamsi* King 25
Guadalupia(?) sp. 24
Guadalupian strata 12,14
Guatemala 6,9,13,16,48,49,62,63,65,66,74,76–78,86,106
Huehuetenango 9
Guizhoupecten sp. 29
Gulf of Mexico
Bartlett Trough 9
Cayman Ridge 9
Gypospirifer Cooper and Grant 100

Habicht (1979) ... 33
Haertocrinus? sp. ... 20
Hall (1852) ... 96,101
Hall (1857) ... 96
Hall (1861) ... 108
Hall and Clarke (1892) ... 40,41
Hall and Clarke (1893) ... 88,100
Hamilton (1966) ... 8
hapala, Hustedia ... 91
Haplistion cf. *H. aeluroglossa* Finks ... 29
hapsida, Composita ... 96
Haydenella Reed ... 62
Hea and Whitman (1960) ... 11
Healdia sp. ... 21
Hedberg and Sass (1937) ... 10,12
Helwig, J ... 6
Hemiptychina Waagen ... 104
Hess Formation ... 14,99
hessensis, Hustedia ... 91
Heteralosia King ... 55
Heterelasma Girty ... 108
Hettner (1892) ... 11
Hicken *et al.* (1972) ... 8
Hildreth (1836) ... 101
hillanus, Dyoros (Dyoros) ... 51
hilli,
  Perrinites ... 16,23
  Spiriferellina ... 103,104
  Spiriferina ... 103
hilli (cf.), *Spiriferellina* ... **8,9** ... 21,*103,104*,125
hirsuta, Holotricharina ... **5** ... 22,27,*70,71*,122
Hoare (1960) ... 49
Hoffstetter (1960) ... 9
Hollinella spp. ... 21,25
Holotricharina Cooper and Grant ... 14,17,30,33,35,*70*,71
  hirsuta Cooper and Grant ... **5** ... 22,27,*70,71*,122
  sparsa Cooper and Grant ... 71
Holotricharina? ... 72
  sp. A ... **5** ... 27,29,30,*71,72*,122
  sp. 1 ... 71,72
Hoover (1975) ... 10,13,82,83
Hoover (1976a) ... 16,31,32,33,36
Hoover (1976b) ... 8,17,31
Hoskingia Campbell ... 104
Howard, J. ... 6
huecoensis,
  Hustedia ... 91
  Neospirifer ... 101
Hueco Formation ... 14
huehuetenanguensis, Echinauris ... 63,65
Hustedia Hall and Clarke ... 14,17,19,20,22,25,27–29,31,33,35,*88*,91,100
  ampullacea Cooper and Grant ... 91
  biparitta Girty ... 91
  catella Cooper and Grant ... 91
  cepacea Cooper and Grant ... 91
  citeria Cooper and Grant ... 91
  compressa Cooper and Grant ... 91
  connorsi Cooper and Grant ... 91
  consata Cooper and Grant ... 90–93
  crepax Cooper and Grant ... 91
  culcitula Cooper and Grant ... 91
  cuneata Cooper and Grant ... 91
  decollatensis Cooper and Grant ... 91
  demissa Cooper and Grant ... 91
  glomerosa Cooper and Grant ... 91
  grandicosta (Davidson) ... 91
  hapala Cooper and Grant ... 91
  hessensis King ... 91
  huecoensis King ... 91
  hyporhachis n. sp. ... **8** ... 5,21,24,25,27,29,30,*88–92*,93,100,125
  inconspicua Cooper and Grant ... 91
  lusca Cooper and Grant ... 91
  narinosa Cooper and Grant ... 91
  opsia Cooper and Grant ... 91
  pugilla Cooper and Grant ... 91
  rupinata Cooper and Grant ... 91
  samiata Cooper and Grant ... 91
  sculptilis Cooper and Grant ... 91
  sicuaniensis Chronic ... 91
  spicata Cooper and Grant ... 91
  stataria Cooper and Grant ... 91
  tomea Cooper and Grant ... 91
  trisecta Cooper and Grant ... 91
  trita Cooper and Grant ... 91
  sp ... **7** ... 20,27,*92*,124
Huxley (1869) ... 39,40
hyporhachis, Hustedia ... **8** ... 5,21,24,25,27,29,30,*88–92*,93,100,125
Hystriculina Muir-Wood and Cooper ... 68

ICZN (1961) ... 102
imbricata, Composita ... 96
inconspicua, Hustedia ... 91
incurvata, Rugatia ... 78,79
indentata, Paucispinifera ... 70
inexpectata, Cooperina ... **4** ... 24,25,*57–61*,121
inflata, Anemonaria ... 67
informis, Derbyia ... 46
?inornata, Anisopyge ... 30
intermedia,
  Paucispinifera ... 70
  Rugatia ... **6** ... 5,22,27,29,76,*77,78*,79,81,123
interrupta, Echinauris ... 63,65,66
intonsa, Cleiothyridina ... 94
intrepidus, Dyoros (Dyoros) ... 51
irregularis,
  Collemataria ... 84
  Echinauris ... 63,65,66
Itaituba Formation ... 10
Ivanova (1951) ... 72
Ives (1861) ... 78
ivesi, Peniculauris ... 76

jisuensis, Echinauris ... 63
Jung, P. ... 6
Juresania Frederiks ... 17,59

kaibabensis (aff.), *Straparollus (Euomphalus)* ... 27,28
Kaibab Formation ... 77,79
Kansas ... 45
Karklins, O. L. [OLK] ... 6,20,21
Kehrer (1938) ... 11
Keyserling and Krozenstern (1846) ... 100
Kier, P. M. [PMK] ... 6,27
King, R. E. (1931) ... 9,47,67,69,70,73,74,76,78,79,85,91,99,101
King, R. E., *et al.* (194) ... 9
King, R. H. (1938) ... 55
King, W. (1846) ... 100
King, W. (1850) ... 40
King, W. (1859) ... 94,104
kingi, Pontisia ... 86
Kinishbia
  sp. ... 27–29
  sp. indet ... 30
Klar, G. ... 6
Kling (1960) ... 9,13
Kochiproductus Dunbar ... 74
Kochiproductus? sp. ... 74–76
Koenig (1825) ... 100
Koken (1889) ... 39
Kozlowski (1914) ... 63,65,66,102
Kozlowskia ... 17

Krotov (1888) ... 53
Krotovia Frederiks ... 70
Kuhn (1949) ... 39,84
Kündig (1938) ... 11
Kutorginella Ivanova ... 14,17,33,35,*72*,73
  lasallensis (Worthen) ... 73
  meridionalis (McKee) ... 73
  mosquensis Ivanova ... 72
  occidentalis (Cooper) ... 73
  parvispinosa (Stehli) ... 73
  robusta Cooper and Grant ... 73
  subquadrata (Cooper) ... 73
  sullivanensis (King) ... 73
  uddeni Cooper and Grant ... 73
  umbonata (Muir-Wood and Cooper) ... 72,73
  cf. *K. umbonata* (Muir-Wood and Cooper) ... **6** ... 20,22,26,27,29, *72–74*,123

Labaia Likharev ... 104
?Lamellospira sp. ... 22
lappacea, Echinauris ... 63–66
lappacea (cf.), *Echinauris* ... **5** ... 18,29,*64,65*,68,122
laqueata, Derbyia ... 41,44
La Quinta Formation ... 11
lasallensis, Kutorginella ... 73
lateralis, Echinauris ... 62,63,65,66
latidorsata, Paucispinifera ... 70
latus, Neospirifer ... 101
Lawrence (1968) ... 18,19
Lee, C. S. [CSL] ... 6,16,23,27
Lee (1975) ... 16
Leonard Formation ... 9
Leonardian strata ... 14,15
Lepidocrania Cooper and Grant ... 39
Lepidospirifer Cooper and Grant ... 100
Leptalosia spondyliformis White and St. John ... 57
Leptodus Kayser ... 83
Leurosina Cooper and Grant ... 49
Leveille (1835) ... 93
Licharewiella Sokolskaya ... 41
Liddle (1946) ... 11
liddlei, Dictyoclostus ... 12
Likharev (1934) ... 94,98
Likharev (1935) ... 55
Likharev (1956) ... 104
Liosotella Cooper ... 67–69,77,78
Lirellaria Cooper and Grant ... 84
Lissochonetes Dunbar and Condra ... 17,49
liumbona, Echinauris ... 63,65,66
liumbona (cf.), *Echinauris* ... **5** ... 20,22,26,27,*65,66*,68,122
Lomita Series ... 10,11
longicosta, Pontisia ... 86
Lopez-Ramos (1969) ... 9
Lophophyllidium ... 28
  aages (Jeffords) ... 20
  sp. cf. *L. pelaeum* (Jeffords) ... 28
  sp. aff. *L. spinosum* Jeffords ... 27
  sp. ... 26,29
Lowenstamia (Stehli) ... 104
lusca, Hustedia ... 91
Lutz-Garihan (1974) ... 95
"*Lyropora*" sp. ... 27

Macuma Formation ... 9
magna,
  Echinauris ... 63,65,66
  Spinifrons ... 81
magnicostata, Pontisia ... 86
magnifica, Meekella ... 48
magnispina, Paucispinifera ... 70
magnus,
  Dyoros (*Dyoros*) ... 51
  Xenosteges ... 56
mansuetus, Neospirifer ... 101
Maorielasma Waterhouse ... 104
Marcou (1858) ... 78,88
Marginifera Waagen ... 17
  sublaevis King ... 67
Marinurnula Waterhouse ... 104,105
marshalli, Collemataria ... 84
Martín B., C. ... 5
Martín B. (1968) ... 12
Martinia McCoy ... 94
Martinothyris Minato ... 98
Martoceras subinterrupta (Krotov) ... 16,27,28
Maxwell (1961) ... 98
McCall, P. ... 6,37
McCoy (1844) ... 92–94
McKee (1938) ... 73,76–79
mckeei,
  Peniculauris ... 74–76
  Rugatia ... 78–79
meduanensis, Craniella ... 39
Meek (1877) ... 63,65,66
Meek and Hayden (1858) ... 45
Meek and Worthen (1873) ... 73
Meekella White and St. John ... 14,17,22,23,32,33,35,*47*,48
  attenuata Girty ... 48
  calathica Cooper and Grant ... 48
  difficilis Girty ... 47
  magnifica Cooper and Grant ... 48
  occidentalis (Newberry) ... 48
  prionota Cooper and Grant ... 48
  skenoides Girty ... **2** ... 21,22,26,27,29,*47–49*,119
  sp. ... 48
Meekospira sp. indet ... 27,30
?Meekospira sp. indet. ... 29
Megadesmus cf. *gryphoides* ... 20
Megard *et al.* (1971) ... 10
Mendes, A ... 5
Menke (1828) ... 39
Merida facies ... 12,13
meridionalis,
  Kutorginella ... 73
  Productus (*Dictyoclostus*) ... 78
Mesolobus Dunbar and Condra ... 49
Metacoceras ... 20
Metriolepis Cooper and Grant ... 102
mexicana, Composita ... 96
Mexican-Central American geosynclinal belt ... 8
Mexico ... 6,8,9,13
  Chiapas ... 9,16
  Coahuila
    Las Delicias ... 9,69
  Gulf of ... 8
  Sonora ... 9
    El Antimonio ... 9
  Yucatan Peninsula ... 8
Meyerhoff (1970) ... 10
Miller and Williams (1945) ... 9,16
Miloradovich (1945) ... 72,77,80
Mimaria Cooper and Grant ... 108,109
Minato (1953) ... 98
miniscula, Composita ... 96
minusculus, Xenosteges ... **4** ... 5,24,25,*55–57*,58,121
minuta, Costicrura ... **8** ... 5,24,25,37,*96,97,98*,125
minutus, Anaptychius ... **10** ... 5,24,25,*107,108*,127
Miréles Formation ... 12
MMH (Ministerio de Energía, Dirección de Geología, Caracas, Venezuela) ... 5,39,40
Molina, D. ... 5

Molina, L. ... 5
Molina, V. ... 5
Molina y Vega, L. M. ... 5
Monos Formation ... 36
Mooreoceras ... 16,27–29
Mora, A. ... 5
Mora, P. ... 5
Mora, S. ... 5
Moreland (1968) ... 17
mormoni, Terebratula ... 88
Morocco ... 23,32
mosquensis, Kutorginella ... 72
Motiscka, P. ... 5
Mucuchachi depositional basin ... 31
Mucuchachi facies ... 12
Mucuchachi Formation ... 12
Mucupatí Series ... 10,11
Muir-Wood, H. M. ... 16,33–35,74
Muir-Wood (1955) ... 106
Muir-Wood (1962) ... 49,53
Muir-Wood and Cooper (1960) ... 30,39,55,59,62,66,68–70, 72,74,76,77,80,82
Müllereid ... 16
mulsa, Cleiothyridina ... 94
Murphy, J. ... 6,10

nana, Cleiothyridina ... 94
nana (cf.), *Cleiothyridina* ... **8** ... 21,*94*,125
nanas, Pontisia ... 86
narinosa, Hustedia ... 91
nasuta,
  Derbyia ... 46
  Spiriferellina ... 104
Naticopsis
  cf. *N. oblatus* Winters ... 23
  sp. ... 30
  sp. indet. ... 28
National Science Foundation ... 5
neali, Neospirifer ... 101
Neal Ranch Formation ... 77
Nebenothyris Minato ... 98
Neochonetes Muir-Wood ... 17,49
  sp. ... 49
Neophricadothyris Likharev ... 14,17,19,27,33,35,94,*98*,99
  bullata Cooper and Grant ... 99
  catatona Cooper and Grant ... 99
  conara Cooper and Grant ... 99
  cordata Cooper and Grant ... 99
  crassibecca Cooper and Grant ... 98,99
  cf. *N. crassibecca* Cooper and Grant ... **8** ... 20,26,27,*98–100*,125
  guadalupensis (Shumard) ... 99
  transversa Cooper and Grant ... 99
Neospirifer Frederiks ... 14,17,33,35,*100*,101
  amphigyus Cooper and Grant ... 101
  apothescelus Cooper and Grant ... 101
  bakeri bakeri King ... 101
  bakeri columbiarus Cooper and Grant ... 101
  cameratus (Morton) ... 101
  formulosus Cooper and Grant ... 101
  huecoensis King ... 101
  latus Dunbar and Condra ... 101
  manuetus Cooper and Grant ... 101
  neali Cooper and Grant ... 101
  notialis Cooper and Grant ... 101
  placidus Cooper and Grant ... 101
  thescelus Cooper and Grant ... 100,101
  triplicatus (Hall) ... 101
  venezuelensis (Gerth) ... **9** ... 20,22,26,27,*100–102*,126
Nepal ... 62
Neuman, R. B. ... 6
Nevada ... 66
nevadensis (cf.), *?Bathymyonia* ... 74
Newberry (1861) ... 48,76,78,79,81
Newell, N. D. [NDN] ... 6,16,20,23–25,27–30,34
Newell, Chronic *et al.* (1949) ... 91,94,96,99,102
Newell, Chronic *et al.* (1953) ... 10,13,91
Newell, Rigby *et al.* (1953) ... 47
New Mexico ... 9
New York ... 23,32
New Zealand ... 37,102,104
Niviconia Cooper and Grant ... 47
NMB (Naturhistorisches Museum Basel, Basel, Switzerland) 6,39,102,126
North (1920) ... 102
Norwood and Pratten (1855) ... 81
Nothopindax Cooper and Grant ... 41
notialis, Neospirifer ... 101
nucella, Composita ... 96
Nuculopsis sp. ... 29
nuda, Spiriferellina ... 104
Nudauris Stehli ... 77

oblatus (cf.), *Naticopsis* ... 23
oblongata,
  Texarina ... 109
  Texasia ... 108
occidentalis,
  Kutorginella ... 73
  Meekella ... 48
  Productus ... 78,79
  Rugatia ... **6** ... 20,26,76,77,*78–80*,81,123
occidentalis parvauris, Rugatia ... 79
Odontospirifer Dunbar ... 102
Oehlert (1888) ... 39
Oehlert (1890) ... 40
Oklahoma ... 57
Oligothyrina Cooper ... 14,104,*105,106*
  alleni Cooper ... 105,106
Oligothyrina? ... 33,35,106
  sp. ... **10** ... 21,30,*106*,127
Oncosarina Cooper and Grant ... 62
Onycochilus sp. indet. ... 28,29
Opik (1934) ... 41
Oppenheim (1937) ... 11
opsia, Hustedia ... 91
opuntia, Echinauris ... 63,65
d'Orbigny (1842) ... 45
Orthonema
  sp. ... 24,28–30
  sp. indet. ... 22,23
?Orthonema sp. indet. ... 25
new genus aff. *Orthonema* ... 24
new genus allied to *Orthonema* ... 27,29
Orthotichia Hall and Clarke ... 40,41
Otsuka Coefficient ... 13,14,16
Ouachita geosynclinal belt ... 8
Owen (1857) ... 47

Pachyphloia sp. ... 23
Pajaud (1968) ... 57
Pakistan ... 62
Paleontological Research Institution (Ithaca, NY, U.S.A.) ... 5
Palaeostylus sp. indet ... 23
Palaeozygopleura sp. indet. ... 23
Palmarito facies ... 12,13,31
Palmarito Formation
  Arnold collection, No. Ar 981-R ... 74,122
  Field No. PRH-71-VE-12 ... 16
  Field No. PRH-71-VE-23 ... 48,49
  locality 1 ... 14–17,19,20,24,35,52,53,66,67,69,73,74,76,77, 79,80,88,92,95,96,98,99,101,102,122–124
  locality 2 ... 14,15,17,20,24,35,50,51,119

locality 3 ..... 14–17,21,22,31,32,35,36,46–49,82,87,88, 90,92–96,103,104,106,119,124–126
locality 4 ..... 14–17,22,32,35,36,43,44,46–49,52–55,65,66,70, 71,73,74,78,82,95,96,101,102,118,119,121–125
locality 5 14,15,17,23,31,32,35,76,77,123
locality 6 14–17,24,25,30,31,35–37,60,61,88,90,121,124–127
block A 24,25,31,32,40,56–58,60,83,84,90,92,97,98,105,108,118
block B 24,25,56–58,83,84,87,88,92,97,98,105,108
block C 17,24,25,32,40,46,47,56–58,60,61,63,64, 83,84,87,88,90,92,97,98,105,108,118
locality 7 ..... 14–17,24,26,35,40,41,48,49,52,53,65,66, 73,74,80,95,96,98–102,118–120,125,126
locality 8 ..... 14–18,26,32,35–37,43,44,48,49,52–55,66,69–74,78, 81,85,86,88,92,95,96,98–102,118,119,121–126
locality 10 ..... 14–17,27,28,31,32,35,45,67,68,72,78, 85–92,95,96,100,118,122,124,125
locality 11 ..... 14–17,24,28,32,35,46,48,49,64,65,67,69,72–74,78,82, 85,86,88,90–92,95,96,109,119,121–125,127
locality 13 ..... 14–17,29,31,32,35,42,43,46,47,54,55,63,64,70, 72,81,88,90–93,95,96,106,118,121,122,124,127
Palmarito Series 10,11
Panchaud, R. 6
pannucia, Derbyia 46
Parafusulina 12,25
durhami 16
sellardsi 16
cf. *P. sellardsi* 24
Paraguay 10
paraindica, Rugatia 78,79
paraindicus, Productus (Dictyoclostus) 77
parallela, Texarina 109
Parallelodon sp. 23,29
Paraspiriferina Reed 102
parasulcata,
Composita 96
Paucispinifera 70
parva,
Cooperina 57–59,61,121
Echinauris 63,65,66
Pontisia 86
parvispinosa, Kutorginella 73
parvus, Dyoros (Lissosia) 51
Passa Dois Series 10
paucicostata, Spiriferellina 104
Paucispinifera Muir-Wood and Cooper 14,17,67,69
auriculata Muir-Wood and Cooper 69,70
costellata Cooper and Grant 67,68,70
indentata (Girty) 70
intermedia Cooper and Grant 70
latidorsata (Girty) 70
magnispina Cooper and Grant 70
parasulcata Cooper and Grant 70
quadrata Cooper and Grant 70
rara Cooper and Grant 70
rectangulata Cooper and Grant 70
spinosa Cooper and Grant 70
sulcata Cooper and Grant 67–70
suspecta Cooper and Grant 70
transversa Cooper and Grant 70
tumida Cooper and Grant 70
Paucispinifera? 33,35,69
cf. *P. sulcata* Cooper and Grant ..... **5** 27,*69*,*70*,122
paucula, Texarina 109
Pavlova (1965) 98
Pawnee Formation, Laberdie Limestone Member 57
Pegmavalvula 25
gloveri Newell and Boyd 24
cf. *gloveri* Newell and Boyd 25,29
pelaeum (cf.), *Lophophyllidium* 28
Peniculauris Muir-Wood and Cooper 14,17,33,35,*74*,*75*,77,80,82
bassi McKee 76
costata Cooper and Grant 76
ivesi (Newberry) 76
mckeei Muir-Wood and Cooper 74–76
peniculifera Cooper and Grant 76
subcostata (King) 76
subcostata latinamericana n. ssp. ..... **6** 5,20,23,*75–77*,78,79,81,123
subcostata subcostata (King) 76
transversa Cooper and Grant 76
peniculifera, Peniculauris 76
perannulata, Anisopyge 28
Permian Ratio 5,6,16,19,33–35
Permophricodothyris Pavlova 98
Perrinites hilli 16,23
Peru 10,13,91
Lake Titicaca 6,86
Petasmaia Cooper and Grant 83
Petrocrania Raymond 14,33,35,*39*,40
diabloensis Cooper and Grant 40
exasperata Cooper and Grant 40
septifera Cooper and Grant 40
teretis Cooper and Grant ..... **1** 24,25,*39*,*40*,118
Philhedra Koken 39
Phricodothyris George 17,98
septata Chronic 99
Pierce *et al.* (1961) 11,12,31,33,36
pilula, Composita 95,96
pilula (cf.), *Composita* ..... **8** 20–22,26,27,29,30,*95*,*96*,125
pilularis, Cleiothyridina 94
placidus, Neospirifer 101
planiextensus, Dyoros (Dyoros) 51
platys, Collemataria 84
Platyworthenia sp. 24
Plectelasma Cooper and Grant 104
Pleurelasma Cooper and Grant 106
Plicatula striato-costata Cox 47
Polymorpharia Cooper and Grant 67
polytreta, Cooperina 57
Pontisia Cooper and Grant 14,33,35,*84*,*85*,86,87
costata Cooper and Grant 86
franklinensis Cooper and Grant 86
kingi Cooper and Grant 86
longicosta (Stehli) 86
magnicostata Cooper and Grant 86
nanas (Stehli) 86
parva Cooper and Grant 86
robusta Cooper and Grant 86
stehlii Cooper and Grant ..... **7** 27,29,84,*85*,*86*,87,124
stehlii stehlii Cooper and Grant 85,87
stehlii tumidosa Cooper and Grant 86,87
cf. *P. stehlii tumidosa* Cooper and Grant ..... **7** 21,*86*,*87*,124
truncata Cooper and Grant 86
ventricola Cooper and Grant 86
wolfcampensis Cooper and Grant 86
sp. 86
portlockianus, Spinifrons 81
prionota, Meekella 48
problematicum wordense, Dielasma 108
productelloides, Echinauris 63,65,66
Productus Sowerby 17
costatus Marcou 78
costatus Sowerby 78
occidentalis Newberry 78,79
Productus (Dictyoclostus)
meridionalis McKee 78
paraindicus McKee 77
Productus Limestone 91
prospera, Composita 96
pseudocameratus, Spiriferella 101
Pseudodielasma Brill 104,106
brilli Cooper and Grant 105
Pseudomonotis sp. 28–30

Pseudopermophorus sp. 29
pugilla, Hustedia 91
Pugnoides
elegans Girty 85
elegans King 85
texanus King 85
texanus Shumard 85
Punctospirifer North 102
pyriformis, Composita 96

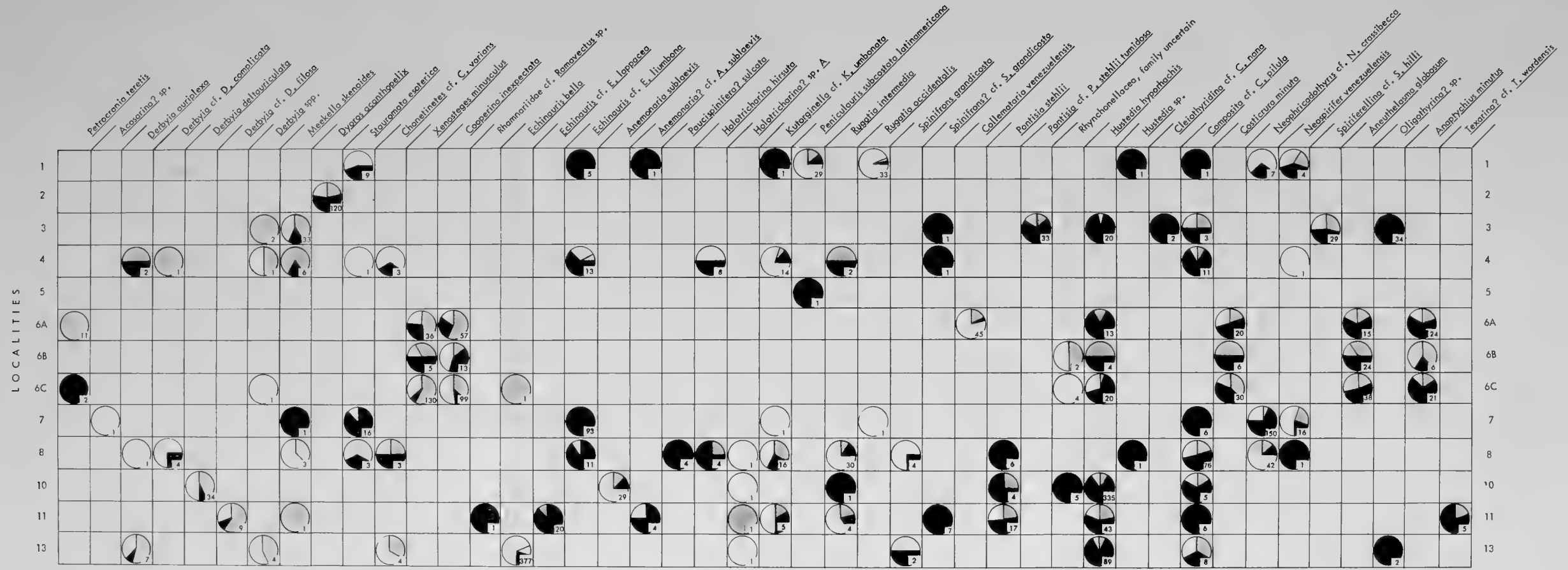
quadrangulatus, Dyoros (Tetragonetes) 51
quadrata, Paucispinifera 70
quadratus,
Spinifrons 80,81
Xenosteges 56
Quadrochonetes Stehli 17,49
Quebec 23,32

Ramavectus Stehli 14,17,59
Ramavectus? 33,35
Ramsbottom (1952) 52,53
rara,
Cleiothyridina 94
Paucispinifera 70
Raymond (1911) 39
rectangulata, Paucispinifera 70
rectimarginata, Cleiothyridina 94
"Red Formations" 11
Reed (1944) 62,102
regularis, Derbyia 41
Retaria umbonata Muir-Wood and Cooper 72
Reticulariina Frederiks 102
Reticulatia Muir-Wood and Cooper 77,80
Retispira sp. indet. 28
Retzius (1781) 39
reversus, Chonetinetes 53,55
Rhamnaria Muir-Wood and Cooper 59
Rhamnariidae cf. *Ramavectus* sp. 4 29,59,62,121
Rhipidomella Oehlert 40
Rhombopora 11
Rhynchonellacea, family uncertain . . . . . 7 . . . . 24,25,27,36,*87,88*,124
Rhynchopora 36
Richthofen (1882) 83
Rigby, J. K. [JKR] 6,22,24,25,27,29
Rivas, A. 5
Road Canyon Formation 14–16,31,33,35,37,43,44,46,48,53,63,64,66–71, 73,74,77,86,87,90,93–96,99,101,108,109
Roadian stage 17
Roberts and Irving (1957) 9
robusta,
Kutorginella 73
Pontisia 86
robustus, Dyoros (Dyoros) 51
Rondon, A. 5
Ross (1967) 10
Roundyella sp. 25
Rowell (1965) 39,40
rossi, Athyris 93
Rugatia Muir-Wood and Cooper 14,17,33,35,*77*,78–80
andersoni Stehli and Grant 77–79
convexa Cooper and Grant 78,79
incurvata (King) 78,79
intermedia n. sp. . . . . 6 . . . . 5,22,27,29,76,*77*,*78*,79,81,123
mckeei Cooper and Grant 78,79
occidentalis (Newberry) . . . . . 6 . . . . 20,26,76,77,*78–80*,81,123
parvauris Cooper and Grant 79
paramdica (McKee) 78,79
Rugosochonetes Sokolskaya 49
rupinata, Hustedia 91

Sabaneta facies 12,31
Sabaneta Formation 12,19,23,27,31
Sabaneta Group 11
Sabaneta Series 11
Salt Range 91
samata, Hustedia 91
Sampling Efficiency Index 5,8,19,35–37
Samtleben (1971) 13,34,72
Sanguinolites sp. 28–30
Santa Rosa Group 9
Macal Series 9
Sapper (1937) 9
Sarganostega Cooper and Grant 102
Sarytcheva (1971) 72
Scenesia Cooper and Grant 102
Schaub (1944) 11
Schizodus canalis Branson 16,20,27
Schizophoria King 40
Schlotheim (1816) 102,104
Schuchert (1913) 104
Schuchert (1935) 10
Schuchert and Cooper (1932) 40
Schuchert and LeVene (1929) 40
Schümann (1969) 22,32
Schwagerina setum 16
Scotese *et al.* (1979) 33
Scrutton, C. T. [CTS] 6,20,21,25–29
sculptilis, Hustedia 91
sellardsi, Parafusulina 16
sellardsi (cf.), *Parafusulina* 24
Sellier de Civrieux (1951) 12
Seminula argentea 101
septata, Phricodothyris 99
septifera, Petrocrania 40
setum, Schwagerina 16
Shagam, R. G. 6
Shagam (1968) 12
Shagam (1972) 12
Shagam and Hargraves (1970) 12
Shaw (1964) 38
Sheehan (1978) 19
Shell and Creole (1964) 12
Shumard (1858) 9
Shumard (1859) 9,99
Shumard (1860) 85
Sicily 108
Siever (1962) 18
Sigma Xi 5
skenoides, Meekella . . . . . 2 . . . . 21,22,26,27,29,*47–49*,119
Skidaway Institute of Oceanography (Savannah, GA, U.S.A.) 6
Skinner Ranch Formation 14,49,74,77,83
Smith, A. G. [AGS] 6,29,30
Sohn, I. G. [IGS] 6,21,25
Sohn (1956) 21
Sokolskaya (1950) 49
Sokolskaya (1960) 41
"*Soleniscus*" sp. indet. 28
solidus, Dyoros (Tetragonetes) 51
solita, Tevarina 109
Sosio Formation 108
Sowerby (1816) 94
Sowerby (1823) 94
Sowerby (1827) 78
sparsa, Holotricharina 77
spatulata, Collemataria 83,84
spicata, Hustedia 91
Spinarella Cooper and Grant 77,80
Spinifrons Stehli 14,17,33,35,77,*80*,81,82
delicatula Cooper and Grant 81
grandicosta n. sp. . . . . 7 . . . . 5,27,30,76,78,79,*80,81*,82,124

magna Cooper and Grant ... 81
portlockianus (Norwood and Pratten) ... 81
quadratus Stehli ... 80,81
sp. ... 80
Spinifrons' ... 22
cf. *S. grandicosta* n. sp. ... **7** ... 21,22,29,*81,82*,124
spinosa, Paucispinifera ... 70
spinosum (aff.), *Lophophyllidium* ... 27
Spirifer Sowerby ... 10,94
ambiguus Sowerby ... 94
cameratus venezuelensis Gerth ... 100
deroysii Leveille ... 93
fasciger Keyserling ... 100
venezuelensis Weisbord ... 100
Spiriferella ... 36
pseudocameratus (Girty) ... 101
Spiriferellina Frederiks ... 14,22,33,35,*102,103*
campestris (White) ... 102
cristata (Schlotheim) ... 104
hilli (Girty) ... 103,104
cf. *S. hilli* (Girty) ... **8,9** ... 21,*103,104*,125
nasuta Cooper and Grant ... 104
nuda Cooper and Grant ... 104
pauciscostata Cooper and Grant ... 104
tricosa Cooper and Grant ... 104
vescula Cooper and Grant ... 104
Spiriferina hilli Girty ... 103
Spiriferinaella Frederiks ... 100,102
Spirorbis ... 25
spondyliformis,
Cooperina ... 58
Leptalosia ... 57
Spuriosa Cooper and Grant ... 59
Squamaria Muir-Wood and Cooper ... 17,75,77,80
Squamularia Gemmellaro ... 98
asiatica Chao ... 98
guadalupensis King ... 99
stalagmium, Composita ... 96
stataria, Hustedia ... 91
Stauromata n. gen. ... 5,14,33,35,49,*51,52*
esoterica n. sp. ... **2,3,4** ... 5,20,22,26,27,50,51,*52,53*,55,119–121
Stehli, F. G ... 5,6,9,10,16,34
Stehli (1954) ... 9,41,47,49,51,52,59,62,70,73,74, 77,80,81,86,88,92,97,102
Stehli (1955) ... 62
Stehli (1957) ... 6
Stehli (1961a) ... 104,105
Stehli (1961b) ... 104,107
Stehli (1964) ... 104
Stehli (1965) ... 104,106
Stehli (1970) ... 33,35
Stehli (1971) ... 6,33
Stehli (1973) ... 33
Stehli and Grant (1970) ... 9,13,34,47–49,62,63,65,66,74–79,86,96,106
Stehli and Grant (1971) ... 33,35–37
Stehli and Wells (1971) ... 15
Stehli *et al.* (1969) ... 6,33
stehlii, Pontisia ... **7** ... 27,29,84,*85,86*,87,124
stehlii stehlii, Pontisia ... 85,87
stehlii tumidosa, Pontisia ... 86,87
stehlii tumidosa (cf.), *Pontisia* ... **7** ... 21,*86,87*,124
Stereochia Grant ... 77
Stictozoster Grant ... 70
Stoyanov (1910) ... 59
Stoyanov (1936) ... 78
Straparollus (*Euomphalus*)
aff. *S.* (*E.*) *kaibabensis* H. Chronic ... 27–29
sp. indet. ... 20,22,24
Streblochondria sp. ... 29
striato-costata, Plicatula ... 47
strigosus, Dyoros (*Tetragonetes*) ... 51
"*Strobeus*" sp. indet. ... 22
strongyle, Composita ... 96
Strophalosiella Likharev ... 55
subcostata, Penicularis ... 76
subcostata latinamericana, Penicularis ... **6** ... 5,20,23,*75–77*, 78,79,81,123
subcostata subcostata, Penicularis ... 76
subcostatus, Aulosteges ... 74,76
subcuneata, Cooperina ... 57,58
subhorrida, Echinauris ... 63,65,66
subinterrupta, Martoceras ... 16,27,28
sublaevis,
Anemonaria ... **5** ... 27,*67,68*,69,70,122
Marginifera ... 67
sublaevis (cf.), *Anemonaria?* ... **5** ... 20,29,*68,69*,122
subliratus, Dyoros (*Dyoros*) ... 51
subquadrata,
Echinauris ... 63,65,66
Kutorginella ... 73
subquadratus, Dyoros (*Tetragonetes*) ... 51
subtilita, Composita ... 96
subtilita peruviana, Composita ... 96
sulcata, Paucispinifera ... 67–70
sulcata (cf.), *Paucispinifera?* ... **5** ... 27,*69,70*,122
Sulcataria Cooper and Grant ... 49
sullivanensis, Kutorginella ... 73
suspecta, Paucispinifera ... 70
Sutton (1946) ... 11,12
Switzerland, Basel ... 10

Taosia
sp. ... 29,30
sp. indet. ... 24
'Taosia sp. indet. ... 20
new genus aff. *Taosia* ... 23,25,29
Taylor Ranch Formation ... 14
tenuis, Dyoros (*Dyoros*) ... 51
Terebratula mormoni Marcou ... 88
Terebratulites cristatus Schlotheim ... 102
teretis, Petrocrania ... **1** ... 24,25,*39,40*,118
Termier and Termier (1957) ... 62
Termier and Termier (1970) ... 57
Termier, Termier, and Pajaud (1966) ... 57,99
texanus, Pugnoides ... 85
Texarina Cooper and Grant ... 14,*108*,109
elongata Cooper and Grant ... 109
oblongata (Cooper and Grant) ... 109
parallela Cooper and Grant ... 109
paucula Cooper and Grant ... 109
solita Cooper and Grant ... 109
wordensis (King) ... 108,109
Texarina' ... 33,35
cf. *T. wordensis* (King) ... **10** ... 29,*108,109*,127
Texasia oblongata Cooper and Grant ... 108
texta, Derbyia ... 44
Thailand ... 25,55–57,62,84,97
Ko Muk ... 57
Thamnosia Cooper and Grant ... 72
Thayer (1979) ... 18–20,31
Thecidellina ... 57
Thedusia Cooper and Grant ... 88
thescelus, Neospirifer ... 100,101
Thomas (1937) ... 41
Thompson and Miller (1949) ... 9,12
Thomson (1926) ... 106,108
Timanotrypa? sp ... 20
Timor ... 62
Titanoceras ... 20
tomea, Hustedia ... 91



Text-figure 4. — Brachiopod occurrences and taphonomic indices in eleven collecting localities within the Palmarito Formation. Circles depict the relative proportions of ventral (white), dorsal (stippled) and articulated (black) valves. The minimum number of individuals represented by these valves, given in the lower right-hand corner of each diagram, is equal to the larger of the dorsal or ventral valve count, added to the articulated valve count

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