

CASPIAN-LIKE RELICT MOLLUSCAN  
FAUNA IN THE SOUTH AMERICAN  
PERMIAN

BRUCE RUNNEGAR AND NORMAN D. NEWELL

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 146 : ARTICLE 1      NEW YORK : 1971



CASPIAN-LIKE RELICT MOLLUSCAN FAUNA  
IN THE SOUTH AMERICAN PERMIAN

BRUCE RUNNEGAR

*University of New England, Armidale, Australia*

NORMAN D. NEWELL

*The American Museum of Natural History  
Columbia University, New York*

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 146 : ARTICLE 1                      NEW YORK : 1971

**BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY**

Volume 146, article 1, pages 1-66, figures 1-27

*Issued October 4, 1971*

*Price: \$3.25 a copy*

## CONTENTS

INTRODUCTION . . . . .	5
Material . . . . .	5
Historical Résumé . . . . .	6
Sources of Data and Acknowledgments . . . . .	8
Abbreviations . . . . .	9
STRATIGRAPHY . . . . .	10
SYSTEMATIC PALEONTOLOGY . . . . .	28
Subclass Anomalodesmata . . . . .	28
Order Pholadomyoidea . . . . .	28
Superfamily Pholadomyacea Gray, 1847 . . . . .	28
Family Megadesmidae Vokes, 1967 . . . . .	28
<i>Plesiocyprinella</i> Holdhaus, 1918 . . . . .	29
<i>Casterella</i> Mendes, 1952 . . . . .	32
<i>Othonella</i> Mendes, 1963 . . . . .	33
<i>Ferrazia</i> Reed, 1932 . . . . .	33
<i>Pyramus</i> Dana, 1847 . . . . .	35
<i>Leptoterraia</i> Beurlen, 1954b . . . . .	37
<i>Jacquesia</i> Mendes, 1944 . . . . .	38
?Family Pholadomyidae Gray, 1847 . . . . .	42
<i>Roxoa</i> Mendes, 1952 . . . . .	42
Subclass Pteriomorpha . . . . .	44
Order Mytiloidea . . . . .	44
Superfamily Mytilacea Rafinesque, 1815 . . . . .	44
Family Mytilidae Rafinesque, 1815 . . . . .	44
<i>Coxesia</i> Mendes, 1952 . . . . .	44
Subclass Heterodonta . . . . .	45
Order Veneroidea . . . . .	45
Superfamily Crassatellacea Férussac, 1822 . . . . .	45
Family Astartidae d'Orbigny, 1844 . . . . .	45
Subfamily Pinzonellinae Beurlen, 1954 . . . . .	45
<i>Pinzonella</i> Reed, 1932 . . . . .	45
Family Uncertain . . . . .	50
<i>Terraia</i> Cox, 1934 . . . . .	50
<i>Leinzia</i> Mendes, 1949 . . . . .	53
?Subclass Palaeoheterodonta . . . . .	56
Order Modiomorphoidea . . . . .	56
Superfamily Modiomorphacea Miller, 1877 . . . . .	56
Family Modiomorphidae Miller, 1877 . . . . .	56
<i>Naiadopsis</i> Mendes, 1952 . . . . .	56
<i>Incertae sedis</i> . . . . .	57
<i>Astartellopsis</i> Beurlen, 1954b . . . . .	57
<i>Barbosaia</i> Mendes, 1952 . . . . .	57
<i>Maackia</i> Mendes, 1954a . . . . .	58
<i>Oliveirara</i> Mendes, 1954a . . . . .	58
<i>Rioclaroa</i> Mezzalira, 1957 . . . . .	59
APPENDIX . . . . .	60
RESUMO . . . . .	61
REFERENCES CITED . . . . .	62



# INTRODUCTION

## ABSTRACT

FOSSILIFEROUS SEDIMENTS of Permian age occupy an area in the Paraná Basin of Brazil, Uruguay, Paraguay, and Argentina equivalent to about one and one-half times the size of the Gulf of Mexico. The Estrada Nova Formation, ranging from 100 to 1000 meters thick near the middle of the Permian section, contains a widely distributed and diverse fauna of bivalve molluscs made known by J. Camargo Mendes and others. Many of these are silicified and very well preserved. The fauna is remarkable in being wholly confined, so far as is known, to the Paraná Basin.

A critical review of the bivalves undertaken in the present paper shows that their family affinities are with marine Gondwana forms found in underlying

strata (Tubarão Group) and in other Gondwana continents. The remarkable endemism of the Estrada Nova fauna and carbon isotope paleosalinities suggest intrabasinal evolutionary radiation under conditions of brackish water and extreme isolation. The history of this relict sea compares favorably with the well-documented, extraordinary history of the Pontian Sea of southeastern Europe of late Cenozoic times and is reminiscent of "sympatric" evolution of the fishes of east African lakes.

The taxonomy of 24 generic and 57 specific names employed for the Permian bivalves is revised and their biologic and ecologic significance is analyzed.

## MATERIAL

When a wholly new assemblage of fossil invertebrates is encountered, it is tempting to assume that it flourished during an interval of time for which there has been no previous geological record. An alternative proposition is that the assemblage represents conditions of extreme isolation. Such an unusual fauna has been made known over the past half-century in undisturbed Permian strata of the Paraná Basin in Brazil, Uruguay, Paraguay, and Argentina. The fauna is represented by excellently preserved silicified shells of bivalve molluscs in dominantly fine-grained calcareous and terrigenous sediments. It is extraordinary because it contains at least 12 genera and possibly two families of bivalves not known from any other part of the world.

Bivalve molluscs normally are conservative, widely distributed organisms, so that the restriction of this fauna to the Paraná Basin is almost without parallel in the fossil record. The only comparable example known to us is the Pontian fauna of late Cenozoic age in southeastern Europe.

Since its discovery in the early part of this century, the Paraná Basin fauna has been difficult to interpret. It was first assumed to be of Triassic age because some of the genera superficially resemble some of the forms found in the

Alpine marine Triassic of southern Europe, but as better collections became available its distinctiveness gradually emerged. In 1947, Gordon wrote that he, K. Caster, J. C. Mendes, and R. Maack were able to confirm a report by Oliveira (1918) that glossopterid plant remains occur in beds overlying the bivalve horizons. Consequently, a Permian age generally has been accepted for the bivalve faunas. The fossils have been extensively studied, and several papers by Mendes of the University of São Paulo have appeared, but Mendes's work has not received the attention outside Brazil it merits. Mendes has demonstrated that the only other organisms found with the bivalves are plants, conchostracans, rare gastropods, and rare vertebrate remains [spines of *Ctenacanthus*, spines and teeth of *Xenacanthus*, scales of the Palaeoniscoidei and Coelacanthini (R. Silva Santos, personal commun.)]. Thus, as the assemblage is taxonomically more restricted than a normal marine fauna, Mendes concluded that the bivalves developed endemically in fresh water during the early Permian after isolation of the Paraná Basin.

Such a hypothesis effectively explains the absence of characteristic late Paleozoic marine groups—corals, bryozoans, brachiopods, ammonoids, and echinoderms—but it does not

explain the absence of annectant small-scale evolutionary stages in the apparently unbroken sequence of strata beneath the bivalve horizons in the Paraná Basin.

Mendes's studies of the Paraná Basin bivalves led him to conclude that none of the species and genera is similar to forms known outside the Basin. Consequently, he was at a loss to explain their family affinities.

Our own familiarity with an unusual family of bivalves from the marine Permian of Australia (Newell, 1956; Runnegar, 1965, 1967, 1969b) has provided us with data not available to Mendes, and we now suggest that many of the endemic genera of the Paraná Basin are derived

from somewhat dissimilar marine forms commonly found in late Carboniferous and Permian sediments of southern continents. If we assume the bivalves lived in normal marine or even estuarine waters, they should appear in marine sediments of similar age that almost certainly occur in Australia, Madagascar, New Zealand, and perhaps India. If the bivalves lived in fresh water, should they not occur in the thick and widespread sequences of fresh-water Permian sediments of South Africa, Australia, and Antarctica? Does the occurrence of this isolated fauna shed any light on the relative positions of South Africa and South America at the close of the Paleozoic?

#### HISTORICAL RÉSUMÉ

In 1918 the Austrian paleontologist Karl Holdhaus published descriptions of two small collections of fossil bivalves sent for identification to the University of Vienna by the Geological Survey of the central government of Brazil. Both collections were from beds now included in the Passa Dois Group and Estrada Nova Formation, but as they came from different areas (Departments of Paraná and São Paulo), different rock types, and contained different species, Holdhaus treated them separately (Holdhaus, 1918).

The collection from São Paulo contained only one species of an obviously new genus which Holdhaus named *Plesiocyprinella* because of its superficial similarity to the Jurassic genus *Plesiocyprina* Fisher. Understandably, he could give no estimate of its age. The second collection contained species now placed in the endemic genera *Leinzia*, *Jacquesia*, and *Terraia*. Holdhaus was impressed by the similarity of these shells to species of *Solenomorpha* and *Sanguinolites* described by McCoy (1844) and Hind (1896–1905, vol. 1) from the marine Lower Carboniferous of Great Britain, and he suggested that the Brazilian species might also be Carboniferous in age. In an appendix to Holdhaus's paper, Oliveira (1918) pointed out that plant remains, including the genus *Glossopteris*, occur several meters above beds containing the fauna described by Holdhaus. Curiously, in view of Holdhaus's comments, Oliveira concluded that the occurrence of *Glossopteris* "fixes the Permian age of the beds

in which the fossils are found." This opinion was widely accepted and for the following decade the age of the Estrada Nova beds was considered to be Lower Permian.

Ten years after Holdhaus's paper appeared, Reed (1928) published a brief description of two small collections which he had received from Alexander du Toit. Both collections were from Paraná, but not from the *Leinzia-Terraia* beds, and none of the species in du Toit's collections had been described by Holdhaus. Reed was unable to find any resemblances between the species he had before him and any known Permian fossils, but he noted "a marked resemblance of the majority of species to well-known Triassic forms"—*Pachycardia rugosa* Hauer, *Anodontophora trapezoidalis* Mansuy, *Trigonodus*, *Myophoria*, *Megalodus*, etc. He concluded that at least the upper part of the Estrada Nova beds should be transferred to the Triassic System.

In a second, larger monograph, Reed (1929) described collections made by Oliveira of the Brazilian Geological Survey from a large number of localities in the Estrada Nova Formation in Paraná. Reed concluded that the small fauna he had described in 1928 and the collection from Paraná described by Holdhaus 10 years earlier represented small samples of two distinct assemblages in the Estrada Nova Formation ("Horizons A and B"), and that both were of Triassic age. Although Reed listed some 53



species, he showed (1928) that the lower fauna is dominated by species of "*Pachycardia*" (now known as *Pinzonella neotropica*) and the upper fauna (Holdhaus, 1918) by species of "*Isoocyprina*," "*Myophoria*," and "*Cuspidaria*" (*Terraia altissima* and *Leinzia similis*). Reed's belief in the Triassic age of the fauna is reflected in the generic and specific names he has applied, such as his use of *Cuspidaria* for species Holdhaus referred to *Solenomorpha*. In part, Reed's nomenclature was reasonable; there is a remarkable similarity between *Pinzonella neotropica* and common Alpine Triassic species of *Pachycardia*. In other cases, however, the resemblances are superficial and based wholly on external form (such as the comparison of *Jacquesia brasiliensis* with *Myophoria*).

Reed published two additional small papers on the Estrada Nova bivalves; the first (1932) deals with collections from two levels in São Paulo and the second (1935) with a fauna from the "*Pachycardia*" beds in Paraná. In these papers Reed was able to show that a third assemblage containing Holdhaus's *Plesiocyprinella carinata* and two new genera (*Ferrazia* and *Pinzonella*) occurs beneath the "*Pachycardia*" assemblage in the Department of São Paulo. He considered this fauna also to be of Triassic age because two of the species were known from the higher horizon, and because the preservation of the fossils was similar to that of the "*Pachycardia*" beds.

A Triassic age of the Estrada Nova bivalve faunas was upheld by Cox (1934) in a short note on the occurrence of three species in northern Uruguay. Cox, however, noted the absence of typical myophoriids characteristic of Triassic marine faunas, and suggested that the Estrada Nova beds may have been deposited under estuarine conditions. He proposed a new generic name, *Terraia*, for some of the species Reed had referred to *Myophoria*.

Reed's Triassic age for the Estrada Nova Formation was accepted for another decade (Mendes, 1944). In 1945, however, Mendes wrote a short article in which he pointed out that the bivalves from the Estrada Nova were really different from Triassic forms with which Reed had compared them, and that interbedded plant remains (mainly arborescent lycopods) suggested Permian rather than Triassic age for the bivalve faunas. This was the first article stressing the endemic nature of the fauna. It also posed an important question. Why is the fauna

of the Estrada Nova Formation so different from other Permian (or Triassic) marine faunas?

One answer was provided in 1948 by the Argentine paleontologist Armando Leanza. Leanza carefully reviewed all the fossils described by Reed and suggested that fragmentary specimens which Reed had identified as a chiton, an ammonite, and an echinoderm would prove to be fragments of plants and crustaceans. He concluded that the Estrada Nova bivalves probably lived in fresh water and cited as evidence the nature of the sediments and the absence of typically marine groups such as brachiopods and cephalopods. Mendes (1952, 1954a) accepted Leanza's suggestion and illustrated Reed's "ammonites" and "echinoderm," showing that they were, indeed, plant remains (1954a). He concluded that the bivalves were totally endemic and therefore of limited use for determining the age of the Estrada Nova beds. He based his assessment of the age of the Estrada Nova Formation on the associated plants (*Glossopteris* and *Lycopodiopsis*), reptiles, and leaiid conchostracans. All subsequent authors have accepted Mendes's conclusions, and the Estrada Nova Formation (and Passa Dois Group) is now generally regarded as Permian in age.

Not all authors, however, have agreed with Mendes's environmental interpretation. In particular the German paleontologist Karl Beurlen (1954b) preferred a brackish environment for the lower bivalve horizons of the Estrada Nova Formation, because he believed that a number of the endemic genera (*Pinzonella*, *Plesiocyprinella*, *Ferrazia*, *Terraia*, and *Cowperesia*) are descended from marine myophoriids and solenomorphae. He argued that the absence of cephalopods and brachiopods can be explained if the waters of the Paraná Basin had been very cold, a situation to be expected after the widespread continental glaciation in the earlier Permian. Unfortunately, although logically valid, Beurlen's arguments were not based on sound taxonomy. Beurlen appears to have been influenced by the similarity in the preservation of a number of unrelated genera, and his grouping of the genera mentioned above into a single new family (Pinzonellidae) has proved to be indefensible.

Our present knowledge of the bivalve fauna of the Estrada Nova Formation is based mainly on the studies of Mendes (1944, 1945, 1949, 1952, 1954a, 1962a, 1963, 1967) and Mezzalana

(1957). In two major papers, (1952, 1954a). Mendes described the stratigraphy and faunas in the richly fossiliferous areas of best exposure, northern São Paulo and central Paraná. He subsequently documented small collections from southern São Paulo and Mato Grosso (1962a, 1963), and published a number of short articles on problems of local stratigraphy (see Mendes, 1967). As a result of Mendes's studies it is clear that almost all the genera and probably all the species of this fauna are truly endemic and are not known to occur outside the Paraná Basin. Should they be expected in South Africa?

An excellent summary in English of the stratigraphy of the Paraná Basin was prepared by a number of Brazilian geologists as part of Brazil's contribution to the First International

Symposium on Gondwana Stratigraphy and Paleontology held in Mar del Plata in October, 1967 (Bigarella, Becker, and Pinto, 1967). This summary supplements a general review of the economic potential of the Paraná Basin prepared for the Brazilian national oil company, Petrobrás, by Sanford and Lange (1960) and contains an excellent historical review of the Estrada Nova Formation and its fauna by Mendes (1967). Most of our stratigraphic data are derived from these and earlier publications. However, as a great deal of drilling has been carried out by Petrobrás in the last 10 years (Rocha-Campos, 1967, fig. 2), it is probable that more detailed information will become available in the future.

#### SOURCES OF DATA AND ACKNOWLEDGMENTS

At the request of the Brazilian government, the United States Geological Survey sent Dr. Mackenzie Gordon, Jr. to Brazil in 1946 and 1947 to assist in the search for coal, and to help train Brazilian geologists. During Gordon's two visits, he participated in a regional study of the Permo-Triassic sediments of the Paraná Basin in Paraná, Santa Catarina, and Rio Grande do Sul, and collected from a number of bivalve localities in the Passa Dois Group (Gordon, 1947). The collection and Gordon's field notes were generously made available for the present study. A second important collection, mainly from the Estrada Nova Formation in northern São Paulo, was donated to the American Museum of Natural History by the director of the Brazilian Geological Survey, the late Dr. P. E. de Oliveira. These two collections, which have yielded representatives of all common genera and species, have been supplemented by photographs made by Newell in 1967 of most of Mendes's figured specimens. Most of the other photographs herein were prepared under Newell's direction by the expert photographer, Mr G. Robert Adlington, of the American Museum.

While preparing taxonomic manuscript for the *Bivalvia* volumes of the *Treatise on Invertebrate Paleontology*, Newell puzzled over the

problems of the Passa Dois bivalves. In correspondence he reviewed some of these problems with Dr. Myra Keen, renowned malacologist of Stanford University, in California. Dr. Keen noted an interesting parallel between the Passa Dois fossils and the Miocene-Pliocene pelecypod radiation within the relict Pontian Sea of the Caspian region of southeastern Europe. Our subsequent studies indicate that the Pontian history does, indeed, provide the key to an understanding of the Passa Dois bivalves. Rapid evolution of marine species within an isolated relict sea of subnormal salinity provided a case that seems to be quite rare in geologic history.

During August and September, 1967, Newell, assisted by his wife, Valerie Zirkle Newell, visited Departamento Nacional da Produção Mineral, Rio de Janeiro, The University of São Paulo, in São Paulo, and the University of Uruguay, in Montevideo, where they studied and photographed Passa Dois specimens and conferred with Drs. P. E. de Oliveira, J. Camargo Mendes, Antonio Rocha-Campos and Rodolfo Mendes Alzola about Passa Dois problems.

Existing collections do not provide sufficiently refined biostratigraphic controls to demonstrate minute grades of speciation implicit in our thesis. It is hoped that our efforts described herein may

stimulate further work on the evolution of the Passa Dois bivalves.

The precise age and environmental tolerances of the Estrada Nova faunas are two outstanding questions in South American geology. To help provide answers we have sought and received technical advice and unpublished information from experts in a number of different fields of competence. As far as possible these contributions are acknowledged at appropriate places in the text. Various aspects of the problem were discussed with Drs. Mackenzie Gordon, Jr., and John Pojeta, Jr., of the United States Geological Survey; Dr. Erle G. Kauffman, Smithsonian Institution; and Dr. Darcy Closs, University of Rio Grande do Sul. We are grateful for their advice and assistance.

The first author's contribution was prepared during the tenure of a National Research Council Postdoctoral Visiting Research Associateship supported by the Smithsonian Institution.

#### ABBREVIATIONS

- AMNH, the American Museum of Natural History, Department of Invertebrate Paleontology  
 BMNH, British Museum (Natural History), Department of Palaeontology  
 CPC, Commonwealth Palaeontological Type Collection, Bureau of Mineral Resources, Canberra  
 DGM, Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Rio de Janeiro  
 DGP, Departamento de Geologia e Paleontologia, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo  
 FHC Pal, Facultad de Humanidades y Ciencias, Universidad de la Republica, Uruguay  
 IGG, Instituto Geografico e Geologico, São Paulo  
 SMC, Sedgwick Museum, Department of Palaeontology  
 USGS, United States Geological Survey, Paleontology and Stratigraphy Branch  
 USNM, United States National Museum, Smithsonian Institution, Division of Invertebrate Paleontology  
 USNM (DM), United States National Museum, Smithsonian Institution, Division of Mollusks

## STRATIGRAPHY

THE PARANÁ BASIN is almost three times as large as the Caspian Sea and one and one-half times as large as the Gulf of Mexico. Its area of about one and one-half million square kilometers covers much of southern Brazil and extends into adjoining parts of Paraguay, Uruguay, and northeast Argentina (fig. 1). The present limits of the Basin are defined by the eroded margins of subhorizontal Devonian and Pennsylvanian sequences (Sanford and Lange, 1960, fig. 2) so that the original size of the Basin is unknown. However, its sediments thicken toward the present structural axis, defined approximately by the course of the Paraná River. Except for local disturbances caused by Mesozoic igneous activity, the post-Devonian sediments are undeformed and normally dip at an angle of less than 1 degree. Because much of the sedimentary pile is fine-grained and soft, the exposures are often very poor.

Sedimentation commenced in the Paraná Basin in the early Devonian and ceased toward the end of the Cretaceous. The basal Devonian sediments overlie folded metamorphic and crystalline basement and in turn are unconformably overlapped by late Paleozoic diamictites, sandstones, and shales (Bigarella, Becker, and Pinto, 1967). The late Paleozoic sediments reach a maximum thickness of about  $1\frac{1}{2}$  miles (2700 meters) near the center of the basin, but surface exposures nearer the Basin margins usually are much thinner. The base of the sequence appears to be middle or late Pennsylvanian in age (Rocha-Campos, 1967, p. 94; Closs, 1967) and its uppermost part may extend into the late Permian or earliest Triassic. A widely distributed oil-shale unit known as the Iratí Formation (Padula, 1969) has been used to divide the late Paleozoic succession into two subequal parts. The upper one (including the Iratí Formation) is known as the Passa Dois Group. The bivalve faunas discussed herein are from the middle part of this unit. Excellent summaries of the stratigraphy of the Passa Dois Group and the underlying Tubarão Group have been prepared by Mendes (1967) and Rocha-Campos (1967).

### TUBARÃO GROUP

The Tubarão Group commences with a thick

sequence of part terrestrial and part marine glaciogene sediments which unconformably overlie pre-Silurian and Devonian basement (Rocha-Campos, 1967; Rocha-Campos, Farfallat, and Yoshido, 1969; Frakes and Crowell, 1969). The glacial influence on these sediments is well demonstrated by the widespread occurrence of striated pavements, dropped clasts, fossil eskers and crevasse fillings, striated and faceted clasts, and rhythmites and diamictites. The glaciogene sediments are succeeded by a more normal sequence of sandstones and shales that pass conformably, and in most areas gradationally, into the Iratí Formation.

An important bivalve fauna occurs in the upper part of the Tubarão Group, approximately 250 meters below the base of the Iratí Formation. A recent revision of this fauna by Rocha-Campos (In press) shows that it contains the marine bivalve genera *Promytilus*, *Myalinella*, *Septmyalina*, *Leiopteria?*, *Aviculopecten*, *Heteropecten*, *Schizodus*, *Stutchburia*, *Oriocrassatella*, *Palaeosolen*, and *Myonia* the bellerophonid *Warthia*, and at least two genera of starfish. The assemblage is best compared with Permian faunas of Australia and New Zealand, and it appears to be a normal marine association of the Gondwana faunal province.

### PASSA DOIS GROUP

The Passa Dois Group conformably overlies the Tubarão Group and is disconformably overlain by Mesozoic sandstones and lavas (Sanford and Lange, 1960, fig. 2). In the Brazilian and Uruguayan parts of the Basin the Passa Dois Group is divided into an upper, thin, fresh-water (red bed) sequence, the Rio do Rasto Formation, a thicker middle sandy-silty unit, the Estrada Nova Formation, and a thin basal bituminous shale, the Iratí Formation. Four distinct facies or lithosomes are recognized in the Estrada Nova Formation on the eastern side of the Paraná Basin, and at least two of these have characteristic bivalve faunas. All of the bivalves from the Passa Dois Group, with the exception of the genus "*Palaeomutela*" and a single specimen of *Maackia* (Beurlen, 1957), are from the Estrada Nova Formation; most occur in the Terezina and Serrinha lithosomes, but a small

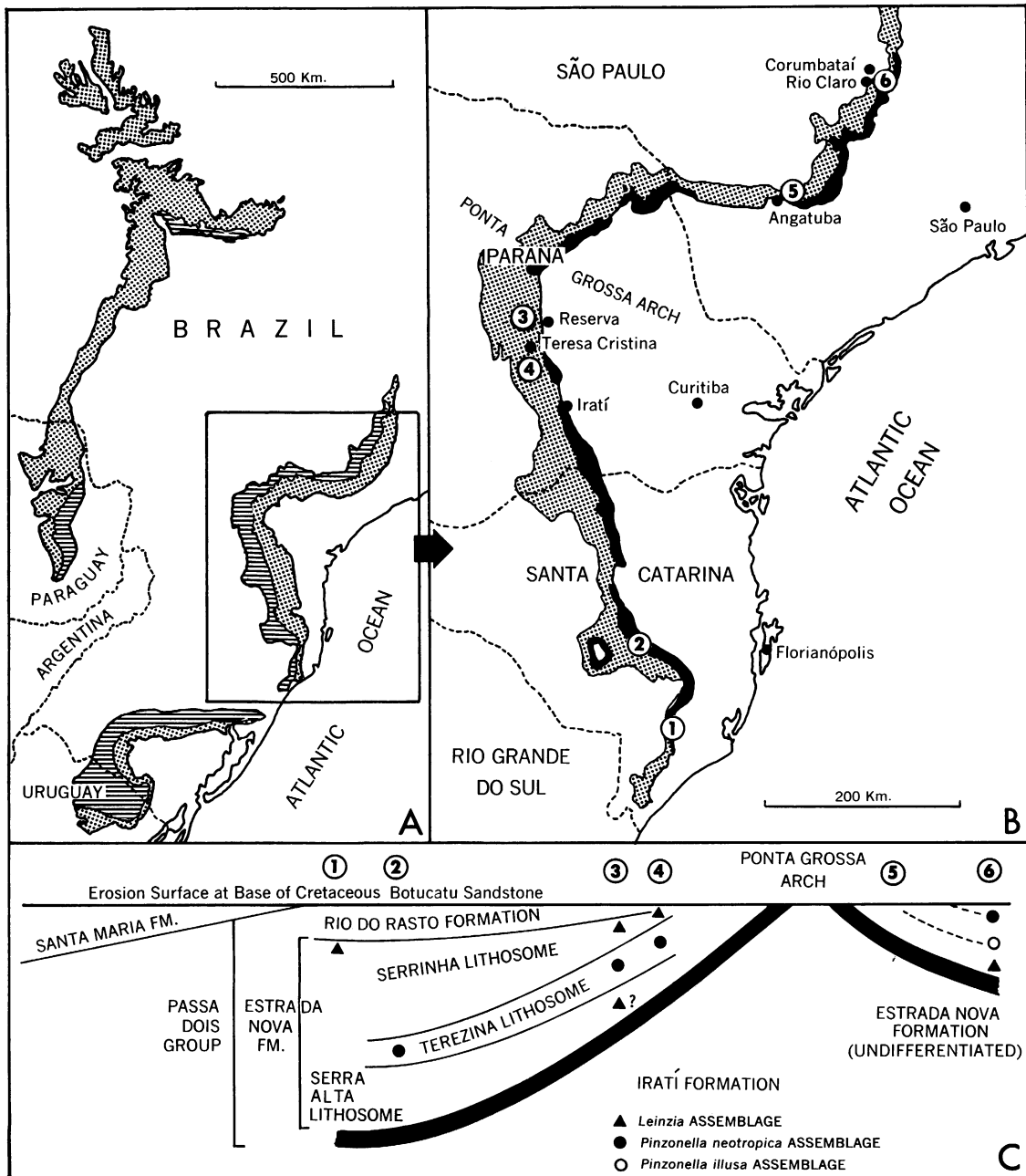


FIG. 1. Distribution of the Passa Dois Group. A. Lower Permian Tubarão Group (stippled) and upper Permian Passa Dois Group (ruled), after Mendes (1967) and Rocha-Campos (1967). B. Passa Dois Group in southeastern Brazil, after Padula (1969). Black, Iratí Formation; shaded, Estrada Nova Formation. Numbered localities refer to measured sections described in the Appendix. C. South to north, diagrammatic section, southeastern Brazil. Not to scale. Locality numbers as in B.

fauna has been found in the Serra Alta lithosome in southeastern Brazil (Mendes, 1954a).

#### SUBDIVISION OF THE ESTRADA NOVA FORMATION

Relatively little information is available regarding the stratigraphy and faunas of the Estrada Nova Formation on the northern, western, and southern margins of the Paraná Basin, and most detailed studies have been based on the eastern areas of outcrop in the Brazilian states of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul (fig. 1). In some of these areas the Estrada Nova Formation has been divided into four lithologic units which are in part laterally equivalent (fig. 1). Mendes (1967) and Salamuni (1963) described these units as follows:

The Serra Alta lithosome is an unlaminated dark gray siltstone containing scattered calcareous concretions. The Paranapanema lithosome is similar but is lighter gray in color, is slightly coarser-grained, and has fewer concretions. The Terezina lithosome typically consists

of a rhythmic alternation of thin, dark gray shales and light gray siltstones interbedded with lenticular or massive beds of silicified oolitic limestone. Mud cracks and asymmetric ripple marks are extremely abundant, and the monotonous repetition of ripple marks produces a characteristic wavy bedding (Mendes, 1967, pl. 48). The Serrinha lithosome is a spheroidally weathering greenish siltstone which contains relatively thick beds of fine- to medium-grained sandstone. In general, the unit is well stratified and ripple marks and mud cracks (which may be larger than those in the Terezina lithosome) are common.

It is significant that bivalve faunas found in the Terezina and Serrinha lithosomes have been used in the past to identify and map these units. This consistent association of the fossil assemblages with particular rock types suggests that the assemblages were environmentally restricted, perhaps by conditions that are reflected in the sediments in which they occur.

## COMPOSITION AND AFFINITIES OF THE ESTRADA NOVA FAUNA

### BIVALVE ASSEMBLAGES

It has been obvious since Reed's (1929) study of the fauna of the Passa Dois Group in Paraná that two distinct assemblages (Reed termed them "Horizons A and B") are present in the Estrada Nova Formation in that area. The lower assemblage, characterized by the species *Pinzonella neotropica* and *Jacquesia brasiliensis*, normally occurs in thin beds of silicified oolite or coarse quartz sandstone (Terezina lithosome; fig. 2), whereas the higher assemblage, characterized by *Leinzia similis* and *Terraia altissima* is restricted to purplish or greenish siltstones (Serrinha lithosome; fig. 3) (Mendes, 1954a, 1967). The terezina assemblage can also be recognized to the north in São Paulo where it occurs near the top of the Estrada Nova Formation (Mendes, 1952). In northeast São Paulo the Serrinha lithosome and *Leinzia* assemblage are missing, presumably because of erosion prior to the deposition of the Cretaceous Botucatu Sandstone.

Two other assemblages occur below the fauna containing *Pinzonella neotropica* and *Jacquesia brasiliensis* in São Paulo (Mendes, 1952, 1962a; Mezzalira, 1957). The higher assemblage is

characterized by *Pinzonella illusa* and *Jacquesia elongata*; it is found in quartz sandstones and oolites similar to those of the Terezina beds (fig. 4), and occurs in the middle part of the Estrada Nova Formation (Mendes, 1952). The lower fauna, characterized by *Leinzia froesi* and *Barbosaia angulata*, also contains *Jacquesia elongata* and *Pinzonella* cf. *illusa* (Mendes, 1949, 1952; Mezzalira, 1957). Most known occurrences are in a fine tuffaceous sandstone.

The species occurring in each of these four assemblages are as follows:

1. *Leinzia froesi* assemblage (Mendes, 1949, 1952; Mezzalira, 1957)
  - ?*Anthraconaia* sp.
  - Barbosaia angulata* Mendes, 1952
  - Casterella* cf. *camargoi* Beurlen, 1954b
  - Ferrazia cardinalis* Reed, 1932
  - Jacquesia elongata* (Holdhaus), 1918
  - Leinzia froesi* Mendes, 1949
  - L. gigantea* Mendes, 1949
  - Pinzonella* cf. *illusa* Reed, 1932
  - Rioclaroa lefeveri* Mezzalira, 1957
2. *Pinzonella illusa* assemblage (Mendes, 1952, 1962a, 1963)

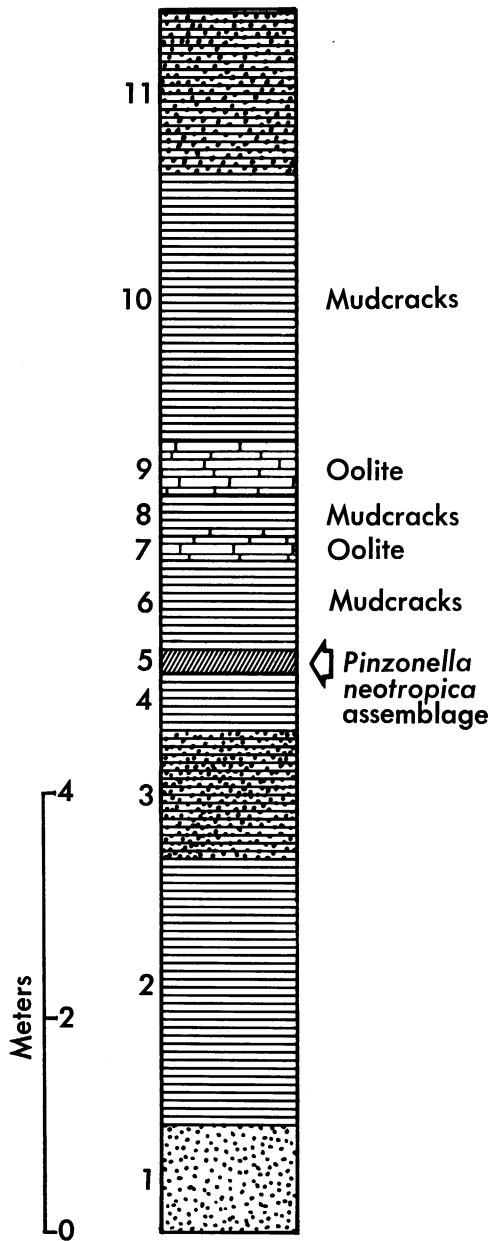


FIG. 2. Terezina lithosome, Estrada Nova Formation, Reboucas, Paraná (Salamuni, 1963). 1. Medium gray siltstone, apparently massive but with irregular stratification. 2. Sandy siltstone with intercalated laminae of silty argillite and undulating bedding. 3. Sandy siltstone and fine sandstone with asymmetric ripple marks and micro-cross stratification. 4. Similar to 2. 5. Shell bed of *Pinzonella neotropica*, *Pyramus anceps*, and other species. 6. Sandy siltstone with conspicuous micro-cross stratification and mudcracks. 7. Unfossiliferous calcareous oolite. 8. Similar to 6. 9. Unfossiliferous calcareous oolite. 10. Sandy siltstone with micro-cross stratification and mudcracks. 11. Similar to 3.

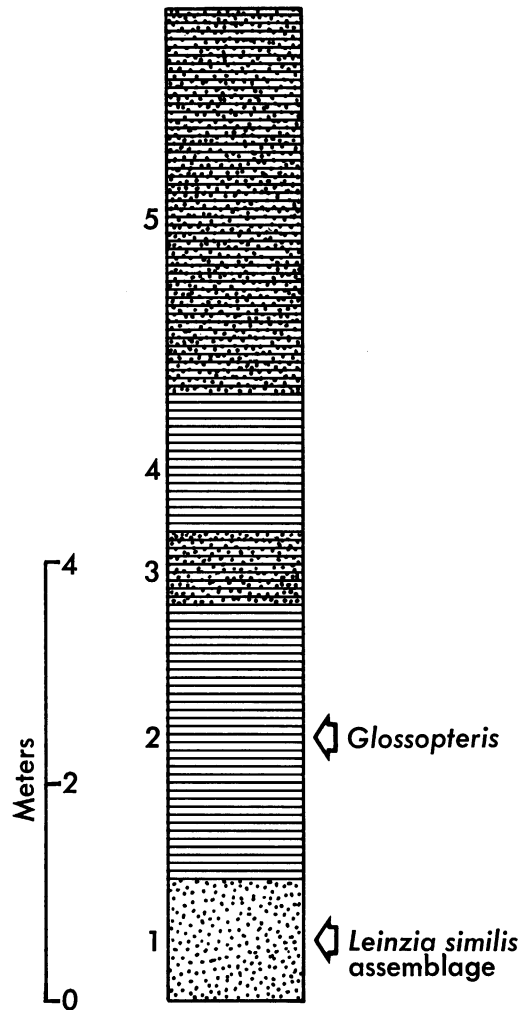


FIG. 3. Serrinha lithosome, Estrada Nova Formation, type area between Mallét and Rio Azul, Paraná (Salamuni, 1963). 1. Sandy siltstone and fine sandstone; lower part containing poorly preserved specimens of *Leinzia similis* and *Terraia altissima*. 2. Gray-green siltstone with irregular bedding. 3. Sandy siltstone and fine sandstone with micro-cross stratification. 4. Argillaceous siltstone with rhythmic bedding, comparable with Terezina lithosome. 5. Fine sandstone, siltstone, and sandy siltstone.

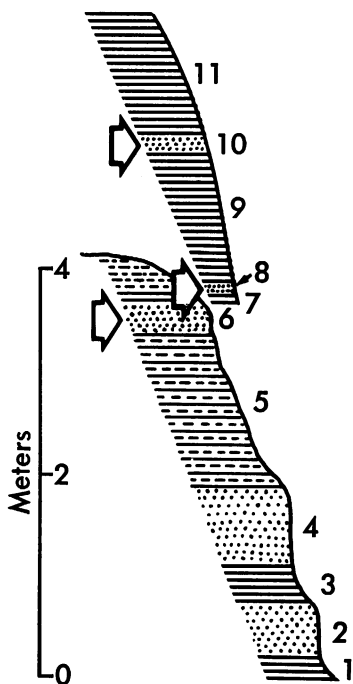


FIG. 4. Section in the middle of the Estrada Nova Formation, west of Rio Clara, São Paulo (Mendes, 1952). 1, 3. Variegated silty shale. 2. Fine sandstone. 4. Bedded gray sandstone, 5, 9, 11. Red silty shale. 6–8, 10. Zone of *Pinzonella illusa* and *Pleisioocyprinella carinata* (*Pinzonella illusa* assemblage; shell beds denoted by arrows). 6. Gray to yellow fine sandstone containing shells. 7. Red-green silty shale. 8. Gray-yellow fine sandstone containing shells. 10. Gray-yellow fine sandstone with shells.

- Casterella gratiosa* Mendes, 1952  
*Coxesia mezzalirai* Mendes, 1952  
*Ferrazia cardinalis* Reed, 1932  
*Jacquesia arcuata* (Mendes), 1962a  
*J. elongata* (Holdhaus), 1918  
*Pinzonella illusa* Reed, 1932  
*Pleisioocyprinella carinata* Holdhaus, 1918  
*Pyramus anceps* (Reed), 1935 [= ?*P. camposi* (Mendes), 1962a]  
 ?*P. cowperesoides* (Mendes), 1962a  
*Roxoa corumbataiensis* Mendes, 1952 [may be conspecific with *R. intrigans* (Mendes), 1944]  
*Terraia aequilateralis* Mendes, 1952
3. *Pinzonella neotropica* assemblage (Mendes, 1952, 1954a)
- Casterella gratiosa* Mendes, 1952  
*Ferrazia cardinalis* Reed, 1932  
*Jacquesia brasiliensis* (Reed), 1929 (very common)  
*J. elongata* (Holdhaus) (rare)  
*Naiadopsis lamellosus* Mendes, 1952

- Pinzonella neotropica* (Reed), 1928  
 “*Pleurophorus*” *bipleura* Reed, 1929  
*Pyramus anceps* (Reed), 1935  
*Roxoa intrigans* (Mendes), 1944  
*Terraia lamegoi* Mendes, 1954
4. *Leinzia similis* assemblage (Mendes, 1954a)  
 ?*Barbosaia* sp.  
*Leinzia similis* (Holdhaus), 1918  
*Oliveiraia pristina* (Reed), 1929  
 ?*Pyramus emerita* (Reed), 1929  
*Terraia altissima* (Holdhaus), 1918  
 mytilid bivalve  
*Dendropupa* sp.

The distribution of fossil bivalves in the Estrada Nova Formation suggests that assemblages containing *Leinzia* (1 and 4) are normally confined to fine-grained sediments (fine sandstones and siltstones), whereas those dominated by *Pinzonella* and *Jacquesia* normally occur in coarse sandstone or silicified oolitic limestone. Although exceptional occurrences have been reported (for example, Mendes 1967, p. 156 has found *Pinzonella neotropica* in a greenish gray siltstone), this model best explains the recurrence of *Leinzia* assemblages at various levels in the Estrada Nova Formation (Mendes, 1949, 1954a, 1962b; Mezzalira, 1957). It also suggests that the difference between assemblages containing *Pinzonella illusa* and *P. neotropica* may reflect a difference in age, as both faunas appear to have inhabited a similar environment.

#### TAXONOMIC CHARACTER OF THE FAUNA

Twenty-four generic names and 57 specific names have been proposed for bivalves from the Passa Dois Group. None of these names has been applied to species or genera found outside the Paraná Basin and most authors have commented on the “highly endemic” nature of the fauna. One purpose of this study is to examine that endemism.

Many of the species from the Passa Dois Group are described from small collections which were not available for study. We have, however, examined representatives of the type species of all but two rare genera, *Maackia* Mendes, 1954a, and *Oliveira* Mendes, 1954a. Our studies suggest that as many as 10 of the generic names can be rejected as junior synonyms and that at least one common species, *Cowperesia anceps* (Reed) can be referred to the Australian Permian genus *Pyramus* Dana, 1847. The classification we have adopted is as follows:



- Family Megadesmidae Vokes, 1967  
*Casterella* Mendes, 1952  
*Ferrazia* Reed, 1932  
*Jacquesia* Mendes, 1944 (= *Holdhausiella* Mendes, 1952, *Favalaia* Mendes, 1952a, ?*Maackia* Mendes, 1954a)  
*Plesiocyprinella* Holdhaus, 1918 (= ?*Othonella* Mendes, 1963)  
*Pyramus* Dana, 1847 (= *Cowperesia* Mendes, 1952, ?*Angatubia* Mendes, 1962a, ?*Leptoterraia* Beurlen, 1954a)
- Family Astartidae d'Orbigny, 1843  
 Subfamily Pinzonellinae Beurlen, 1954  
*Pinzonella* Reed, 1932 (= *Pinzonellopsis* Mendes, 1944)
- Family Mytilidae Rafinesque, 1815  
*Coxesia* Mendes, 1952
- Family Modiomorphidae Miller, 1877  
*Naiadopsis* Mendes, 1952
- Family Pholadomyidae? Gray, 1847  
*Roxoa* Mendes, 1952
- Family uncertain  
*Terraia* Cox, 1934 (= *Terraioopsis* Beurlen, 1954b)  
*Leinzia* Mendes, 1949
- Incertae sedis*  
*Astartellopsis* Beurlen, 1954b  
*Barbosaia* Mendes, 1952  
*Rioclaroa* Mezzalira, 1957

Many of the genera listed above are rare components of the Passa Dois fauna; the common elements are species of *Jacquesia*, *Plesiocyprinella*, *Pyramus*, *Pinzonella*, *Terraia*, and *Leinzia*. In this context the abundance of megadesmid genera is of particular interest as it suggests a close link between the faunas of the Paraná Basin and the Permian marine faunas of Australia and New Zealand.

#### ORIGIN OF THE ESTRADA NOVA FAUNA

Only one of the 14 genera listed above is known to occur outside the Paraná Basin, but a number of the endemic genera are closely related to forms that are common in marine Permian deposits of the Southern Hemisphere. For example *Casterella*, *Ferrazia*, and *Plesiocyprinella* are clearly related to the Australian genera *Megadesmus* and *Astartila*; and *Jacquesia* is allied to the Australian genus *Myonia*. The origin of most of

the other genera is not so obvious, but they are probably derived from a number of unrelated late Paleozoic marine stocks (the Astartidae, Modiomorphidae, Mytilidae, Pholadomyidae, etc.) which are found in the Tubarão Group of the Paraná Basin (Reed, 1930; Rocha-Campos, In press), the Copocabana Group of Peru (Newell, Chronic, and Roberts, 1953), and the Bonete Formation of Argentina (Harrington, 1955). These faunas contain widely distributed late Paleozoic marine genera and presumably represent a small but representative sample of the pre-Passa Dois marine community.

It has been suggested by several authors (Leanza, 1948; Mendes, 1952, 1954a; Beurlen, 1954b) that the unique fauna of the Passa Dois Group developed in brackish or fresh-water conditions after the Paraná Basin became geographically isolated. The most important objection to this hypothesis has been the unexplained absence of morphologically intermediate forms in the upper part of the Tubarão Group, and the obvious difficulty of a benthonic fauna surviving the euxinic conditions that must have existed on a basin-wide scale at the time of formation of the Iratí oil shales.

Perhaps a solution to both problems is provided by the present-day distribution of benthonic organisms in the Black Sea (fig. 5), in which anaerobic conditions below a depth of 150 meters restrict the bottom-living animals to the margins of the Sea. As a result, the area occupied by benthonic organisms in the Black Sea is less than 24 per cent of the total.

If the fauna of the Paraná Basin had a similar distribution at the time of deposition of the Iratí Formation most, if not all, of its record may have been lost through subsequent erosion of the Basin margins. The bivalve genera of the Estrada Nova Formation are found in extremely shallow-water sediments and it is reasonable to assume that their ancestors may also have inhabited a littoral environment. Consequently, the best place to search for ancestors of the Estrada Nova bivalves may be in marginal equivalents of the Iratí Formation where a shallow water fauna might have survived.

## AGE OF THE ESTRADA NOVA FORMATION

Because of its unique characteristics, the age of the Estrada Nova fauna is difficult to determine. The existence of Permian marine faunas in the underlying Tubarão Group (Rocha-Campos, 1967) and a Middle to Upper Triassic reptile fauna and plants in the overlying Santa Maria Formation (C. B. Cox, 1968; Gordon and Brown, 1952) provide reliable upper and lower limits, but there remain alternative possibilities that the Estrada Nova Formation dates from the late Permian or early Triassic.

## EVIDENCE FOR A PERMIAN AGE

Glossopterid plant remains are relatively common in the Serrinha beds of the Estrada Nova Formation, in three cases occurring 0.5 meter below and 5 and 20 meters above beds containing *Leinzia similis* and *Terraia altissima* (stratigraphic section 3: Mendes, 1954a, pp. 47, 70; Oliveira, 1918, p. 30; fig. 3 in this paper). *Glossopteris* occurs rarely in the Rio do Rasto Formation (Gordon, 1947, p. 12), uncommonly in the Terezina beds of the Estrada Nova Formation (Mendes, 1954a, pp. 51, 67, pl. 1, fig. 3) and commonly in the Tubarão Group (Read, 1941). It is significant that the Santa Maria Formation, which lies between the Rio do Rasto Formation and the Botucatu Sandstone contains a *Dicriodidium* flora (Bortoluzzi and Barberena, 1967).

*Glossopteris* appears to have been a deciduous, seed-bearing plant with winged spores. It could have been, and probably was, widely dispersed by the wind. Recent palynological studies of late Permian and early Triassic nonmarine sediments in eastern Australia (Hennelly, 1959; Evans, 1967; R. Helby, unpublished data) reviewed by Balme (1969) have shown that a rapid microfloral change accompanies the disappearance of the *Glossopteris* flora. In the Bowen Basin, Queensland, the abruptness of this change may be accentuated by a depositional unconformity of unknown duration (Evans, 1966), but in the Sydney Basin, New South Wales, the sequence appears to be continuous (R. Helby, personal commun.). The succeeding microfloras, characterized by the genus *Taeniaesporites*, are probably of Scythian age because *Taeniaesporites* is not known from Permian strata in Australia, India, the Salt Range, or Madagascar, but is associated with early Scythian ammonoid faunas in many parts of the world (Balme, 1969). Although the

first representatives of the succeeding *Dicriodidium* flora do not appear immediately,<sup>1</sup> glossopterid plant remains are not known from rocks that have yielded *Taeniaesporites* or its associated forms.<sup>2</sup> For this reason all rocks containing *Glossopteris* in Australia are considered to be Permian, and a Permian rather than a Triassic age for the Estrada Nova Formation thus seems more likely.

The occurrence of leaïid conchostracans in the Rio do Rasto Formation (Reed, 1929; Mendes, 1954b) and the presence of large arborescent lycopods in the Estrada Nova Formation (Mendes, 1967, pl. 61, figs. 1, 2) are also evidence for a pre-Triassic age for the Estrada Nova Formation as neither group is known to occur above the Permian (Paul Tasch, written commun.; F. Heuber, personal commun.). This is also true for the fish genus *Ctenacanthus* (R. Silva Santos, personal commun.). Even so, this argument cannot be carried too far as there is no a priori reason why both groups should be extinguished at the end of the Paleozoic, and it is often difficult to date the nonmarine sediments in which they occur.

Although the bivalve fauna of the Estrada Nova Formation clearly is different from any other known fauna, its closest similarity is to the Permian marine faunas from Australia, New Zealand, India, and South America. There are no similarities to the known Lower Triassic marine faunas from Australia (Dickins and McTavish, 1963; Fleming, 1966; Runnegar, 1969a), which are cosmopolitan and resemble Lower Triassic assemblages from other parts of the world.

## EVIDENCE AGAINST A PERMIAN AGE

We are especially concerned about establishing the age of the Estrada Nova Formation for

<sup>1</sup>According to Balme (1969) the *Dicriodidium* flora did not become well established until the late Lower Triassic. There is equivocal evidence for the presence of *Dicriodidium* below a mid-Scythian ammonoid fauna in southeast Queensland (Runnegar and Ferguson, 1969, p. 258) but additional mapping will be needed to confirm this occurrence.

<sup>2</sup>Bharadwaj and Srivastava (1969) reported finding *Glossopteris*, *Dicriodidium*, and a late Lower Triassic microflora in a carbonaceous shale from northern peninsular India. It is not clear from their work whether all of these fossils are from a single exposure. We are unable to assess the significance of their discovery.

the following reason: Lowermost Triassic marine faunas notoriously lack many groups of marine invertebrates—corals, bryozoans, brachiopods, crinoids, and even gastropods—commonly found in Paleozoic rocks. Most Lower Triassic faunas are dominated by epifaunal bivalves and ceratitic ammonoids. Does the unusual association of the Estrada Nova Formation therefore simply reflect an early Triassic age? This possibility would offer an acceptable alternative to the suggestion that the bivalve faunas of the Estrada Nova Formation developed in a fresh- or brackish-water environment, since the paleontological argument for such a conclusion would then be seriously weakened. Thus it is conceivable that the Estrada Nova Formation contains an earliest Triassic marine fauna which developed after the extinction of many other Paleozoic marine stocks. It is also possible that, as in the Permian, this fauna was not widely distributed but was confined to the area known as the Gondwana faunal province.

Such a suggestion is as difficult to confirm as it is to dispute because so little is known about latest Permian and earliest Triassic marine faunas. Fossiliferous marine sediments of both periods are extremely rare and in most areas where marine sediments of both ages are juxta-

posed, the boundary is represented by a hiatus of unknown duration (Kummel and Teichert, 1966; Newell, 1967; Balme, 1969; Tozer, 1969). Consequently, the precise age of the Estrada Nova fauna is still uncertain. At present, the occurrence of glossopterid plant remains within and above the Estrada Nova Formation provides the best indication of a Permian age for the bivalve fauna, but such evidence is by no means conclusive as there is no a priori reason for assuming that the extinction of this flora coincided with the extinctions of marine invertebrates that mark the end of the Permian period. Furthermore, it is quite possible that *Glossopteris* may have lingered on in some areas and many paleontologists are inclined to regard the first appearance of an organism of greater stratigraphic value than its last record. However, the presence of *Glossopteris*, coupled with the absence of marine groups such as ceratites, brittle stars, and pectinoid bivalves, which are widely distributed in the earliest Triassic marine faunas, suggests that the Estrada Nova fauna is not a typical marine fauna of the early Triassic, and for the present it seems more reasonable to conclude that the fauna is Permian rather than Triassic in age.

## ENVIRONMENTAL ANALYSIS THE CASPIAN BASIN—AN ENVIRONMENTAL MODEL

Most paleoecological studies rely heavily on modern environmental processes and phenomena to support inferences about the geologic past (Laporte, 1968). In searching for an analog for the Estrada Nova fauna, we were impressed by a parallel between the late Cenozoic evolution of the Caspian region and the late Paleozoic history of the Paraná Basin.

The Caspian Sea has an average salinity of about 15 parts per thousand and contains a molluscan fauna, which, until foreign species were introduced by man, was dominated by brackish-water endemic genera and species which apparently developed *in situ* during the Pliocene (Ebersin, 1965). The Pliocene bivalve faunas are exceedingly diverse, having yielded some 36 genera and five subfamilies of cardiids, all apparently derived from species of the

common Mediterranean cockle, *Cerastoderma*. A significant number of the brackish-water forms are still living in the Caspian and Azov seas (Zenkevitch, 1963), so their environmental tolerances are well known.

The molluscs of the Caspian region were first described by Andrussov (1897, 1900, 1903). By sampling successive horizons he was able to show that a brackish-water Pontian fauna replaced a normal Mediterranean fauna in response to a gradual lowering of the salinity of the pre-Pontian sea (Zenkevitch, 1963, p. 356). Andrussov explained that the Pontian fauna is formed not only by the gradual elimination of stenohaline species, but also by the evolution of numerous new species and genera within the brackish environment (Zenkevitch, 1963, p. 354; Gillet, 1946; Ebersin, 1965). This apparent

parallel with the diversification of the Megadesmidae in the Estrada Nova fauna suggests that the Pontian-Caspian Sea may form a useful model for an environmental analysis of the Paraná Basin.

GENERAL SIMILARITIES OF THE  
PONTIAN-CASPIAN AND PARANÁ SEAS

The present-day Caspian Sea has an area of 460,000 km<sup>2</sup>, and is about one-third as large as the Paraná Basin. Although the Caspian is the largest enclosed body of water in the world, the Pontian Lake-Sea was almost three times its size (Zenkevitch, 1963, fig. 174), and thus almost as

large as the Paraná Basin. Perhaps a water body of this order of magnitude is needed to provide sufficient space for effective radiation within a geographically restricted environment.

The climates of the Paraná Basin and the Pontian-Caspian sea may also have been similar. The widespread occurrence of glacial sediments in the Tubarão Group suggests that the Paraná Basin had a temperate climate and may have been partly covered by ice in winter. The deeper parts of the Basin may therefore have been temporarily stagnant because of temperature stratification of the surface waters during summer months. If fresh water was continuously supplied

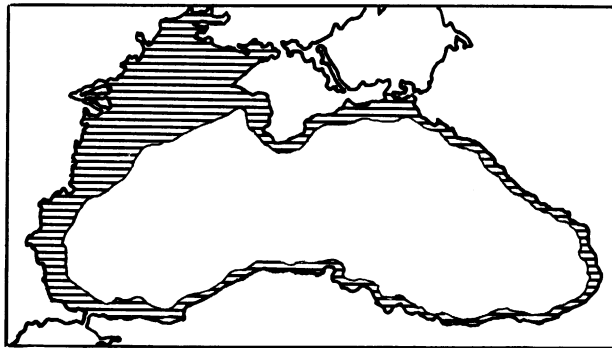


FIG. 5. Distribution of zoobenthos (shaded) in the Black Sea (Zenkevitch, 1963).

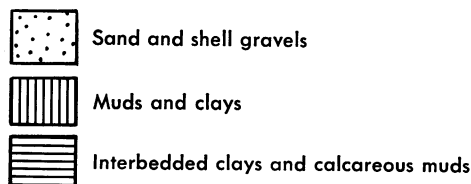
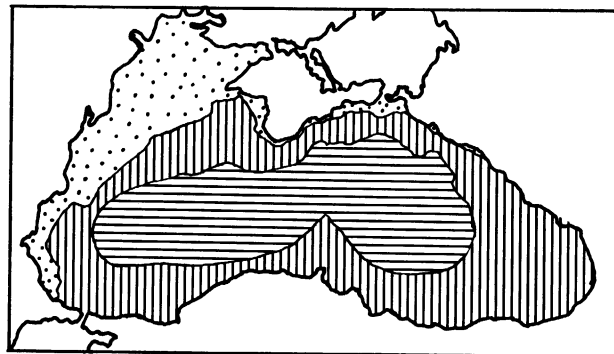


FIG. 6. Distribution of recent bottom sediments in the Black Sea (Zenkevitch, 1963). Compare distribution of benthonic organisms, figure 5.

at the surface, the lower density of the warmer, less saline surface waters may at times have induced a permanent stratification of the water column. Permanent stratification exists today in the Black Sea, where there is almost no circulation below a depth of 150 meters (Zenkevitch, 1963, p. 388). The deeper parts of the Sea are therefore anaerobic and the only forms of life found within this zone are sulfate-reducing bacteria. A similar situation seems to have occurred on a much wider scale in the Caspian region during the Upper Miocene, just before the freshening that led to the development of the Pontian fauna (Zenkevitch, 1963, pp. 355-356). As mentioned previously, the Iratí Formation could have formed in a comparable period of widespread stagnation of the bottom waters in the Paraná Basin.

In contrast to the Iratí Formation, the bivalve-bearing horizons of the Estrada Nova Formation probably were deposited in well-oxygenated, littoral, and in some cases subaerial, environments. Ample evidence for this conclusion is provided by widespread occurrences of shallow-water sedimentary structures (oolitic sands, clay galls, and mud cracks; Mendes, 1954a, fig. 8; 1967, pls. 44, 51; Salamuni, 1963), and the differential sorting of left and right valves of the more common bivalves. Such environments are found near the margins of the Caspian Sea, particularly in its northern part, where a huge area has a depth of less than 10 meters (Zenkevitch, 1963, p. 540). Because the Sea is surrounded by relatively flat land, the shorelines of the Caspian are poorly defined and may recede up to 20 km. owing to the effect of on-shore and off-shore winds (Zenkevitch, 1963, p. 542). Similar conditions in the Paraná Basin could explain the widespread distribution of desiccation structures in the Estrada Nova Formation.

Most of the water supplied to the Caspian Sea comes from the Volga River. River water contains more calcium and magnesium carbonates than does sea water so the Caspian has a higher concentration of these salts than normal sea water, and calcareous oolitic sands are forming along its eastern shore (Zenkevitch, 1963, pp. 544, 551). However, in contrast to the rest of the Caspian, the inlets along the eastern shore are hypersaline because of arid climate and absence of a supply of fresh water. Whether the oolites form only in these saline or hypersaline

areas is not clear, but as a general rule calcareous oolites are characteristic of waters of normal to high salinity.<sup>1</sup>

It is clear, therefore, that the distribution of high- and low-salinity waters in the Caspian Sea is complex, and although most of the Sea is brackish, the salinity of marginal areas can vary from a few parts per thousand near the mouth of the Volga to as much as 200 parts per thousand in some of the eastern bays (Zenkevitch, 1963, p. 551). The salinity of the shallow marginal regions of the Paraná Basin may therefore have been quite variable and may even have fluctuated with the supply of fresh rain water. It should be noted that all of the bivalve faunas of the Estrada Nova Formation are found in sediments deposited in a very shallow-water-to-subaerial environment.

It is instructive to compare the composition of the present-day Caspian fauna with the fossils recovered from the Passa Dois Group. According to Zenkevitch (1963, pp. 568-570), many typically marine groups are missing from the Caspian, or are represented by few species. Fish, crustaceans, and molluscs comprise about 60 per cent of all free-living species and an even higher percentage of the total biomass. There is a complete absence of radiolaria, corals, brachiopods, chitons, scaphopods, cephalopods, and echinoderms, whereas foraminifera, sponges, bryozoans, gastropods, and many groups of bivalves are poorly represented. Many species are restricted to the Caspian and the endemism of the bivalves is obvious.

There is an interesting parallel with the fauna of the Passa Dois Group which has yielded sponge spicules, crustaceans (conchostracans and malacostracans), bivalves, rare gastropods, fish scales, and two aquatic reptiles (*Mesosaurus* and *Stereosternum*) but no corals, bryozoans, brachiopods, cephalopods, or echinoderms. Impoverished faunas may result from either low or high salinities (Parker, 1960; Nicol, 1965) but the absence of brachiopods, echinoderms, and marine gastropods from the Estrada Nova Formation argues for a fresh- or brackish-water environment. In this context it is interesting to note that marine gastropods are relatively common in the high salinity assemblages of Laguna

<sup>1</sup>Oolites are known from fresh-water sediments; Bradley (1929) described calcareous oolites from the Laney Shale Member of the Green River Formation, Wyoming.

Madre (Parker, 1959) and in several Permian faunas from the southwest United States that appear to have lived in a similar environment (Nicol, 1965) but are less common in the low salinity waters of the Mississippi delta and Caspian Sea.

Of the 37 species of gastropods occurring in the Caspian Sea, at least 23 belong to fresh-water families and most of these are endemic (Zenkevitch, 1963, p. 567). Only two species of gastropods have been found in the Passa Dois Group and both appear to be fresh-water or terrestrial forms (E. L. Yochelson, personal commun.).

Although there are gross similarities in the molluscan faunas of the Passa Dois Group and Caspian Sea, there is one important difference. The present assemblage of bivalves in the Caspian Sea is a mixture of euryhaline fresh-water genera (e.g., *Unio*, *Dreissena*), stenohaline relict genera which developed in the late Pliocene (e.g., *Monodacna*, *Adacna*, *Didacna*), and euryhaline marine forms that are able to exist in the low salinity environment (*Cerastoderma edule*, *Mytilaster*). There is little evidence for a similar threefold or even twofold origin for the Passa Dois faunas. Frenguelli (1945) and Mendes (1954a) have referred poorly preserved shells from the Rio do Rasto Formation to the late Paleozoic fresh-water genus *Palaemutela*, but no fresh-water forms are known from the better preserved Estrada Nova faunas. There are also no widely distributed marine species, so that although the Passa Dois faunas are more taxonomically diverse than the Pontian-Caspian faunas (in terms of number of families), they appear to have developed from a single source.

Nevertheless, the Pontian-Caspian sediments and molluscan faunas provide a useful model for an environmental analysis of the Paraná Basin; and we now propose to compare several different parts of the Passa Dois Group with their more recent environmental analogs in the Pontian-Caspian region.

#### PALEOGEOGRAPHIC SETTING OF THE PARANÁ BASIN

Interest in the distribution of late Paleozoic glacial sediments in the Southern Hemisphere has stimulated detailed studies of the Tubarão Group in the Paraná Basin (Rocha-Campos, 1967; Frakes and Crowell, 1969). The directions of sediment transport and ice movement along

the eastern and western margins of the Basin are now well documented (Rocha-Campos, 1967, fig. 8) and a broad picture of the early Permian paleogeography of the Basin has emerged (Rocha-Campos, Farfallat, and Yoshido, 1969).

For example, it is known that the center of ice movement lay to the east of the present eastern edge of the Basin and that the sediments deposited on the eastern side are dominantly continental. It is obvious, at this point, that the relationship of Africa to South America must be considered, because the similarity of the glacial sediments of the Tubarão Group to those of the Dwyka Series of South Africa has long been used as evidence for continental drift (Martin, 1961). The similarity is so striking (Martin, 1961) that to ignore the possibility that the Paraná Basin may once have extended into Africa would be unreasonable, particularly in view of the independent geophysical evidence for sea floor spreading which has become available in the last decade. Nevertheless there is no evidence for the existence of the Estrada Nova fauna in Africa although nonmarine sediments of an apparently equivalent age are widely distributed. This suggests that if the two continents were connected, the Estrada Nova bivalves may have been unable to invade fresh water.

#### ENVIRONMENTS IN THE PASSA DOIS GROUP IRATÍ FORMATION

The Iratí Formation is the basal part of the Passa Dois Group on the eastern side of the Paraná Basin (Padula, 1969; Mendes, 1967). Its outcrop begins in São Paulo and extends more or less continuously for 1700 km. to the northern border of Uruguay (Padula, 1969, figs. 1-3). Lithologically the Iratí Formation consists of dark gray and brown to black oil shale and light to dark gray nonbituminous shales with thin interbeds of fine-grained limestone and dolomite. The percentage of limestone and dolomite increases to the north and in São Paulo the Formation consists of a rhythmic alternation of limestone and bituminous shale (Mendes, 1967, pl. 42). The even, and in some places almost varvelike bedding, and the presence of articulated reptile skeletons (Mendes, 1967, pl. 55) indicate that the Iratí Formation was deposited in quiet and probably relatively deep water. Apart from plant remains and a single poorly preserved bivalve (Beurlen, 1957), the only fossils recovered from the Iratí Formation are

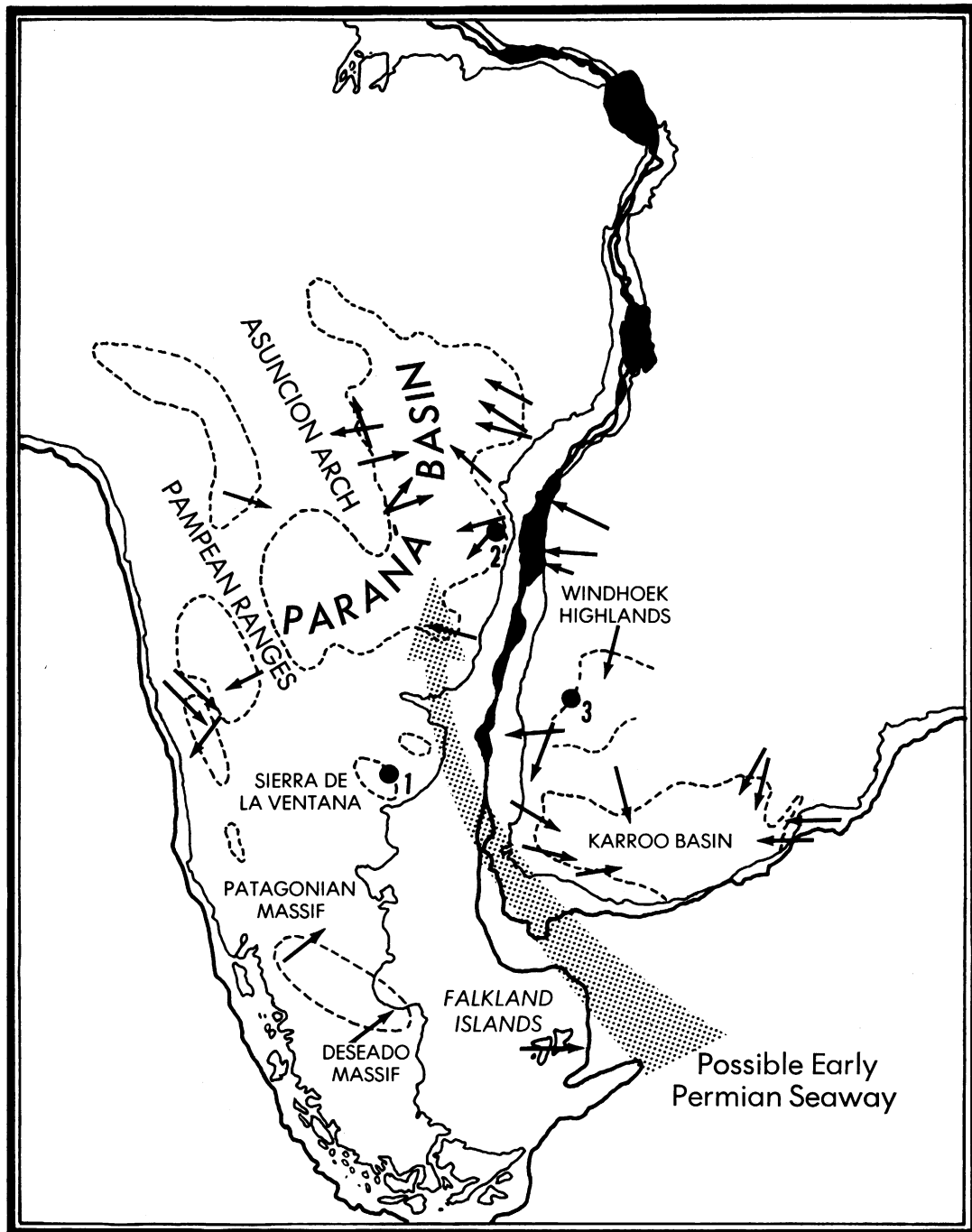


FIG. 7. Palaeogeographic setting of the Paraná Basin in the Lower Permian, prior to the deposition of the Passa Dois Group. The continental margins are fitted at the 500 fathom isobath (after Bullard, Everett, and Smith, 1965) with overlaps shown in black. Late Paleozoic continental and marine sediments occur in areas indicated by dashed lines, and the arrows indicate directions of sediment transport (after Martin (1961), Rocha-Campos (1967), Frakes and Crowell (1967, 1969), and Stratten (1969)). Lower Permian marine faunas occur in three areas marked by black spots: 1 and 3 contain *Eurydesma* (Harrington, 1955; Dickins, 1961) and are possibly contemporaneous; 2 occurs some 250 meters below the Passa Dois Group (Rocha-Campos, 1967) and may be the same age as 1 and 3. An early Permian seaway may have extended into Brazil through the area subsequently occupied by the South Atlantic basin. It is unlikely that the Paraná Basin extended into South Africa.

insects, fish, crustaceans, and the reptiles *Mesosaurus* and *Stereosternum*. A similar assemblage occurs in the "White Band" of the Dwyka Series in South Africa (Haughton, 1963; Padula, 1969).

#### PONTIAN-BLACK SEA ANALOG

An acceptable model for the Paraná Basin during the time of deposition of the Iratí Formation may be provided by present conditions in the Black Sea. Similar conditions seem to have also existed in the Caspian region just before the development of the Pontian fauna (Zenkevitch, 1963, p. 355).

At present the bottom waters of the Black Sea are cold, dense, and stagnant, and there is almost no circulation below a depth of 100 to 150 meters. Consequently, the deeper parts of the sea are anaerobic, and benthonic organisms are restricted to the margins of the sea (fig. 5). The distribution of the benthos is sharply reflected in the distribution of bottom sediments (fig. 6), with an outer zone of sand and skeletal material and an inner zone of well-laminated fine clays and muds. The high content of organic carbon and calcium carbonate in the fine-grained deposits of the anaerobic zone is reminiscent of the Iratí Formation, which seems to have formed in a similar environment.

The fossils found in the Iratí Formation are probably useless as indicators of the depositional environment, because they were either washed in (plants and insects) or were nektonic (fish, crustaceans, and reptiles) and could have lived in well-oxygenated surface waters. The excellent lamination of the Iratí shales and limestones demonstrates that the sediments were not reworked by burrowing animals, and it is reasonable to assume that benthonic organisms were restricted by anaerobic bottom conditions to the shallow, well-oxygenated margins of the Basin.

It is difficult to estimate the salinity of the Paraná Basin during the time of deposition of the Iratí Formation. Presumably the stagnation that appears to have caused the anaerobic conditions resulted from density stratification of the water column, so there may have been a significant increase in salinity with depth, particularly if the sea was being gradually freshened by discharge from rivers. Keith (1969) has found widely variable ratios of isotopic carbon ( $C^{13}:C^{12}$ ) in several samples of limestone and dolomite from the Iratí Formation, and by com-

parison with the carbon-isotope ratios of recent carbonates (Keith and Parker, 1965), has suggested (written commun.) that except for one sample, the Iratí Formation was deposited in a "marine to marginal marine" environment.

#### ESTRADA NOVA FORMATION

The Iratí Formation grades vertically upward into the Estrada Nova Formation. In general, the lower part of the Estrada Nova is a massive, unstratified, gray siltstone lacking the well-laminated bituminous layers that characterize the Iratí. Fossils are rare, but small bivalve faunas are known from the lower part of the Estrada Nova Formation in São Paulo (Mendes, 1949, 1952, 1967, p. 147; Mezzalira, 1957), and a single locality in the Serra Alta lithosome of Paraná has yielded two bivalve species (Mendes, 1954a), and the "conchostracan" *Acantholeaia* (Almeida, 1950).

#### PONTIAN-CASPIAN ANALOG

If we assume that the lithological change from the Iratí Formation to the basal part of the Estrada Nova Formation reflects a gradual recovery from anaerobic bottom conditions, it may be possible to use the present-day Caspian Sea as a model for the Paraná Basin during early Estrada Nova time. The decrease in oxygen content with depth in the Caspian Sea is not nearly as pronounced as in the Black Sea so that a much larger area of the Caspian is occupied by benthonic organisms (Zenkevitch, 1963, fig. 288). However, the number of organisms drops off rapidly below depths of about 100 meters, and the deeper parts of the Sea are inhabited by crustaceans and oligochaete and polychaete worms. Molluscs characteristically are absent from the deeper waters.

It is possible that the Serra Alta and Parapanema lithosomes of the Estrada Nova Formation were formed in essentially the same environment and that the absence of bedding in both units is because of the reworking by soft-bodied animals not represented in the fossil record. Where bivalves are present, the environment may have been transitional to that of Terezina and Serrinha beds which seem to have been deposited in very shallow water.

#### TEREZINA LITHOSOME

Syngenetic sedimentary structures are not



unequivocal indicators of depositional environment, however, there is little doubt that the Terezina and Serrinha lithosomes of the Estrada Nova Formation were deposited in shallow waters or a subaerial environment. Salamuni (1963) has studied the syngenetic structures of both units in some detail, and has concluded that they were deposited on a tidal flat or a fluvial flood plain. Because of the irregular bedding, the frequent occurrence of mud cracks (Salamuni, 1963, fig. 11c, 12a-c, 13b; Mendes, 1967, pls. 44, 51), and the presence of red beds, Salamuni preferred a continental to a marine environment.

Strictly speaking, the Terezina lithosome is limited to Santa Catarina and Paraná states, but as we are primarily concerned with the Estrada Nova bivalves, we shall treat similar faunas from São Paulo state at this time. In all three states bivalve faunas containing the genus *Pinzonella* normally are found in one of two rock types—a clean, well-sorted silicified oolitic limestone (Mendes, 1954a, fig. 8) or a moderately well-sorted quartz sandstone. In Paraná and Santa Catarina these thin oolitic or sandy beds form an integral part of the Terezina lithosome (fig. 2), but in São Paulo they form only a minor part of the Estrada Nova Formation (Mendes, 1952, 1962a). However, in São Paulo there are two distinct assemblages of this type in the Estrada Nova Formation, each characterized by a differ-

ent species of *Pinzonella*. Both are found in quartz sandstone as well as silicified oolitic limestone.

Faunas occurring in rocks of these types normally are dominated by disarticulated valves of *Pinzonella*. It is noteworthy therefore that Mendes and Petri (1950) measured unequal numbers of left and right valves in a biometrical study of several species of *Pinzonella*. For example, they measured 81 left and 30 right valves of *P. illusa* from one locality in São Paulo, and 64 left and 38 right valves from a second locality in the same area. This discrepancy suggested that the valves may have been differentially sorted. Consequently, we examined the largest collections available to us from single localities. The results are presented in table 1. A simple chi-squared test shows that the valves of *Pinzonella illusa* from the first locality and *Jacquesia brasiliensis* from the second locality are significantly sorted at or above the 99 per cent confidence level, comparable with results obtained by Behrens and Watson (1969) on Texas beaches. As neither of our species is markedly unequivalved, the differential sorting cannot be caused by winnowing. Behrens and Watson were able to demonstrate that differential sorting takes place in the swash zone of wave action, and significantly sorted populations (>99% confidence level) can therefore be used as an indicator of an intertidal environment. The presence of calcareous oolitic sands and the abundance of

TABLE 1  
SORTING OF PELECYPOD VALVES FROM TWO LOCALITIES IN THE ESTRADA NOVA FORMATION<sup>a</sup>

	Left Valves	Right Valves	Articulated	$\chi^2$	Confidence Level, %
Locality A <sup>b</sup>					
<i>Pinzonella illusa</i>	411	224	17	46.6	99.5
<i>Terraia aequilateralis</i>	35	23	0	2.48	90-95
<i>Plesiocyprinella carinata</i>	24	28	1	0.30	60-70
<i>Jacquesia elongata</i>	3	4	0	—	—
<i>Coxesia mezzalirai</i>	1	0	1	—	—
<i>Casterella gratiosa</i>	1	1	0	—	—
<i>Ferrazia cardinalis</i>	0	1	0	—	—
Locality B <sup>c</sup>					
<i>Pinzonella neotropica</i>	59	44	0	2.1	80-90
<i>Jacquesia brasiliensis</i>	26	6	0	12.3	99.5
<i>Pyramus anceps</i>	2	2	0	—	—

<sup>a</sup>Mendes, 1952, p. 50.

<sup>b</sup>Chácara Pedra Azul, Cidade de Rio Clara, São Paulo.

<sup>c</sup>"A volta da Piedra Branca," Rio Ivai, about 3 km. downstream from, and nearly 2 km. northwest of, Teresa Cristina, Paraná.

mud cracks and ripple marks (fig. 2) reinforces the view that the faunas containing *Pinzonella* accumulated on mud flats around a lake or sea.

Because the bivalve assemblages found in these beds are transported, or winnowed, associations, it is difficult to draw definitive conclusions concerning the environments in which they lived. Nonetheless, there are several general features of the faunas that can be used for a cautious paleoecological interpretation.

First, at many localities the taxonomic diversity is greater than that found in most present-day fresh-water environments, even though one or two species normally dominate the assemblage. In the Corumbataí region of São Paulo, for example, nine genera belonging to five different families occur in the lower *Pinzonella illusa* assemblage, and eight genera and five families are found in the upper *P. neotropica* assemblage. Exceptionally, four or five families of living bivalves will be found in fresh-water streams in one area [for example, the rivers of eastern China contain representatives of the Unionidae, Pisidiidae, Corbiculidae, and Mytilidae (J. P. E. Morrison, personal commun.)], but most fluvial faunas contain only two or three families.

Second, with the exception of rare fresh-water mytilids and the unique brackish- to fresh-water lyonsiid *Guianadesma* (Morrison, 1943), living and younger fossil relatives of the genera found in the Estrada Nova Formation do not appear to have invaded fresh water. By contrast, many marine groups of bivalves have and still do invade waters of very low salinity, both in estuaries (Parker, 1959) and in isolated lakes (Zenkevitch, 1963). Moreover, in almost all areas where estuarine and fresh-water faunas intergrade, a clear distinction can be made between true fresh-water groups (unionids, mutelids, corbiculids, pisidiids, and dreissenids), which inhabit waters whose salinity is generally less than about three parts per thousand, and the most euryhaline elements of marine faunas (cardiids, mytilids, *Macoma*, *Mya*, oysters, etc.), which are normally found in waters with at least five parts per thousand salinity (Parker, 1959; Zenkevitch, 1963). It follows that the taxonomic composition of the *Pinzonella* assemblages in the Estrada Nova Formation suggests a salinity of at least four to five parts per thousand for the shallow marginal areas of the Paraná Basin in which the molluscs lived. Such a con-

TABLE 2  
CARBON ISOTOPE RATIOS FROM LIMESTONES OF THE  
PASSA DOIS GROUP (Keith, 1969)<sup>a</sup>

	C <sup>13</sup> ‰	Salinity Estimated by Analogy with Living Faunas
Rio do Rasto Formation	-4.48	
	-5.83	Fresh
	-5.32	
Serrinha Lithosome		
Estrada Nova Formation	-1.16	Slightly brackish
Terezina Lithosome		
Estrada Nova Formation	+0.71	Brackish
Terezina equivalent in	+0.88	
São Paulo	+0.30	Brackish
Iratí Formation	Very variable	No data

<sup>a</sup>Samples with low Carbon 13:Carbon 12 ratios (C<sup>13</sup> < -2‰) indicate a continental environment of deposition (Allen and Keith, 1965). There is good agreement between Keith's work and generalizations that can be made from the fossil assemblages.

clusion is supported by Keith's (1969) study of the carbon isotopic composition of a shell bed from the Terezina lithosome (table 2), which suggests that the depositional environment of the unit was probably "dominantly marine or marginal marine."

Only very rare elements of the *Pinzonella* assemblages (*Coxesia* and *Naiadopsis*) appear to have been epifaunal, and all of the commoner species probably were active burrowers either lacking extensively fused mantle margins (*Pinzonella* and possibly *Terraia*) or with only short retractable siphons (*Casterella*, *Ferrazia*, *Jacquesia*, *Plesiocyprinella*, and *Pyramus*). Only *Roxoa* appears to have been a deep burrowing form. According to Stanley (1968, pp. 221, 223), present-day nonsiphonate infaunal bivalves like *Astarte* and *Neotrigonia* are sluggish burrowers that live largely in subtidal environments. As *Pinzonella*, the commonest genus in the Estrada Nova faunas, appears to be related to the Astartidae, it probably also lacked siphons; and, by implication, may also have lived subtidally. By contrast, the *Donax*-like shape of *Terraia aequilateralis* (fig. 21D, E, H) suggests that it may have been an active and efficient burrower, despite the fact that it may also have lacked extensively fused

mantle margins. The remaining siphonate genera probably burrowed about as inefficiently as *Cardium* or *Mercenaria* (Trueman, 1968), for they are relatively robust, thick shells with pedal muscle scars of comparable or smaller relative size.

Although all these bivalves commonly are found in beds of oolitic sand, it is quite possible they did not live in areas of active oolite formation. Such areas in the Bahamas are almost devoid of plant and animal life (Newell et al., 1959, p. 219), probably in contrast to the areas of stabilized oolite. Clearly, it is therefore difficult to arrive at any specific conclusions concerning the habitat of the bivalves of the *Pinzonella* assemblages.

In Australia, members of the Megadesmidae are found in very shallow water sediments (for example, Runnegar and Ferguson, 1969, p. 253) and the available evidence indicates their South American relatives occupied a similar habitat.

#### PONTIAN-CASPIAN LITTORAL AND SUBLITTORAL ANALOG

A large part of the northern Caspian has a water depth of less than 10 meters, and it is in this area that the densest concentration of molluscs occurs (Zenkevitch, 1963, p. 614). At depths of 2 to 12 meters bivalves average 91 per cent of the total biomass and are found inhabiting both hard and soft bottoms. On both substrates the communities are composed of byssally attached species of *Dreissena* and shallow-burrowing cardiid genera. Similar assemblages are found in the late Cenozoic Pontian deposits where the taxonomic diversity was even higher than it is today in the Caspian. It seems probable that the bivalves found with *Pinzonella* in the Estrada Nova Formation may have inhabited areas of similar water depth in the Paraná Basin, forming shell accumulations in the littoral and sublittoral environment.

#### SERRINHA LITHOSOME

Lithologically, the Serrinha lithosome is similar to the Terezina except that it lacks beds of silicified oolitic limestone and coquinas of silicified shells. It contains more sandstone, and all the fossils are preserved as iron-stained casts and molds. The faunas in this unit are not as diverse as those of the Terezina lithosome and because they are often poorly preserved have not been so extensively collected. Therefore, we have

examined collections from the following two localities in some detail:

1) USGS locality 22836: 25-cm. bed of gray to yellowish siltstone, in road cut at 109.7 km. on the road from Prudentopolis to Guarapuava, Paraná (see Mendes, 1954a, pp. 56, 67, 70). The fauna contains three common and two very rare species:

- 40 per cent *Dendropupa* sp. (maximum size 4 mm.)
- 39 per cent *Terraia altissima* (normally disarticulated and commonly broken, most 3–5 mm. in size)
- 21 per cent *Leinzia similis* (frequently articulated and normally unbroken, 35–45 mm. long)
- 1 per cent mytilid bivalve, possibly *Coxesia* (1 mm.), and gastropod

An immediately underlying siltstone has well preserved *Glossopteris* and other plants (Mendes, 1954a; Mackenzie Gordon, personal commun.) and a micaceous shale containing conchostracans (USGS G-81-47) occurs about 57 meters lower in the sequence.

2) USGS locality 22829: light purplish gray siltstone, 41.3 meters below the base of Rio do Rasto Formation, on the Santa Clara-Urubici road, north slope of Morro do Panelão, 6.5 miles (10.35 km.) by road south of Santa Clara, Municipality Bom Retiro, Santa Catarina. Many of the shells from this locality are crushed and difficult to identify. Accordingly, no attempt was made to count individuals of each species. The fauna is slightly more diverse than that of USGS locality 22836, but it is obviously a similar association.

- Terraia altissima* (common, up to 20 mm. in length)
- Leinzia similis* (common, 30–40 mm. in length)
- Terraia bipleura* (uncommon)
- ?*Dendropupa* sp. (uncommon)
- Jacquesia* cf. *elongata* (uncommon)
- ?*Ferrazia* sp. (rare)
- large indeterminate bivalve (rare)

The greater diversity of this fauna may indicate a slightly different environment, or the rarer elements may have been mechanically introduced. Presumably, at some localities one could expect to find representatives of both the *Leinzia* and *Pinzonella* assemblages.

Ellis L. Yochelson, of the United States Geological Survey, has kindly examined the gastropods from both localities and has provided us with the following statement:

“U.S.G.S. locality 22836 has yielded a large number of external impressions of gastropods. In

spite of the large variation which they show at first glance, I believe that all except one belong to a single species. The specimens are moderately high-spired but the apical area is beehive-shaped rather than sharply pointed. In the aperture of one specimen there is a suggestion of an apical tooth. The specimens may be reasonably assigned to *Dendropupa* Dawson.

"In the United States this genus occurs in the Upper Pennsylvanian Monongahela Series and continues upward at least into the Ninevah Limestone of the Greene Formation of the Dunkard Series, that is, in beds presumed to be of early Permian age. Specimens commonly are distorted and seem to be thin shelled. This tendency towards distortion combined with the allometric change of the younger shell gives the impression of diversity in what is an impoverished fauna, quite similar to the Brazilian material.

"In the Ninevah Limestone and in the Karniowice beds of probably Upper Carboniferous age near Krakow, Poland, an extremely slender form occurs along with abundant *Dendropupa*; this is probably a new genus. The one unique specimen in the Brazilian collection cannot be compared closely with these others because it is not well preserved, but again there is a similarity.

"Field work in the Dunkard and a brief visit to the Karniowice locality has convinced me that *Dendropupa* is not a marine gastropod. I believe that the question of whether it is fresh-water or terrestrial is impossible to answer from an interpretation of the shell morphology. My impression is that its distribution in the outcrop is best explained by assuming that it lived on reeds just above the surface of a lake. Specimens occur in both limestones and shales though I have never before seen examples in a fine siltstone. *Dendropupa* might be transported to a brackish water area, but in the two areas where

I have collected it several lines of field evidence support a lacustrine environment.

"The few specimens from U.S.G.S. locality 22829 are very poorly preserved. Insofar as they show features of general size and shape similar to those in the larger collection, I would be inclined to also assign them to *Dendropupa* and to suspect a non-marine environment."

The conchostracans, plants, and gastropods all suggest a fresh-water environment for the Serrinha beds. Interestingly, the anterior prong shown by *Leinzia* is similar to a structure found in the living fresh-water unionid *Arconaia* (fig. 24H, I), but as the function of this structure in *Arconaia* is unknown, no significance at present can be attached to this observation. It is not clear whether *Terraia* lived in fresh or saline waters; however, because the relatively robust shells of *Terraia* are broken, it may not have been associated with the other forms during life.

The available evidence points to a fresh- or slightly brackish-water environment for this fauna. Similar living assemblages showing an equivalent degree of diversity and grossly comparable taxonomic composition occur near permanent river mouths and in delta distributaries in the Gulf of Mexico (Parker, 1956, 1960) and the Caspian Sea (Zenkevitch, 1963, p. 614).

#### RIO DO RASTO FORMATION

In the Brazilian states of Paraná, Santa Catarina, and Rio Grande do Sul the Serrinha lithosome of the Estrada Nova Formation is succeeded gradually by red beds of the Rio do Rasto Formation. The sedimentary structures (Bigarella and Salamuni, 1967, p. 260), widespread occurrence of plant remains and conchostracans, and the isotopic ratios of analyzed carbonates (table 2, after Keith, 1969) all argue for a continental depositional environment for this unit.

#### CONCLUSIONS

The late tertiary history of the Caspian region is exceedingly complex. At times, the whole of the area now occupied by the Black, Caspian, Azov, and possibly Aral seas, was incorporated in one huge inland sea, whereas at

other times (as at present), several smaller basins were isolated from one another. The situation is further complicated by salinity gradients that may isolate two or more communities occupying otherwise similar environments in the

same basin (Zenkevitch, 1963). If, as seems reasonable, a similar degree of complexity is assumed to have existed in the Paraná Basin, it is obviously impossible to compile an accurate picture of the spatial distribution of depositional environments with the very limited amount of stratigraphic data available.

It is assumed that evolution in most of the Estrada Nova phyla was much more rapid than in related forms of the open sea, at rates that

were generally high because of geographic fragmentation and extreme isolation effected, no doubt, by ecological barriers such as sand bars and salinity gradients. Just why these barriers were relatively more effective than ordinarily is the case is not clear. In any event, the Paraná and Pontian-Caspian examples illustrate endemism to a marked degree that is quite unusual in the history of marine molluscs.

## SYSTEMATIC PALEONTOLOGY

### SUBCLASS ANOMALODESMATA ORDER PHOLADOMYOIDA

#### SUPERFAMILY PHOLADOMYACEA GRAY, 1847

#### FAMILY MEGADESMIDAE VOKES, 1967

DISCUSSION: A compact group of late Paleozoic infaunal bivalves that appear to have had nacreous shells and short siphons are referred to this family. Because they were active burrowers, the shells are robust and have a stout external ligament; they lack teeth or have a blunt tooth in the right or both valves.

All the genera previously placed in the family were first described from the marine Permian of eastern Australia, where they are common and conspicuous components of the faunas. Several genera have since been identified in Western Australia (Dickins, 1956, 1957, 1963), West Pakistan (Reed, 1936), South America (Reed, 1930; Harrington, 1955; Rocha-Campos, In press), Siberia (Popov, 1957; Dickins, 1963, p. 23), Japan (Nakazawa and Newell, 1968), and New Zealand (Waterhouse, 1969), but they are normally abundant only in deposits of the Gondwana faunal province. For example, only one rare species from the rich silicified Permian faunas of southwest Texas and Wyoming (Newell, Chronic, and Roberts, 1953, fig. 84; Boyd and Newell, 1968) can be satisfactorily referred to this family.

Most of the Australian megadesmid shells are unusually large so that small accessory muscle scars and fine details of the hinge and ligament are well preserved (Runnegar, 1966, 1967, 1968). However, as most occur as external and internal molds, the hinges were poorly known until modern casting techniques were developed and applied (Newell, 1956). By contrast, the silicified bivalves from the Estrada Nova Formation are easily extracted and cleaned by mechanical means, so that their hinges have always been well known (Holdhaus, 1918; Reed, 1932). Ironically, it is only because of recent studies of the Australian genera (Newell, 1956; Dickins, 1956, 1957, 1963; Waterhouse, 1965, 1969; Runnegar, 1965, 1966, 1967, 1969b) that it is now possible to refer some of the genera from the Estrada Nova Formation to the Megadesmidae.

The family can therefore be expanded to include the following forms:<sup>1</sup>

*Astartila* Dana, 1847  
*Australomya* Runnegar, 1969  
*Casterella* Mendes, 1952  
*Ferrazia* Reed, 1932  
*Jacquesia* Mendes, 1944  
*Megadesmus* Sowerby, 1838  
*Myonia* Dana, 1847  
*Plesiocyprinella* Holdhaus, 1918  
*Pleurikodonta* Runnegar, 1965  
*Pyramus* Dana, 1847

THE MEGADESMID HINGE: Apart from gross similarities in shape, the most important character shared by the genera from Brazil and Argentina is the structure of the hinge.<sup>2</sup> It is therefore pertinent to examine the megadesmid hinge in some detail and to consider its origin and development.

Fortunately, the nominate genus, *Megadesmus*, is a typical and relatively unspecialized member of the family.

*Megadesmus* has a large, blunt tooth in the right valve and a corresponding socket in the left valve. In most species the socket results from a ventral depression of the cardinal valve margin (Runnegar, 1965, pl. 14, figs. 6, 9, 10; 1969b, pl. 19, fig. 4), but in *Megadesmus gryphoides* it forms a short, deep notch in the margin of the valve (Runnegar, 1967, pl. 3, fig. 14). In all species of *Megadesmus* in which the hinge is well known, the tooth results from an abrupt S-shaped bend in the valve margin beneath the beak (Runnegar, 1965, pl. 14, figs. 6, 8), and the anterior dorsal margin of the right valve slightly overlaps that of the left (Runnegar, 1967, pl. 3, fig. 14). Other megadesmid genera in most cases

<sup>1</sup>Names we have rejected as junior synonyms include *Angatubia* Mendes, 1962, *Clarkia* de Koninck, 1876, *Cleobis* Dana, 1847, *Cowperesia* Mendes, 1952, *Favalia* Mendes, 1962, *Globicarina* Waterhouse, 1965, *Holdhausiella* Mendes, 1952, *Maeonia* Dana, 1848, *Myofossa* Waterhouse, 1969, *Notomya* McCoy, 1847, *Pachydomus* Morris, 1845, *Pachymyonia* Dun, 1932, *Pyramia* Dana, 1849, and possibly *Leptoterraia* Buerlen, 1954, *Maackia* Mendes, 1954, and *Othonella* Mendes, 1963. It is not yet clear whether *Crassiconcha* Netschajew, 1894, and *Ochotomya* Polubotka, 1966 should be referred to this family as well.

<sup>2</sup>However, some other, possibly unrelated groups have evolved similar hinges. For example, see figure 27.

show some modification of this basic plan or lack teeth altogether.

The hinge of *Pyramus concentricus* (fig. 12A) is essentially the same as that of *Megadesmus gryphoides* except that the edge of the left valve in front of the socket is thickened. The socket is therefore deep and triangular, and its projecting anterior edge functions as a second tooth. This "tooth" is even more obvious in the type species, *Pyramus myiformis* (Newell, 1956, fig. 4d), and the species from Brazil "*Cowperesia*" *anceps* (figs. 12C-H), now also referred to *Pyramus*. As Waterhouse has emphasized (1966, p. 551), a second tooth may also be present in the left valve of *Astartila intrepida*, but in *Astartila* the tooth is small and conical and thus different from the thickened valve edge of *Pyramus*.

The genera *Plesiocyprinella*, *Ferrazia*, and *Casterella* from Brazil have hinges of the type found in *Megadesmus* (figs. 8-11) but in the Brazilian forms the hinge is a little more complex. For example, in *Plesiocyprinella* the ventral face of the tooth is concave and there is a corresponding prominent ridge in the middle of the socket of the left valve. However, in juvenile specimens of *Plesiocyprinella* the groove and ridge are poorly developed (fig. 8C) and the hinges of *Plesiocyprinella* and *Megadesmus* are then remarkably similar. The hinges of *Casterella* and *Ferrazia* are less well known, but they are clearly related to *Plesiocyprinella* and *Megadesmus*. From their similarity in external shape, it seems probable that both *Ferrazia* and *Casterella* developed from *Plesiocyprinella* after the isolation of the Paraná Basin. It is interesting to note that although the differences among *Casterella*, *Ferrazia*, and *Plesiocyprinella* parallel those that distinguish *Pyramus*, *Astartila*, *Pleurikodonta*, and *Megadesmus* (Runnegar, 1966), the three genera from Brazil are obviously more closely related to one another than they are to any of the Australian forms. Their obvious similarity is due mainly to an unusual expansion of the anterior part of the shell, which may be related to possession of a large and active foot. A similar expansion distinguishes a fourth genus from Brazil, *Jacquesia*, from its Australian counterpart, *Myonia*, and is found in the unrelated but associated species *Roxoa intricans*, *Terraia aequilateralis*, and *T. lamegoi*. The significance of this feature is not well understood, but its occurrence in several unrelated lines suggests that it is an environmental adaptation, perhaps, as in *Donax*,

correlated with the need for rapid initial fixation in a surf-zone habitat (Trueman, Brand, and Davis, 1966).

A second, less easily explained difference between the megadesmids from the Estrada Nova Formation and those from the Australian Permian is the absence of a pedal levator muscle scar in all of the Brazilian species of well-known musculature. It is possible that the disappearance of this muscle was dependent on the anterior expansion of the shell (because the foot could no longer be supported by a muscle attached in the umbonal region), but this suggestion does not explain its absence in *Pyramus anceps*, which is not as anteriorly expanded, and in other respects resembles species of *Pyramus* from Australia. Apart from the fact that this muscle is missing in all the Estrada Nova megadesmids, its absence is probably not very significant. The levator scar is quite small in a number of Australian species and often disappears in larger shells.

The oldest known representatives of the Megadesmidae are *Myonia pollocki* (Maxwell, 1964, pl. 3, figs. 13-17) from the Upper Carboniferous of Queensland and an undescribed species of *Pyramus* from the *Marginirugus barringtonensis* zone (Namurian), New South Wales. In South America, the family first appears in the Lower Permian Bonete Formation of Argentina (Harrington, 1955) and the Tubarão Group of Brazil. Both faunas contain species of *Myonia* which could have given rise to *Jacquesia*, but so far *Pyramus* and *Megadesmus* have not been reported from South American Lower Permian faunas.<sup>1</sup>

#### PLESIOCYPRINELLA HOLDHAUS, 1918

TYPE SPECIES: *Plesiocyprinella carinata* Holdhaus, 1918, by monotypy.

SYNONYM: ?*Othonella* Mendes, 1963.

#### *Plesiocyprinella carinata* Holdhaus, 1918

Figures 8, 9

*Plesiocyprinella carinata* HOLDHAUS, 1918, p. 21, pl. 2, figs. 1-5. REED, 1932, p. 485, pl. 19, fig. 13.

MENDES, 1944, p. 52; 1952, p. 85, pl. 1, figs. 10-11; pl. 2, fig. 9; 1967, pl. 59, fig. 6.

? *Plesiocyprinella carinata* REED, 1929, p. 77. MENDES, 1954a, p. 108.

<sup>1</sup>*Pyramus* has recently been discovered in the Patagonian region of Argentina (Carlos R. Gonzales, written commun.), and a *Megadesmus*-like bivalve has been found in the Lower Permian of Rio Grande do Sul (specimens provided by D. Cloos).

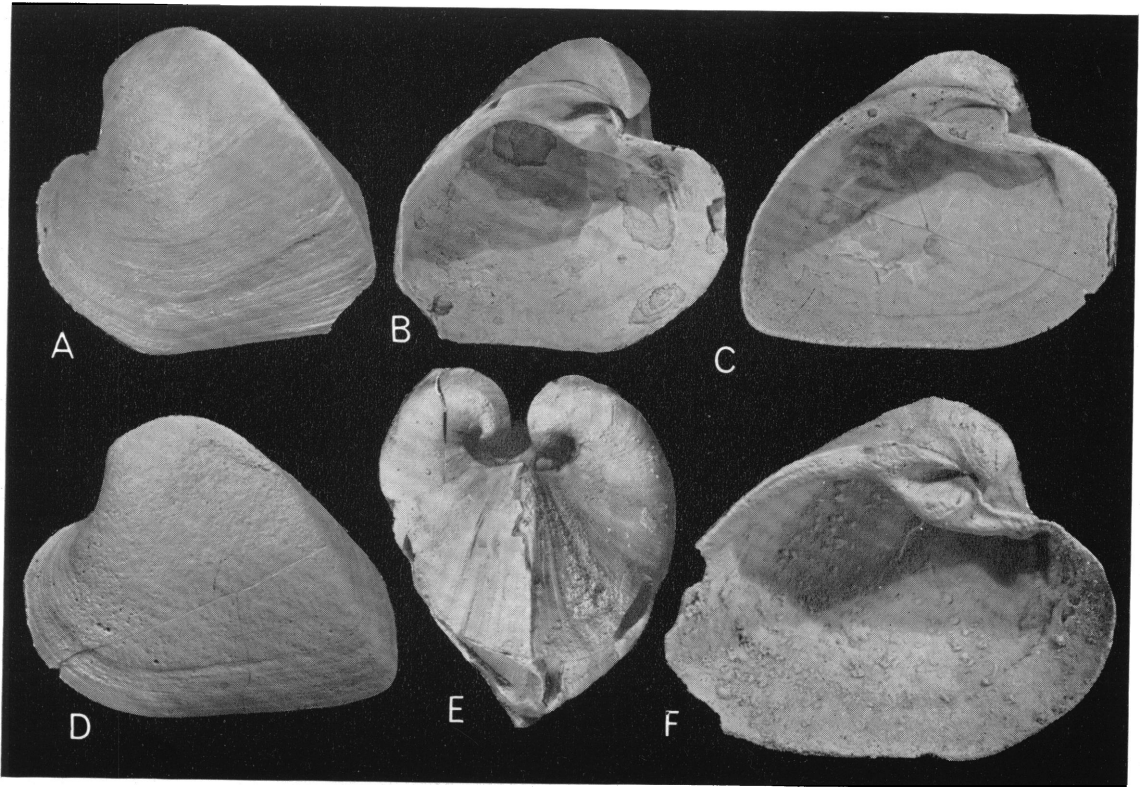


FIG. 8. *Plesiocyprinella carinata* Holdhaus. Middle Estrada Nova Formation, northeastern São Paulo. A, B. Left valve, AMNH 28975, Pedra Azul, about 6 km. west of Rio Claro.  $\times 1$ . C, D. Smaller left valve with hinge similar to *Megadesmus*, AMNH 28976, Pedra Azul, about 6 km. west of Rio Claro.  $\times 2$ . E. Anterior view of a bivalved specimen, DGM 5020-1, Culik farm, 2 km. northeast of Ferraz station, Rio Claro.  $\times 1.70$ . F. Left valve, DGM 5022-1, Culik farm, 2 km. northeast of Ferraz station, Rio Claro.  $\times 2$ .

*Plesiocyprinella* BEURLIN, 1954b, pl. 1, fig. 2a, b.  
 ? *Plesiocyprinella* cf. *carinata* MEZZALIRA, 1957, p. 50.  
 ? *Casterella* cf. *camargoi* Beurlen: MEZZALIRA, 1957,  
 p. 49, pl. 2, fig. 4.

TYPE MATERIAL: Specimens figured by Holdhaus (1918) from a *Pinzonella illusa* assemblage, middle part of Estrada Nova Formation, near Corumbataí, São Paulo (not examined).

DESCRIPTION: Shell medium-sized (maximum length approximately 45 mm.), equivalved, with subcentral beaks and rounded to angular posterior umbonal carina; umbones high, prosogyral, enrolled, but separated in life by massive inter-umbonal tooth of right valve; lunule and escutcheon absent; shell margins closed or rarely with small but well-defined siphonal gape (fig. 9C); valves smooth except for widely spaced growth lamellae. Ligament opisthodontic, parivincular, external, attached to short, robust nymphs; hinge with massive cardinal tooth in

right valve, formed, as in *Megadesmus*, from S-shaped flexure in valve margin; ventral surface of tooth concave, fitting prominent ridge or boss in center of socket of left valve; left valve socket otherwise similar to that of *Megadesmus* (Runnegar, 1965, pl. 14, figs. 9, 10) except that it lies wholly within valve commissure; lateral teeth absent. Adductor muscle scars subquadrate, small, subequal; posterior scar placed behind umbonal carina; pallial line relatively narrow, continuous, without pallial sinus; anterior and posterior pedal retractor scars above adductor scars, protractor and levator scars not observed.

STRATIGRAPHIC RANGE: *Pinzonella illusa* and *Leinzia froesi* assemblages, lower part of Estrada Nova Formation, northeastern São Paulo (Mendes, 1952; Mezzalira, 1957). There are also two records of this species from the Estrada Nova Formation in Paraná. The first is by Reed



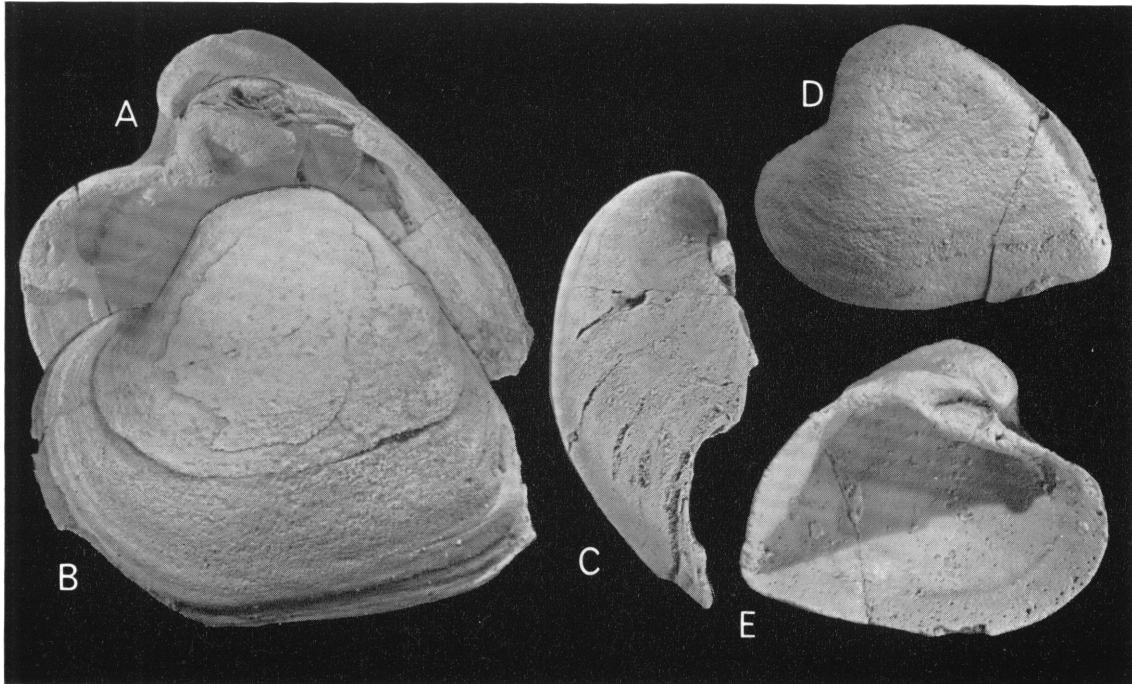


FIG. 9. *Plesiocyprinella carinata* Holdhaus. Middle Estrada Nova Formation, northeastern São Paulo. A. Bifid tooth of right valve, AMNH 28979, Pedra Azul, about 6 km. west of Rio Claro.  $\times 1.5$ . B, C. Left valve with small siphonal gape shown by growth lamellae, AMNH 28977, Pedra Azul, about 6 km. west of Rio Claro.  $\times 2$ . D, E. Left Valve, DGM 5021-1. Culik farm, 2 km. northeast of Ferraz station, Rio Claro.  $\times 2$ .

(1929, p. 77) who reported "several imperfect specimens" from two localities near Rio Claro do Sul, close to the southern border of Paraná. Both localities are in the Terezina lithosome of the Estrada Nova Formation, and subsequent collections by Mendes (1954a, pp. 45, 67, 75) and Gordon (1947, USGS locality 22834) have failed to yield additional specimens. It seems possible that Reed misidentified a few poorly preserved specimens of *Jacquesia brasiliensis*, which abounds at these localities.

The second record is from the Reserva plateau of central Paraná (Mendes, 1954a, p. 108), but in this case *Plesiocyprinella* occurs with species normally found with *Pinzonella illusa*, namely *Jacquesia elongata*, *Casterella gratiosa*, and *Ferrazia cardinalis*. The stratigraphic position of this locality is not well known (Carvalho, 1937, p. 56), but Mendes (1954a) concluded that it probably lies within the Terezina beds of the Estrada Nova Formation because the fossils occur in a silicified oolitic limestone. However, Reserva is situated on the eastern side of an out-

crop belt of the Estrada Nova Formation 60 km. wide (Padula, 1969, fig. 2), so the locality may be closer to the base of the Formation than the localities near Tereza Cristina (formerly Terezina). A similar assemblage is also found in a silicified oolite at Angatuba, some 275 km. to the northeast (Mendes, 1962a).

**DISCUSSION:** The only species that resemble *Plesiocyprinella carinata* in shape are the type species of *Casterella*, *C. gratiosa*, a very poorly illustrated second species of ?*Casterella*, *C. camargoi* Beurlen (1954c, p. 16, fig. f), and the type species of *Othonella*, *O. araguaiana*. The only well-illustrated specimen referred to ?*Casterella camargoi* is close to *Plesiocyprinella carinata* in external form (Mezzalira, 1957, pl. 2, fig. 4) and may well be a crushed specimen of *P. carinata*.

*Casterella gratiosa* is externally similar to *P. carinata* except that it sometimes lacks an angular umbonal carina. Most specimens also have a small siphonal gape (fig. 10C), but a similar gape may occur in rare specimens of *Plesiocyprinella* (fig. 9C). Mendes (1952, p. 102)

reported that the pallial line of *C. gratiosa* has a small sinus, but no illustration of the sinus has been published. It may be expected, however, that individuals with a well-developed siphonal gape would also have a small pallial sinus, and both characters are known to vary intraspecifically in *Pyramus laevis* from eastern Australia.

The hinges of the specimens of *Casterella gratiosa* figured originally by Mendes (1952, pl. 1, fig. 6a, b; pl. 3, figs. 9, 10) are edentulous, but Mendes (1962a) subsequently reported small teeth of the sort found in *Megadesmus*, *Plesiocyprinella*, and *Ferrazia* in specimens of *C. gratiosa* from the Angatuba district of São Paulo. The hinge of one of these specimens is illustrated in figure 10, together with an edentulous left valve from the type area (northeastern São Paulo). It is unlikely that the absence of teeth in specimens from the type area is caused solely by wear (although many shells are severely abraded) because the socket is missing as well as the tooth, and it can be assumed that the hinge of *Casterella* must have been quite variable. It is of interest to note that many of the described specimens of *C. Gratiosa* are relatively small and that at least in the type area, *C. Gratiosa* is always associated with *Plesiocyprinella carinata*. It follows that there is a slight possibility that the two species are conspecific, as the hinge of *P. carinata* is also quite variable, and may be reduced in smaller individuals.

Paradoxically, until the relationship between these two species is resolved by a detailed study of large collections from northeastern São Paulo and Angatuba, the status of *Casterella* as a distinct genus must remain uncertain. If the two forms can be shown to be consistently distinct, the differences in hinge structure are sufficient to warrant generic separation because the same criterion is currently being used to separate the Australian genera *Megadesmus* and *Astartila*.<sup>1</sup>

<sup>1</sup>Runnegar (1965) and Waterhouse (1965) believed that the absence of an anterior pedal protractor scar assisted in distinguishing *Astartila* from *Megadesmus*, but Runnegar pointed out that the muscle may still have been present while attached to the sheath of the anterior adductor instead of the shell. R. E. Wass, Sydney University, has since found this scar on an undescribed species of *Astartila* from the Farley Formation, New South Wales (personal commun.), and it is also visible on a topotype of *Astartila intrepida* (USNM locality 3588a). Thus, the only remaining differences between *Astartila* and *Megadesmus* are (slightly) in shape and in the structure of the hinge (Waterhouse, 1966, p. 551).

However, if *Plesiocyprinella carinata* and *Casterella gratiosa* belong to one variable species, the total variation in hinge structure would exceed that known to occur in any one Australian species (or even genus), and the reasons for separating *Megadesmus*, *Astartila*, and *Pleurikodonta* would have to be reassessed.

The type specimens of a third Brazilian genus of this group, *Othonella* Mendes, 1963, are poorly preserved (Mendes, 1963, figs. 3, 4) but the shape and visible dentition suggest that it may also be conspecific with *Plesiocyprinella carinata*.

In Australia and New Zealand, genera belonging to the Megadesmidae can usually be identified at a glance, indicating that the shape of the valves (as in most other families) is the primary basis for generic recognition. Experience has shown that similarly shaped species are united by other characters, the most important of which is the structure of the hinge. The differences in shape and dentition between *Plesiocyprinella carinata* and its closest Australian relatives, *Megadesmus gryphoides* and *M. nobilissimus* (Runnegar, 1965), are equivalent to those between *Megadesmus* and *Pyramus*, and are thus considered sufficient for generic separation. *Plesiocyprinella* is distinguished by its high, en-rolled umbones, its angular umbonal carina, expanded anterior margin, and massive, complex hinge.

#### CASTERELLA MENDES, 1952

TYPE SPECIES: *Casterella gratiosa* Mendes, 1952, by monotypy and original designation.

OTHER SPECIES: ?*Casterella camargoi* Beurlen, 1954c, p. 16, fig. f; Mezzalira, 1957, p. 49, pl. 2, fig. 4.

#### *Casterella gratiosa* Mendes, 1952

Figure 10

*Pleuromya* aff. *mactroides* Schloth: MENDES, 1944, p. 56, pl. 1, fig. 5.

*Casterella gratiosa* MENDES, 1952, p. 101, pl. 1, fig. 6a, b; pl. 3, figs. 9, 10; 1954a, pl. 94; 1962a, p. 47, pl. 2, fig. 1, text-figs. 4, 5.

TYPE MATERIAL: The lectotype (here designated) is DGP 7-58 (Mendes, 1952, pl. 1, fig. 6a, b) from a *Pinzonella illusa* assemblage, Estrada Nova Formation, in an exposure on the right of the road from Ajapi to Ferraz, near the bank of the Corumbataí River, Municipality Rio Claro, São Paulo.

DESCRIPTION: Shell medium-sized (maximum

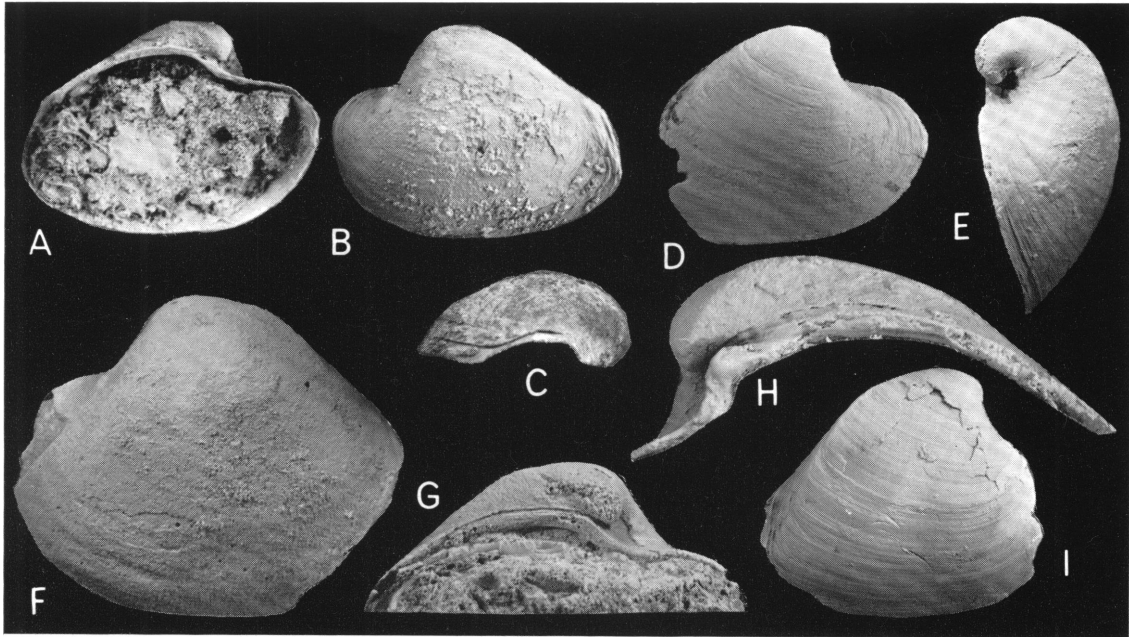


FIG. 10. *Casterella gratiosa* Mendes, type species of *Casterella*, *Pinzonella illusa* assemblage. Estrada Nova Formation, São Paulo. A-C. Left valve with well-defined siphonal gape, DGP 7-949, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo.  $\times 1.4$ . D. Right valve, Manoel Pereira Primo property.  $\times 1$ . E. Left valve, anterior, DGP 948, Manoel Pereira Primo property.  $\times 2$ . F, G. Left Valve with edentulous hinge, AMNH 28979, Pedra Azul farm, about 6 km. west of Rio Claro.  $\times 2$ . H, I. Right valve, DGP 1124, Manoel Pereira Primo property.  $\times 2$ . and  $\times 1$ , respectively.

length approximately 40 mm.), anteriorly expanded, with subcentral beaks, and rounded to distinctly angular posterior umbonal slopes; beaks high and prosogyral; lunule and escutcheon absent; valve margins closed anteriorly and ventrally but with small siphonal gape; valves smooth except for widely spaced growth lamellae. Ligament opisthodetic, parivincular, external, attached to short robust nymphs; hinge edentulous or with small blunt tooth in right valve and shallow socket in left; lateral teeth absent; musculature not observed.

STRATIGRAPHIC RANGE: *Pinzonella illusa* assemblage São Paulo (Mendes, 1952; 1962a); Reserva plateau (stratigraphic position uncertain).

DISCUSSION: The affiliations of *C. gratiosa* are considered in the discussion of *Plesiocyprinella carinata*.

#### OTHONELLA MENDES, 1963

TYPE SPECIES: *Othonella araguiana* Mendes, 1963, by monotypy and original designation.

#### *Othonella araguiana* Mendes, 1963

*Othonella araguiana* MENDES, 1963, p. 61, figs. 3, 4.

TYPE MATERIAL: DGP 7-980, 7-981, 7-982, 7-983 (Mendes, 1963, fig. 4), *Pinzonella illusa* assemblage, Estrada Nova Formation, Mato Grosso.

DISCUSSION: The affiliations of *O. araguiana* are considered in the discussion of *Plesiocyprinella carinata*.

#### FERRAZIA REED, 1932

TYPE SPECIES: *Ferrazia cardinalis* Reed, 1932 by monotypy.

OTHER SPECIES: *Ferrazia simplicarinata* Mezzalana 1957, p. 46, pl. 2, fig. 3; Mendes, 1962a, fig. 9.

#### *Ferrazia cardinalis* Reed, 1932

Figure 11

*Ferrazia cardinalis* REED, 1932, p. 480, pl. 19, figs. 1-5.

*Ferrazia cardinalis*: MENDES, 1944, p. 66; 1952, p. 82, pl. 3, fig. 1a, b; 1962a, p. 51, pl. 2, text-figs. 7-9; 1967, p. 59, figs. 4, 5.

*Ferrazia*: BEURLEN, 1954b, pl. 1, fig. 3a, b.

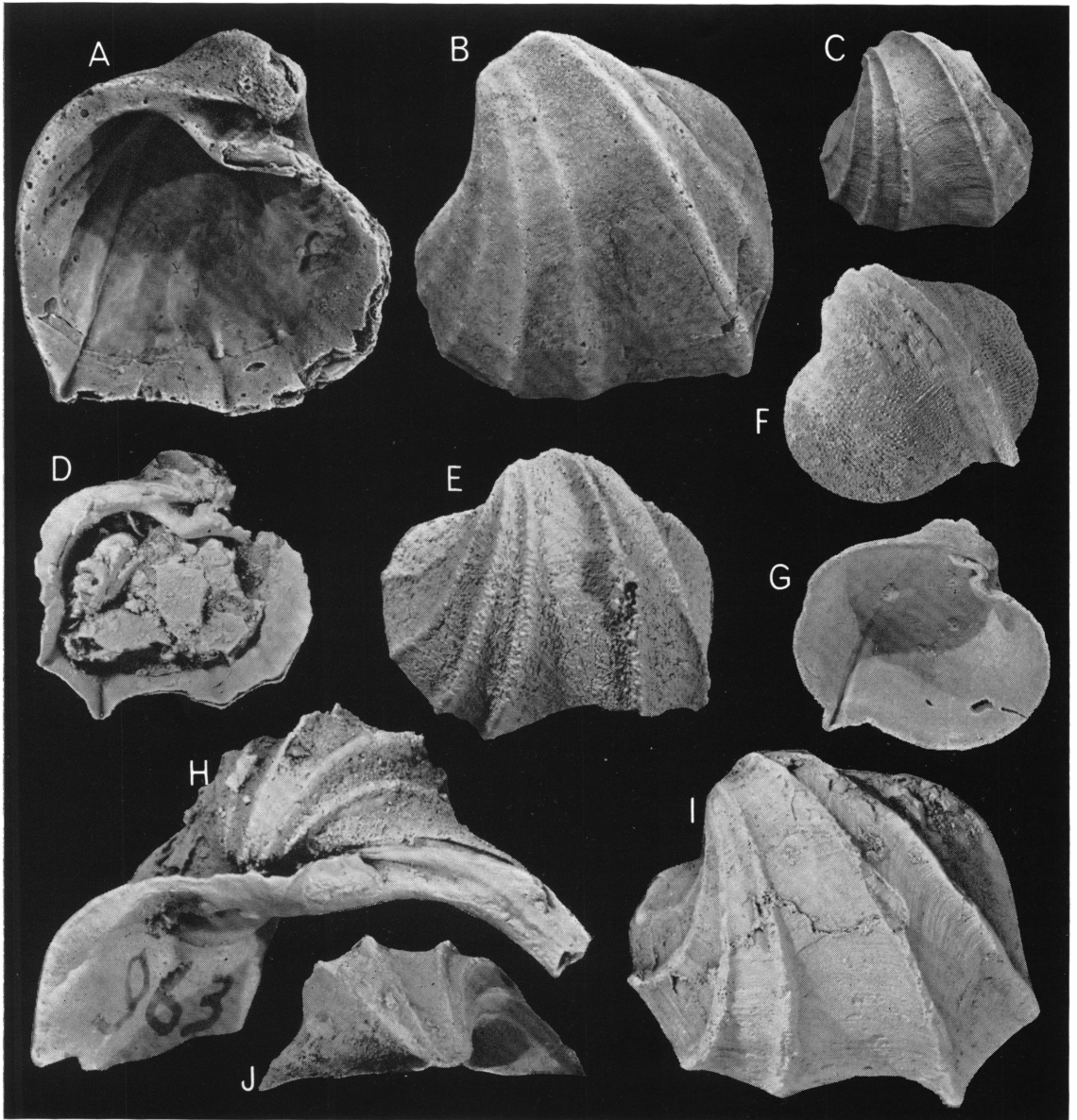


FIG. 11. *Ferrazia cardinalis* Reed, Estrada Nova Formation. A, B. Left valve; compare with *Plesiocyprinella carinata* of figure 8; AMNH 28980, Morro Azul farm, Rio Claro, São Paulo.  $\times 2$ . C. Left valve, DGM 4014, 19+100 km. on railroad between Ferraz and Ajapi, Rio Claro, São Paulo.  $\times 1$ . D. Interior, left valve, DGP7-959, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo.  $\times 0.8$ . E. Left valve, DGM 4409a-1, road near Prudentópolis, Paraná.  $\times 2$ . F, G. An unnamed genus of living Verticordiidae, for comparison with *Ferrazia cardinalis*. Left valve, 495 fathoms off Cagayan Island, Jolo Sea, Philippines, USNM 165745.  $\times 2$ . H. Right valve with single tooth behind beak, DGP 7-963, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo. Approximately  $\times 3.3$ . I, J. Left valve, DGP 7-958, Manoel Pereira Primo property.  $\times 2.0$  and  $\times 1.6$ , respectively.

**TYPE MATERIAL:** Specimens illustrated by Reed (1932), *Pinzonella illusa* assemblage; now kept at the University Museum, Tübingen (not examined).

**DESCRIPTION:** Shell small to medium-sized (attaining a length of 30 mm.), equivalved, anteriorly expanded, tumid, ornamented with 6–9 angular radial plicae, one of which coincides with the posterior umbonal ridge; umbones high, prosogyral, enrolled; lunule and escutcheon absent; valve margins closed; primary ligament opisthodontic, parivincular, external, attached to short robust nymphs; hinge with blunt tooth in right valve and socket in left; lower edge of socket may be thickened, as in *Plesiocyprinella*, to function as second tooth; adductor muscle scars small, subquadrate; posterior scar placed behind umbonal carina; pallial line continuous, without pallial sinus; anterior and posterior pedal retractor scars above adductor scars; protractor and levator scars not observed.

**STRATIGRAPHIC RANGE:** *Pinzonella illusa* assemblage São Paulo (Mendes, 1952, 1962a) and Mato Grosso (Mendes, 1963); *Pinzonella neotropica* assemblage Paraná (USGS locality 22837=locality 17 of Mendes, 1954a, p. 67); Reserva plateau, Paraná (stratigraphic position uncertain).

**DISCUSSION:** When Reed proposed the genus *Ferrazia* he was looking for related Triassic forms and it is hardly surprising that he compared *F. cardinalis* with coarsely ribbed Triassic species now placed in the myophoriid genus *Costatoria*. However, as Reed noted, the hinge of *Ferrazia* is unlike that of any known myophoriid, and the two genera are only grossly homeomorphic. Mendes (1952, p. 82) and Beurlen (1954a) subsequently drew attention to the similarity between the hinges of *Plesiocyprinella* and *Ferrazia*, and there is little doubt that the two genera are closely related. The shell characters of *Ferrazia cardinalis* and *Plesiocyprinella carinata* are essentially the same except that *Ferrazia* is ornamented with 6–9 angular radial plicae, one of which corresponds to the single umbonal carina of *Plesiocyprinella*. In *Ferrazia* this carina may continue ventrally as a short blunt spine [as in *Myonia morrissi* (Runnegar, 1967, pl. 5, fig. 1)]. The differences between *Ferrazia* and *Plesiocyprinella* seem to be equivalent to those between *Costatoria* and *Schizodus* (Myophoriidae), *Halicardissa* and *Halicardia* (Verticordiidae, see Soot-

Ryen, 1966), or *Pleurikodonta* and *Astartila* (Megadesmidae), so that it is reasonable to treat them as separate genera.

*Ferrazia* is remarkably similar in shape to an undescribed living verticordiid genus known from two left valves dredged from 500 fathoms in the Philippines; but the verticordiid genus has only a single keel-like carina, a partly internal ligament, and somewhat different dentition (fig. 11F–G). Its similarity to *Ferrazia* is certainly due to convergence, but the two genera provide an excellent example of the repetition of form within one major lineage.

#### PYRAMUS DANA, 1847

Figure 12

**TYPE SPECIES:** *Pyramus myiformis* Dana, 1847, by subsequent designation of Newell (1956, p. 7).

**OTHER SPECIES:** *Megadesmus laevis* Sowerby, 1838; *Edmondia concentrica* Etheridge, 1872; *Pseudocorbula anceps* Reed, 1935; ?*Angatubia Cowperesoides* Mendes, 1962; *Pyramus planus* Nakazawa and Newell, 1968.

**SYNONYMS:** *Notomya* McCoy, 1847; *Pyramia* Dana, 1849; *Clarkia* de Koninck, 1876; *Cowperesia* Mendes, 1952; ?*Leptoterraia* Beurlen, 1954; ?*Angatubia* Mendes, 1962.

**SUMMARY OF GENERIC CHARACTERS:** Shell oval, equivalved, with low umbones, inwardly directed beaks, and rounded to angular posterior umbonal slopes; lunule and escutcheon narrow, often poorly defined; valve margins closed anteriorly and ventrally but usually with small siphonal gape; shell smooth or with ornament of coarse concentric ribs; ligament opisthodontic, parivincular, external, attached to short dorsally reflected nymphs; hinge virtually edentulous or with variably developed tooth beneath beak of right valve and socket in left; valve margin in front of socket may be thickened to fit beneath corresponding edge of right valve; true lateral teeth absent; adductor muscle scars subequal; pallial line relatively wide, continuous, not extended above adductor scars; pallial sinus small or absent; pedal protractor and anterior and posterior retractor scars present in all species; levator scar present in most species at apex of umbonal cavity.

**DISCUSSION:** *Pyramia* and *Clarkia* have the same type species as *Pyramus* and are therefore objective synonyms. The type species of *Pyramus* and *Notomya* were independently described from the same locality and appear to be conspecific

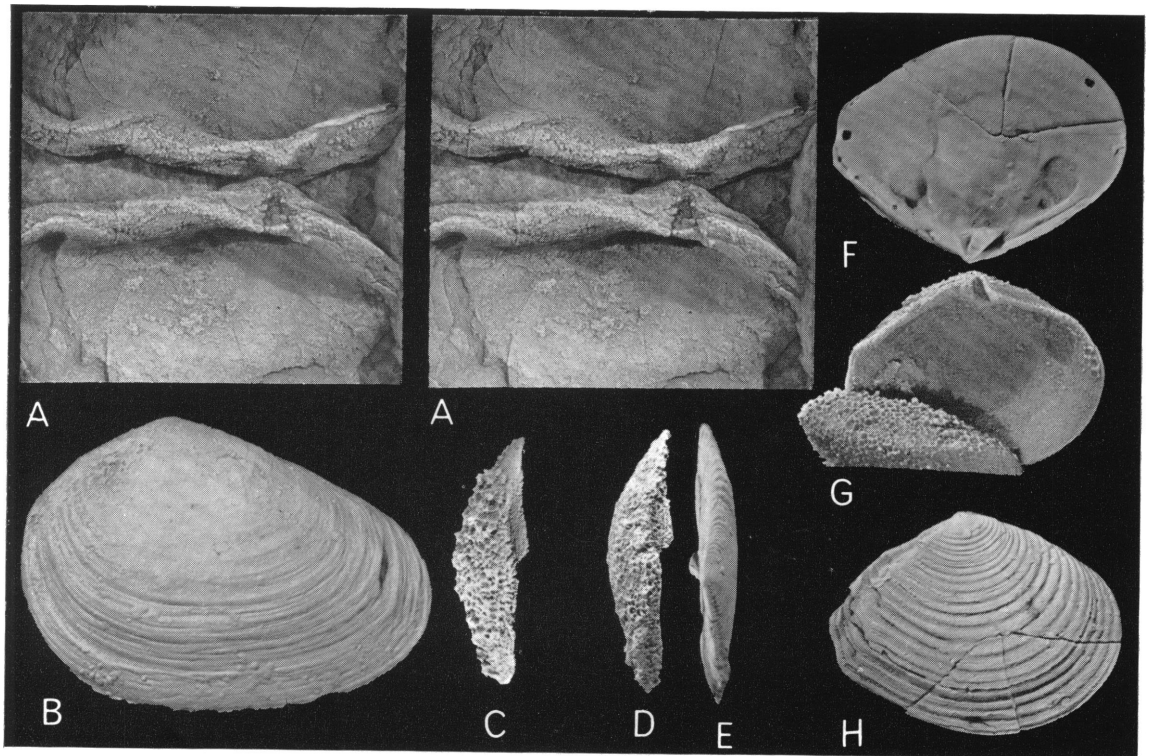


FIG. 12. Genus *Pyramus*. A. *Pyramus concentricus* (Etheridge), Lizzie Creek Volcanics, Lower Permian, Queensland, Australia; stereopair of hinge, CPC 7495, CPC locality SL. 199.  $\times 1$ . B. *Pyramus cowperesoides* (Mendes), type species of ?*Angatubia* Mendes, DGP 7-944, *Pinzonella illusa* assemblage, Estrada Nova Formation, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo.  $\times 3$ . C-H. *Pyramus anceps* (Reed), type species of *Cowperesia* Mendes, *Pinzonella illusa* and *P. neotropica* assemblages, Estrada Nova Formation. E, F, H. Right valve, DGP 7-52, Raven farm, Corumbataí, São Paulo.  $\times 2.5$ . C, G. Left valve, USNM 165746, USGS locality 22831, near Piedra Branca, Ivaí River, 3 km. downstream from Teresa Cristina, Reserva, Paraná.  $\times 2.5$ . D. Left valve, USNM 165747, Estrada Nova Formation.  $\times 2.5$ .

(Newell, 1956; Runnegar, 1967) although some authors have placed them in separate subgenera (Dickins, 1963; Waterhouse, 1965).

The morphology of the type species of *Cowperesia*, *Pseudocorbula anceps* Reed, 1935, is well known from excellently preserved silicified shells from São Paulo and Paraná (Mendes, 1952, 1954a; this paper, fig. 12C-H). *Cowperesia anceps* is similar to Australian species of *Pyramus* in shape and ornament and particularly in the structure of its hinge (fig. 12), but differs in being small and compressed, in having a deeper and much narrower lunule and escutcheon, and in lacking a pedal levator scar. Its pallial sinus is also a little deeper than that of most Australian species and the pallial line is further from the margins of the valves. Undoubtedly, many of

these characters are related to the unusually compressed form of the shell and therefore should not be considered independent differences. (It may, for example, be useful to make a functional comparison between *Cowperesia anceps* and living species of the genus *Pandora* (family Pandoridae), which also have compressed, relatively thick shells, similar external ornament, a withdrawn pallial line, and reflected, overlapping valve margins).

*Pyramus planus* from the Upper Permian of Japan (Nakazawa and Newell, 1968) has a deeper pallial sinus than *Cowperesia anceps* and very small teeth so that both characters are known to vary considerably within the genus. The differences between *C. anceps* and other species of *Pyramus* are probably not as important

as the similarities (shape, ornament, hinge structure, musculature) and *Cowperesia* can be treated as junior subjective synonym.

A second genus from the Paraná Basin, named *Angatubia* by Mendes (1962a), is externally similar to *Pyramus* but lacks hinge teeth. The genus is based on a single species from a *Pinzonella illusa* assemblage in southern São Paulo and is named *cowperesoides* because of its resemblance to "*Cowperesia*" *anceps*. Drawings by Mendes (1962a) suggest that it has feeble teeth of the same type as *Pyramus anceps*, but the specimens are abraded and it is difficult to be certain of the original structure of the hinge. Nevertheless, when the characters available are used, it is difficult to separate *Angatubia* from species of *Pyramus* with poorly developed teeth, and it seems likely that *Angatubia* will prove to be a junior synonym of *Pyramus*.

***Pyramus anceps* (Reed), 1935**

Figure 12C-H

*Anodontophora* aff. *trapezoidalis* Mansuay (pars.): REED, 1928, p. 41, pl. 1, figs. 7, 8.

*Pseudocorbula anceps* REED, 1935, p. 34, pl. 1, figs. 1-3a.

*Pseudocorbula subtriangularis* REED, 1935, p. 35, pl. 1, fig. 4.

*Pseudocorbula anceps*: MENDES, 1944, p. 67.

*Pseudocorbula triangularis* MENDES, 1944, p. 65, pl. 2, fig. 6a, b.

*Pseudocorbula camaquensis* MENDES, 1944, p. 64, pl. 2, figs. 4a, b, 5.

*Cowperesia anceps*: MENDES, 1952, p. 88, pl. 2, fig. 3a, b, pl. 4, figs. 2a-5b; 1954a, p. 94, pl. 2, figs. 1, 7; 1967, pl. 57, figs. 5, 6.

?*Cowperesia* cf. *anceps*: MEZZALIRA, 1957, p. 50.

?*Cowperesia camposi* MENDES, 1962a, p. 48, pl. 1, fig. 1, pl. 2, fig. 3.

**TYPE MATERIAL:** Sedgwick Museum, Cambridge, F1201-5, 1215, 1217, from an assemblage containing *Pinzonella neotropica* in the Terezina lithosome of the Estrada Nova Formation near Rio Claro do Sul, Paraná. The lectotype (here designated) is F12101, an incomplete left valve figured by Reed (1935, pl. 1, fig. 2a, b).

**DESCRIPTION:** Shell small (maximum length generally less than 2 mm.), equivalved, compressed, with low, centrally placed orthogyral beaks; lunule and escutcheon narrow but well-defined; valve margins closed anteriorly and ventrally but with small siphonal gape; ornament of regularly spaced concentric ribs; ligament opisthodontic, parivincular, external, attached to small nymphs set well down in the

escutcheon; hinge with large forwardly inclined triangular tooth beneath beak of right valve and triangular socket in left valve; anterior dorsal margin of left valve thickened to project beneath corresponding edge of right valve; adductor muscle scars relatively small, rounded; pallial line continuous, distant from valve margin, with small but well-defined sinus; anterior and posterior pedal retractor scars well defined, anterior scar often separated from anterior adductor; pedal protractor scar visible in one specimen (fig. 12F) attached to dorsal edge of adductor; levator scar not visible.

**STRATIGRAPHIC RANGE:** *Pinzonella illusa* and *P. neotropica* assemblages, Estrada Nova Formation, São Paulo and Paraná (Mendes, 1952, 1954a).

**DISCUSSION:** The specimens of *Pyramus anceps* illustrated by Mendes (1952) demonstrate the variability of this species. In general, the beaks are further from the anterior margin than they are in other species of *Pyramus*, and the valves are less convex. The dentition is well-developed and in this respect *P. anceps* resembles *P. ?concentricus* from the Lower Permian of eastern Australia (fig. 12A), although the two species clearly differ in shape and external ornament (Runnegar, 1967). A second Australian species, *Pyramus laevis*, has ornament like that in *P. anceps* (Runnegar, 1967) but is much larger and has poorly developed teeth (Runnegar, 1969b).

It is generally agreed that *Pseudocorbula subtriangularis* Reed, 1935, *P. triangularis* Mendes, 1944, and *P. camaquensis* Mendes, 1944 are junior synonyms of *P. anceps* (Mendes, 1952). *Cowperesia camposi* Mendes, 1962a, may also be conspecific as the type specimens resemble Reed's original illustrations of *P. anceps*, and only small differences in external ornament separate the two species.

**LEPTOTERRAIA BEURLLEN, 1954b**

**TYPE SPECIES:** *Pseudocorbula emerita* Reed, 1929, by original designation.

**OTHER SPECIES:** ?*Leptoterraia longissima* Beurlen 1954b for *Anodontophora* aff. *munsteri* Wissmann and *A. cf. recta* Gumbel (Reed, 1929); *Leptoterraia caudata* Beurlen 1954b is a *nomen nudum*.

**TYPE MATERIAL:** Three specimens figured by Reed (1929, pl. 2, figs. 4-6), from the Estrada Nova Formation (Serrinha lithosome) near Serrinha, Paraná; collection of Departamento

Nacional da Producao Mineral, Rio de Janeiro (not examined).

DISCUSSION: The type specimens of *Pseudocorbula emerita* are crushed internal and external molds of a small oval shell with an angular umbonal carina (perhaps accentuated by crushing), and a triangular socket in the left valve (Mendes, 1954a, pl. 3, fig. 9). Mendes (1954a, p. 96) considered *P. emerita* belonged to the genus *Cowperesia*, which if true, would make *Leptoterraia* a junior synonym of *Pyramus*. There is, however, a distinct possibility that the type specimen of *P. emerita* belongs to another species (*Solenomorpha altissima* Holdhaus, 1918) commonly found in the upper part of the Estrada Nova Formation in Paraná. Cox (1934) made *S. altissima* the type species of the genus *Terraia* so that in either case *Leptoterraia* can be suppressed in favor of an older name.

#### JACQUESIA MENDES, 1944

TYPE SPECIES: *Myophoriopsis brasiliense* Reed, 1929. (by original designation).

OTHER SPECIES: *Sanguinolites elongatus* Holdhaus, 1918, p. 16, pl. 1, fig. 13; ?*Holdhausiella almeidai* Mendes, 1952, p. 99, pl. 2, figs. 7-8; *Favalia arcuata* Mendes, 1962, p. 49, pl. 1, figs. 4-6.

SYNONYMS: *Holdhausiella* Mendes, 1952; *Favalia* Mendes, 1962a.

SUMMARY OF GENERIC CHARACTERS: Shell equivalved, carinate, with a shallow lateral sulcus and a characteristically straight dorsal margin in front of the beaks; umbones low to moderately high; prosogyral, approximately one-third of valve length from anterior margin; lunule and escutcheon present in all species but



FIG. 13. *Myonia taoensis* (Reed). Composite internal mold of right valve, USNM 165753, Tubarão Group, Lower Permian, Taio, Municipality Rio do Sul, Santa Catarina.  $\times 0.75$

sometimes poorly defined; valve margins closed, shell smooth: lunular area of right valve thickened, particularly below beak, to project beneath corresponding edge of left valve; ligament opisthodontic, parivincular, external, attached to relatively short nymphs; adductor muscle scars small, subquadrate, posterior scar set high on valve behind umbonal carina; pallial line relatively wide, continuous, without a sinus; anterior and posterior pedal retractor scars well defined, often separated from adductor scars; anterior retractor scar connected to adductor scar by isthmus, probably caused by insertion of pedal protractor muscle; levator muscle apparently absent (musculature known only from type species).

DISCUSSION: Beurlen (1953) drew attention to the similarity of shape and hinge structure to the type species of *Holdhausiella* and *Jacquesia*. He illustrated a species of *Jacquesia* which he considered to be intermediate, and suggested that stratigraphic evidence indicated that *Holdhausiella* gave rise to *Jacquesia*. The information available to us supports this conclusion, but the differences between *Jacquesia brasiliensis* and *Holdhausiella elongata* are small enough so that both species might be accommodated in the same genus. The two species are alike in all characters except degree of valve elongation, a feature we do not regard as significant at the generic level. The differences are equivalent to those between the Australian species *Myonia elongata* and *M. morrisoni* (Runnegar, 1967), and there is a parallel variation in form in the two genera. Some authors (Dickins, 1963; Waterhouse, 1965) have placed *Myonia elongata* and *M. morrisoni* in separate genera (*Myonia* and *Pachymyonia*), and presumably would separate *Jacquesia* and *Holdhausiella*, but we are of the opinion that these differences distinguish species rather than genera, unless it can be shown that two well-defined groups of species are involved. As both *Jacquesia* and *Holdhausiella* contain only one, or at the most two, species it is simpler to consider them synonymous.

Mendes (1962a) proposed a third genus, *Favalia*, for a single species from the lower part of the Estrada Nova Formation in São Paulo. *Favalia arcuata* is similar to "*Holdhausiella*" *elongata* but is a little less inflated and lacks a well-defined tooth in the right valve. These differences are not sufficient to distinguish the two species at a generic level, and *Favalia* is con-



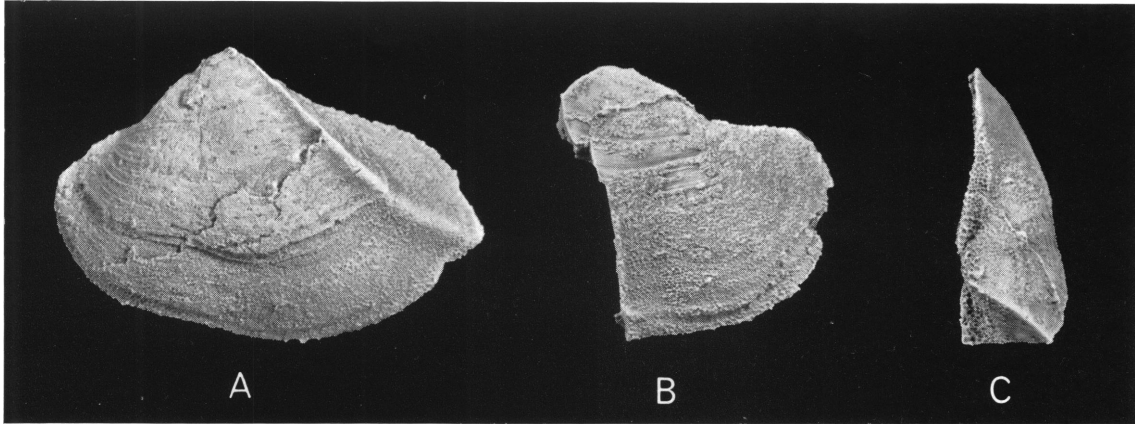


FIG. 14. A-C. *Jacquesia brasiliensis* (Reed), type species of *Jacquesia* Mendes, *Pinzonella neotropica* assemblage, Estrada Nova Formation, on the road ascending Serra Geral from Serra Alto to Lajes, Santa Catarina, USGS locality 2230. A. Left valve, USNM 165748.  $\times 0.8$ . B, C. Right valve shown for comparison with *J. elongata*, USNM 165749.  $\times 1.5$ .

sidered to be a junior synonym of *Holdhausiella* and hence of *Jacquesia*.

*Jacquesia* is externally similar to the Australian genus *Myonia*, except that the anterior part of the shell is expanded (fig. 12B), and the umbones are farther from the front of the shell. The hinge is also different as *Myonia* is edentulous (Runnegar, 1967, pl. 5, fig. 15; 1968, pl. 19, fig. 1), whereas all three species of *Jacquesia* have some form of blunt "tooth" in the right valve. In addition, the type species of *Jacquesia* lacks the pedal levator muscle scar found on the anterior side of the umbonal cavity in all species of *Myonia*.

*Jacquesia elongata* and *J. arcuata* occur below *J. brasiliensis* in the Estrada Nova Formation (Mendes, 1952, 1962b) and it is reasonable to assume that *J. brasiliensis* developed from one of these species. It follows that the oldest species of *Jacquesia* may have been elongate, edentulous shells, similar to the type species of *Myonia* (see Runnegar, 1967). It is therefore interesting to note that *Myonia tayoensis* (Reed), 1930 from the underlying Tubarão Group (fig. 13) is comparable with *Jacquesia arcuata* in shape and conceivably has been the species from which *Jacquesia* developed.

***Jacquesia brasiliensis* (Reed), 1929**  
Figures 14, 15

*Sanguinolites* sp. ind. ?HOLDHAUS, 1918, p. 19, pl. 1, fig. 12.

*Myophoria* (*Myophoriopsis*) aff. *carinata* Bittner: REED, 1928, p. 44, pl. 1, figs. 6, 6a, b.

*Myophoria* (*Myophoriopsis*) aff. *lineata* (Münster): REED, 1928, p. 43, pl. 1, fig. 2.

*Myophoriopsis brasiliense* REED, 1929, p. 73, pl. 5, fig. 1, 1a.

? *Myophoria martialis* REED, 1929, p. 31, pl. 3, figs. 14-17.

*Myophoriopsis brasiliensis*: REED, 1932, p. 485.

*Terraia angusta* REED, 1935, p. 36, pl. 1, fig. 7.

*Terraia martialis*: REED, 1935, p. 36, pl. 1, figs. 6, 6a.

*Jacquesia brasiliensis*: MENDES, 1944, p. 63, pl. 2, figs. 1-3; 1952, p. 107, pl. 3, fig. 3a, b, pl. 4, figs. 8, 9a, b; 1954a, p. 98, pl. 2, figs. 2-3; 1967, pl. 59, figs. 1-3; BEURLEN, 1953, p. 21, pl. 1, figs. 1, 2, text-figs. 1c, 2c.

*Jacquesia carinata* BEURLEN, 1953, p. 24, pl. 1, figs. 3, 4, text-figs. 1a, 2a.

*Jacquesia angusta*: BEURLEN, 1953, p. 22, pl. 1, fig. 6, text-figs. 1b, 2b.

TYPE MATERIAL: Single specimen figured by Reed (1929, pl. 5, fig. 1) from a *Pinzonella neotropica* assemblage, Estrada Nova Formation near Roxo Roiz (now Rio Azul), southern Paraná (Holdhaus, 1918; Mendes, 1954a, pp. 47, 67, 75). Although Reed included a number of other specimens in this species, it is obvious from his description that this specimen should be made the lectotype.

DESCRIPTION: Shell medium-sized (maximum length approximately 40 mm.), equivalved, with subcentral, prosogyral beaks, well-defined lateral sulcus, and carinate umbonal ridge; umbones

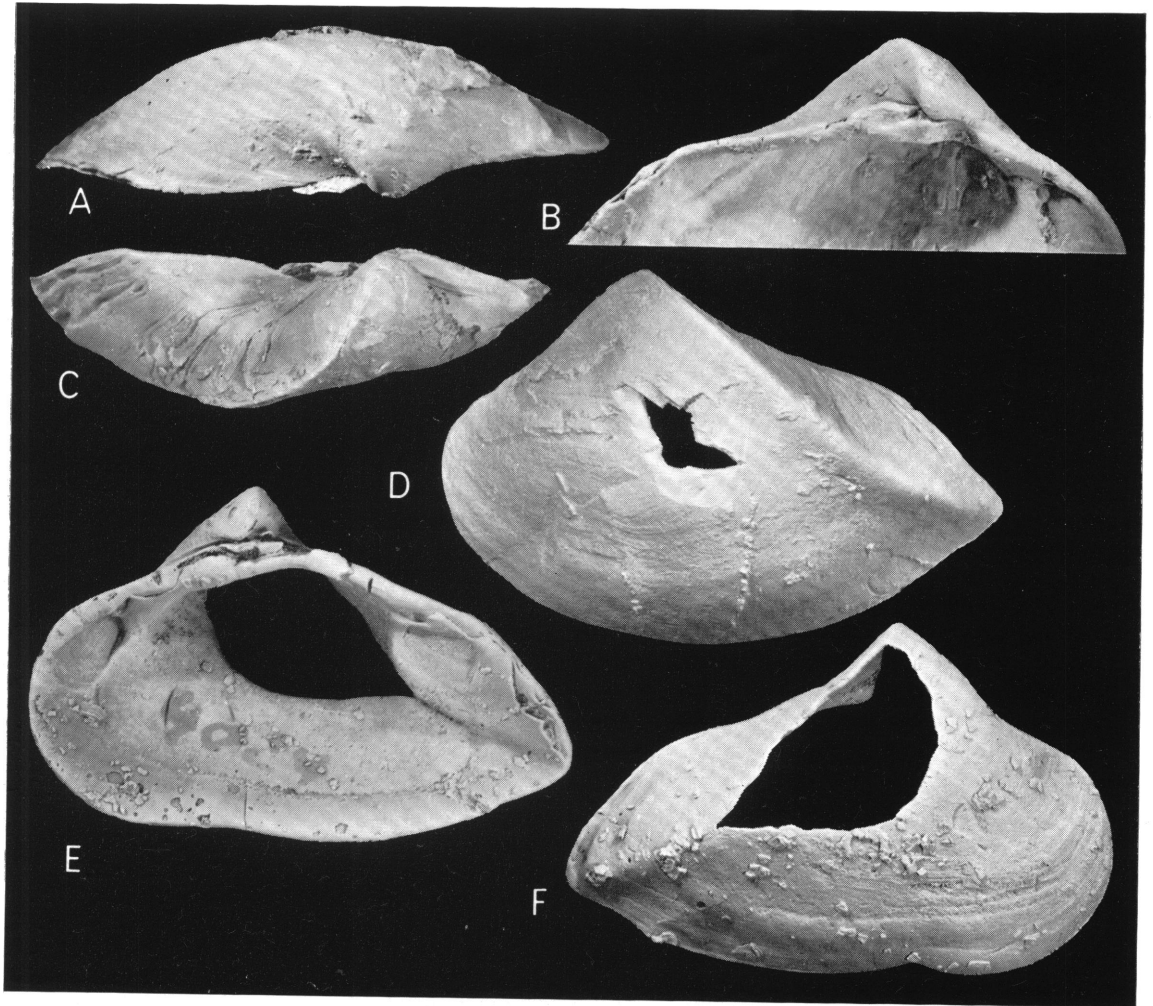


FIG. 15. *Jacquesia brasiliensis* (Reed), type species of *Jacquesia* Mendes, *Pinzonella neotropica* assemblage, Estrada Nova Formation, Sgarboza farm, about 1.5 km. northeast of Corumbataí railroad station, Municipality Rio Claro, São Paulo. A, B. Left valve, DGM 4024.4. C. Right valve, hinge view, DGM 4024.3.  $\times 2$ . D. Left valve, DGM 4024.2. E, F. Right valve, DGM 4024.  $\times 2$ .

moderately high and well defined; anterior umbonal slope distinctly concave in lateral view; lunule and escutcheon present but sometimes poorly defined; valve margins closed; shell generally smooth but area behind umbonal carina may be roughened by irregular growth lamellae; ligament opisthodontic, parivincular, external, supported by short, robust nymphs; lunular area of right valve thickened, particularly below beak, to project beneath corresponding edge of left valve; ventral surface of left valve hinge concave, particularly below beak, to receive thickened edge of right valve; muscula-

ture as for genus.

DISCUSSION: *Jacquesia brasiliensis* is a short, relatively robust species, not easily confused with the elongate shells of *J. elongata* and *J. arcuata*.

In 1944, Mendes placed Reed's species *Myophoria martialis* in synonymy with *J. brasiliensis*, but he subsequently treated it as a separate species (Mendes, 1952, p. 107). We have not had an opportunity to examine the type specimens of *M. martialis*, but Reed's drawings suggest that Mendes may have been correct in uniting the two species. *Terraia angusta* Reed and *Jacquesia*

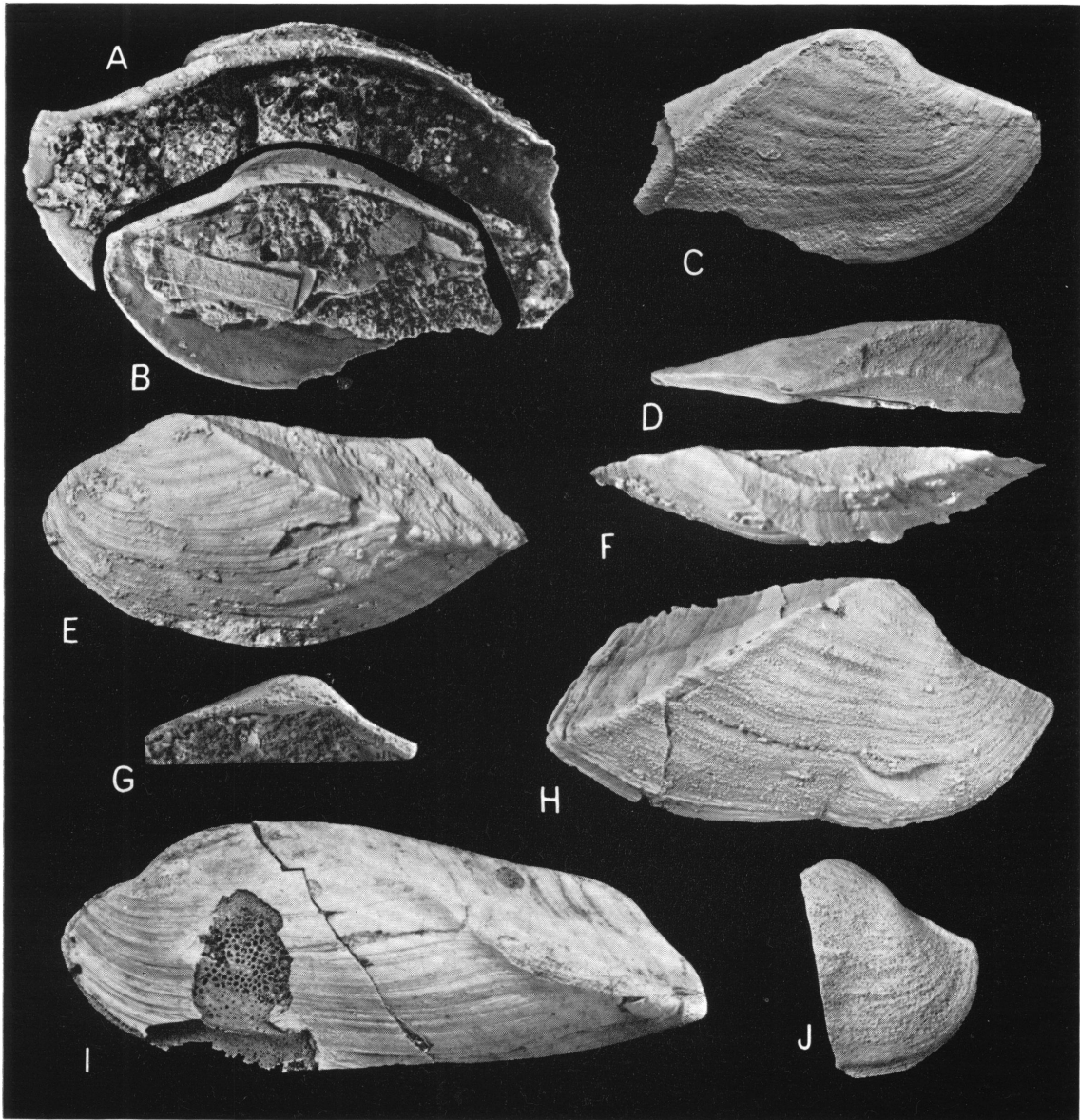


FIG. 16. A-J. *Jacquesia elongata* (Holdhaus), type species of *Holdhausiella* Mendes, *Pinzonella illusa*, and *P. neotropica* assemblages, Estrada Nova Formation. A. Hinge view right valve, DGP 1125, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo.  $\times 4.0$ . B-D. Right valve, USNM 165752, 5 km. west of Bom Successo, Santa Catarina, USGS locality 22825.  $\times 2$ . E, F. Left valve, DGP 7-966, Manoel Pereira Primo property.  $\times 1.8$ . G. Left valve, USNM 165751, 5 km. west of Bom Successo, Santa Catarina.  $\times 1.5$ . H. Right valve, DGP 965, Manoel Pereira Primo property.  $\times 1.7$ . I. Left valve, DGM 4019, Barreiro, Planalto da Reserva, Paraná.  $\times 2.0$ . J. Right valve, USNM 165750, road from Tres Bicos to Reserva, Paraná.  $\times 2$ .

*carinata* are both based on fragmentary and possibly crushed specimens which seem to fit within the limits of variation of *J. brasiliensis*. Accordingly they have been treated as junior synonyms.

***Jacquesia elongata* (Holdhaus), 1918**  
Figure 16

*Sanguinolites elongatus* HOLDHAUS, 1918, p. 16, pl. 1, fig. 13.

?*Pleurophorus* cf. *elongatus* (Moore) non HOLDHAUS:

REED, 1929, p. 79.

?*Pleurophorus* cf. *elongatus* (Moore): REED, 1935, p. 37.

*Pleurophorus* cf. *elongatus* (Moore): MENDES, 1944, p. 53, pl. 1, fig. 4.

*Holdhausiella elongata* (Holdhaus): MENDES, 1952, p. 97, pl. 1, fig. 7a, b, pl. 2, figs. 4-6b, pl. 4, fig. 1; 1954a, p. 97, pl. 2, fig. 5; 1962a, p. 52, pl. 2, figs. 4-5; 1967, pl. 59, fig. 7; MEZZALIRA, 1957, p. 48, pl. 1, fig. 6.

?*Holdhausiella mendesi* BEURLIN, 1953, p. 15, fig. 1f-g.

TYPE MATERIAL: Single specimen figured by Holdhaus (1918, pl. 1, fig. 13) from a *Pinzonella neotropica* assemblage, Estrada Nova Formation, near the Agua Quente River, approximately 15 km. west of Reboucas, southern Paraná (Mendes, 1954a, p. 50).

DESCRIPTION: Shell small to medium-sized (maximum length approximately 45 mm.), equivalved, posteriorly expanded, with shallow lateral sulcus and carinate umbonal ridge; umbones low, prosogyral, posterior umbonal slope convex or slightly concave in lateral view, anterior umbonal slope concave; cardinal margin normally extended in front of beaks to form rounded, angular, or even pointed junction with anterior valve margin; shell smooth; lunule and escutcheon narrow, normally well defined; ligament opisthodontic, parivincular, external, attached to relatively short nymphs; dentition as in *J. brasiliensis* but tooth and socket not as strongly developed; musculature unknown.

STRATIGRAPHIC RANGE: *Leinzia froesi*, *Pinzonella illusa*, and *P. neotropica* assemblages, Estrada Nova Formation, São Paulo and Paraná (Mendes, 1952, 1954a, 1962b; Mezzalira, 1957).

DISCUSSION: The only demonstrable differences between *J. elongata* and *J. brasiliensis* are in shape, as both species have quite similar dentition (figs. 14C; 16A, C, D, G; 15B, E) and a characteristic extension of the anterior cardinal margin. Like *J. brasiliensis*, *J. elongata* differs from Australian and South American species of *Myonia* in having a tooth in the right valve, and in having the anterior part of the shell expanded.

Some specimens of *J. elongata* develop a small winglike extension at the anterior end of the hinge (fig. 16A). It is interesting to speculate whether this wing is functionally analogous to the anterior projection of *Leinzia*, and if so, whether it has any environmental significance. The only living infaunal bivalve known to have

a similar process is the rare Asiatic unionid *Arconaia* Conrad (fig. 24H, I).

### ***Jacquesia arcuata* (Mendes) 1962**

Figure 17A-G

*Favalia arcuata* MENDES, 1962a, p. 49, pl. 1, figs. 4-6, text-fig. 6.

TYPE MATERIAL: The lectotype (here designated) is DGP 7-955 (Mendes, 1962a, pl. 1, fig. 6; this paper fig. 16G) from a *Pinzonella illusa* assemblage, Estrada Nova Formation, near Angatuba, southern São Paulo.

DESCRIPTION: Shell small (maximum length approximately 25 mm.), equivalved, posteriorly expanded, with very shallow lateral sulcus, and rounded to distinctly angular umbonal ridge; umbones low, prosogyral, posterior umbonal slope gently convex to slightly concave; anterior margin rounded, shell smooth; lunule and escutcheon very narrow, not well defined; ligament opisthodontic, parivincular, external, attached to small, narrow nymphs; right valve with obscure thickening below beak which may function as a tooth; hinge of left valve poorly known but apparently edentulous; musculature unknown.

STRATIGRAPHIC RANGE: *Pinzonella illusa* assemblage, Estrada Nova Formation, São Paulo (Mendes, 1962b).

DISCUSSION: Very few specimens of *J. arcuata* have been collected, therefore its internal morphology is not well known. The hinge is almost edentulous but the anterior cardinal margin of the right valve seems to project slightly, as in other species of *Jacquesia*. Externally, *J. arcuata* resembles *J. elongata*, but is distinguished by its less angular umbonal carina, narrower escutcheon and post-carinal area, and less angular anterior valve margin.

### ?FAMILY PHOLADOMYIDAE GRAY, 1847

#### **ROXOA MENDES, 1952**

TYPE SPECIES: *Anoplophora intricans* Mendes, 1944, by original designation.

OTHER SPECIES: *Roxoa corumbataiensis* Mendes, 1952, p. 105, pl. 3, fig. 4; Beurlin, 1954b, p. 105, pl. 3, fig. 4.

#### ***Roxoa intricans* (Mendes), 1944**

Figure 18F-I

*Anoplophora intricans* MENDES, 1944, p. 68, pl. 2, fig. 7.  
*Roxoa intrigans*: MENDES, 1952, p. 104, pl. 3, figs. 8a, b, 11.

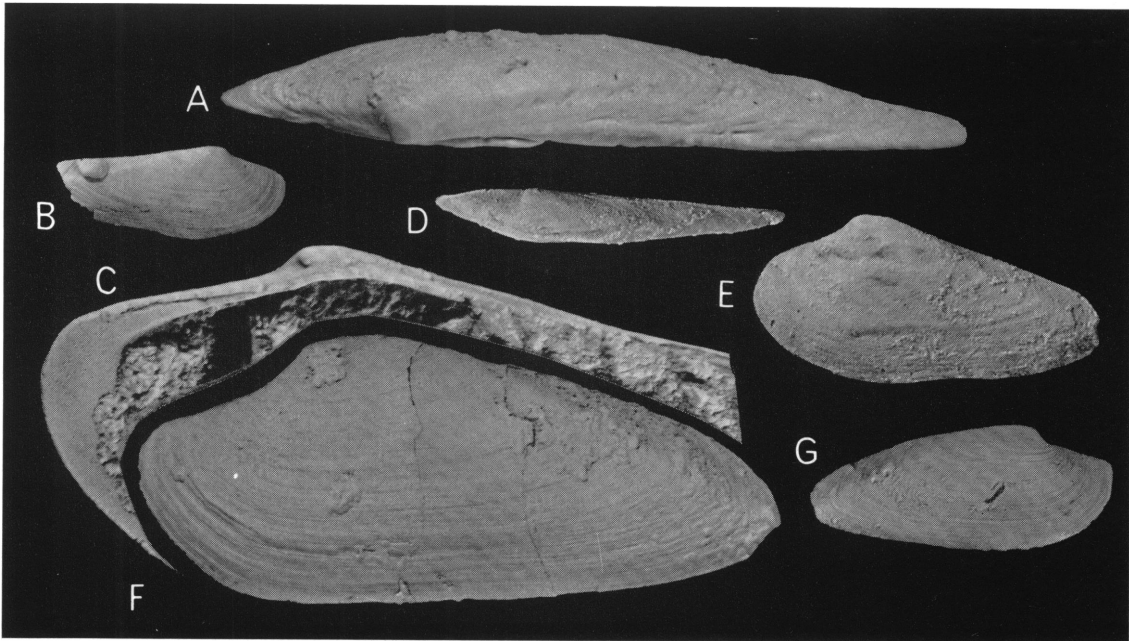


FIG. 17. A-G. *Jacquesia arcuata* (Mendes), type species of *Favalia* Mendes, *Pinzonella illusa* assemblage, Estrada Nova Formation, São Paulo. A. Dorsal view of right valve, DGP 7-954, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo.  $\times 4$ . B. Right valve, DGP 7-954, Manoel Pereira Primo property.  $\times 1$ . C. Right valve hinge, DGP 9-957, Manoel Pereira Primo property.  $\times 4$ . D, E. Left valve, USNM 165754, near Morro Grande, Municipality Rio Claro (USGS locality 22838).  $\times 2$ . F. Left valve, DGP 7-956, Manoel Pereira Primo property.  $\times 3.5$ . G. Lectotype, right valve, DGP 7-955, Manoel Pereira Primo property.  $\times 1.5$ .

**TYPE MATERIAL:** The lectotype (here designated) is DGM4016 (Mendes, 1952, pl. 3, fig. 8; this paper, fig. 18H, I), *Pinzonella neotropica* assemblage, Estrada Nova Formation, Sgarboza farm, about 1.5 km. northeast of Corumbataí railway station, São Paulo (Mendes, 1952, p. 51).

**DESCRIPTION:** Shell smooth, medium-sized (length of lectotype approximately 35 mm.), oval to kidney-shaped, with shallow to deep lateral sulcus and evenly rounded anterior and posterior margins; umbones low, prosogyral, approximately one-third valve length from anterior margin; no lunule or escutcheon; valve margins closed anteriorly and ventrally but apparently with small siphonal gape; ligament external, opisthodontic, parivincular; hinge edentulous; posterior adductor scar relatively small and rounded, anterior scar not observed but presumably similar in size; pallial line con-

tinuous, with deep pallial sinus.

**STRATIGRAPHIC RANGE:** *Pinzonella neotropica* assemblage, Estrada Nova Formation, São Paulo. Very few specimens of *Roxoa* have been recovered from the Estrada Nova Formation, and it is not yet clear whether *R. intricans* and *R. corumbataiensis* should really be treated as distinct species. *Roxoa corumbataiensis* occurs in the *Pinzonella illusa* assemblages in São Paulo.

**DISCUSSION:** *Roxoa* is an edentulous shell with a deep pallial sinus. It differs from *Wilkingia* mainly in having the anterior part of the shell expanded so that the beaks are placed about one-third the shell length from the anterior valve margin. *Roxoa* is thus externally similar to *Mya*, *Panope*, or *Macoma*, and like these genera was probably a deep burrower. The edentulous hinge suggests that *Roxoa* is probably related to *Wilkingia* and we have tentatively included both genera in the same family (*Pholadomyidae*).

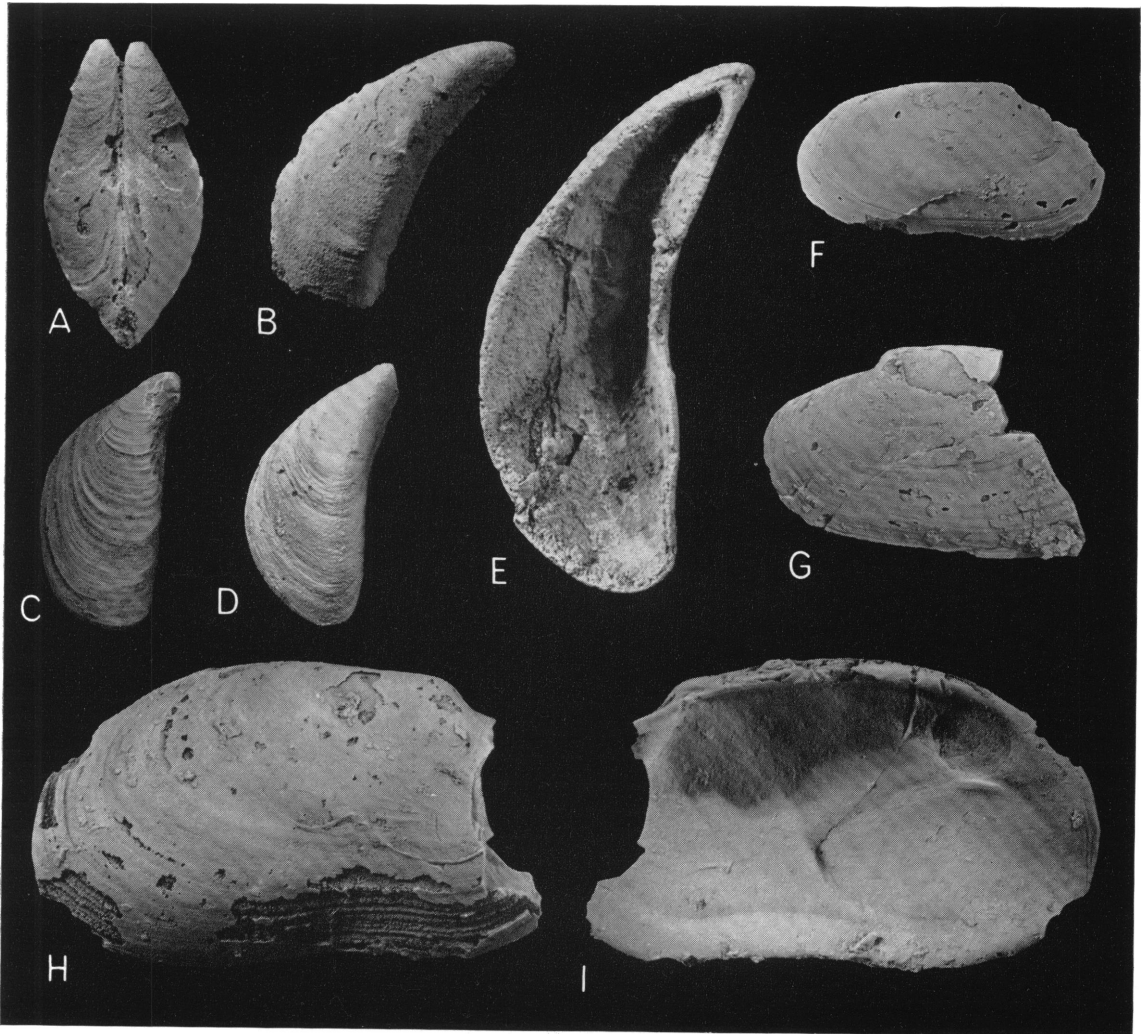


FIG. 18. A, B, D, E. *Coxesia mezzalirai* Mendes, type species of *Coxesia* Mendes *Pinzonella illusa* assemblages, Estrada Nova Formation, São Paulo state. A, B. Articulated specimen, AMNH 28991, Pedra Azul farm, about 6 km. west of Rio Claro.  $\times 3$ . C. *Sinomytilus* sp., USNM 165767, modern fresh-water mytilid for comparison with *Coxesia mezzalirai*.  $\times 3$ . D. Right valve, DGM 4025, 99+100 km. on railroad between Ferraz and Ajapi, Municipality Rio Claro.  $\times 2$ . E. Left valve, interior, DGM 4411, Culik farm, about 2 km. northeast of Ferraz railroad station, Municipality Rio Claro.  $\times 3$ . F-I. *Roxoa intricans* Mendes, type species of *Roxoa* Mendes, *Pinzonella neotropica* assemblage, Estrada Nova Formation, São Paulo state. F. Right valve, DGP 7-64, Roven farm, about 1.5 km. northeast of Corumbataí railroad station, Municipality Rio Claro.  $\times 2$ . G. Anterior part of left valve, AMNH 28990, Camaquan, Municipality Rio Claro.  $\times 1.5$ . H, I. Lectotype, DGM 4016, right valve, Sgarboza farm, about 1.5 km. northeast of Corumbataí railroad station, Municipality Rio Claro.  $\times 2.5$ .

SUBCLASS PTERIOMORPHA  
 ORDER MYTILOIDA  
 SUPERFAMILY MYTILACEA RAFINESQUE,  
 1815  
 FAMILY Mytilidae RAFINESQUE, 1815  
 COXESIA MENDES, 1952

TYPE SPECIES: *Coxesia mezzalirai* Mendes, 1952 by monotypy and original designation.

DISCUSSION: *Coxesia mezzalirai* (fig. 18A, B, D, E) is an equivalved mytilid having a strong external resemblance to living species of the nonmarine dreissenids *Congerina*, *Dreissena*, and

*Mytilopsis*, and the fresh-water mytilids *Sinomytilus* (fig. 18C) and *Limnoperna*. It differs from the Dreissenidae internally, in lacking a stout umbonal septum to support the anterior adductor muscle, and from other late Paleozoic mytilids such as *Promytilus* (Newell, 1942) in lacking a small lobe at the anterior margin of the valve. In lateral view *Coxesia* is thinner, more falcate, and has a more strongly curved (although equivalently angular) umbonal ridge than living species of *Sinomytilus*, characters it shares with the Dreissenidae and the Western Australian estuarine mytilid *Xenostrobus* (Wilson, 1967).

In view of its antiquity, *Coxesia* is probably different from *Sinomytilus* and other similarly shaped living mytilids, most of which seem to inhabit fresh or brackish water. It is also similar in shape to the Jurassic marine mytilid, *Falcimytilus* Cox, but *Falcimytilus* has an even more angular umbonal ridge and is less convex behind the umbonal ridge.

***Coxesia mezzalirai* Mendes, 1952**

Figure 18A, B, D, E

*Coxesia mezzalirai* MENDES, 1952, p. 110, pl. 3, figs. 2a, b; pl. 4, fig. 6; 1967, pl. 57, fig. 9.

**TYPE MATERIAL:** The lectotype (here designated) is DGP 7-36 (Mendes, 1952, pl. 3, figs. 2a, b) from a *Pinzonella illusa* assemblage, Estrada Nova Formation, Culik farm, Ferraz, Municipality Rio Claro, São Paulo.

**Description:** Shell small (maximum length approximately 20 mm.), equivalved, strongly falcate, with terminal beaks, and slightly to strongly curved umbonal ridge; ligament apparently of type found in *Mytilus*; teeth or denticles appear to be absent; musculature not observed.

**DISCUSSION:** *Coxesia* is a very rare component of the Estrada Nova faunas, and so far has only been confidently identified from the *Pinzonella illusa* assemblages of São Paulo. It cannot be readily confused with other late Paleozoic mytilids.

**SUBCLASS HETERODONTA  
ORDER VENEROIDA**

**SUPERFAMILY CRASSATELLACEA  
FÉRUSAC, 1822**

**FAMILY ASTARTIDAE D'ORBIGNY, 1844**

**SUBFAMILY PINZONELLINAE BEURLEN,  
1954**

**PINZONELLA REED, 1932**

**TYPE SPECIES:** *Pinzonella illusa* Reed, 1932, by subsequent designation of Mendes (1952, p. 72).

**OTHER SPECIES:** *Pachycardia neotropica* Reed, 1928, p. 44, pl. 1, figs. 3, 3a, b.

**SYNONYM:** *Pinzonellopsis* Mendes, 1944.

**DISCUSSION:** *Pinzonella illusa* is a small equivalved shell, externally similar to *Astartella*, with large, sometimes radially striated cardinal teeth and an obscure posterior lateral socket in the left valve. The posterior edge of the right valve fits into this socket so that the edge of the left valve slightly overlaps that of the right. The ligament is small, parivincular, and external, set in a well-defined escutcheon; a lunule is present but is poorly defined. As in *Astartella*, an obscure umbonal carina runs from the beaks to the posterior ventral margin.

The adductor scars are small, equally impressed, and subequal; a large pedal retractor scar occurs above each adductor scar, and a row of several small muscle pits occurs in the umbonal cavity. The internal margins of the valves are not denticulate.

*Pinzonella neotropica* is similar to *P. illusa* but is slightly inequivalved and triangular rather than oval in outline. The hinge plate of the left valve is interrupted by a deep notch which corresponds to the posterior cardinal socket of *P. illusa*. Both species are now placed in the same genus. When Mendes first studied the fauna of the Estrada Nova Formation, however, he recognized five species, two of which (*P. similis* Reed, 1929 and *P. trigonia* Mendes, 1944) are closely related to *P. illusa*, and one (*P. occidentalis* Reed, 1929) that is similar to *P. neotropica*. Mendes believed that the differences between the two groups of species were sufficient to distinguish them generically, and he made *P. occidentalis* the type species of a new genus, *Pinzonellopsis*. It is very much to Mendes's credit that he was subsequently able to show painstakingly that three of the five specific names are junior synonyms, and that only two variable species, *P. illusa* and *P. neotropica*, are present in the Estrada Nova Formation (Mendes and Petri, 1950; Mendes, 1952). He therefore recommended that the name *Pinzonellopsis* be suppressed as a junior synonym of *Pinzonella*.

In the only well-established sequence containing both *Pinzonella illusa* and *P. neotropica* (southern and central São Paulo), *P. illusa* invariably occurs beneath *P. neotropica* (Mendes, 1952; Mezzalira, 1957), and it is probable *P. neotropica* developed from the older species.

*Pinzonella illusa* should therefore be closer to the form from which *Pinzonella* is derived.

As small overlap of the type found in *P. illusa* is unknown in paleoheterodont stocks (unionids, trigonioids), *Pinzonella* is probably related either to late Paleozoic carditacean genera such as *Permophorus*, or to the conservative Astartellinae; its similarity in shape to *Astartella* suggests the latter group. The relatively small size of *Pinzonella illusa*, its obscure umbonal ridge and sub-rectangular posterior valve margin are characteristic features found in many species of *Astartella*. The dorsal accessory musculature of *Astartella* is not well known, but a series of small muscle pits like those of *P. illusa* are present in at least one Tertiary astartid (J. Pojeta, Jr., personal commun.).

The dentition of *P. illusa* could be derived from that of late Paleozoic astartids such as *Astartella vera* (Boyd and Newell, 1968, fig. 6) by reducing the lateral teeth and enlarging the cardinal teeth. The enlargement of the cardinal teeth seems to result in a breakdown of the hinge plate, particularly in the left valve.

Boyd and Newell (1968) have introduced the subfamily Astartellinae for late Paleozoic astartid genera which have fewer cardinal teeth than in Mesozoic and Cenozoic astartids, and slightly different anterior lateral dentition. The morphological differences between *Pinzonella* and *Astartella* are greater than those between *Astartella* and *Astarte*, and it could be argued that they should be placed in separate families. However, there is a significant morphological gap between *P. neotropica* and *P. illusa*, and it is reasonable to assume that *Pinzonella* was a rapidly evolving, variable genus. For this reason we have decided to refer it to a separate subfamily of the Astartidae rather than to a different family.

***Pinzonella illusa* Reed, 1932**

Figure 19A–D, H–N

*Pinzonella illusa* REED, 1932, p. 482, pl. 19, figs. 6–11.

MENDES, 1944, p. 49; 1952, p. 75, pl. 1, figs. 2a, b, 3a, b, 4; 1962a, p. 53, pl. 1, fig. 9; 1963, fig. 2; 1967, pl. 57, fig. 4. BEURLEN, 1954b, pl. 1, fig. 1a, b.

*Pinzonella similis* REED, 1932, p. 484, pl. 19, figs. 12, 12a; 1935, p. 38. MENDES, 1944, p. 49, pl. 1, fig. 3. ?*Pinzonella* cf. *illusa*: REED, 1935, p. 41, pl. 1, figs. 13, 13a.

*Pinzonella trigonia* MENDES, 1944, p. 48, pl. 1, figs. 1, 2a, b.

*Pinzonella* cf. *illusa*: MEZZALIRA, 1957, p. 50.

TYPE MATERIAL: University Museum, Tübingen (not examined); specimens figured by Reed (1932) from *Pinzonella illusa* assemblage, middle part of Estrada Nova Formation between Ferraz and "Morro Grande," Municipality Rio Claro, São Paulo. (Details of the fossil localities in this area are given by Mendes (1952)).

DESCRIPTION: Shell small (maximum length approximately 25 mm.), equivalved, oval; umbones rounded, prosogyral, poorly defined umbonal ridge, and well-defined, wide escutcheon; as in *Astartella* (fig. 19E–G) escutcheon long and ridge defining it extends to posterior margin of shell; posterior valve margin rounded to almost square, and anterior and ventral margins rounded; lunule present but poorly defined; valve margins closed; shell smooth anteriorly but roughened behind umbonal ridge by projecting imbricate growth lamellae; no lateral sulcus but obscure ridge occurs in corresponding position on inside of valves; ligament external, opisthodontic, parivincular, attached to short narrow nymphs; hinge plate of right valve has large bulbous tooth below beak, separated by shallow socket from anterior edge of valve; behind tooth is a deep socket, bordered posteriorly by obscure cardinal tooth that lies beneath ligament nymph; left valve hinge plate has, correspondingly, two well-defined sockets separated by a strong tooth and small tooth below ligament nymph; in some specimens there may also be a small tooth near anterior valve margin, but true anterior lateral teeth absent; most well-preserved left valves have obscure posterior lateral tooth behind ligament groove; this tooth best seen in dorsal view parallel to commissure because it projects slightly beyond edge of valve; posterior edge of right valve functions as lateral tooth and fits beneath corresponding edge of left valve (fig. 19A, K, N); ventral surface may be slightly concave to leave room for tooth in left valve. From Boyd and Newell's (1968) terminology, the hinge formula may be written as follows:

	RV lo-nOIOIo				
Posterior					Anterior
	LV IOl-nloIOl				

Adductor muscle scars small, circular, anterior scar deeply impressed; pallial line narrow, continuous, without pallial sinus; relatively



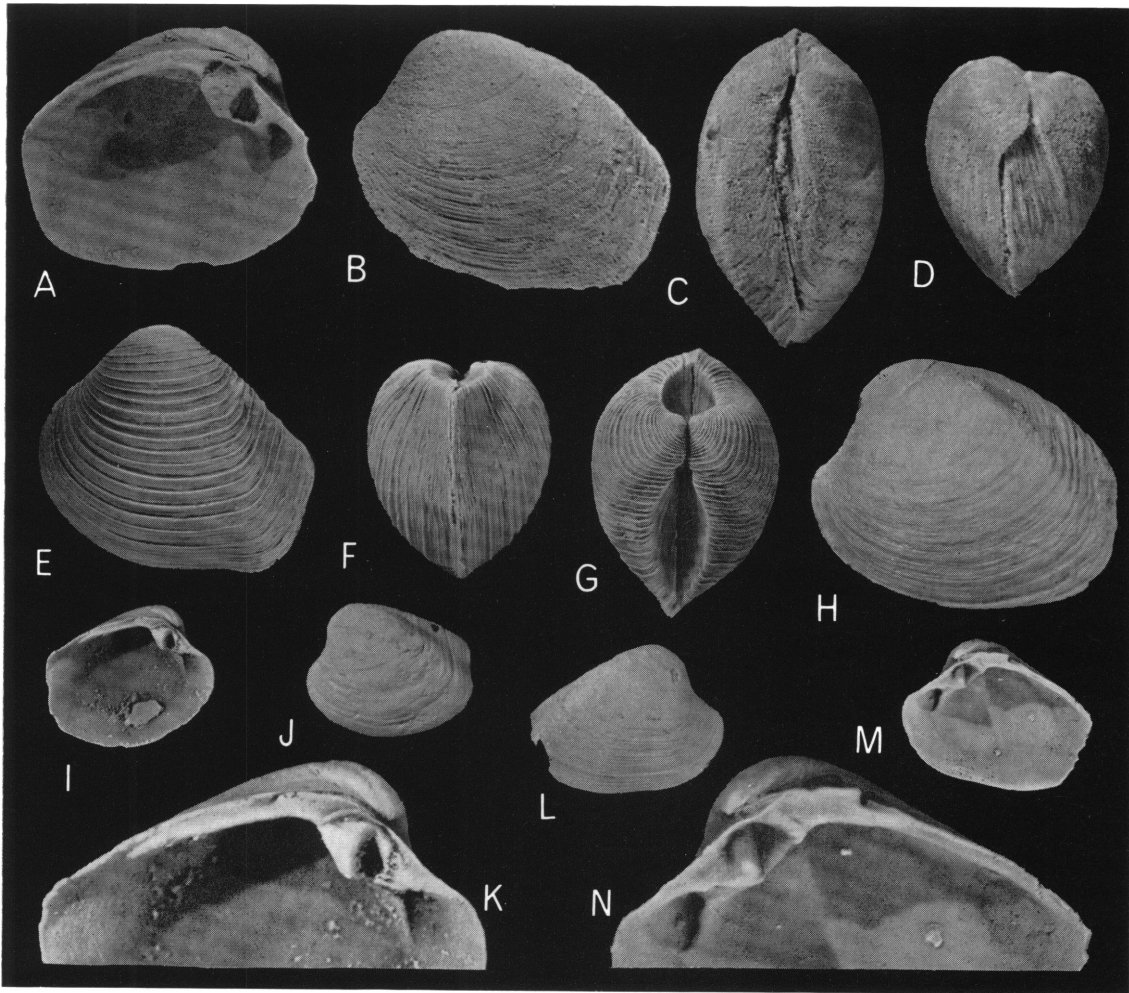


FIG. 19. A–D, H–N. *Pinzonella illusa* Reed, type species of *Pinzonella* Reed, Estrada Nova Formation, state of São Paulo. A. Interior of left valve, AMNH 28981, Culik farm, about 2 km. northeast of Ferraz railroad station, Municipality Rio Claro.  $\times 2$ . B–D. An articulated specimen, AMNH 28982, Culik farm, about 2 km. northeast of Ferraz railroad station, Municipality Rio Claro,  $\times 3$ . E–G. *Astartella vera* Hall, USNM 165755, Graford Formation, Upper Pennsylvanian, near Martin's Lake, 2 km. southwest of Bridgeport, Texas, figured for comparison.  $\times 2$ . H. Left valve, *Pinzonella illusa* Reed, DGM 4415–1, 19+100 km. on railroad between Ferraz and Ajapi, Municipality Rio Claro,  $\times 1.6$ . I, J. Left valve, DGP, uncatalogued, Manoel Pereira Primo property, Buenos District, near Angatuba, São Paulo.  $\times 2$ . K. Same as I, J.  $\times 5$ . L, M. Right valve, AMNH 28983, Manoel Pereira Primo property.  $\times 2$ . N. Same as L, M.  $\times 5$ .

large anterior and posterior pedal retractor scars above adductor scars, anterior pedal scar situated on lower edge of hinge plate as in living heterodonts like *Mercenaria*; from three to five small irregular scars on anterior side of umbonal cavity that may have supported foot and/or viscera.

STRATIGRAPHIC RANGE: *Pinzonella illusa* and

*Leinzia froesi* assemblages, lower and middle parts of the Estrada Nova Formation, São Paulo (Mendes, 1949, 1952, 1962b; Mezzalira, 1957) and Mato Grosso (Mendes, 1963).

DISCUSSION: The shape of *Pinzonella illusa* readily distinguishes it from *P. neotropica* (figs. 19A, 20E), and only poorly preserved specimens are likely to be confused.

***Pinzonella neotropica* (Reed), 1928**

Figure 20

*Pachycardia neotropica* REED, 1928, p. 44, pl. 1, figs. 3, 3a, b; 1929, p. 71, pl. 5, figs. 2-6a, 1932, p. 485; 1935, p. 37.

*Pachycardia* aff. *rugosa* HAUER: REED, 1928, p. 40, pl. 1, fig. 1.

*Pachycardia rugosa* Hauer var. *occidentalis* REED, 1929, p. 71, pl. 5, figs. 7-10; 1932, p. 485.

*Pinzonellopsis occidentalis*: MENDES, 1944, p. 60, pl. 1, fig. 7a, b.

*Pinzonella neotropica*: MENDES, 1952, p. 77, pl. 1, fig. 5a, b, pl. 2, figs. 1, 2a, b; 1954a, p. 107, pl. 2, figs. 4, 6; 1967, pl. 57, figs. 1-3.

*Pinzonella (Pinzonella) elongata* BEURLEN, 1954c, p. 13, pl. 3, fig. 5; pl. 4, figs. 6, 8.

**TYPE MATERIAL:** The lectotype (here designated) is the single specimen figured by Reed (1928, pl. 1, figs. 3, 3a, b) from the Terezina lithosome, Estrada Nova Formation, "a few kilometers" to the west of Rio Claro do Sul, Paraná.

**DESCRIPTION:** Shell small to medium-sized (maximum length approximately 30 mm.), sub-triangular, with obvious prosogyral beaks and well-defined escutcheon; posterior valve margin rounded to pointed in lateral view, anterior margin rounded; lunule present but poorly defined; valve margins closed; ornament consisting of scattered, well-defined growth lamellae; shallow lateral sulcus and obvious thickening of corresponding part of shell interior (fig. 20B); valves slightly different in shape but apparently similar in size; umbo of left valve higher and more strongly enrolled than that of right valve (fig. 20B, E) and umbonal ridge better defined (fig. 20B, E) and umbonal ridge better defined on left valve; ligament external, opisthodontic, parivincular, attached to short dorsally reflected nymphs; hinge plate of right valve has large triangular cardinal tooth followed posteriorly by deep socket; posterior edge of socket may also function as cardinal tooth; left valve has, correspondingly bulbous cardinal tooth surrounded on each side by deep sockets; as in right valve there are no lateral teeth, but lower edge of ligament nymph may function as small cardinal tooth. From Boyd and Newell's (1968) terminology, the hinge formula may be written as follows:

	RV	nIOI	
Posterior			Anterior
	LV	nOIO	

The adductor muscle scars small and circular; anterior scar deeply impressed; well-defined

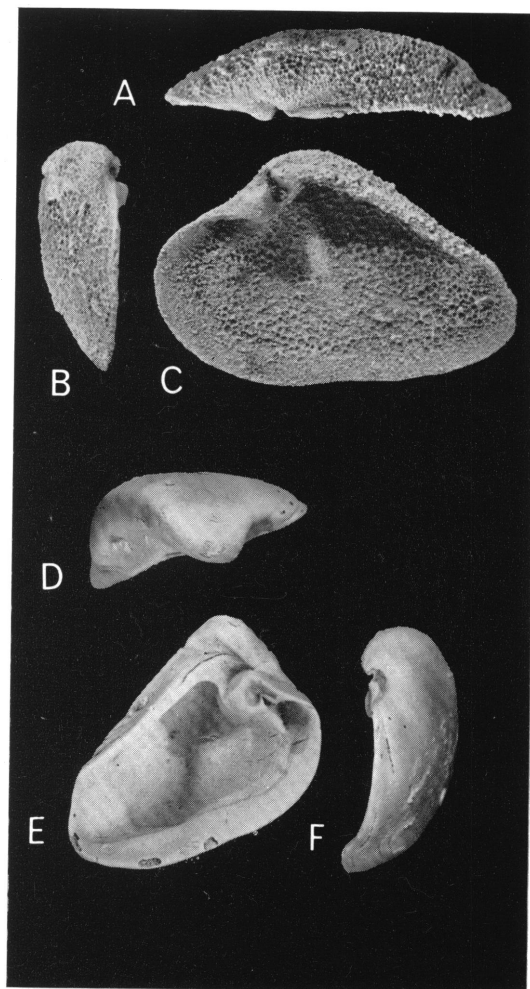


FIG. 20. *Pinzonella neotropica* (Reed), type species of *Pinzonellopsis* Mendes, middle and upper Estrada Nova Formation, states of São Paulo and Paraná. A-C. Right valve with impressions of oolite grains, USNM 165756, Piedra Branca, Ivaí River, about 3 km. downstream from Teresa Cristina, Reserva, Paraná.  $\times 2$ . D-F. Left valve, AMNH 28985, Sgarboza farm, about 1.5 km. northeast of Corumbataí railroad station, Municipality Rio Claro, São Paulo state.  $\times 2$ .

pedal retractor scars occur above each adductor scar and short row of pedal or visceral muscle scars present on anterior side of umbonal cavity; pallial line thin, continuous, not extended above adductor scars, and without pallial sinus.

**STRATIGRAPHIC RANGE:** Middle part of the Estrada Nova Formation, São Paulo, Paraná, and Santa Catarina (Mendes, 1952, 1954a;

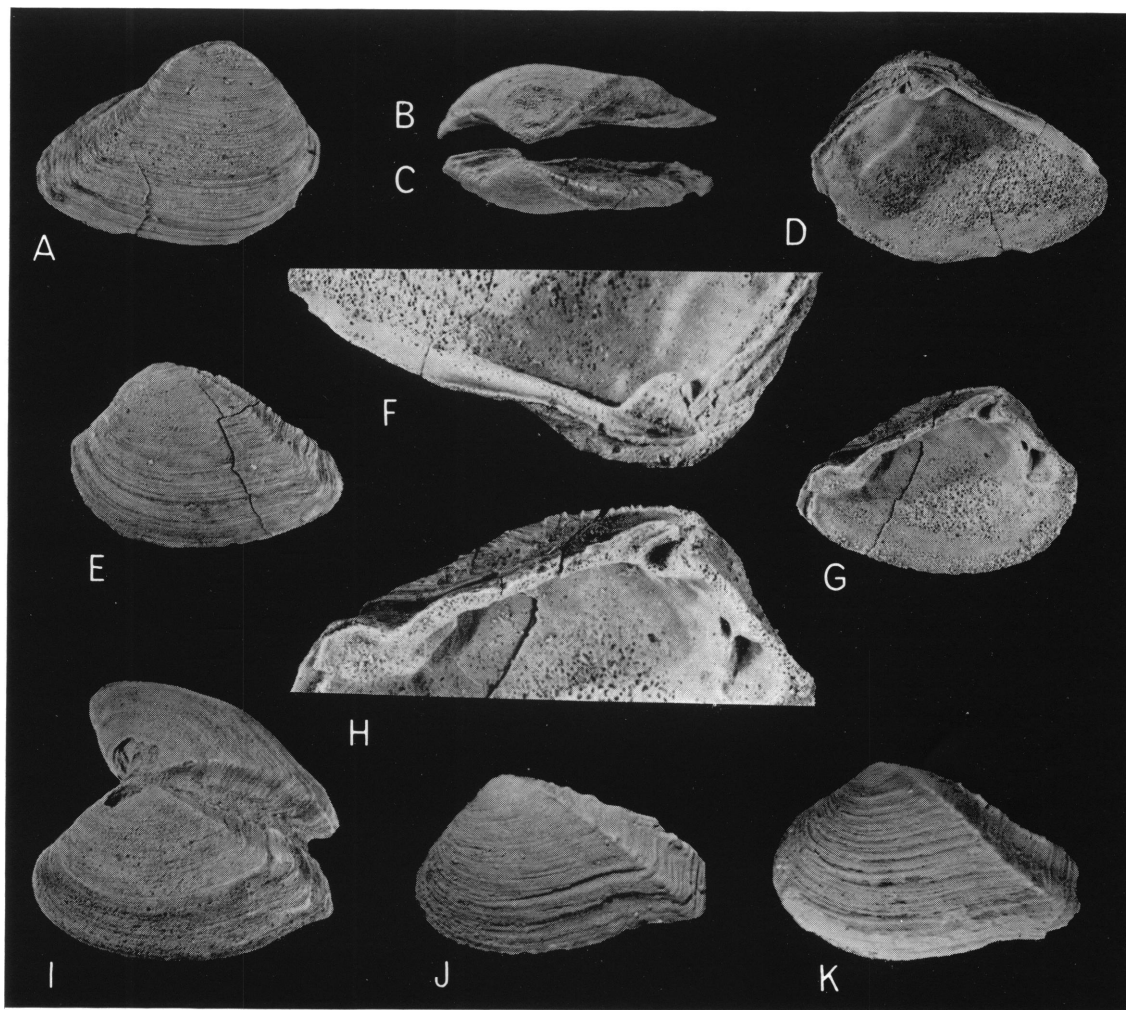


FIG. 21. *Terraia altissima* (Holdhaus), type species of both *Terraia* Cox and *Terraioipsis* Beurlen, Passa Dois Group, near Cerro hospital, right bank of Rio Negro, northern Uruguay. A, B, D. Right valve, BMNH L61069.  $\times 2.20$ . F. Right valve, BMNH L61069.  $\times 4$ . C, E, G. Left valve, BMNH L61070.  $\times 2.20$ . H. Left valve, BMNH L61070.  $\times 4.2$ . I. Articulated specimen, AMNH 28986.  $\times 2$ . J, K. Left valves, FAC Pal. 1868 and 1869, respectively.  $\times 2$ .

USGS collections). It is possible that a badly preserved left valve from Paraguay figured by Reed (1935, pl. 1, figs. 13, 13a) also belongs to this species.

DISCUSSION: Beurlen's rather poorly illustrated species *Pinzonella elongata* is based on three valves from the Terezina lithosome of the Estrada Nova Formation between Prudentópolis and Teresa Cristina, Paraná. These specimens appear to belong to *P. neotropica* which is common at localities in this area.

In 1957, Mezzalira illustrated two very small

shells from the lower part of the Estrada Nova Formation in northeastern São Paulo which he referred to *P. elongata*. We have five similar valves from a *Pinzonella illusa* assemblage, Pedra Azul farm, Municipality Rio Claro, São Paulo, and it seems possible that these and Mezzalira's specimens may belong to an undescribed species of *Pinzonella*. However, as all the available specimens are very small, they may only be unusually elongate juvenile specimens of *P. illusa*. So far as we know, *P. illusa* and *P. neotropica* do not occur at the same locality.

## FAMILY UNCERTAIN

## TERRAIA COX, 1934

TYPE SPECIES: *Solenomorpha altissima* Holdhaus, 1918, by original designation.

OTHER SPECIES: ?*Pleurophorus bipleura* Reed, 1929, p. 47, pl. 4, figs. 8-10; *Terraia aequilateralis* Mendes, 1952, p. 92, pl. 1, figs. 8a, b; 9; *Terraia lamegoi* Mendes, 1954a, p. 111, pl. 2, fig. 12; pl. 3, fig. 1; ?*Terraia*? *erichseni* Mendes, 1954a, p. 112, pl. 3, fig. 2, the last two species known only from fragments.

SYNONYM: *Terraioopsis* Beurlen, 1954b.

DISCUSSION: When Cox proposed *Terraia* he made "the species here identified with *Solenomorpha altissima* Holdhaus" the type species. Beurlen (1954b) believed the specimens Cox was referring to belonged to a different genus so that he made *Solenomorpha altissima* Holdhaus non Cox the type species of a new genus, *Terraioopsis*. However, as zoological nomenclature can only be concerned with the names applied to taxa, Cox's designation of *Solenomorpha altissima* Holdhaus as the type species is valid, and *Terraioopsis* is a junior objective synonym.

The type locality of *Terraia altissima* is in the Serrinha lithosome of the Estrada Nova Formation in southern Paraná. Unfortunately, most specimens which have been collected from this rock unit are poorly preserved and many critical features, including the structure of the hinge, are not well known. The specimens figured by Cox (1934; this paper fig. 21A-F, G, I) from near Cerro Hospital, northern Uruguay, are well preserved and appear to belong to the same species (Mendes, 1954a), despite Beurlen's assertions to the contrary. We have therefore based our understanding of *Terraia altissima* on a small collection from the Uruguayan locality (fig. 21A-K).

An older, excellently preserved species named *Terraia aequilateralis* by Mendes (1952) occurs in the lower part of the Estrada Nova Formation in São Paulo. *Terraia aequilateralis* resembles *T. altissima* in having a large triangular tooth in the right valve and a deep socket in the left valve, but differs in its *Donax*-like shape and in lacking a well-defined escutcheon. The similarity in the hinges of the two species (figs. 21, 22) suggests that they are congeneric even though *T. altissima* has an obscure posterior lateral tooth that is missing from *T. aequilateralis*.

A third, less well-known species, *Terraia bi-*

*pleura* (Reed) (fig. 23A, B) also has a similar hinge; this species is important because it appears to be intermediate between *T. altissima* and *Leinzia similis* (fig. 17A-E). All three species have a large triangular cardinal tooth in the right valve, bordered posteriorly by a narrow cardinal socket, and anteriorly by a long shallow depression which apparently receives the corresponding edge of the left valve (figs. 21D, F; 24G). From Boyd and Newell's (1968) notation, the hinge formulas for the three species may be written as follows:

		<i>Terraia altissima</i>
	RV	IOI—nloIol—I
Posterior		
	LV	I—noIolo—I
		<i>Terraia bipleura</i>
	RV	IOI—nloI—I
		<i>Leinzia similis</i>
	RV	?—n?OI—Iol
	LV	I—noIol—I

Similarity in the hinges of these three species, together with their gross resemblance in shape, suggests that *Terraia* and *Leinzia* may be related, and we are tentatively placing them in the same family, but the affinities of this family are uncertain. The only late Paleozoic shell with comparable dentition seems to be the North American Permian genus *Alula* Girty (fig. 27), which, like *Terraia altissima*, has anterior and posterior lateral sockets on either side of a massive cardinal tooth in the right valve. *Alula* is also difficult to classify because it is not clearly related to other well-defined heterodont or palaeoheterodont stocks, so that it is even more difficult to determine the origin of *Leinzia* and *Terraia*.

SUMMARY OF GENERIC CHARACTERS: Shell medium-sized, triangular, equivalved, with centrally placed beaks and angular carina extending from beaks to posterior ventral margin beaks prosogyral or orthogyral; well-defined escutcheon or second umbonal carina present in two species; lunule absent; valve margins; closed; shell smooth except for irregular fine growth lines; ligament opisthodontic, parivincular, external, attached to short, dorsally reflected nymphs; hinge with large triangular cardinal tooth in right valve and corresponding deep-floored socket in left valve; tooth and socket followed posteriorly by one or more small cardinal teeth; obscure posterior lateral tooth

and socket in right valve of type species but not present in other species; anterior lateral socket well defined in right valve of all species, to receive thickened margin of left valve; adductor muscle scars subequal, deeply impressed, each normally separated from well-defined pedal retractor scars; protractor and levator scars not observed; pallial line thin, continuous, without sinus.

***Terraia altissima*** (Holdhaus), 1918

Figure 21

*Solenomorpha altissima* HOLDHAUS, 1918, p. 12, pl. 1, figs. 8-10.

*Isocyprina reducta* REED, 1929, p. 41, pl. 1, figs. 11-17.

*Terraia altissima*: COX, 1934, p. 271, pl. 10, figs. 1a-c; 2a, b, 4, 5. MENDES, 1944, p. 51; 1954a, p. 109, pl. 3, figs. 3, 7, 10, 11.

*Terraioopsis altissima*: MENDES, 1967, pl. 57, fig. 11.<sup>1</sup>

**TYPE MATERIAL:** Specimens figured by Holdhaus (1918) from the upper part of the Estrada Nova Formation, approximately 6 km. northwest of Mallét, southern Paraná (details of the locality are given by Holdhaus, 1918 (and accompanying map) and Mendes, 1949, p. 22).

**DESCRIPTION:** Shell relatively small (maximum length approximately 25 mm.), equivalved, with two well-defined posterior umbonal carinae, inner of which delimits a long and relatively deep escutcheon; beaks relatively low, prosogyral; valve margins closed; ornament consisting of irregularly spaced growth lines which may become distinctly lamellose behind umbonal carina; ligament opisthodic, parivincular, external, attached to small, dorsally reflected nymphs; hinge with large triangular cardinal tooth in right valve and a second obscure tooth between large tooth and ligament nymph; left valve has, correspondingly, obvious triangular socket bordered posteriorly by narrow tooth and socket; anterior and posterior dorsal margins of left valve function as lateral teeth by fitting beneath edges of right valve; obscure posterior lateral tooth present in right valve but no corresponding tooth below anterior lateral socket. From Boyd and Newell's (1968) terminology, the hinge formula may be written as follows:

RV IOI—nloIol—Iol

Posterior Anterior

LV I—nolOlo—I

The adductor muscles small, subequal; each surmounted by circular pedal retractor scar; pallial line thin, continuous, without a sinus.

**STRATIGRAPHIC RANGE:** Upper part of Estrada Nova Formation, Paraná and Santa Catarina (Mendes, 1954a; USGS collections). The species also occurs at a locality near Cerro Hospital, northern Uruguay (Cox, 1934), but the stratigraphic position of this locality is unknown.

**DISCUSSION:** *Terraia altissima* is easily distinguished from *T. aequilateralis* because it has less centrally placed beaks and lacks a massive anterior lateral tooth in the left valve. *Terraia bipleura* is closer to *T. altissima* but the carina bordering its escutcheon does not coincide with the posterior dorsal margin of the valve.

***Terraia aequilateralis*** Mendes, 1952

Figure 22

*Terraia altissima*: MENDES, 1944, p. 51.

*Terraia aequilateralis* MENDES, 1952, p. 92, pl. 1, figs. 8a, b, 9; 1962, p. 54, pl. 1, figs. 7, 2; 1962a, pl. 57, figs. 7, 8. MEZZALIRA, 1957, p. 50, pl. 2, fig. 2. BEURLEN, 1957, figs. 3, 4.

**TYPE MATERIAL:** The lectotype (here designated) is DGP 7-25 (Mendes, 1952, pl. 1, figs. 8a, b) from a *Pinzonella illusa* assemblage, Estrada Nova Formation, Göss Farm, Ferraz, Municipality Rio Claro, São Paulo.

**DESCRIPTION:** Shell small to medium-sized (maximum length approximately 25 mm.), equivalved, anteriorly elongated with subcentral orthogyral beaks; umbonal carina very well defined, separating flattened postcarinal area from remainder of shell; ornament generally inconspicuous except on postcarinal slopes where growth lamellae may become roughened and lamellose; ligament short, opisthodic, attached to tiny dorsally reflected nymphs set in obscure cordate escutcheon; hinge with large triangular tooth in center of hinge plate of right valve, bordered posteriorly by two or three narrow subparallel teeth (fig. 22B, G); left valve has correspondingly deep-floored socket and two or three narrow cardinal teeth; in front of socket there is large wedge-shaped lateral tooth fitting into well-defined anterior lateral socket in right valve; posterior lateral teeth absent from both valves. From Boyd and Newell's (1968) terminology, the hinge formula may be written as follows:

<sup>1</sup>See Mendes (1954a, p. 109) for extended synonymy.

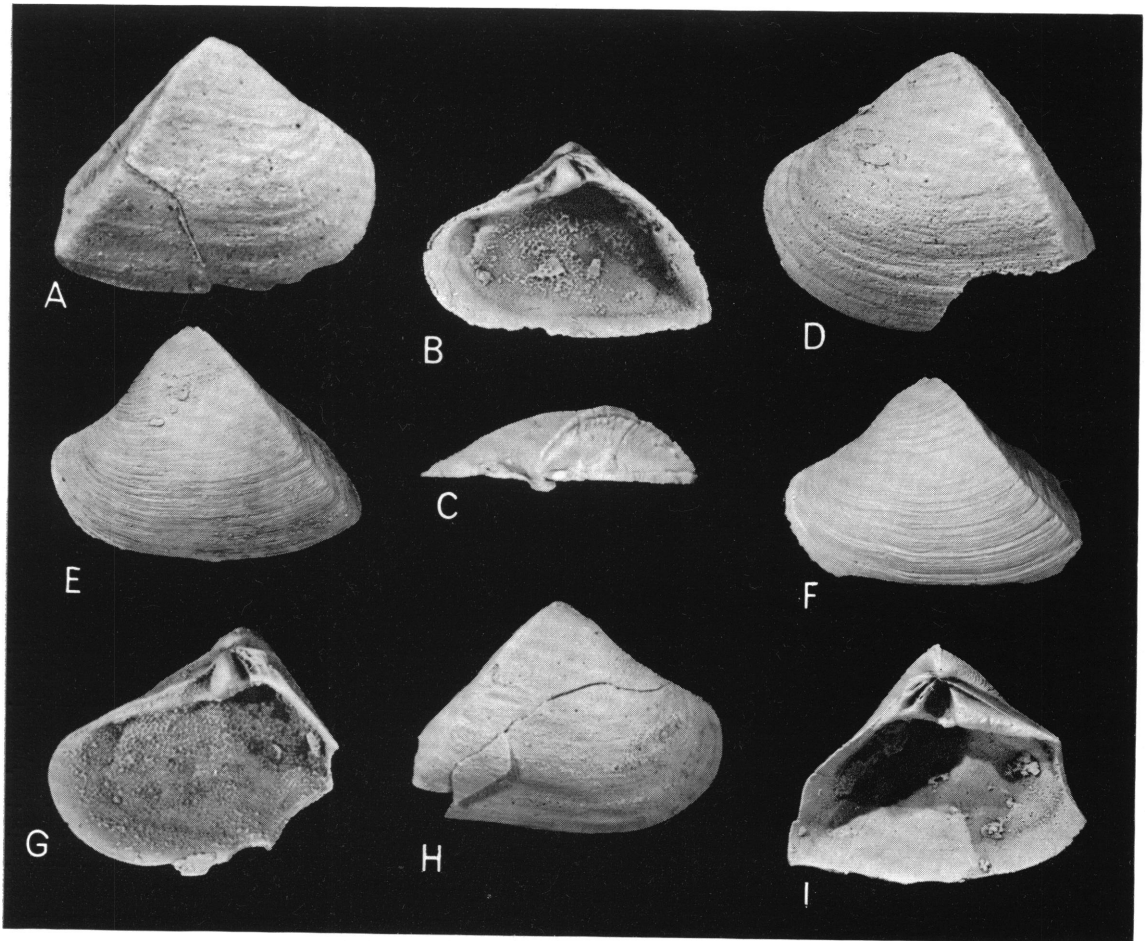


FIG. 22. *Terraia aequilateralis* Mendes, *Pinzonella illusa* assemblage, Estrada Nova Formation, São Paulo state. A, H. Right valves, Lote Sgarboza, Corumbatai, Municipality Rio Claro, DGM, not catalogued.  $\times 2$ . B, C. Right valve, DGP, not catalogued, Manoel Pereira Primo property, Buenos district, near Angatuba, São Paulo.  $\times 2$ . D. Left valve, DGM 4412, Culik farm, about 2 km. northeast of Ferraz railroad station, Municipality Rio Claro.  $\times 2$ . E. Left valve, DGP 7-974, Manoel Pereira Primo property.  $\times 3$ . F. Left valve, DGP 7-972, Manoel Pereira Primo property.  $\times 2.4$ . G. Right valve, DGP 1126, Manoel Pereira Primo property.  $\times 2.4$ . I. Left valve, DGP 7-976.  $\times 2.2$ .

Posterior                    RV nloloI—OI                    Anterior  
                                   LV nololoO—Io

The adductor muscles small, subcircular, subequal; because shell is relatively thick anterior scar is deeply impressed; each scar merged with lower edge of well-defined pedal retractor scar; pallial line narrow, continuous, and lacks sinus; it does not extend above adductor scars.

STRATIGRAPHIC RANGE: *Pinzonella illusa* assemblages, Estrada Nova Formation, São Paulo (Mendes, 1952, 1962b). A single valve associated

with *Pinzonella neotropica* in the Terezina lithosome of the Estrada Nova Formation was described as *Terraia lamegoi* by Mendes (1954a). From Mendes's illustrations it is difficult to see how this species differs from *T. aequilateralis* and it is therefore possible that *T. aequilateralis* also occurs in the higher assemblage.

***Terraia bipleura* (Reed) 1939**

Figure 23

? *Pleurophorus bipleura* REED, 1929, p. 47, pl. 4, figs. 8-10.

*Leinzia bipleura*: LANGE, 1954, p. 69.

**TYPE MATERIAL:** Specimens figured by Reed (1929) from the Serrinha lithosome, Estrada Nova Formation, approximately 6 km. northwest of Mallét, southern Paraná (see Holdhaus, 1918).

**DESCRIPTION:** Shell small (maximum length approximately 20 mm.), elongate, with sub-central beaks and two angular posterior carinae; ornament consisting of inconspicuous growth lamellae; hinge with large triangular tooth in right valve followed posteriorly by small second cardinal tooth; posterior lateral teeth absent, but well-defined anterior lateral socket parallel to valve margin (fig. 23B); hinge of left valve unknown; anterior adductor scar rounded with well-defined pedal retractor scar joined to upper edge; pallial line and posterior musculature not observed.

**STRATIGRAPHIC RANGE:** Serrinha lithosome, Estrada Nova Formation, Paraná and Santa Catarina.

**DISCUSSION:** The hinge and shape of *Terraia bipleura* clearly relate it to *T. altissima*. Mendes (1954a, p. 110) tentatively regarded ?*Pleurophorus bipleura* a junior synonym of *T. altissima*, but the admittedly small collections available to us suggest that the two species are probably distinct. *Terraia bipleura* has a wider area behind the second carina and appears to be somewhat more transverse.

#### LEINZIA MENDES, 1949

**TYPE SPECIES:** *Solenomorpha similis* Holdhaus, 1918, by original designation.

**OTHER SPECIES:** *Leinzia froesi* Mendes, 1949, p. 23, pl. 2, fig. 1; Mezzalira, 1957, p. 51, pl. 2, fig. 5; *Leinzia gigantea* Mendes, 1949, p. 26, pl. 2, fig. 2.

**SYNONYM:** ?*Acantholeaia* Almeida, 1950.

#### *Leinzia similis* (Holdhaus), 1918

Figure 24D-G, J

*Solenomorpha similis* HOLDHAUS, 1918, p. 6, pl. 1, figs. 1-5.

*Cuspidaria similis*: REED, 1929, p. 45, pl. 4, figs. 1-5, 11?

*Leinzia similis*: MENDES: 1949, p. 14, pl. 1, figs. 1-5; 1954a, p. 100, pl. 3, fig. 4; 1967, pl. 57, fig. 10. BEURLIN, 1954b, pl. 5, fig. 48, pl. 6, fig. 60.

**TYPE MATERIAL:** Specimens figured by Holdhaus (1918) from the upper part of the Estrada Nova Formation, approximately 6 km. northwest of Mallét, southern Paraná (details of the locality are given by Holdhaus, 1918 (and

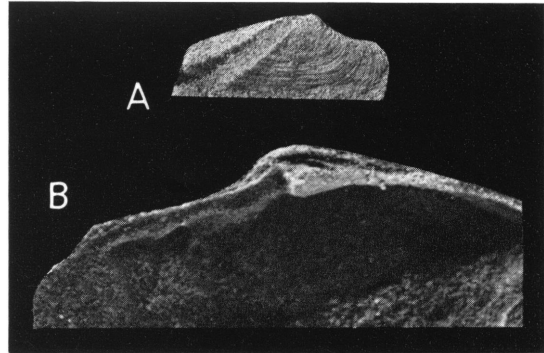


FIG. 23. *Terraia bipleura* (Reed), Serrinha lithosome, Estrada Nova Formation, 41 meters below Rio do Rasto Formation, on Santa Clara-Urubici road, north of Morro do Panelão, 10.3 km. south of Santa Clara, Municipality Bom Retiro, state of Santa Catarina (USGS locality 22829). A. Latex cast of right valve, USNM 165757.  $\times 3$ . B. Hinge of another latex cast, USNM 165758.  $\times 5$ .

accompanying map) and Mendes, 1949, p. 22).

**DESCRIPTION:** Shell small to medium-sized (observed maximum length approximately 17 mm.), equivalved, very elongate, compressed, with extraordinary projection at anterior end of hinge; umbonal carina well defined, extending diagonally from beak to posterior-ventral valve margin; beaks low, ill defined, situated approximately one-quarter to one-third of valve length from anterior end of shell; dorsal and ventral margins subparallel in lateral view, dorsal margin gently concave on both sides of beak; posterior margin distinctly concave; valves ornamented with regularly spaced angular concentric rugae which extend on to anterior projection and may produce series of low knobs where they intersect umbonal carina; rugae not visible behind umbonal carina but may reappear as small lamellose or spinose projections along posterior dorsal margin; as there are at least twice as many spinose projections as rugae, other growth increments must also produce projections along dorsal valve margin; some specimens also show traces of fine growth lines between rugae; ligament external, apparently opisthodontic, attached to tiny nymphs occurring just behind beaks; hinge with inclined triangular tooth below beak of right valve and well-defined socket in left valve; small elongate tooth on posterior side of socket, fitting a narrow groove behind tooth in right valve; ligament nymphs

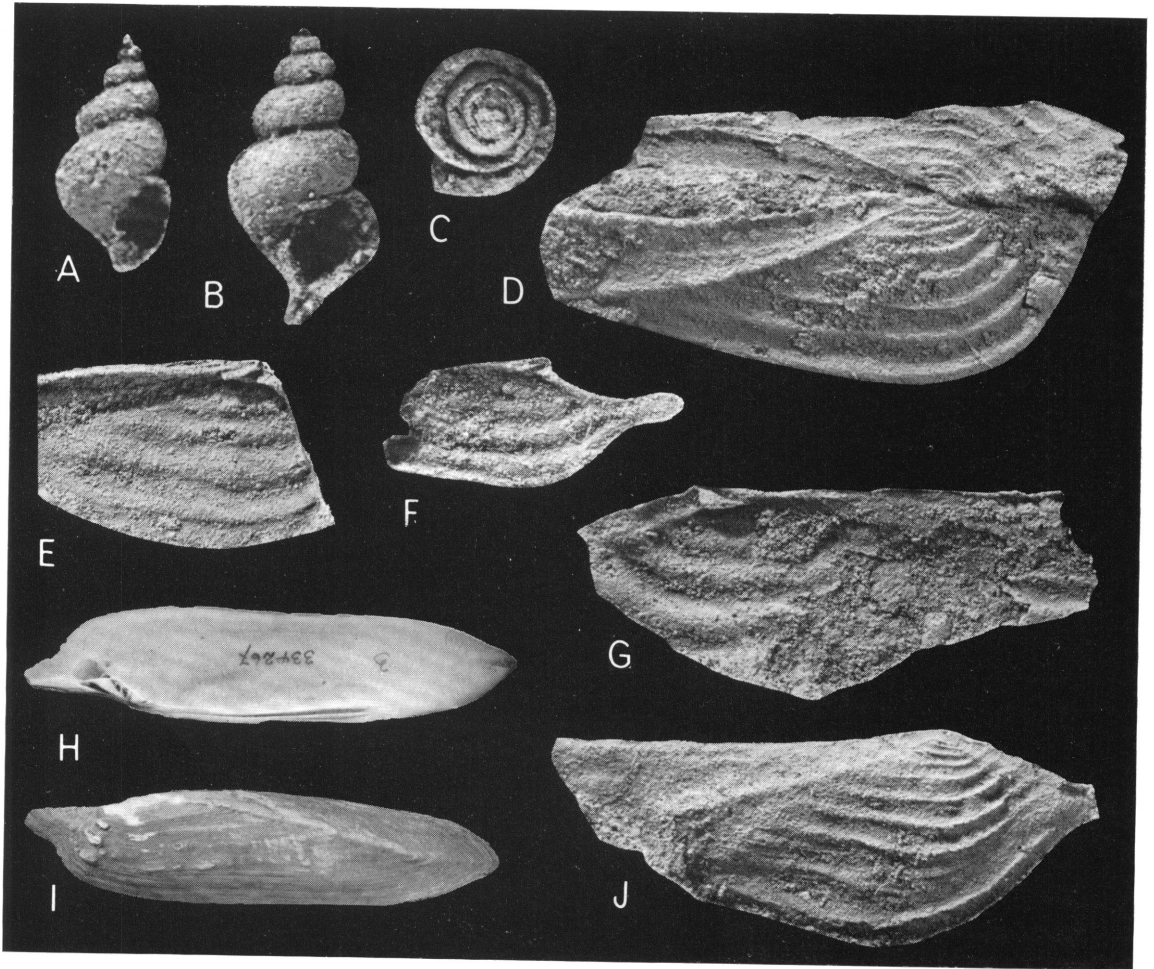


FIG. 24. A-C. *Dendropupa* sp. Latex casts, USNM 165764-6, respectively, Serrinha lithosome, Estrada Nova Formation, road cut km. 109.7 on road from Prudentópolis to Guarapuaua, state of Paraná (USGS locality 22836). D-G, J. *Leinzia similis* (Holdhaus), type species of *Leinzia* Mendes, Serrinha lithosome, latex casts, Estrada Nova Formation, road cut, km. 109.7 from Prudentópolis to Guarapuaua, Paraná (USGS locality 22836).  $\times 4$ . H, I. *Arconaia lanceolata* Len, a modern unionid from Soochow, China, homeomorph of *Leinzia similis*, USNM 334267.  $\times 1$ .

not involved in dentition but edge of right valve in front of tooth slightly concave and probably receives thickened edge of left valve; musculature unknown; in small shells anterior margin is angular (fig. 24J) but anterior projection does not begin to develop until shell almost a centimeter long.

**STRATIGRAPHIC RANGE:** Upper part of Estrada Nova Formation, Paraná and Santa Catarina (Mendes, 1954a, USGS collections).

**DISCUSSION:** *Leinzia* has such an extraordinary shape that we have toyed with the possibility

that it may have been an unusual bivalved arthropod rather than a mollusc. We have rejected that possibility because the shells have fine growth striae, small ligament nymphs, well-developed cardinal teeth, and a non rectilinear hinge. None of these features is normally found in bivalved arthropods and there are theoretical reasons why the first two should not occur.

The external ornament of *Leinzia* is similar to the external ornament of some bivalved arthropods, and it seems possible that tiny specimens of *Leinzia* have been described as a genus of concho-



stracans, *Acantholeaia*, by Almeida (1950). *Acantholeaia* is an unusual conchostracan (Chernysheva, 1960), and if the umbonal areas of *Leinzia similis* (fig. 24D) are compared with Almeida's illustrations of *Acantholeaia regoi* (Almeida, 1950, pl. 1, figs. 1-4), the only significant difference seems to be that for a given valve height, *A. regoi* has approximately twice as many growth rugae as *L. similis*. In *A. regoi* each growth lamella produces a single spine along the posterior cardinal margin (Almeida, 1950, fig. 2), but as there are fewer growth lamellae in *L. similis*, the spines are not so closely spaced and, apparently, not so large.

*Acantholeaia regoi* was described from a locality in the Serra Alta lithosome of the lower part of the Estrada Nova Formation in southern Paraná (see stratigraphic Section 3). It therefore occurs at a similar stratigraphic position as does *Leinzia froesi* (= *L. gigantea* Mendes?) which is found in the basal part of the Estrada Nova Formation farther to the north (Mendes, 1949; Mezzalira, 1957). According to Mendes (1949, p. 24), *L. froesi* has relatively fine concentric ornament and a straighter cardinal margin than has *L. similis*, and the finer ornament of *Acantholeaia regoi* may indicate that it is conspecific with *L. froesi* rather than with *L. similis*.

The affinities of *Leinzia* still remain obscure. When Holdhaus first described *L. similis* he was unaware of the curious anterior prolongation of its hinge, and he placed it in the Carboniferous genus *Solenomorpha*. Reed (1929), also unaware that the projection existed, compared *L. similis* with Bittner's Alpine Triassic species of *Cuspidaria* [sic], probably because he believed the Estrada Nova bivalves to be of Middle or Upper Triassic age. He also noted a similarity to Jurassic species of *Cercomya* but pointed out that the hinge of *Leinzia* was poorly known. When Mendes (1949) discovered the anterior prong he felt that *Leinzia* could have been a pteroid, but he subsequently changed his mind because *Leinzia* obviously lacks so many pteroid characters (Mendes, 1954a, p. 100).

Holdhaus (1918), Leanza (1948), and Beurlen (1954b) have commented on the similarity of the hinges of *Leinzia similis* and an associated species, *Solenomorpha altissima* Holdhaus. Cox (1934) made *S. altissima* the type species of the genus *Terraia*, which he believed was related to *Pseudocorbula* and *Myophoriopsis* (Family Myophoricardiidae). According to Beurlen (1954b),

*Leinzia* may have developed from "*Terraiopsis*" (= *Terraia*) after the Paraná Basin became isolated. He cited a poorly known species, *Leinzia curta* Beurlen (1954b, explanation to pl. 4) as a possible intermediate because it is an elongate shell but lacks an anterior prong. This species is so poorly documented that it may never again be identified, and in any case there is no evidence that it is related to *Leinzia* or *Terraia*. However, there is one species that occurs with *Leinzia similis* and *Terraia altissima* that may be morphologically intermediate although it is obviously closer to the latter species. The species is ?*Pleurophorus bipleura* Reed 1929, considered by Mendes (1954a) to be close to or conspecific with *Terraia altissima*, but referred to *Leinzia* by Lange (1954, p. 69). It is a relatively elongate shell with two strongly-defined posterior carinae (fig. 23B), one of which seems to border an unusually wide escutcheon. The hinge of the right valve (fig. 23B) has a well-defined triangular tooth like that of *Leinzia similis*, but until the morphology of this species is thoroughly documented, its relationship to *Leinzia* will be difficult to prove. In summary therefore, the circumstantial evidence of its occurrence with *Terraia altissima* and *T. bipleura*, together with the similarity of the hinges of all three species, suggests that *Leinzia similis* may be closely related to the other two species. As the affinities of *Terraia* are not well understood, *Leinzia* is even more difficult to classify.

Because of its remarkably elongate shape, *Leinzia* has been tentatively placed in the Solenomorphidae (Newell, 1969). At present it is difficult to present an effective argument either for or against such an assignment because the morphology of the constituent genera is so poorly known.

One living bivalve, a rare Asiatic unionid named *Arconaia*, has an anterior extension of the hinge that resembles the anterior prong of *Leinzia* (fig. 24H, I). Unfortunately, the life habits of *Arconaia* are unknown so that the function of this projection is not clear; presumably *Arconaia* lives partially buried so the projection is probably functionally different from the anterior auricle of some pteroids (Kauffman, 1969). *Leinzia* also seems to have been infaunal, although it is possible that it was a bysally attached epifaunal form, functionally analogous to very elongate pteroids such as *Monopteria* and *Ensipteria* (Nakazawa and Newell, 1968).

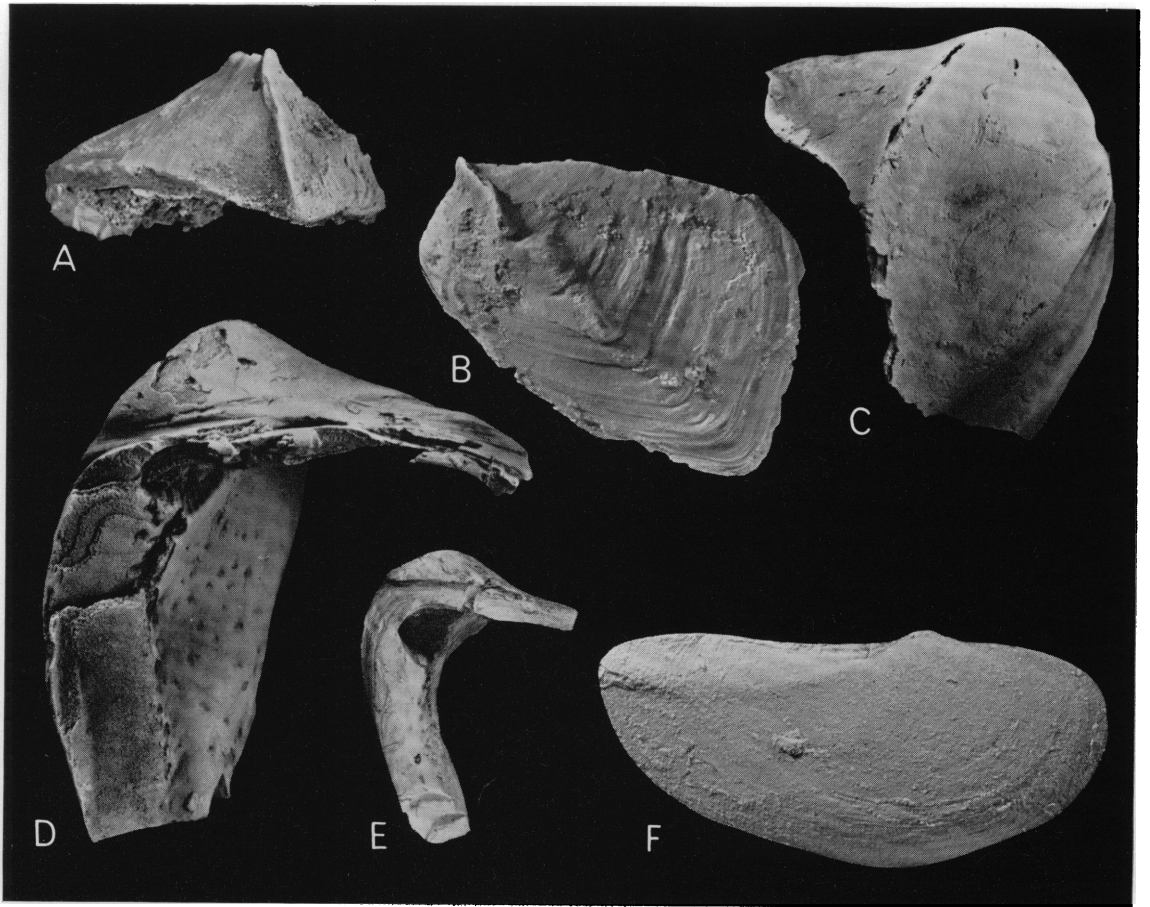


FIG. 25. A–E. *Naiadopsis lamellosus* Mendes, type species of *Naiadopsis*, *Pinzonella neotropica* assemblage, Estrada Nova Formation, states of São Paulo and Paraná. A, B. Dorsal and lateral views of left valve, from float near base of hill on Teresa Cristina–Apu Carena road, just beyond intersection with road to Ponta Grossa, central Paraná, USGS locality 22827.  $\times 1.5$ . C, D. Fragment of right valve, DGM 5015. Chácara Sgarboza, Corumbataí, Municipality Rio Claro.  $\times 1.5$  and  $\times 2$  respectively. E. Another fragmentary right valve, DGM 4022, Sgarboza farm, about 1.5 km. northeast of Corumbataí railroad station, Municipality Rio Claro, São Paulo state.  $\times 1$ . F. *Rioclaroa lefeveri* Mezzalira, IGG 601, type species of *Rioclaroa* Mezzalira, holotype, 7 km. on old road from Rio Claro to Piracicaba, São Paulo state.  $\times 4$ .

?SUBCLASS PALAEOHETERODONTA  
ORDER MODIOMORPHOIDA

SUPERFAMILY MODIOMORPHACEA

MILLER, 1877

FAMILY MODIOMORPHIDAE MILLER,  
1877

NAIADOPSIS MENDES, 1952

TYPE SPECIES: *Naiadopsis lamellosus* Mendes, 1952, by monotypy and original designation.

DISCUSSION: *Naiadopsis* is a thick anisomyarian shell which has an angular or even nodose umbonal carina extending from the beaks to the

posterior ventral margin. Although no articulated specimens are known, it appears to have been more or less equivalved. The anterior adductor is small and deeply impressed. From it extends a pitted pallial line which encloses an area of the shell studded with pits caused by muscles that attached the mantle to the shell. Because of its shape, *Naiadopsis* has been classified with the late Paleozoic myalinids (Vokes, 1967); however, it lacks a duplivincular ligament and has a narrow escutcheon (fig. 25D, B) and therefore is probably better allied with

middle and late Paleozoic genera such as *Modiomorpha* and *Goniophora*. It differs from *Goniophora* in shape and possibly in lacking hinge teeth.

***Naiadopsis lamellosus* Mendes, 1952**

Figure 25A-E

*Myoconcha* sp. MENDES, 1944, pl. 69, pl. 2, fig. 8.

*Naiadopsis lamellosus* MENDES, 1952, p. 113, pl. 3, figs. 5-7; pl. 4, figs. 7a, b; 1954a, pl. 102, pl. 2, fig. 10.

**TYPE MATERIAL:** The lectotype (here designated) is DGP 7-19 (Mendes, 1952, pl. 3, fig. 6) from a *Pinzonella neotropica* assemblage, Estrada Nova Formation, outcrop 5.5 km. from Santo Antonio da Platina, on the road to Joaquim Tabora, Paraná.

**DESCRIPTION:** Shell relatively large (maximum length approximately 35 mm.), apparently equivalved, very thick; angular umbonal carina extends from beak to posterior ventral margin; in well-preserved specimens, such as lectotype, shell distinctly modioliform, with pronounced anterior lobe housing anterior adductor muscle; ligament apparently external, parivincular, set in well-defined escutcheon (fig. 25A), attached to irregular, dorsally reflected nymphs; hinge without teeth but massively thickened by interumbonal growth; anterior adductor muscle relatively large, circular, deeply impressed; posterior scar obscure but apparently much larger; both scars connected by pallial line pitted in some specimens near anterior adductor (fig. 25D); well-defined pedal/byssal retractor scar placed above anterior adductor (Mendes, 1952, pl. 3, fig. 6).

**STRATIGRAPHIC RANGE:** *Pinzonella neotropica* assemblages, Estrada Nova Formation, São Paulo and Paraná (Mendes, 1952, 1954a).

**INCERTAE SEDIS**

**ASTARTELLOPSIS BEURLEN, 1954**

**TYPE SPECIES:** *Astartellopsis prosoclina* Beurlen (1954b, p. 128), by original designation.

**OTHER SPECIES:** *Astartellopsis nana* Beurlen "1953" (1954, p. 73); *nomen nudum*.

***Astartellopsis prosoclina* Beurlen, 1954b**

*Astarte* cf. *triasina* Roemer: REED, 1929, pl. 49, pl. 3, figs. 2-8.

*Astartellopsis prosoclina* BEURLEN, 1954b, p. 128.

**DISCUSSION:** Reed's figures of this species suggest that it is a small astartid with well-

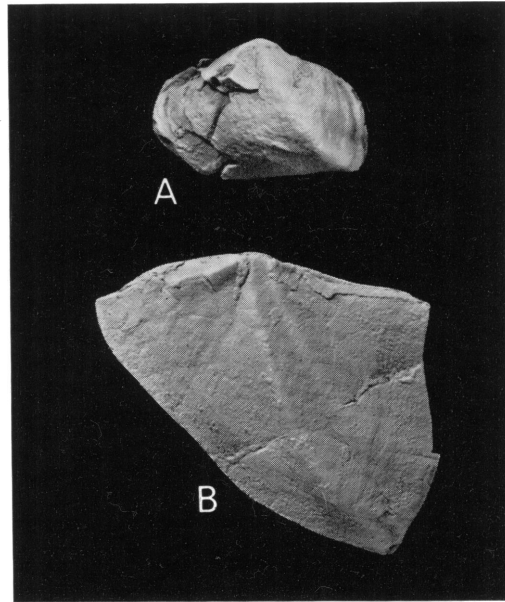


FIG. 26. A. *Maackia iratiensis* Beurlen, DGM 4532-1, holotype, supposedly from the Iratí Formation in a borehole, São Mateus do Sul, Paraná.  $\times 2$ . B. *Barbosaia angulata* Mendes, DGP 7-78, lectotype of the type species of *Barbosaia* Mendes, lower part of the Estrada Nova Formation, Santa Terezina, km. 192 on road to Xarqueada, Rio Corumbataí, Piracicaba, São Paulo state.  $\times 2.25$ .

developed cardinal teeth and high pointed umbones. We have no material that resembles Reed's illustrations, and it seems possible that the species is based on broken umbonal fragments of *Terraia altissima*.

**BARBOSAIA MENDES, 1952**

**TYPE SPECIES:** *Barbosaia angulata* Mendes, 1954a, p. 93, pl. 3, fig. 5.

**OTHER SPECIES:** ?*Barbosaia gordonii* Mendes, 1954a, p. 93, pl. 3, fig. 5.

***Barbosaia angulata* Mendes, 1952**

Figure 26B

*Barbosaia angulata* MENDES, 1952, p. 70, pl. 1, fig. 1.

BEURLEN, 1954c, p. 18, fig. C. MEZZALIRA, 1957, p. 47, pl. 2, fig. 6.

**TYPE MATERIAL:** The lectotype (here designated) is DGP 7-78 (Mendes, 1952, pl. 1, fig. 1; present paper, fig. 26B), from the lower part of the Estrada Nova Formation, Bairro de Santa Terezinha, Piracicaba, São Paulo state.

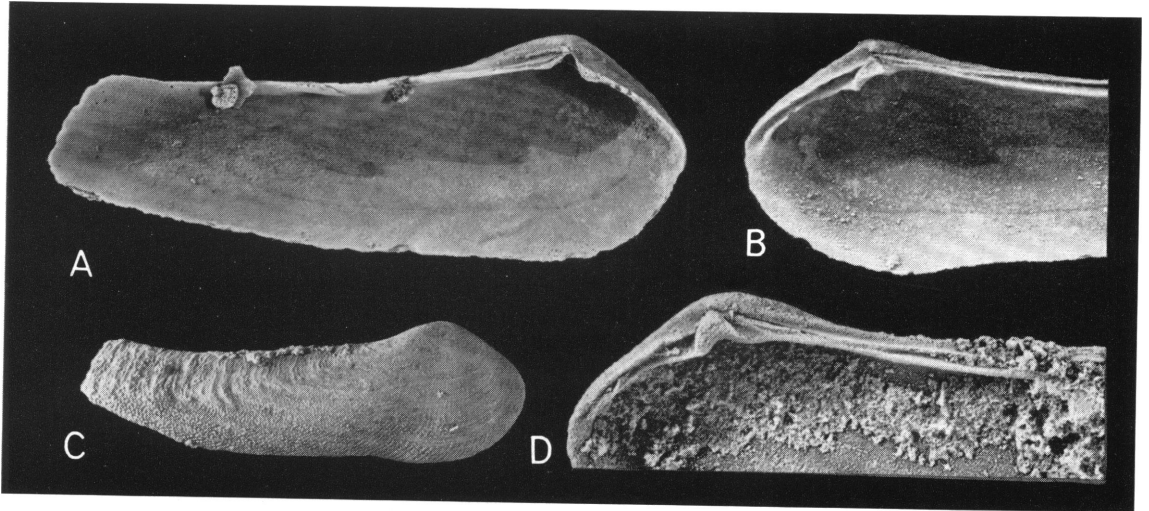


FIG. 27. *Alula squamulifera* Girty, type species of *Alula*, for comparison with the Megadesmidae, Permian, lower Getaway Limestone, 0.3 km. south of U.S. highway 62, near bench mark 5426, Guadalupe Mountains, Texas (AMNH locality 512).  $\times 3$ . A. Left valve, AMNH 28987.  $\times 3$ . B. Right valve, AMNH 28988.  $\times 3$ . C, D. Right valve.  $\times 2$  and  $\times 4$ , respectively.

**DISCUSSION:** The affinities of this fossil remain obscure as its hinge and musculature are unknown. From its shape it appears to have been an epifaunal shell belonging to the subclass Pteriomorpha.

**STRATIGRAPHIC RANGE:** *Barbosaia* is only known from the lower part of the Estrada Nova Formation in São Paulo state.

#### MAACKIA MENDES, 1954a

**TYPE SPECIES:** *Maackia contorta* Mendes, 1954a, by monotypy and original designation.

**OTHER SPECIES:** *Maackia iratiensis* Beurlen, 1957, p. 2, figs. 1-5.

#### *Maackia contorta* Mendes, 1954a

*Maackia contorta* MENDES, 1954a, p. 101, pl. 2, figs. 8, 9; ?pl. 3, fig. 6. BEURLLEN, 1957, fig. 2.

**TYPE MATERIAL:** Specimens figured by Mendes (1954, pl. 2, figs. 8, 9; DGP 7-158) from the Serra Alta lithosome, Estrada Nova Formation, at km. 78.6 on the road from Ponta Grossa to Prudentópolis, Paraná State.

**DISCUSSION:** According to Mendes (1954a) the feature which distinguishes *Maackia* is the presence of two posterior carina, the lower of which is strong and the upper weak; internal characters are unknown. The only illustrated specimens of *Maackia* are poorly preserved, and *M. contorta* could easily be based on poorly preserved speci-

mens of *Jacquesia* in which the edge of the escutcheon is strong enough to look like a second carina.

*Maackia iratiensis* (fig. 26A) is based on a single specimen and is noteworthy only because it is supposed to come from below the Iratí Formation; if so, it is the oldest bivalve that belongs to the Estrada Nova fauna.

#### OLIVEIRAIA MENDES, 1954a.

**TYPE SPECIES:** *Thracia pristina* Reed, 1929, by monotypy.

**SYNONYM:** *Thraciomorpha* Beurlen, 1954b.

#### *Oliveiraia pristina* (Reed), 1929

*Thracia pristina* REED, 1929, p. 51, pl. 2, fig. 15.

*Thracia perversa* REED, 1929, p. 53, pl. 2, figs. 17, 18.

*Gonodon* (*Schafhäullia*) cf. *astartiformis* MÜNSTER: REED, 1929, p. 57, pl. 3, fig. 11.

*Oliveiraia pristina*: MENDES, 1954a, p. 104, pl. 3, fig. 8.

*Thraciomorpha perversa*: LANGE, 1954, p. 69.

*Thraciomorpha pristina*: LANGE, 1954, p. 69.

?*Thraciomorpha* (?)*prolata* BEURLLEN "1953," 1954, p. 69.

**TYPE MATERIAL:** The holotype (by monotypy) is DGM 1279 (Reed, 1929, pl. 2, fig. 15; Mendes, 1954a, pl. 3, fig. 8) from the Serrinha lithosome, Estrada Nova Formation, approximately 6 km. northwest of Mallét, southern Paraná.

**DISCUSSION:** Vokes (1967, p. 339) treated

*Thraciomorpha* Beurlen 1954b as a senior synonym of *Oliveiraia*, a name which he assumed Beurlen introduced because *Oliveiraia* was preoccupied. In fact, Beurlen pointed out that because of a delay in publication, his name (*Thraciomorpha*) lost priority to *Oliveiraia*. *Thraciomorpha* does not appear in the text of Beurlen's paper but is used in Lange's paper in the same volume.

The hinge and musculature of *Oliveiraia* are unknown so that its affinities remain obscure. Its external shape suggests it may be related to *Terraia altissima*. It has been found only in the Serrinha lithosome of the Estrada Nova Formation in Paraná.

**RIOCLAROA MEZZALIRA, 1957**

TYPE SPECIES: *Rioclaroa lefevrei* Mezzalira, 1957, by original designation.

***Rioclaroa lefevrei* Mezzalira, 1957**

Figure 25F

*Rioclaroa lefevrei* MEZZALIRA, 1957, p. 45, pl. 1, figs. 1, 2.

TYPE MATERIAL: The lectotype (here designated) is IGG 602-1, (Mezzalira, 1957, pl. 1, fig. 1; present paper fig. 25F) from the basal part of the Estrada Nova Formation on the old road from Rio Claro to Piracicba, 7 km. from Rio Claro, Municipality Rio Claro, São Paulo.

DISCUSSION: The hinge and musculature of *Rioclaroa* are unknown so the affinities of this genus remain obscure.

## APPENDIX

### STRATIGRAPHIC SECTIONS

SECTION 1, TYPE SECTION OF THE PASSA DOIS GROUP, SANTA CATARINA: The stratigraphy of the type section has been summarized by Mendes (1967). As in most other places, the Passa Dois Group conformably overlies the Permian Tubarão Group and is locally unconformably, and regionally unconformably overlain by a Cretaceous aeolian sandstone, the Botucatu Formation. The following units occur in the Passa Dois Group in its type area (Mendes, 1967, pp. 151–154) (no fossils are known from this section):

Rio do Rasto Formation (36 meters)

Estrada Nova Formation

Serrinha lithosome (40 meters)

Serra Alta lithosome (260 meters with small intercalations of Terezina lithosome near the top)

Irati Formation (30 meters)

SECTION 2, URUBICI–SANTA CLARA AND LAJES–RIO DO SUL ROADS, SOUTHERN SANTA CATARINA: This section has been assembled by combining two partial sections of the Passa Dois Group measured by Mackenzie Gordon and Victor Dequech (United States Geological Survey) in November, 1946. The first section on the road from Urubici to Santa Clara was measured from the base of the Botucatu Formation and includes the Rio do Rasto Formation and almost all of the Serrinha lithosome of the Estrada Nova.

Rio do Rasto Formation (36.2 meters)

Estrada Nova Formation

Serrinha lithosome (169+ meters to base of section)

Bivalve USGS locality 22829 containing *Leinzia similis* and *Terraia altissima* occurs 41.3 meters below the base of the Rio do Rasto Formation, and a bed containing fish scales occurs 6.6 meters below the bivalve locality.

The second section measured on the road from Lajes to Rio do Sul covers the interval from the Irati Formation to the lower part of the Serrinha lithosome, Estrada Nova Formation.

Estrada Nova Formation

Serrinha lithosome (37.3 meters to top of section)

transition beds (20.5 meters)

Terezina lithosome (157.8 meters)

Irati Formation (no thickness given)

Bivalve USGS locality 22830 occurs 27.3 meters below the base of the Serrinha lithosome. This fauna is dominated by *Pinzonella neotropica*.

SECTION 3, PONTA GROSSO–GUARAPUAVA ROAD, SOUTHERN PARANÁ. This section was examined by Gordon in 1947, and is described in some detail by Mendes (1954a, p. 53). Unfortunately, no thicknesses are given for the complete section, and normally only small exposures in road cuts and roadside ditches have been described. The Passa Dois Group is exposed between km. posts 78 and 128.

The contact between the Irati Formation and the Serra Alta Facies of the Estrada Nova Formation is exposed near km. 79 (Mendes, 1954a, p. 55, fig. 16). A small fauna containing the bivalves *Maackia* and *Kidodia* [*sic*] and the “conchostracan” *Acantholeaia* (Mendes, 1954b, pl. 14, fig. 12) occurs some 60 meters above the base of the Serra Alta lithosome.

A contact between sediments of the Serra Alta type and those of the Terezina type occurs in a quarry at Manduri (km. 89) and beds of the Terezina lithosome are exposed about 10 km. farther along the road (Mendes, 1954a). One of the latter exposures, a road cut at 98 km., contains bivalves (mainly *Pinzonella neotropica* and *Jacquesia brasiliensis*) in a silicified oolite (USGS 22837; Mendes, 1954a, p. 67). Sommer (1954) has also described a charophytacean alga *Leonardosia* from this locality.

The base of the Serrinha lithosome occurs near 99 km. and fossiliferous horizons within this unit occur at km. 105, 106, and 109.8 (Mendes, 1954a, p. 67). The last locality (USGS 22836) containing *Leinzia similis*, *Terraia altissima*, and *Dendropupa*, occurs about 50 cm. above a bed with *Glossopieris* and other plants.

A marked change in lithology near 112 km. (Mendes, 1954a, p. 5) probably indicates the base of the Rio do Rasto Formation.

SECTION 4, RAILROAD BETWEEN THE CORUMBATAÍ RIVER AND CAMAQUA, NORTHEAST SÃO PAULO. This section is described in detail by

Mendes (1952, p. 33). The Paranapanema lithosome is the only subdivision of the Estrada Nova Formation recognized in São Paulo; it corresponds to the lower 50+ meters of the Corumbataí Formation of Mendes (1952), now considered equivalent to the Estrada Nova Formation. The Rio do Rasto Formation thins and disappears in northern Paraná (Gordon, 1947, p. 13), so that in São Paulo the Botucatu Formation rests directly on the Estrada Nova.

Because of the negligible dip, barometric measurements have been used to estimate the thickness of the Estrada Nova Formation in São Paulo. The validity of this method is demonstrated if the measured heights of a number of localities of the two major bivalve horizons are compared (data from Mendes, 1952).

<i>Pinzonella illusa</i> horizon	<i>Pinzonella neotropica</i> horizon
575 meters	612 meters
575	615
564	612
570	615
580	615
576	
575	
575	
562	
572	

Using this method, Mendes estimated that

approximately 77 meters of Estrada Nova Formation occur between the base of the Botucatu Formation and the water level of the Corumbataí River in the section being discussed. The two bivalve horizons (*Pinzonella neotropica* and *P. illusa*) occur 1 and 52 meters below the upper contact of the Estrada Nova Formation.

In the same paper, Mendes (p. 42) mentioned the occurrence of *Barbosaia* and *Holdhausiella* in siltstones near the mouth of the Corumbataí River. Although this outcrop is close to outcrops of the Iratí Formation, local tectonic deformation prevents an accurate determination of its stratigraphic position. Subsequently, Mezzalana (1957) located other localities of this fauna (which was found to include *Leinzia*), the most important of which occurs on the edge of the Claro River. Presumably over the relatively short distance (10 km.) between this locality and the base of the section described above, the water levels of the rivers should be more or less the same, so that the total thickness of the Estrada Nova Formation is probably not more than 100 meters. The fauna with *Leinzia*, *Barbosaia*, and *Holdhausiella* probably occurs within the lower 30–40 meters of the Formation. [Mendes (1949) has also reported *Leinzia* and *Pinzonella* cf. *illusa* from the basal part of the Estrada Nova Formation in a well near Anhemby, central São Paulo.]

## RESUMO<sup>1</sup>

Na Bacia do Paraná do Brasil, Uruguai, Paraguai e Argentina, sedimentosossilíferos de idade permiana ocupam uma área equivalente, ou uma vez e meia maior do que a do Golfo do México. A Formação Estrada Nova, cuja espessura varia 100 a 1.000 metros, corresponde à parte média da secção permiana e contém uma fauna de moluscos bivalves amplamente distribuída e diversificada, estudada anteriormente por J. Camargo Mendes e outros.

Muitos dos bivalves são silicificados e muito bem preservados. A fauna é notável por estar totalmente confinada, pelo que se conhece presentemente, à Bacia do Paraná.

<sup>1</sup>Translation by Dr. A. C. Rocha-Campos, University of São Paulo, Brazil.

Uma revisão crítica dos bivalves, aqui apresentada, demonstra que suas afinidades familiares são com formas marinhas gonduânicas que ocorrem nas camadas subjacentes (Grupo Tubarão) e em outros continentes gonduânicos. O notável endemismo da fauna da Formação Estrada Nova e as paleosalinidades determinadas pelo método dos isótopos de carbônio sugerem evolução *in situ*, sob condições de água salobra e extremo isolamento. A história desse mar residual compara-se bem com o caso, quase único, do Mar Pontiano do sudoeste europeu, durante o Cenozóico.

Revisa-se a taxonomia de 24 nomes genéricos e 57 nomes específicos utilizados para os bivalves permianos e analisa-se o seu significado biológico e ecológico.

## REFERENCES CITED

- ALLEN, P., AND M. L. KEITH  
1965. Carbon isotope ratios and palaeosalinities of Purbeck Wealden carbonates. *Nature*, vol. 208, no. 5017, pp. 1278-1280.
- ALMEIDA, FERNANDO FLAVIO, MARQUES DE  
1950. *Acantholeaia*, um novo gênero de Leaiadidae. *Notas Prelim. Estud. Div. Geol. Min. Brasil*, no. 51, 6 pp., 5 figs.
- ANDRUSSOV, N. I.  
1897. Fossile und lebende Dreissendiae Eurasiens. *Trav. Soc. Imp. Nat. St. Pétersbourg*, vol. 25, pt. 5, 683 pp., 15 figs. (In Russian), 115 pp. (French résumé), Atlas 20 pls.  
1900. Fossile und lebende Dreissenidae Eurasiens. *Ibid.*, Erste Suppl. vol. 29, no. 5, pt. 4, pp. 1-74, pls. 1, 2.  
1903. Studien über die Brackwassercardiiden. *Mem. Acad. Imp. Sci. St. Pétersbourg, sér. 8*, vol. 13, no. 3, pp. 1-82, pls. 1-7.
- BALME, B. E.  
1969. The Permian-Triassic boundary in Australia. *Geol. Soc. Australia Special Publ.* no. 2, pp. 99-112.
- BEHRENS, E. W., AND R. L. WATSON  
1969. Differential sorting of pelecypod valves in the swash zone. *Jour. Sediment. Petrology*, vol. 39, no. 1, pp. 159-165.
- BEURLEN, K.  
1953. Considerações sobre alguns lamelibrânquios das Camadas Terezina, no Paraná. *Div. Geol. Min. Brasil*, no. 142, 41 pp., 1 pl., 2 figs.  
1954a. Horizontes fossilíferos das Camadas Serra Alta do Paraná. *Ibid.*, no. 152, 30 pp., 1 pl., 2 figs.  
1954b. As faunas de lamelibrânquios do sistema Gondwanico no Paraná. In Lange, F. W. (ed.), *Paleontologia do Paraná, Volume Comemorativo do 1º Centenário do Estado do Paraná*, Curitiba, Brasil, pp. 107-136, pls. 1-7.  
1954c. Algumas observações sobre a associação faunística nas Camadas Terezina (série Passa Dois) do Paraná. *Arq. Mus. Paranaense, new ser. Geol.* 1, 20 pp., pls. 1-4.  
1957. Um lamelibrânquio do Folhelho Iratí de São Mateus do Sul, Estado do Paraná. *Notas Prelim. Estud. Div. Geol. Min. Brasil*, no. 98, 5 pp.
- BHARADWAJ, D. C., AND S. C. SRIVASTAVA  
1969. A Triassic mioflora from India. *Palaeontographica*, vol. 125, sect. B, pt. 4-6, pp. 119-149, pls. 24-29.
- BIGARELLA, J. J., R. D. BECKER, AND I. D. PINTO (EDS.)  
1967. Problems in Brazilian Gondwana Geology, First Internatl. Symp. Gondwana Stratigr. Palaeont., Curitiba, Paraná Brazil, 344 pp.
- BIGARELLA, J. J., AND R. SALAMUNI  
1967. Some palaeogeographic and palaeotectonic features of the Paraná Basin. In Bigarella, J. J., R. D. Becker, and I. D. Pinto (eds.) *Problems in Brazilian Gondwana Geology. First Internatl. Symp. Gondwana Stratigr. Palaeont., Curitiba*, pp. 235-301, pls. 74-80.
- BORTOLUZZI, C. A., AND M. C. BARBARENA  
1967. The Santa Maria beds in Rio Grande do Sul (Brazil). In Bigarella, J. J., R. D. Becker, and I. D. Pinto (eds.) *Problems in Brazilian Gondwana Geology. First Internatl. Symp. Gondwana Stratigr. Palaeont., Curitiba*, pp. 169-195, pls. 63-73.
- BOYD, DONALD W., AND N. D. NEWELL  
1968. Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera. *Amer. Mus. Novitates*, no. 2328, pp. 1-52.
- BRADLEY, W. H.  
1929. Algae reefs and oolites of the Green River Formation. *U.S. Geol. Surv. Prof. Paper* 154, pp. 203-223, pls. 28-48.
- BULLARD, SIR EDWARD, J. E. EVERETT, AND A. GILBERT SMITH  
1965. The fit of the continents around the Atlantic. In Blackett, P. M. S., Sir Edward Bullard and S. K. Runcorn, *A symposium on Continental Drift*, pp. 41-51.
- CARVALHO, P. F. DE  
1937. Estado do Paraná. *Serv. Geol. Min. Brazil, Relat. Anual Dir.* 1937, pp. 49-62.
- CHEARNYSHEVA, N. E. (ED.)  
1960. *Osnovy paleontologii, Spravochnik dlya Paleontologov i Geologiv SSSR*, (vol. 8). *Chelenistonogie, Trilobitoobraznye i Rakoobraznye*, Moscow, Gosudar. Nauch-Tekh Izd. Lit. Geol. i Okhrane Nedr., 515 pp.
- CLOSS, D.  
1967. Intercalations of goniatites in the Gondwanic glacial beds of Uruguay. *Abstracts. 1 Simposio Internacional sobre estratigrafia y Paleontologia del Gondwana. Asoc. Geol. Argentina*, pp. 9-10.
- COX, C. B.  
1968. The Chanares (Argentina) Triassic reptile fauna. IV. The Dicynodont fauna. *Breviora*, no. 295, pp. 1-27.
- COX, L. R.  
1934. Triassic Lamellibranchia from Uruguay. *Ann. Mag. Nat. Hist.*, ser. 10, vol. 13, pp. 264-273, pl. 10.
- COX, L. R. ET AL.  
1969. Part N-Mollusca 6 (Bivalvia) vols. 1-2. In



- Moore, R. C. (ed.), Treatise on invertebrate paleontology. Boulder, Geol. Soc. Amer. and Univ. of Kansas, 952 pp., 6198 figs.
- DICKINS, J. M.  
 1956. Permian pelecypods from the Carnarvon Basin, western Australia. Bull. Australian Bur. Min. Resources, no. 29, 42 pp., 6 pls.  
 1957. Lower Permian pelecypods and gastropods from the Carnarvon Basin, Western Australia. *Ibid.*, no. 41, 55 pp., 10 pls.  
 1961. *Eurydesma* and *Peruwispira* from the Dwyka beds of South Africa. Palaeontology, vol. 4, pt. 1, pp. 138-148, pl. 18.  
 1963. Permian pelecypods and gastropods from western Australia. Bull. Australian Bur. Min. Resources, no. 63, 150 pp., 26 pls.
- DICKINS, J. M., AND R. A. McTAVISH  
 1963. Lower marine fossils from the Beagle Ridge (BMR 10) Bore, Perth Basin, Western Australia. Geol. Soc. Australia Jour., vol. 10, pt. 1, pp. 123-140, pls. 1, 2.
- EBERSIN, A. G.  
 1965. Sistema i Filogenia Solonovotvodnykh Kardiid. Molloski. Voprosy Teorii i Prikladnoi Malokologii. Tezisy Dokl., Sb. 2, Izd. Zool. in-ta AN SSSR.  
 1965. Sistema i filogeniya solonovotvodnykh Kardiid. Akad. Nauk S.S.S.R., Zool. Inst., Mollyuski-Voprosi., Teoreticheskoy; Prikladnoy Malakologii. Tezisy dokladov., Sbornik Vtoroy [System and phylogeny of brackish-water Cardiidae. 2nd Conf. on Study of Mollusca: Problems of theoretical and applied malacology: Abstr.], vol. 2, pp. 11-25, 5 figs.
- EVANS, P. R.  
 1966. Mesozoic stratigraphic palynology in Australia. Australian Oil Gas Jour., vol. 12, no. 6, pp. 58-63.  
 [MS.] Upper Carboniferous and Permian palynological stages and their distribution in eastern Australia. Rec. Australian Bur. Min. Resources, 1967/69, pp. 1-13.
- FLEMING, P. J. G.  
 1966. Eotriassic marine bivalves from the Maryborough Basin, southeast Queensland. Queensland Geol. Surv., Publ. 333, Palaeont. Paper 8, pp. 17-29, pls. 7-9.
- FRAKES, L. A., AND J. C. CROWELL  
 1967. Facies and paleogeography of late Paleozoic Lafonian diamictite, Falkland Islands, Bull. Geol. Soc. Amer., vol. 78, no. 1, pp. 37-58.  
 1969. Late Paleozoic glaciation: I. South America. *Ibid.*, vol. 80, pp. 1007-1042, 4 pls.
- FRENGUELLI, J.  
 1945. Moluscos continentales en el Paleozoico superior y en el Triasico de la Argentina. La Plata Universidad, Museo. Notas Paleont., vol. 10, no. 83, pp. 181-204.
- GILLET, S.  
 1946. Lamellibranches dulcicoles, les limnocardiidés. Rev. Sci., Paris, vol. 84, fasc. 6 (no. 3258), pp. 343-353, 11 figs.
- GORDON, M., JR.  
 1947. Classification of the Gondwanic rocks of Paraná, Santa Caterina, and Rio Grande do Sul. Notas Prelim. Estud. Div. Geol. Min. Brasil, no. 38, 19 pp.
- GORDON, MACKENSIE, AND ROLAND W. BROWN  
 1952. Plantas Triássicas do sul do Brasil. Notas preliminares e estudos, Número 54, Dept. Nac. Produção Min. Div. de Geol. Min., Div. de Geol. Min., 7 pp.
- HARRINGTON, H. J.  
 1955. The Permian *Eurydesma* fauna of eastern Argentina. Jour. Paleont., vol. 29, no. 1, pp. 112-128, pls. 23-26.
- HAUGHTON, S. H.  
 1963. Stratigraphic history of Africa south of the Sahara. New York, Hafner, xii+368 pp., 45 figs.
- HENNELLY, J. P. F.  
 1959. Spores and pollen grains from a Permian-Triassic transition in New South Wales. Proc. Linnean Soc. New South Wales, vol. 83, pt. 3, pp. 363-369.
- HIND, W.  
 1896-1905. A monograph of the British Carboniferous Lamellibranchiata. Palaeont. Soc., vol. 1 (1896-1900), 486 pp., 54 pls.; vol. 2 (1901-1905), 222 pp., 25 pls.
- HOLDHAUS, K.  
 1918. Sobre alguns lamellibranchios fosseis do sul do Brasil. Serv. Geol. Min. Brasil, Monogr. 2, pp. 1-24, pls. 1, 2.
- KAUFMAN, E. G.  
 1969. Form, function and evolution. In Moore, R. C. (ed.), Treatise on invertebrate paleontology, Part N, Mollusca 6, Bivalvia. Boulder, the Geol. Soc. Amer. and the Univ. of Kansas, pp. N129-N205.
- KEITH, M. L.  
 1969. Isotopic composition of carbonates from the Karroo and comparison with the Passa Dois group of Brazil. Proc. Simp. Internac. Sobre estratigrafia y Paleont., Gondwana, pp. 775-778.
- KEITH, M. L., AND R. H. PARKER  
 1965. Local variation of C<sup>13</sup> and O<sup>18</sup> content of mollusk shells and the relatively minor temperature effect in marginal marine environments. Marine Geol., vol. 3, no. 1-2, pp. 115-129.
- KUMMEL, B., AND C. TEICHERT  
 1966. Relations between the Permian and Triassic

- formations in the Salt Range and Trans-Indus ranges, West Pakistan. *Neues Jahrb. Geol. Paläont. Abhandl.*, vol. 125, Festband Schindewolf, pp. 297, 333, pls. 27, 28.
- LANGE, F. W.  
1954. Paleontologia do Paraná. *In* Lange, F. W. (ed.), *Paleontologia do Paraná, Volume Comemorativo do 1º Centenário do Estado do Paraná, Curitiba, Brasil, Comissão de Comemorações do Centenário do Paraná*, pp. 1-105.
- LAPORTE, L. F.  
1968. Ancient environments. Englewood Cliffs, Prentice-Hall, Inc., 115 pp.
- LEANZA, A. F.  
1948. El llamado Triasico marino de Brasil, Paraguay, Uruguay y la Argentina. *Rev. Asoc. Geol. Argentina*, vol. 3, no. 3, pp. 219-244, 3 pls.
- LYUTKEVICH, E. M., AND O. B. LOBANOVA  
1960. Peletzipody Permi Sovetskogo Sektora Arktiki [Permian pelecypods of the Soviet Arctic]. *Vsesoiz. Neft. Nauchno-Issled. Geol.-Razv. Inst. Trudy, Vyp. 149*, pp. 1-294, pls. 1-35.
- MCCOY, F.  
1844. A synopsis of the characters of the Carboniferous limestone fossils of Ireland. Dublin, privately published, 207 pp., 29 pls.
- MARTIN, H.  
1961. The hypothesis of continental drift in the light of recent advances of geological knowledge in Brazil and in Southwest Africa. *Geol. Soc. South Africa, Annex-vol. 64, Alex. L. DuToit Mem. Lect. no. 7*, 47 pp., 5 pls.
- MAXWELL, W. G. H.  
1964. The geology of the Yarrol region. Part 1, Biostratigraphy. Univ. Queensland, Dept. Geol. Papers, vol. 5, no. 9, pp. 1-79, pls. 1-14.
- MENDES, J. C.  
1944. Lamelibranquios Triassicos de Rio Claro (Estado de São Paulo). *Fac. Fil. Cien. Letras, Univ. São Paulo, Bol. 45, Geol 1*, pp. 41-76, 2 pls.  
1945. Considerações sobre a Estratigrafia e idade do formação Estrada Nova. *Ibid.*, Bol. 50, Geol. 2, pp. 27-34.  
1949. Novos lamelibranquios fosseis da serie Passa Dois, sul do Brasil. *Div. Geol. Min. Brazil, Bol. 133, Geol. 40 pp.*, 5 pls.  
1952. A foramao Corumbataí na região di Rio Corumbataí (estratigrafia e descrição dos lamelibranquios). *Univ. de São Paulo, Fac. Fil., Cien Letras, Univ. São Paulo, Bol. 145, Geol. 8, 119 pp.*, 4 pls.  
1954a. Contribuição à estratigrafia da serie Passa Dois no estado do Paraná. *Ibid.*, Bol. 175, Geol. 10, 119 pp., 3 pls.  
1954b. Conchostracos Permianos do Sul do Brasil. *In* Lange, F. W. (ed.), *Paleontologia do Paraná, Volume Comemorativo do 1º Centenário do Estado do Paraná, Curitiba, Brasil, Comissão de Comemorações do Centenário do Paraná*, 11 pp., 153-164, pls. 12-14.  
1962a. Lamelibranquios Permianos do Oólito de Angatuba, estado de São Paulo (Formação Corumbataí). *Bol. Soc. Brasil. Geol.*, vol. 11, no. 1, pp. 37-56, 2 pls.  
1962b. Recorrenca de facies no Grupo Passa Dois (Permiano) observada no Perfil Irati-Relógio, Paraná. *Ibid.*, vol. 11, no. 2, pp. 75-81.  
1963. Lamelibranquios Permianos do Estado de Mato Grosso (Formação Estrada Nova). *Ibid.*, vol. 11, no. 1-2, pp. 57-64.  
1967. The Passa Dois group (The Brazilian portion of the Paraná Basin). *In* Bigarella, J. J., R. D. Becker, and I. D. Pinto (eds.). *Problems in Brazilian Gondwana Geology, First Internatl. Symp. Gondwana Stratigr. Paleont., Curitiba*, pp. 119-166, pls. 41-61.
- MENDES, J. C., AND S. PETRI  
1950. Estudos biométricos de certas espécies de *Pinzonella e Pinzonellopis*. *An. Acad. Brasil. Cien.*, vol. 22, no. 11, pp. 99-106.
- MEZZALIRA, S.  
1957. Ocorrencias fossilíferas novas de série Passa Dois na região Limeira-Rio Clara piracicaba. *Soc. Brasileira Geol., Bd., vol. 6, no. 2*, pp. 37-59.
- MOORE, R. C. ET AL.  
1969. *Treatise on Invertebrate Paleontology Part N, vol. 1 (of 3), Mollusca 6, Bivalvia*. Boulder, Colorado, The Geological Society of America, Inc. 489 pp.
- MORRISON, J. P. E.  
1943. A new type of fresh water clam from British Guiana. *Nautilus*, vol. 57, no. 2, pp. 46-52, pl. 8.
- NAKAZAWA, K., AND N. D. NEWELL  
1968. Permian bivalves of Japan. *Mem. Fac. Sci., Kyoto Univ., Geol. Min.*, vol. 35, no. 1, pp. 1-108, pls. 1-11.
- NEWELL, N. D.  
1942. Late Paleozoic pelecypods: Mytilacea. *Kansas State Geol. Surv.*, vol. 10, no. 2, 115 pp., 20 pls.  
1956. Primitive desmodont pelecypods of the Australian Permian. *Amer. Mus. Novitates*, no. 1799, pp. 1-13.  
1967. Paraconformities, *In* *Essays in Paleontology*

- and Stratigraphy, R. C. Moore Commemorative Volume, Univ. Kansas Special Publ. no. 2, Lawrence, pp. 349-367.
1969. Systematic description. In Moore, R. C. (ed.), Treatise on invertebrate paleontology, Part N, Mollusca 6, Bivalvia, Boulder, the Geol. Soc. Amer. and the Univ. of Kansas, pp. N818-N827.
- NEWELL, N. D., J. CHRONIC, AND T. G. ROBERTS  
1953. Upper Paleozoic of Peru. Geol. Soc. Amer., Mem. 58, 276 pp., 44 pls.
- NEWELL, N. D., J. IMBRIE, E. G. PURDY, AND D. L. THURBER  
1959. Organism communities and bottom facies, Great Bahama Bank. Bull. Amer. Mus. Nat. Hist., vol. 117, art. 4, pp. 181-228, pls. 58-69.
- NICOL, D.  
1965. An ecological analysis of four Permian molluscan faunas. Nautilus, vol. 78, no. 3, pp. 86-95.
- OLIVEIRA, E. P. DE  
1918. Posição estratigráfica dos lamelibranquios descritos na memoria do Professor Holdhaus. Serv. Geol. Mineral. Brasil, Monograph 2, pp. 27-32.
- PADULA, V. T.  
1969. Oil shale of Permian Irati Formation, Brazil. Bull. Amer. Assoc. Petrol. Geol., vol. 53, no. 3, pp. 591-602.
- PARKER, R. H.  
1956. Macro-invertebrate assemblages as indicators of sedimentary environments in east Mississippi delta region. Bull. Amer. Assoc. Petrol. Geol., vol. 40, no. 2, pp. 295-376, pls. 1-8.  
1959. Macro-invertebrate assemblages of central Texas. *Ibid.*, vol. 43, no. 9, pp. 2100-2166.  
1960. Ecology and distributional patterns of marine macro-invertebrates, northern Gulf of Mexico. In Shepard, F. P. and others (eds.), Recent Sediments, northwest Gulf of Mexico. Tulsa, Oklahoma, Amer. Assoc. Petrol. Geol., pp. 302-337.
- POPOV, YU. N.  
1957. Nekotorye Permskie Peletsipody, Gastropody i Ammonity Verkhoyan'ya [Some Permian pelecypods, gastropods and ammonites of Verkhoyansk]. Nauchno-issled. Inst. Geol., Arkt., Sb. Stat. Paleont. Biostratigr., Vyp. 1, pp. 45-60, pls. 1-3.
- READ, C. B.  
1941. Fossil plants from the late Paleozoic of Parana and Santa Catarina. Serv. Geol. Min. Brasil, Monogr. 12, pp. 11-102, 8 pls.
- REED, F. R. C.  
1928. Triassic fossils from Brazil. Ann. Mag. Nat. Hist., ser. 10, vol. 2, pp. 39-48, pl. 1.
1929. Faunas Triassicas do Brasil. Serv. Geol. Min. Brasil, Monogr. 9, pp. 1-83, pls. 1-5.
1930. A new Permo-Carboniferous fauna from Brazil. *Ibid.*, Monogr. 10, pp. 1-45, pls. 1-8.
1932. Some new Triassic fossils from Brazil. Ann. Mag. Nat. Hist., ser. 10, vol. 10, pp. 479-487, pl. 19.
1935. Some Triassic lamellibranchs from Brazil and Paraguay. Geol. Mag., vol. 72, pp. 33-42, pl. 1.
1936. Some fossils from the *Eurydesma* beds (Punjabian) of the Salt Range. Mem. Geol. Surv. India, Palaeont. Indica, new ser., vol. 23, no. 1, pp. 1-36.
- ROCHA-CAMPOS, A. C.  
1967. The Tubarão group in the Brazilian portion of the Paraná Basin. In Bigarella, J. J., R. D. Becker, and I. D. Pinto (eds.), Problems in Brazilian Gondwana Geology—1. First Internat. Symp. Gondwana Stratigr. Palaeont., Curitiba, pp. 27-102, pls. 3-35. [In Press.] Moluscos fósseis de Taió, S. C., Paleontologia e elementos da geologia da area.
- ROCHA-CAMPOS, A. C., J. E. S. FARJALLAT, AND R. YOSHIDA  
1969. Facies e paleogeografia do sub grupo Itararé na Bacia do Paraná. Acad. Brasil. Cien. An., vol. 41, no. 2, pp. 211-213.
- RUNNEGAR, B.  
1965. The bivalves *Megadesmus* Sowerby and *Astartila* Dana from the Permian of eastern Australia. Jour. Geol. Soc. Australia, vol. 12, pt. 2, pp. 227-252.  
1966. Systematics and biology of some desmodont bivalves from the Australian Permian. *Ibid.*, vol. 13, pt. 2, pp. 373-386.  
1967. Desmodont bivalves from the Permian of eastern Australia. Bull. Australian Bur. Min. Resources, no. 96, 108 pp. 13 pls.  
1968. Preserved ligaments in Australian Permian bivalves. Palaeontology, vol. 11, pt. 1, pp. 94-103, pls. 19-20.  
1969a. A lower Triassic ammonoid fauna from southeast Queensland. Jour. Paleont., vol. 43, no. 3, pp. 818-828, pls. 103-104.  
1969b. Permian fossils from the southern extremity of the Sydney Basin. In Campbell, K. S. W. (ed.), Stratigraphy and palaeontology: essays in honour of Dorothy Hill, Canberra, Australia, A.N.U. Press, pp. 276-298, pls. 18-20.
- RUNNEGAR, B., AND J. A. FERGUSON  
1969. Stratigraphy of the Permian and Lower Triassic marine sediments of the Gympie district, Queensland. Univ. Queensland, Dept. Geol., Papers, vol. 6, no. 9, pp. 247-281, pls. 1-6.

- SALAMUNI, R.  
1963. Estruturas sedimentares singenéticas e sua significação na série Passa Dois. Univ. Paraná Bol., Geol. 12, 90 pp.
- SANFORD, R. M., AND F. W. LANGE  
1960. Basin-study approach to oil evaluation of Paraná Miogeosyncline, South Brazil. Bull. Amer. Assoc. Petrol. Geol., vol. 44, no. 8, pp. 1316-1370.
- SOMMER, F. W.  
1954. Contribuição à Paleofitografia do Paraná. In Lange, F. W. (ed.), Paleontologia do Paraná, Curitiba, Paraná, Brasil, Comissão de Comemorações do Centenário do Paraná. pp. 175-194, pls. 15-20.
- SOOT-RYEN, T.  
1966. Revision of the pelecypods from the Michael Sars North Atlantic deep-sea expedition, 1910, with notes on the family Verticordiidae and other interesting species. Sarsia, vol. 24, pp. 1-31, 3 pls.
- STANLEY, S. M.  
1968. Post-paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation. Jour. Paleont., vol. 42, no. 1, pp. 214-229, 13 figs.
- TOZER, E. T.  
1969. Xenodiscacean ammonoids and their bearing on the discrimination of the Permian-Triassic boundary. Geol. Mag., vol. 106, no. 4, pp. 348-361, pl. 16.
- TRUEMAN, E. R.  
1968. A comparative account of the burrowing process of species of *Mastra* and other bivalves. Proc. Malacol. Soc., vol. 38, pt. 2, pp. 139-151.
- TRUEMAN, E. R., A. R. BRAND, AND P. DAVIS  
1966. The dynamics of burrowing of some common littoral bivalves. Jour. Exp. Biol., vol. 44, pp. 469-492.
- VOKES, H. E.  
1967. Genera of the Bivalvia: a systematic and bibliographic catalogue. Bull. Amer. Paleont., vol. 51, no. 232, pp. 111-393.
- WATERHOUSE, J. B.  
1965. Generic diagnoses for some burrowing bivalves of the Australian Permian. Malacologia, vol. 2, no. 3, pp. 367-380.  
1966. On the validity of the Permian bivalve family Pachydomidae Fischer 1887. Jour. Geol. Soc. Australia, vol. 13, no. 2, pp. 543-559, pls. 15-17.  
1969. The Permian bivalve genera, *Myonia*, *Megadesmus*, *Vacunella* and their allies, and their occurrences in New Zealand. New Zealand Geol. Surv. Paleont. Bull. no. 41, 141 pp., pls. 1-23.
- WILSON, B. R.  
1967. A new generic name for three Recent and one fossil species of Mytilidae (Mollusca: Bivalvia) in southern Australasia, with re-description of the species. Proc. Malacol. Soc. London, vol. 37, no. 4, pp. 279-295, pl. 37.
- ZENKEVITCH, L.  
1963. Biology of the seas of the U.S.S.R. (Translated by S. Botcharaskaya), New York, Interscience, 955 pp.



