AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2829, pp. 1–40, figs. 1–62 October 21, 1985

Permian Gastropods from Perak, Malaysia. Part 3. The Murchisoniids, Cerithiids, Loxonematids, and Subulitids

ROGER L. BATTEN[1]

ABSTRACT

This is the final part of a study of Permian gastropods from the *Misellina claudiae* zone from the H. S. Lee Mine No. 8, near Kampar, Perak, Malaysia. The fauna constitutes one of the richest and most diverse known in the Permian—91 species of 52 genera. Included in this portion of the study are analyses of species of the murchisoniids, loxonematids, cerithiids, subulitids, nerineids, pyramidellids, and trochids. This study now provides the best documented Permian gastropod fauna of the Eastern Hemisphere. There are 33 new species of a total of 41 and 4 new genera described herein. The genera belong to the Murchisoniidae, Loxonematacea (incertae sedis), Procerithiidae, and the Nerineidae; the latter two families are important Mesozoic groups reported for the first time in the Paleozoic. The presence of these and other dominant post-Triassic families and the presence of Paleozoic groups in the Triassic serve as additional evidence that a catastrophic event did not affect gastropods at the end of the Permian as it might have in nonmolluscan groups. Of interest is the recognition of a number of species which have very similar morphologies to species from the North American Pennsylvanian, particularly among *Retispira, Naticopsis, Trachidomia, Worthenia, Orthonema,* and *Pseudozygopleura.* The presence of an unusually large number of siphonate species (18) in the fauna may indicate the beginning of the exploitation of infauna habitats, perhaps in response to the origin of predation.

INTRODUCTION

This study completes the description of the Permian Malaysian gastropods. It was based on the marine molluscan fauna found at a single locality, Lee Mine No. 8 near Kampar, Perak [map of Malaysia sheet 2n/9, old series (MR 90356)]; see Batten, 1972, p. 5 for details. As stated in the first part of this study (Batten, 1972, p. 5), the preservation is quite

[1] Curator, Department of Invertebrates, American Museum of Natural History.

Copyright © American Museum of Natural History 1985 ISSN 0003-0082 / Price $3.95

uneven; much of the surface detail is preserved in fine, powdery calcite dust which is so fragile that merely touching the surface may destroy details. In consequence, there are fairly large numbers (more than 300 of a total of 646 studied) of specimens which can be placed in high-level categories only. Many of these are high-spired, many-whorled forms that suggest placement in the Cerithiacea and do not seem to fit into any of the groups described herein. Other specimens appear to belong to some of the trochid and subulitid families. On the whole, this gives the fauna a far more Mesozoic appearance than would appear to be true from the illustrations and synoptic classification. I cannot overemphasize the importance of these indescribable specimens in judging the nature of this fauna.

There is an unusually large number of siphonate species in this fauna (some 18) compared to all other known Permian faunas where one or two may be present. Some of the siphonate species are in groups such as the murchisoniids which are always holostomous (with apertures which do not have siphonal notches indicating siphons). This may reflect an early trend into the infaunal realm (see the conclusions for a more detailed discussion).

The fauna is dominated by gastropods, but corals, scaphopods, bivalves, brachiopods, and cephalopods are present along with fusulinids and other Foraminifera. Based on fusulinids, the unnamed white-colored limestone which contains the fauna is dated as Late Artinskian–Early Guadalupian and is included in the *Misellina claudiae* zone (Jones, Gobbett, and Kobayashi, 1966, p. 328). As mentioned in the earlier reports, this Tethyan fauna containing 92 gastropod species is, with the exception of the Lower Getaway Limestone fauna of the Guadalupe Mountains, Texas, the richest known thus far in the Permian. The fauna is composed of both endemic and cosmopolitan species and has several unusual and important characteristics, such as the presence of the earliest known nerineid, *Prodiozoptyxis permiana* (new genus and species). The endemic forms *Loxosonia* (new genus), *Acrospira* (new genus), and *Sinozyga* (new genus), have exaggerated morphological features, such as siphons, unknown in other members of the families. Mention should again be made of the disjunctive distributions of *Sallya, Dichostasia, Lacunospira,* and *Lamellospira* known only from this Lee Mine locality and in several horizons in the Permian of the southwestern United States. There are several examples of disjunct distributions involving distances of thousands of miles in the Paleozoic marine faunas. Another example is the Cambrian molluscan (*Hypseloconus*) fauna found in the north central United States and the Ellsworth Mountains of Antarctica. In this case about 10 genera are found in common; in fact, the species are nearly identical (Yochelson, personal commun., 1983).

An important observation made during the course of this study was to find a number of iterative morphotypic species between North American Pennsylvanian and the Malaysian Permian of the genera *Naticopsis* McCoy, 1844, *Trachydomia* Meek and Worthen, 1866, *Retispira* Knight, 1945, *Worthenia* DeKoninck, 1883, *Orthonema* Meek and Worthen, 1862, and *Pseudozygopleura* Knight, 1930. Bayer and McGhee (1984) have shown that repeated morphologies of ammonites are intimately correlated with directional changes in the physical environment in the Middle Jurassic Basin of Germany. These morphologies are not derived from evolutionary lineages because they are repeated in unrelated lineages involving endemic and immigrant groups. Yet, in each of three cycles the morphological sequence is exactly repeated. I suspect that the repeated species morphologies of the above genera are not directly linked genetically to the North American species but are convergent on them and reflect similar environments in different parts of the Tethys.

In the case of the Malaysian species there are, in addition to some identical features of North American Pennsylvanian species, sufficient differences to recognize them as being distinct. For example, if I should throw species from both areas together I would have no trouble separating them. In critical features such as the two spiral ribs defining the outer whorl face, *Orthonema rectimurum* n. sp. is identical to *Orthonema salteri* Meek and Worthen, 1860, yet in details of the secondary ornament such as the threads near the sutures, the two species are distinct. The Malaysian *Orthonema nakazawai* n. sp., *O. rectimurum* n. sp., *O. tirusum* n. sp., and *O. knighti* n. sp. have the following iterative counterparts in the North American Pennsylvanian: *O. marvinwelleri* Knight, 1934, *O. liratum* Sayre, 1930, *O. salteri* Meek and Worthen, 1860, and *O. inornatum* Knight, 1934. Knight (1934) was the first and only reviewer of the genus *Orthonema* which, at that time, was known only by 10 species from the North American Pennsylvanian. Because species of the genus are represented by only a single or few specimens at any locality, inter- and intraspecific variation remained unknown. This study furnishes some introspection into this variation.

It is difficult to compare the composition of the known Tethyan Permian faunas owing to the variation in time, ecology, and geographic distribution. The physically closest faunas are those described by Delpey (1942) in Cambodia and by Yin (1983) and Wang and Xi (1980) from Yunnan and Guizhou. The Cambodian fauna is almost identical to the Malaysian fauna in many groups, but it lacks the diversity; unfortunately, Delpey did not report the size of her samples and we cannot compare frequencies. The Sosio and Tunisian faunas are quite similar and are related to the Western Hemisphere faunas rather than to the eastern Tethyan faunas. The Yunnan and Guizhou faunas lack many of the species represented in the Malaysian fauna. Obviously, this difference is due to the more complete sampling of the Malaysian Permian because of the unique preservation. The Salt Range fauna has a few conservative bellerophontid genera and many endemic species, making comparisons difficult.

One of the most important observations made in this study was an incurrent siphonal notch in *Paleostylus* as represented by the Asian Tethyan species. In consequence, *Paleostylus* senso stricto (the type species *P. pupoides* Mansuy, 1914 was described from Southeast Asia) must be removed from the Loxonematacea, which are exclusively holostomous. The concept of *Paleostylus* as a member of the loxonematid pseudozygopleurids was introduced by Knight in 1936. My conclusion is to place the genus in the Cerithiacea based on the presence of the siphonal notch and features shared with Jurassic cerithids, including nearly vertical, straight growth lines. This represents a major systematics change.

There is a serious systematics consequence of this discovery—over 50 species of Carboniferous and Permian pseudozygopleurids have been assigned to this genus. They are clearly holostomous and firmly placed as distinct members of this family. They are somewhat similar to *Paleostylus,* namely in having vertical ribbing on flattened whorls and a high-spired many-whorled shell. This ribbing ranges from typical slightly curved pseudozygopleurid ornament to the straight ribbing seen in the cerithids. See page 11 for a more detailed discussion.

Finally, I should point out that the recognition of a new genus of nerineids in the Paleozoic *Prodiozoptyxis* may appear difficult to justify. However, the presence of apomorphic nerineid features, such as internal folds, in this new genus suggests placement in this family rather than in the campanilids as discussed in the systematics of *Prodiozoptyxis.* The nerineids undergo a rapid diversification in the Jurassic and Cretaceous. When the first species appeared in the Bajocian, they already had parietal and columellar folds. Huddleston (1889, p. 497) reports 26 species from the Inferior Oolite and these show a range from simple folds to rather complex infolding of the principal folds.

The literature does not indicate the presence of nerineids in the Triassic; however, there is an undescribed species in the Norian fauna of Idaho (Seven Devils Formation). In that species there is a single mid-whorl parietal fold. The shell is very high-spired with flattened, slightly concave whorls much like the common Jurassic genus *Nerinea* Deshays, 1827. The only real gap is the absence of a nereinid in the Middle Triassic (none are present in the St. Cassian fauna).

I cannot judge from Huddleston's illustrations whether all of the 26 species he described belong to *Nerinea.* I suspect they do not because he was extremely conservative in using generic determinations; for example, he used *Pleurotomaria* where none of the species are currently assigned to that genus. In fact, I doubt that all of the species would be considered valid by today's standards. In any event, the illustrations show an interesting sequence of increasingly complex internal folds. The Permian species falls well within the range of that Inferior Oolite sequence.

ACKNOWLEDGMENTS

I again thank Dr. Derek J. Gobbett of Cambridge University (formerly of the University of Malaysia) for sending me the specimens that form the basis of this study. Dr. Keiji Nakazawa of Kyoto University deserves special thanks for sending vital additional specimens collected during the Southeastern Scientific Expedition made by members of the Ozaka City and Kyoto universities. I thank Mr. G. Robert Adlington and Mr. Peter Harries for the bulk of the photographs made of poorly photogenic material.

SYMBOLS AND ABBREVIATIONS

The following abbreviations are used: **AMNH** American Museum of Natural History. **H** shell height. In most cases this measurement is estimated because the protoconch and earliest whorls are frequently broken off. The height is approximated by measuring the distance between the base of the shell and the intersection of eye-piece goniometer cross-hairs, which are touching the later whorls to measure the spiral angle, and are extended above the top of the shell at the position of the tip of the protoconch. In many cases the protoconch height is not related to the logarithmic progression of the teleoconch; it may be higher or lower. **W** shell width. **WhH** whorl height. **WhW** whorl width. **SpAng** the spiral angle.

The numbers in parentheses in the synoptic classification are the numbers of specimens of each species studied.

SYNOPTIC CLASSIFICATION

Class Gastropoda
  Subclass Prosobranchia
    Order Archeogastropoda
      Suborder Murchisoniina
        Superfamily Murchisoniacea Koken, 1896
          Family Murchisoniidae Koken, 1896
            Genus *Murchisonia* d'Archiac and deVerneuil, 1841
              Subgenus *M.* (*Donaldospira*) Batten, 1966
                M. (*D.*) *malaysia,* new species .... (21)
            Genus *Stegocoelia* Donald, 1892
              Subgenus *S.* (*Taosia*) Girty, 1939
                S. (*T.*) *bengkaka,* new species .... (10)
            Genus *Goniasma* Tomlin, 1930
                Goniasma, species .... (1)
            Genus *Cibecuia* Winters, 1963
                C. divarica, new species .... (4)
            Genus *Loxosonia,* new genus
                L. hormotoma, new species .... (6)
                L. zygopleuroides, new species .... (3)
    Order Mesogastropoda Theile, 1925
        Superfamily Loxonematacea Koken, 1889
          Family Pseudozygopleuridae Knight, 1930
            Genus *Pseudozygopleura* Knight, 1930
              Subgenus *P.* (*Pseudozygopleura*) Knight, 1930
                P. (*P.*) *pleurozyga,* new species .... (8)
                P. (*P.*) *obliqua,* new species .... (4)
                P. (*P.*) *convexus,* new species .... (6)
                P. (*P.*) *lirata,* new species .... (12)
                P. (*P.*), species .... (2)
              Subgenus *P.* (*Leptozyga*) Knight, 1930
                P. (*L.*) cf. *venustus* Hoare and Sturgeon, 1981 .... (4)
              Subgenus *P.* (*Stephanozyga*) Knight, 1939
                P. (*S.*), species .... (1)

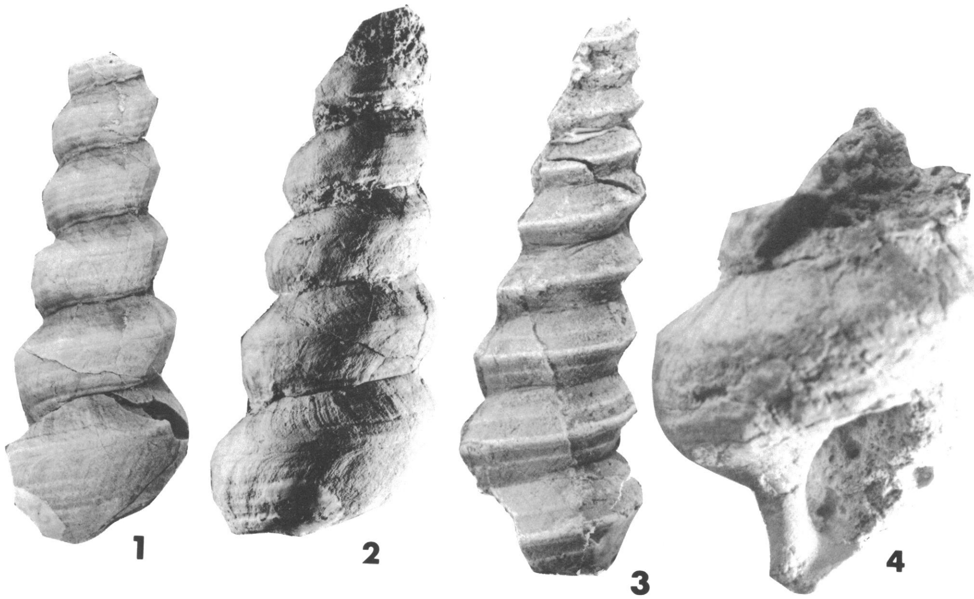
ORDER ARCHEOGASTROPODA

SUBORDER MURCHISONIINA COX AND KNIGHT, 1960

DISCUSSION: Cox and Knight (1960) constructed this suborder because of some morphological differences between the pleurotomarians and the high-spired murchisoniids and also because they recognized that the murchisoniids were ancestral to the loxonematids and the cerithids and hence distinct from the pleurotomarians which they resemble. Some genera have incipient abapical apertural canals whereas the pleurotomarians are holostomous. They have a three-layered crossed-lamellar wall as opposed to the nacroprismatic wall of all known pleurotomarians, which serves, in part, to separate the two suborders. The crossed-lamellar structure is of the form of short first-order lamellae with opposing sets of second-order lamellae at relatively low angles. This type of structure is commonly encountered in many archaeogastropod groups, such as the euomphalids, bellerophontids, and neritaceans (see Batten, 1984, p. 12). The centrally located selenizone indicates that they retained paired aspidobranch ctenidia and rhipidoglossate radula. With this group as the ancestral stock of two mesogastropod superfamilies (Cerithiacea and Loxonematacea), it is clear that both the archeogastropods and the mesogastropods are polyphyletic since the trochids also appear to have given rise to a number of mesogastropod families.

FAMILY MURCHISONIIDAE KOKEN, 1896

DISCUSSION: Knight et al. (1960) have discussed the morphological range of the genera included in this family. They concluded that one of the most important morphological complexes in the family was that of the placement of the selenizone. For example, *Goniasma* Tomlin, 1930 has a selenizone immediately underlying a centrally located keel or periphery, while *S.* (*Hypergonia*) Donald, 1892 has a selenizone immediately overlying the periphery. *M.* (*Donaldospira*) Batten, 1966 has a selenizone on the periphery so that half of it is above and half below, resulting in a convex selenizone. The family is relatively conservative with a low speciation rate in the Upper Paleozoic. Inter- and intrapopulation variation is low. Only a few specimens of a single species occur in most faunas. At AMNH locality 512 in the lower Getaway limestone at Pine Springs, Guadalupe Mountains, Texas, the richest Permian fauna yet to be found has about 100 specimens belonging to five species. The Lee Mine fauna has 43 specimens belonging to six species.



FIGS. 1–4. *Murchisonia* (*Donaldospira*) *malaysia*. **1.** Holotype, AMNH 42782, side view, ×1.5. **2.** Paratype, AMNH 42784, side view with low-angled lighting to show the selenizone bisected by the angular periphery; this is a more rounded variant, ×1.5 mm. **3.** Paratype, AMNH 42785, side view of a turriculate variant, ×2. **4.** Paratype, AMNH 42788, apertural view of a fragment showing the well-developed siphonal trough; the unorthodox side lighting from the right is necessary to cast a shadow on the trough, ×2.

Murchisonia (*Donaldospira*) Batten, 1966

TYPE SPECIES: *Murchisonia pertusa* deKoninck, 1883, p. 15, pl. 33, figs. 50, 51; from the v3b (=D_2) zone at Vise, Belgium.

DISCUSSION: Batten (1966, p. 68) recognized seven species in the Devonian and Lower Carboniferous (confined to western Europe) as belonging to this subgenus; thus far it has not been identified in the Pennsylvanian or elsewhere in the Permian. The preservation of these specimens is such that little surface detail, such as growth lines, is available for analysis. For example, the curious patterned punctation found in the type species *M.* (*D.*) *pertusa* was not observable. It is possible that some of the silicified specimens identified as *Stegocoelia* (Donald, 1889) in the Permian of west Texas may be *Donaldospira,* but the coarse silicification has destroyed fine growth lines in every specimen examined, hence preventing proper taxonomic assignment. The shell shapes, position of the periphery on the whorl, and other features are nearly identical in both groups. Only the position of the selenizone, along with its associated characteristics, can be used to distinguish them.

***Murchisonia* (*Donaldospira*) *malaysia*,**
new species
Figures 1–4

DIAGNOSIS: Large, turritelliform snails with a convex selenizone forming the periphery; early whorls angulate with prominent peripheries, older whorls rounded with peripheries less well defined; selenizone ornamented with fine spiral threads and with collabral nodes; upper whorl surface convex, flat, or slightly concave with two or more spiral threads; alveozone flat to concave with one medial spiral thread; basal margin marked by a prominent spiral rib; base with one or more spiral threads or ribs. Siphonal groove well developed.

DISCUSSION: The population sample averaged about twice that of the type species *M.* (*D.*) *pertusa*. It differs from *Murchisonia dussaulti* Mansuy, 1914 in having a broad, flat upper whorl surface, with a more rapid whorl expansion rate. The fine spiral ornament is more numerous on the base and has a well-developed siphonal groove. The first known specimen of the subgenus to have the aperture preserved is shown in figure 4. The siphonal canal is more tapered and narrow than in any related group. The nature of the selenizone is unknown in *M.* (*D.*) *dussaulti.* I have not recognized the species in other faunas.

The early whorls of this species are turriculate with prominently developed peripheries; older whorls are more rounded with the periphery less well defined. This feature varies among specimens; some are more turriculate throughout ontogeny. **Twenty-one specimens.**

MEASUREMENTS: Holotype AMNH 42782, H 47.1 (e) mm, W 17.1 mm, SpAng 13°; paratype AMNH 42783, H 40.2 (e) mm, W 13.8 mm, SpAng 14.5°; paratype AMNH 42784, H 58.2 (e) mm, W 18.7 mm, SpAng 16.0°; paratype AMNH 42785, H 59.2 (e) mm, W 20.2 mm, SpAng 16.0°; paratype AMNH 42786, H 51.6 (e) mm, W 20.6 mm, SpAng 19.0°; paratype AMNH 42787, H 61.9 (e) mm, W 28.0 mm, SpAng 14.5°; paratype AMNH 42788, H 85.1 (e) mm, W 26.8 mm, SpAng 14.5°. (e) = estimated height, the specimen is broken.

Stegocoelia (*Taosia*) Girty, 1939

TYPE SPECIES: *S.* (*T.*) *copei* (White), 1881, p. 31, pl. 3, figs. 10a, b.

DISCUSSION: This subgenus is widely distributed in upper Paleozoic rocks but only one or several specimens occur at any one locality.

***Stegocoelia* (*Taosia*) *bengkaka*, new species**

Figures 5–6

DIAGNOSIS: Relative high-spired, turriculate shells with a strongly noded periphery located low on the whorl. Sutures are located just below the periphery. A well-defined spiral cord is adjacent to the upper suture. There may be fine collabral threads developed on the periphery and upper spiral cord. The selenizone is located midway between the suture and the periphery on the flattened or slightly concavoconvex upper whorl face. The base is somewhat flattened and minutely phaneromphalus. The columellar lip has an elongate, centrally located callus which slightly reflexes the lip. A spiral thread is located in the middle of the base; no other spiral ornament was observed.

DISCUSSION: This specimen is virtually identical to *S.* (*T.*) *crenulata* Girty, 1939, a ubiquitous species in the Pennsylvanian and Permian of the Western Hemisphere. It is not preserved well so that the growth lines and perhaps fine ornament are not observable. However, the basic morphology cannot be separated from that of *S.* (*T.*) *crenulata.* To the best of my knowledge, this subgenus is thus far unknown in the Eastern Hemisphere with the exception of a specimen I have identified from the highest Permian in Greece.

SPECIMENS: Ten; two other specimens are from the Sin Thong Hing Mine near Kampar and marked "Upper Paleozoic" on the Department of Geology label (University of Malaysia).

MEASUREMENTS: Holotype AMNH 42789, H 8.0 mm, W 2.9 mm, WhH 1.5 mm, WhW 2.9 mm; large paratype AMNH 42790, H 21.0 mm, W 8.9 mm, WhH 4.2 mm, WhW 8.9 mm.

ETYMOLOGY: *Bengkak,* Malay for swelling.

Stegocoelia (*Stegocoelia*) sp.

Figure 7

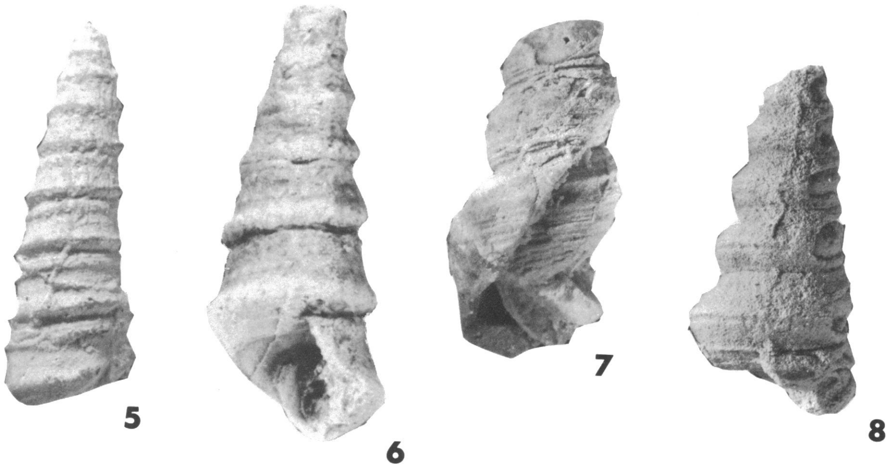
DESCRIPTION: High-spired, turriculate shells with the periphery below midwhorl; the upper selenizone margin forms the periphery; the lower selenizone margin defines a narrow, flat selenizone. The upper whorl face is slightly convexoconcave; the lower whorl face is about one-third the size of the upper whorl face and the sutures are sharply defined.

DISCUSSION: There is only a single specimen of this taxon and the preservation of the shell is so poor that nothing can be discussed of the ornament or other morphology except the selenizone and associated characters. **One specimen.**

MEASUREMENTS: AMNH 42791, H 14.7 mm, W 5.7 mm, SpAng 29°.

Genus *Goniasma* Tomlin, 1930

TYPE SPECIES: *Murchisonia lasallensis* Worthen, 1930.



FIGS. 5–8. **5.** *Stegocoelia* (*Taosia*) *bengkaka*. Holotype, AMNH 42789, side view, ×6.6. **6.** Paratype, AMNH 42790, apertural view, note strong rib on periphery, ×2.5. **7.** *Stegocoelia* (*Stegocoelia*) sp., AMNH 42791, side view of fragment, ×3. **8.** *Goniasma* sp., AMNH 42792, side view, ×4.

DISCUSSION: As far as I am aware this is the first report of the genus outside North America. The type species is from the Pennsylvanian of Illinois. Three species have been described from the Pennsylvanian and Permian of the western United States. The genus is based on the selenizone location; it is just below the periphery, with the upper selenizone margin forming the periphery.

Goniasma sp.
Figure 8

DISCUSSION: One specimen in this fauna is clearly a member of this genus. The preservation is too poor to describe the species characteristics. The whorls are evenly convex and there are several spiral cords. The upper margin of the selenizone marks the periphery. The selenizone is strongly concave and the margins rounded and well developed. The upper whorl surface has a well-developed spiral cord in the center. The whorls embrace on a spiral cord which forms the edge of the base. The base is narrowly phaneromphalus. **One specimen.**

MEASUREMENTS: AMNH 42792, H 12.3 mm, W 5.6 mm, SpAng 21°.

Cibecuia Winters, 1963

TYPE SPECIES: *C. cedarensis* Winters, 1963, p. 38, pl. 4, figs. 5a–6b.

DISCUSSION: *C. divarica*, new species, is the only other species of the genus. *Cibecuia* previously has been known only from the Permian Kaibab Formation of eastern Arizona and from a single fragment from the Bone Spring Formation, Sierra Diablo Mountains of western Texas. This is yet another example of a disjunct distribution involving the southwestern United States and Malaysia.

Cibecuia divarica, new species
Figure 9

DIAGNOSIS: High-spired shells with whorl profile smooth and whorl face flat; selenizone just above midwhorl, the lower selenizone margin marks its midwhorl; selenizone margins impressed; base delineated by a spiral keel; numerous collabral, elongated nodes on upper whorl surface adjacent to the suture; collabral threads are formed on the outer whorl surface from the lower selenizone margin to the basal periphery; whorls embrace just below the spiral keel; base ornamented by two equally spaced and developed ribs; base is flat to slightly concave.

DISCUSSION: This species is remarkably similar to the type and the previously only known species, *C. cedarensis* Winters, 1963. It differs in that the whorl profile is less stepped than that of *C. cedarensis* because the lower part of the whorl is more fully de-

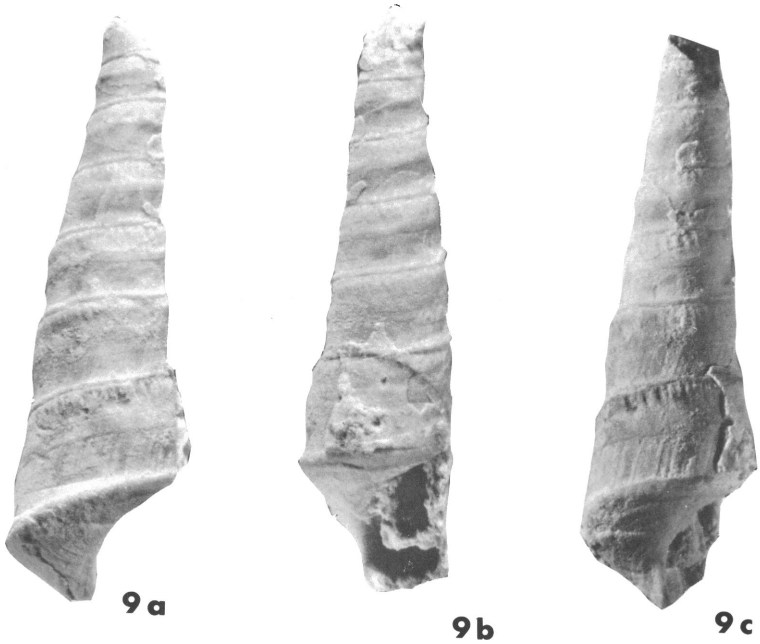


FIG. 9. *Cibecuia divarica,* holotype, AMNH 42793; (**a**) side view, ×4.5; (**b**) apertural view, ×4.5, low-angled lighting was used to bring out details of selenizone and subsutural ornament; (**c**) side view, ×4.5 with low-angle light to bring out details.

veloped than that of the whorl near the suture. The sutural nodes are more numerous and finer than that of the type species. In all other features the two species are identical. **Four specimens.**

MEASUREMENTS: Holotype AMNH 42793, H 15.00 mm, W 4.3 mm, WhH 3.0 mm., WhW 4.3 mm, SpAng 12°; paratype AMNH 42794, H 8.00 mm, W 3.5 mm, WhH 2.1 mm, WhW 3.5 mm, SpAng 12°; paratype AMNH 42795, WhH 3.2 mm, WhW 5.5 mm.

ETYMOLOGY: *Divaricatus,* Lat. spread.

Loxisonia, New Genus

DIAGNOSIS: Moderately high-spired, fusiform shells with a selenizone located near the suture on the upper whorl surface; whorls elongate, rounded; sutures embrace whorls below the rounded peripheral region; selenizone margins sharply defined by narrow grooves; ornament, if present, consists of collabral ribs or threads, is more developed on the outer whorl face; columellar lip reflexed into a narrow funicle or callus; siphonal canal is short and shallow.

DISCUSSION: The shell shape and the collabral ornament of this genus is highly convergent on the fusiform shells of the loxonematids, but the presence of a well-developed selenizone and siphonal canal is typical of the murchisonids. *Loxisonia* differs from the murchisonids *Aclisina* and *Stegocoelia* in having the selenizone much higher on the whorl (near the suture), in having a siphonal canal, and by having rounded whorls with no spiral ornament, keels, or sharply defined periphery. I have found specimens of the genus illustrated in an unpublished manuscript illustration of the Permian of Crimea written by O. Toumansky in the late 1930s or early 1940s.

ETYMOLOGY: *Loxos,* Gk. sloping; *sohn,* Gk. related to.

Loxisonia hormotoma, new species

Figures 10–11

DIAGNOSIS: A moderately high-spired shell with elongate, rounded to somewhat flattened whorls with a relatively narrow selenizone, apparently without margins, located near the suture; the suture is sharp and deeply impressed; ornament is faintly developed collabral threads or ribs which are barely raised above the whorl surface and are rounded to somewhat flattened; whorls embrace well below the rounded periphery located at midwhorl; the base is rounded and continuous with the outer whorl surface; siphonal canal well developed and narrow; hemiomphalus to anomphalus.

DISCUSSION: This species differs from *L. zygopleuroides* in being an order of magnitude larger and with the ornament faintly developed; the shell shape is more variable, ranging from a compressed form with more tightly coiled, flattened whorls to a loosely coiled form with more inflated whorls and a rounded base.

SPECIMENS: Six; all specimens are broken but with from five to nine whorls preserved.

MEASUREMENTS: Holotype AMNH 42796, H 10.5 mm, W 3.55 mm, SpAng 21°; paratype AMNH 42797, H 5.1 mm, W 2.01 mm, SpAng 17°; paratype AMNH 42798, H 4.20 mm, W 1.53 mm, SpAng 16°; paratype AMNH 42799, H 3.20 mm, W 1.10 mm, SpAng 14°.

ETYMOLOGY: *Hormos,* Gk. chain; *tomas,* Gk. cut.

Loxisonia zygopleuroides, new species
Figure 12

DIAGNOSIS: Shell with smooth, rounded whorls except at the selenizone and upper whorl surface above it which are flattened relative to the rest of the whorl; the selenizone is flat to concave with asymmetric lunulae; the selenizone is located higher on the whorl; ornament is strongly developed collabral ribs which are rounded between the suture and the selenizone; the ribs are strongly arcuate on the lower whorl face forming a deep sinus adjacent to the selenizone; ornament absent on the base; siphonal notch short; anomphalus.

DISCUSSION: This species is strongly convergent on the pseudozygopleurid *P. sinuosia* Knight, 1930 in the shape of the shell, the whorl profile, the collabral ribs, the shape of the base, and the reflexed columellar lip. It differs from the pseudozygopleurids in having a well-developed selenizone which interrupts the collabral ribs above the midwhorl.

SPECIMENS: Three; all specimens are broken so that only the last two whorls are present.

MEASUREMENTS: Holotype AMNH 42800, H 7.0 mm, W 3.2 mm, SpAng 14°; paratype AMNH 42801, H 6.0 mm, W 2.8 mm, SpAng 12°; paratype AMNH 42802, H 12.0 mm, W 6.0 mm, SpAng 20°.

ETYMOLOGY: *Zygon,* Gr. yoke; *pleuron,* Gr. rib.

ORDER MESOGASTROPODA THIELE, 1925

DISCUSSION: Extinct members of this order, particularly of the Paleozoic, are recognized by comparison of shell morphology with extant groups. This is reinforced by assuming that extinct members of higher taxa share ordinal features with their living sister groups. Occasionally, a living relict of an extinct group is discovered such as the monoplacophoran *Neopilina. Abyssochrysos melanoides* Tomlin, 1927, a living species, was found which may possibly be a member of the otherwise extinct superfamily Loxonematacea Koken, 1889 (Houbrick, 1979). Thiele (1931), Wenz (1938), Taylor and Sohl (1962), and others had placed the family Abyssochrysidae in the superfamily Cerithiacea. The Cerithiacea have living representatives so that the taxonomic placement within the living mesogastropods is secure.

FAMILY PSEUDOZYGOPLEURIDAE KNIGHT, 1930

DISCUSSION: This family and others of the Loxonematacea have been suggested as mesogastropods based on the recognition of the living *Abyssochrysos melanoides* Tomlin, 1927 as being loxonematid rather than cerithiacean (Houbrick, 1979) as previously believed. This is based on the presence of closed pallial gonoducts and a large penislike organ which excludes it from the cerithids which have open pallial gonoducts and an aphallic condition in males (Houbrick, 1979, pp. 14–15).

There is a persistent recognition problem involving the families Zygopleuridae Wenz, 1938, Pseudozygopleuridae Knight, 1931, and Palaeozygopleuridae Horný, 1955 (see Hoare and Sturgeon 1978, pp. 850–852 for further discussion). Knight (1930, pp. 8–12) recognized the Paleozoic pseudozygopleurids as being distinct from the Mesozoic zygopleurids on the basis that the first four whorls are ornamented by features differing from those of an adult shell. Horný (1955) discovered several genera in the Devonian of Czechoslovakia which are identical to adult pseudozygopleurid shells except that the early whorls are unornamented. Subsequent to these finds, other species in the late Paleozoic have been found to have unornamented early whorls as well, and these have been called by various pseudozygopleurid generic names (Hoare, 1980). The problem is that without the early whorls preserved (the usual state), it is impossible to place shells in either family. In addition, the specter of homeomorphy is present. I see no reason why this problem could not be simply resolved by broadening the definition of the pseudozygopleurids to include the forms with smooth early whorls, hence synonymizing the palaeozygopleurids.

In the case of the Mesozoic zygopleurids, the main phyletic path has evolved away from the pseudozygopleurid bauplan. Only *Katosira* Koken, 1892, *Zygopleura* Koken, 1892, and *Tyrsoecus* Kittl, 1892 are similar to the Paleozoic families. Hence, there is merit to retaining the zygopleurids as a distinct entity. I would suggest that the above three genera could be placed in the Pseudozygopleuridae, but it is beyond the scope of this study to make such revisions.

Genus *Pseudozygopleura* Knight, 1930

TYPE SPECIES: *Loxonema semicostatum* Meek, 1872.

DISCUSSION: Knight (1930) originally set up four subgenera based on shell shape and ornament: *P.* (*Stephanozyga*), *P.* (*Pseudozygopleura*), *P.* (*Leptozyga*), and *P.* (*Progozyga*). Since that time two major revisions of the genus were effected by Knight et al. (1960) and Hoare and Sturgeon (1981). The former placed the four subgenera in the genus *Paleostylus*. This cannot be supported by current knowledge as documented by Hoare and Sturgeon (1981, p. 572).

Pseudozygopleura is not found in most faunas of the Tethyan Permian and, hence, we know little of its distribution. It is found in Crimean Permian but is curiously absent from the larger, better known faunas such as those in Tunisia, Sicily, or Greece. Even in the Texas Permian it is poorly represented.

P. (*Pseudozygopleura*) *pleurozyga*, new species

Figure 13

DIAGNOSIS: Shell high-spired with very weak spiral ornament on the periphery and with slightly sigmoid collabral ribbing that is well developed across the whorl. The convex whorl profile has a slight depression forming a trough just below the suture but is separated from it by poorly developed interference nodes on the ribs adjacent to the suture. Ribbing is weakly developed in the trough. A weakly formed periphery is present on the lower whorl face. The base is smoothly rounded. The ornament is evenly developed on all whorls except for the nuclear whorls and the base where it is subdued.

DISCUSSION: The presence of a shallow trough just beneath the suture is an important and unique feature. This and the related feature of the disappearance of ornament in the trough make this a distinctive species unrelated to any others described. There is variation in the development of the collabral ribbing from evenly formed ribs to those that are well developed only at the suture and on the outer portions of the periphery. In some specimens, the trough is very faint and only a slight weakening of the ribbing marks the position of the trough. **Eight specimens.**

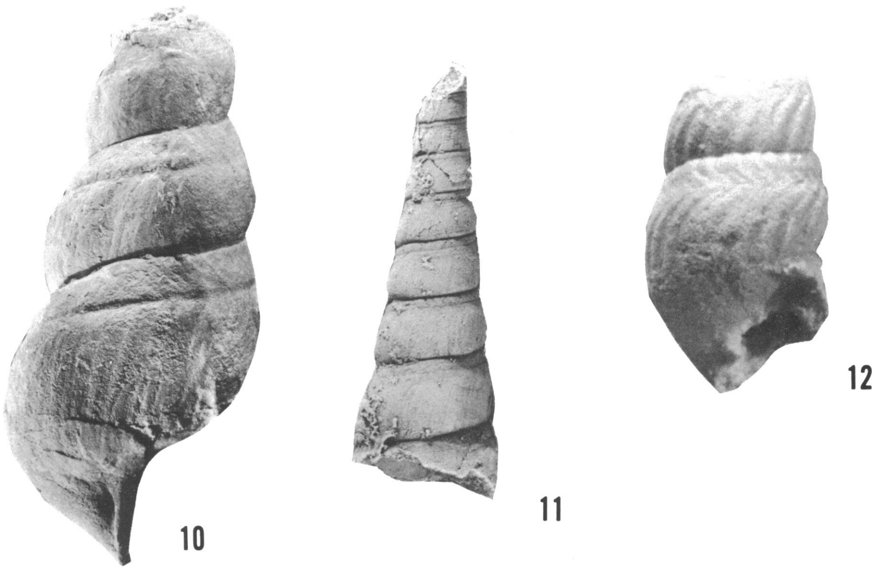
MEASUREMENTS: Holotype AMNH 42803, H 20.2 mm, W 8.4 mm, WhH 4.1 mm, WhW 7.3 mm; paratype AMNH 42804, broken WhH 3.7 mm, WhW 6.7 mm.

ETYMOLOGY: *Pleura,* Gk. ribs; *zygon,* Gk. yoke.

P. (*Pseudozygopleura*) *obliqua*, new species

Figure 14

DIAGNOSIS: High-spired shell with moderately, but evenly, inflated whorls, with the upper whorl surface slightly flattened. The collabral ribbing is straight but oblique to the suture. Each whorl has ribbing aligned with ribbing in adjacent whorls. Ribs are fully developed from suture to suture. Ribbing may be fine or coarse. Ornament weakens during growth so that earlier whorls are more strongly ornamented, the final two whorls with faint, rounded ribs or growth lines only. The pe-



FIGS. 10–12. **10.** *Loxosonia hormotoma,* holotype, AMNH 42796, apertural view, note siphonal trough, ×0.5. **11.** Paratype, AMNH 42799, side view of fragment, ×1. **12.** *Loxosonia zygopleura,* holotype, AMNH 42800, apertural view, ×8.

riphery is low on the whorls and the base is somewhat flattened. The whorls embrace just below the periphery. The ornament on the base consists of faint collabral threads.

DISCUSSION: Except for *P.* (*P.*) *semicostatum* (Meek), 1872 the type species, and *P.* (*P.*) *terebra* Knight, 1930, most species have the ornament fully developed throughout ontogeny. Some specimens may lose ornament in species that normally retain full ornamentation. I doubt that it has phyletic significance. The ribbing in this species and the very evenly developed whorl profile is quite distinctive. It most closely resembles *P.* (*P.*) *mucronotus* Hoare and Sturgeon, 1981, in the obtuse ribbing and evenly formed ribs; it differs from that species by having more inflated whorls and straight ribs. **Four specimens.**

MEASUREMENTS: Holotype AMNH 42805, H 24.0 mm, W 8.4 mm, WhH 3.8 mm, WhW 7.2 mm, SpAng 18°; paratype AMNH 42806, H 15.2 mm, W 2.9 mm, WhH 2.9 mm, WhW 6.2 mm, SpAng 18°.

ETYMOLOGY: *Obliquus,* Lat. slanting.

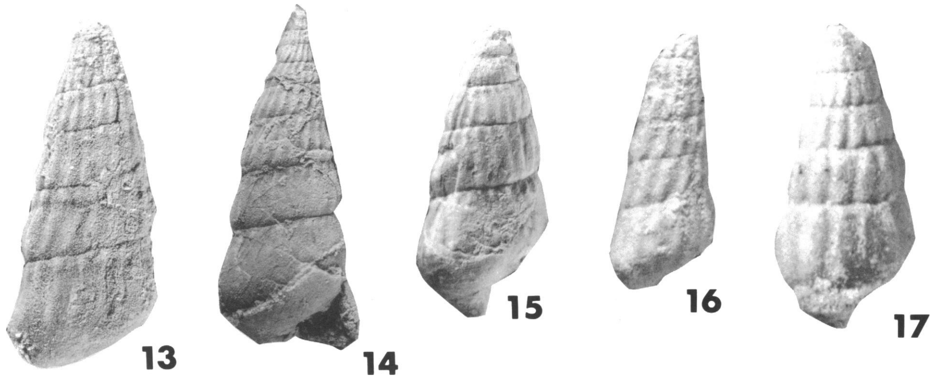
***P.* (*Pseudozygopleura*) *convexus*,**
new species
Figure 15

DIAGNOSIS: The shell is moderately high-spired with an evenly convex whorl profile with a midwhorl periphery and vertical, straight collabral ribs. The ribbing is well developed and sharply delimited with full development across the whorl. Weakly reinforced interference nodes are found on collabral ribs immediately adjacent to the suture. The sutures are sharply defined and deep. Whorls embrace on the edge of an ill-defined low periphery. The base is evenly rounded.

DISCUSSION: The variation noted in this species involves the whorl expansion rate causing some specimens to be more trochoid or lower spired than most other species in shell shape. Some specimens have somewhat finer ribs than that of the holotype. This species resembles *P.* (*P.*) *inornata* Knight, 1930 in the development of the ribbing, but the whorl profile is more inflated and the base more rounded. It is similar to *P.* (*P.*) *pugonis* Hoare and Sturgeon (1981) in the shape of the whorl but has finer ribbing. There does not seem to be any other described species outside North America that is similar to this one. **Six specimens.**

MEASUREMENTS: Holotype AMNH 42807, H 8.1 mm, W 3.9 mm, WhH 2.2 mm, WhW 3.9 mm, SpAng 26°; paratype AMNH 42808, broken WhH 3.6 mm, WhW 6.2 mm, SpAng 24°.

ETYMOLOGY: *Convexus,* Lat. arched.



FIGS. 13–17. *Pseudozygopleura* (*Pseudozygopleura*). **13.** *P.* (*P.*) *pleurozyga,* holotype, AMNH 42803, side view, ×2. **14.** *P.* (*P.*) *obliqua,* holotype, AMNH 42805, apertural view (aperture broken), ×2. **15.** *P.* (*P.*) *convexus,* holotype, AMNH 42807, side view, ×4.5. **16.** *P.* (*P.*) *lirata,* holotype, AMNH 42809, side view, ×8. **17.** *P.* (*P.*) sp., AMNH 42811, side view, ×12.5.

***P.* (*Pseudozygopleura*) *lirata*,** new species
Figure 16

DIAGNOSIS: A small, turriculate shell with flattened whorl profiles and flattened base with a lira marking the lower margin of the outer whorl face. The outer whorl face slopes outward to a sharply defined periphery low on the whorl. Collabral ribs are straight, moderately well developed, and nearly vertical over the whorl face. Ornament is uniformly developed over the entire shell. The suture is sharply defined but shallow. The base is flatly rounded with reduced to absent ornament.

DISCUSSION: The most distinguishing feature of this species is the flattened base delimited by a lira which forms the boundary between the base and the outer whorl face. To my knowledge, this is a unique feature to the genus. There is some variation in the development of the collabral ribs from numerous fine ribs to fewer coarser ribs. The whorl profile tends to be flattened but may be evenly convex and sloping toward the low-lying periphery. The species somewhat resembles several flat-based species described by Hoare and Sturgeon (1981) such as *P.* (*P.*) *gradatus* in the flattened whorl profile and base but differs in having a basal peripheral lira and an unornamented base. **Twelve specimens.**

MEASUREMENTS: Holotype AMNH 42809, H 4.8 mm, W 1.9 mm, WhH 0.8 mm, WhW 1.7 mm, SpAng 18°; paratype AMNH 42810, H 4.6 mm, W 2.3 mm, WhH 0.9 mm, WhW 1.7 mm, SpAng 16°.

ETYMOLOGY: *Lira,* Lat. for ridge.

P. (*Pseudozygopleura*), species
Figure 17

DISCUSSION: Two specimens are sufficiently distinct to include as a separate species. The whorl profile is evenly inflated with a flattened outer whorl face with well-developed, slightly arched, collabral ribs which are distinct in being fully developed from suture to the base. The suture is deeply incised. None of the other species have this unique rib development. Since only the illustrated specimen is well preserved, I have refrained from formalizing this species. **Two specimens.**

MEASUREMENTS: AMNH 42811, H 3.7 mm, W 1.7 mm, SpAng 38°.

P. (*Leptozyga*) Knight, 1930

TYPE SPECIES: *P.* (*Leptozyga*) *minuta* Knight, 1930, p. 63, pl. 4, fig. 2.

P. (*Leptozyga*) cf. *venustus*
Hoare and Sturgeon, 1981
Figure 18

P. Leptozyga venustus Hoare and Sturgeon, 1981, p. 584, pl. 1, figs. 13–14.

DISCUSSION: Several specimens are so close in morphology to this species that I can detect no important differences between them. They show the same evenly convex whorl profiles and fine, numerous collabral threads. The base is rounded and anomphalus. One tiny specimen has coarser threads than those illustrated by Hoare and Sturgeon. **Four specimens.**

MEASUREMENTS: AMNH 42812, H 11.5 mm, W 4.7 mm, WhH 1.9 mm, WhW 3.0 mm, SpAng 2.5°.

P. (*Stephanozyga*) Knight, 1930

TYPE SPECIES: *P.* (*Stephanozyga*) *nodosa* (Girty), 1915.

P. (*Stephanozyga*) sp.
Figure 19

DISCUSSION: A single, poorly preserved specimen is probably a member of this subgenus. It resembles the type species in having a concavo-convex whorl profile with a very low periphery. Suture embrace beneath the periphery. The periphery is noded with collabral ribs which disappear just above the peripheral ridge. Sutures are shallow and sharply defined. The subgenus is very rarely encountered, known only from a few horizons in the Pennsylvanian Des Moines Series in the Mississippi Valley. **One specimen.**

MEASUREMENTS: AMNH 42813, H 4.6 mm, W 2.6 mm, WhH 1.1 mm, WhW 2.3 mm, SpAng 22°.

Hemizyga (*Hemizyga*) Girty, 1915

TYPE SPECIES: *H. elegans* Girty, 1915.

Hemizyga globosa, new species
Figures 20a, b

DIAGNOSIS: Moderately high-spired forms with globose whorls with numerous fine, evenly developed collabral ribbing on all whorls. Sutures are sharply defined and relatively deep. A sutural ramp is narrow and slanted toward the suture. The early whorls have coarse ribs which become finer in later whorls. The adult whorl may be unornamented. Whorls embrace well below the rounded periphery located at midwhorl.

DISCUSSION: Two well-preserved specimens with inflated, convex whorls have numerous, rounded collabral ribs; are fine except for the unornamented adult whorl. The shell is thin and the aperture is holostomous. The columellar lip is straight. The ornament is subdued on the base and it is cryptomphalus. It resembles the Silurian *Auriptygma* Perner, 1903 in the shape of the aperture, ornament pattern, and thinness of the shell. It differs from most species of *Hemizyga* in lacking revolving ornament. However, the earliest whorls are not preserved so that it is possible that there might be revolving ornament on the earlier whorls as in some species. I have found no other species similar to this specimen. **Two specimens.**

MEASUREMENTS: Holotype AMNH 42814, H 22.4 mm, W 13.6 mm, SpAng 34°; paratype AMNH 42815, H 22.4 mm, W 13.5 mm, SpAng 44°.

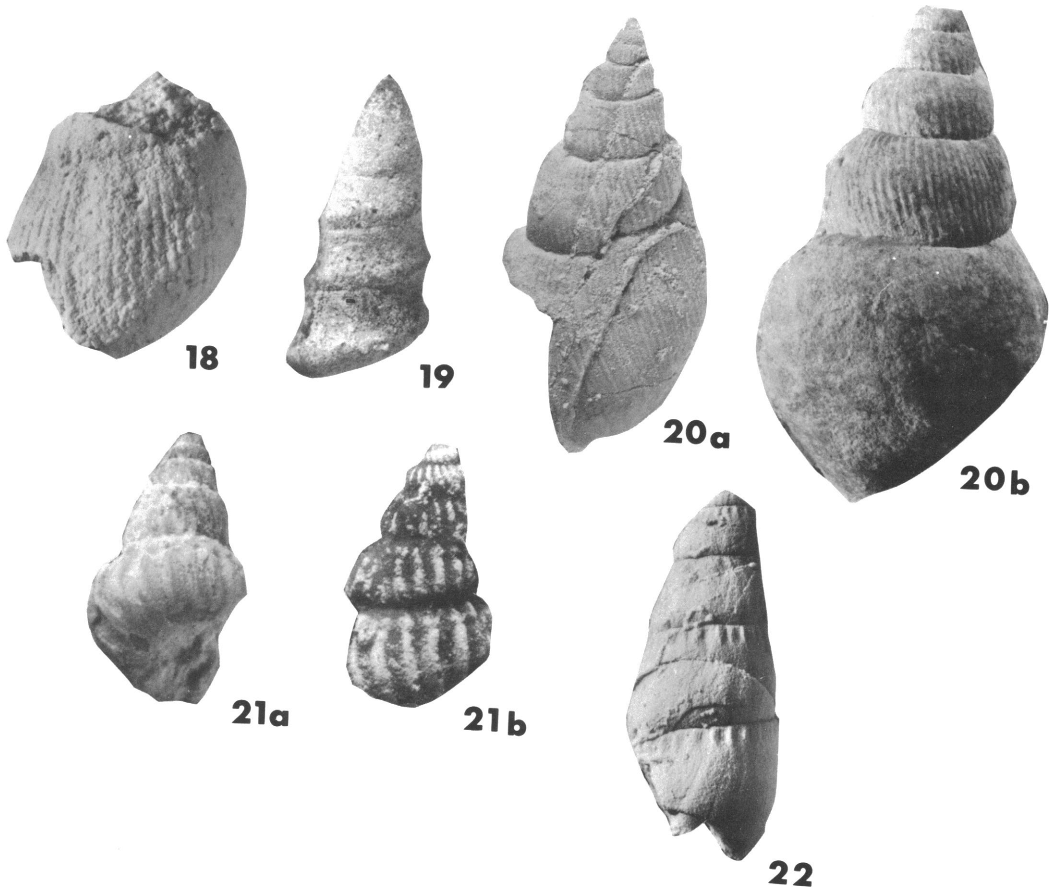
Hemizyga (*Plocezyga*) Knight, 1930

TYPE SPECIES: *Plocezyga corona* Knight, 1930.

DISCUSSION: Knight considered this subgenus as belonging to *Hemizyga* based on the presence of spiral ornament, an arcuate columella, and a subcircular whorl cross section. Hoare and Sturgeon (1981, p. 171) discovered that the genus *Hemizyga* does not have a pseudozygopleurid embryonic whorl, based on examination of the type *H.* (*H.*) *elegans* (Girty), 1915. They defined the new genus *Gamizyga* to include all species having pseudozygopleurid embryonic whorls and having the characteristic spiral ornament identical to that of *Hemizyga,* placing *Plocezyga* in the new genus plus 18 new species. They did not specify the nature of the embryonic whorls (nor did Knight in the original descriptions). Again, a dual system does not seem logical. I will continue to be conservative, believing that the presence or absence of the intricate embryonic whorls is not sufficient to construct a dual classification and will retain this subgenus in *Hemizyga.*

H.* (*Plocezyga*) *serocorona, new species
Figures 21a, b

DIAGNOSIS: Trochiform shells with strongly formed collabral ribs with faint spiral threads which appear to be confined to the whorl surface between the ribs, but this may be a matter of preservation. The ribs are evenly developed over the whorl surface except immediately adjacent to the suture. Whorls embrace just below the periphery. The



FIGS. 18–22. **18.** *P.* (*Leptozyga*) cf. *venustus* Hoare and Sturgeon, 1981, AMNH 42812, oblique side view, ×12.5. **19.** *P.* (*Stephanozyga*) sp., AMNH 42813, side view, ×7. **20.** *Hemizyga* (*Hemizyga*) *globosa*; (**a**) holotype, AMNH 42814, oblique side view, ×2.5; (**b**) paratype, AMNH 42815, side view of adult whorl in low lighting to show lack of ornament, ×3. **21.** *Hemizyga* (*Plocezyga*) *serocorona*; (**a**) holotype, AMNH 42816, oblique basal view, note open umbilicus, ×7; (**b**) paratype, AMNH 42817, side view lightly coated to show lack of ornament or ribs, ×8. **22.** *Microptychis permiana,* holotype, AMNH 42818, side view with low lighting to show the sinus just under the subsutural nodes, ×4.5.

base is somewhat flattened and phaneromphalus. The columella is arcuate. The shell is relatively thin and the sutures are sharply incised.

DISCUSSION: The whorl profile varies from globose to somewhat flattened. The shell shape ranges from low trochiform to almost turbinform. This species comes closest to the type species *H.* (*Plocezyga*) *corona* in the relative intensity of the collabral ribs, the shell shape, and whorl profile. **Three specimens.**

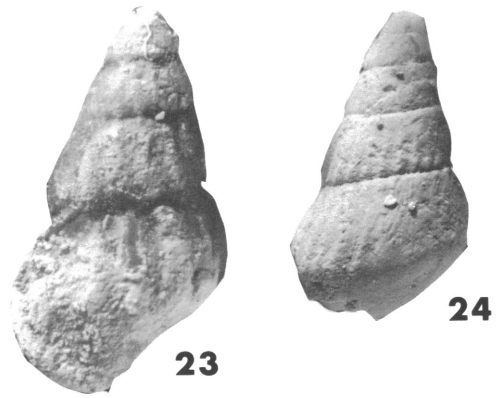
MEASUREMENTS: Holotype AMNH 42816, H 4.4 mm, W 2.6 mm, SpAng 33°; paratype AMNH 42817, H 30.0 mm, W 22.5 mm, SpAng 42°.

ETYMOLOGY: *Serus,* Lat. late; *corona,* Lat. crown.

Microptychis Longstaff, 1912

TYPE SPECIES: *Microptychis wrighti* Longstaff, 1912, p. 307, pl. 30, figs. 6a, b.

DISCUSSION: This is the first described species of the genus in the Permian. It is rel-



FIGS. 23–24. **23.** *Acrospira cristata,* holotype, AMNH 42819, side view, note varix formed at the outer lip, ×10.5. **24.** *Acrospira* sp., AMNH 42821, side view, ×10.5.

atively common in the European Lower Carboniferous but rare in the Pennsylvanian. The Crimean species has strong noding adjacent to the suture, identical to that of *Paleostylus* suggesting that it is a transitional form between the two genera. It helps to clarify the relationship between them and the pseudozygopleurids which lack a sinus. Hoare (1981, p. 1039) described the new genus *Anozyga* to include forms which he described as being *Microptychis*-like with pseudozygopleurid embryonic whorls. His illustrations seem to indicate that it lacks a sinus and has fewer, more inflated whorls than *Microptychis* sensu stricto.

Microptychis permiana, new species
Figure 22

DIAGNOSIS: High-spired shells with slightly inflated whorls with elongate collabral nodes immediately adjacent to the suture. Sutures sharply impressed. Whorls embrace just below a lowly positioned periphery. Growth lines are sigmoidal, forming a broad sinus just below the ring of collabral nodes. Elongate collabral nodes disappear just above the sinus. The whorl face is flattened in the sinus region but becomes convex and sloping downward to the periphery. The base is rounded, without ornament. Possibly minutely phaneromphalus.

DISCUSSION: This species differs from the undescribed Crimean species by having the whorls more inflated, with weaker, more elongate collabral nodes and no spiral thread adjacent to the suture. The sinus is deeper than that of the Crimean species. There appear to be several species in the Crimean Permian. This species resembles *M. subconstricta* (DeKoninck), 1881 from the European Carboniferous in shell shape and whorl profile but differs in having coarser ribbing and a deeper sinus. This beautifully preserved fragment is so distinctive that there is no question that it represents a new Permian species of the genus. **One specimen.**

MEASUREMENTS: AMNH 42818, H 2.7 mm, W 4.3 mm.

ETYMOLOGY: Permian, a geological system.

SUPERFAMILY LOXONEMATACEA, INCERTAE SEDIS

DISCUSSION: A new genus, *Acrospira,* which is almost identical in external morphology to *Procerithiopsis* Mansuy, 1914, but lacks columellar folds, is assigned to the loxonematids. The dominance of collabral ribbing in this superfamily, along with a high-spired shell, has influenced workers to assign species to this group even though, I suspect, they do not belong. A case in point was the acceptance for many years of *Paleostylus* as a member, although clearly it belongs to Cerithiacea because it is siphonate. In any event, I too am influenced by the presence of collabral ribbing in *Acrospira* and place it in this group.

Acrospira, New Genus

DIAGNOSIS: Trochoid shells with collabral ribbing and adult varix. The shell is moderately high spired with about seven whorls. The whorl profile is evenly convex with well-developed collabral ribbing which is more fully developed in the broad peripheral region. The suture is deeply impressed and whorls embrace below the broad periphery. The aperture is holostomous and the adult aperture has a greatly thickened outer lip formed into a large varix. The base is rounded with no ornament and is anomphalus.

DISCUSSION: This genus is quite close to that of *Procerithiopsis* Mansuy, 1914, in many features but has an adult apertural varix and lacks the two columellar folds which are generic level determinates. I have not found any other species that resembles these shells. Further, as far as I am aware, *Procerithiopsis* has not been reported elsewhere other than by Mansuy; yet the genus is valid.

ETYMOLOGY: *Akron,* Gk. top; *spira,* Gk. twist.

Acrospira cristata, new species
Figure 23

DIAGNOSIS: Same as that of the genus.

DISCUSSION: The most notable variation among the nine specimens is the change in the whorl profile from evenly rounded to flattened. The collabral ribbing varies somewhat in the number (hence intensity) of ribs per whorl, a feature also noted in species of pseudozygopleurids. The whorls embrace just below the periphery, but if the whorl profile is flattened, then the embracement position will cause the sutures to appear more deeply incised. **Nine specimens.**

MEASUREMENTS: Holotype AMNH 42819, H 4.6 mm, W 2.7 mm, WhH 1.1 mm, WhW 2.0 mm, SpAng 38°; paratype AMNH 42820, H 3.9 mm, W 2.2 mm, WhH 1.0 mm, WhW 0.8 mm, SpAng 40°.

ETYMOLOGY: *Crista,* Lat. crest or ridge.

Acrospira, species
Figure 24

DESCRIPTION: The shell with seven to eight whorls with numerous fine collabral threads which are collabral sloping downward from the suture to the aperture. Whorls embrace at periphery and are inflated with gently convex outer whorl face which slopes downward and outward to a periphery that is low on the whorls. The base is flatly rounded and anomphalus.

DISCUSSION: This species differs from *A. cristata* in having less inflated whorls, with finer ribbing and only a moderate amount of thickening at the aperture and no sharply defined varix. Whorls embrace higher on the shell, at the periphery. Only three complete shells are known and they are not sufficiently detailed to formalize. This species is strikingly similar to *Procerithiopsis ambigua* Mansuy, 1914 but lacks an umbilicus and columellar folds. **Three specimens.**

MEASUREMENTS: AMNH 42821, H 6.0 mm, W 3.5 mm, WhH 1.5 mm, WhW 2.8 mm, SpAng 41°.

SUPERFAMILY CERITHIACEA FLEMING, 1822
FAMILY TURRITELLIDAE WOODWARD, 1851

The Paleozoic genera, *Acanthonema* Sherzer and Grabau, 1908, *Callispira* Nelson, 1947, and *Orthonema* Meek and Worthen, 1862 previously placed in this family contain species that all differ from Mesozoic and Cenozoic genera by having an aperture with the outer lip straight and nearly vertical. All post-Paleozoic genera either have broad sinuses with the greatest depth at the center of the aperture or have anal notches near the suture. Knight (1934, p. 436) first observed this sinus in *O. bilineatum* Mark, 1912, *O. schucherti* Knight, 1934, and *O. inornatum* Knight, 1934. Most species, such as *O. conicum* Meek and Worthen, 1866, have a straight, nearly vertical, outer lip with some specimens showing a slight backward oblique swing near the suture marking an incipient anal notch. Even though the sinuosity is the most defining feature of the Turritellidae, the absence of the sinuous outer lip in some species has not been regarded as significant in Paleozoic species.

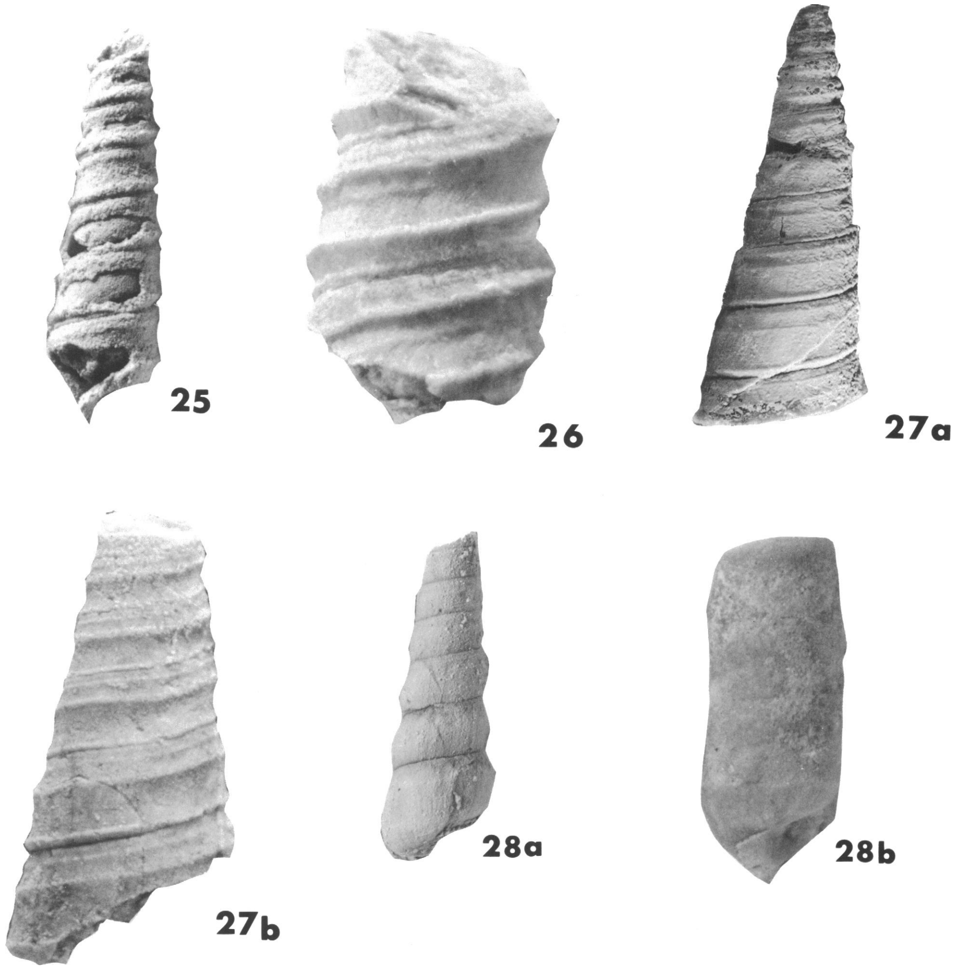
It is interesting to note that no species of turritellids are to be found in the uppermost Permian and throughout the entire Triassic! The earliest occurrence of a Mesozoic turritellid is from the Jurassic Inferior Oolite of Great Britain (Huddleston, 1889). Those species are high-spired with rounded whorls having a few spiral ribs and a broad, shallow sinus.

Genus *Orthonema*
Meek and Worthen, 1862

TYPE SPECIES: *Eunema*? *salteri* Meek and Worthen, 1961.

DISCUSSION: *Orthonema* is seemingly a conservative genus, being represented in the upper Paleozoic by 16 species. In most occurrences it is known by a single specimen at localities where large numbers of other gastropod species are found.

The basis for species recognition is the spiral ornament which usually consists of two groups of carinae each near the top or base of the whorl and separated by a flat or slightly concave outer whorl face. In some species only a single carina may be present at the base of the whorl, or there may be more than



FIGS. 25–28. *Orthonema*. **25.** *O. rectimurum*, holotype, AMNH 42822, side view, ×5. **26.** *O. nakazawai*, holotype, AMNH 42824, side view of fragment, ×7. **27.** *O. tirusum*; (**a**) holotype, AMNH 42827, side view, ×4.5; (**b**) paratype, AMNH 42828, side view showing the principal spiral rib low on the outer, foreshortened whorl face, ×6. **28.** *O. knighti*; (**a**) holotype, AMNH 42830, side view, ×3; (**b**) paratype, AMNH 42831, side view with low lighting to emphasize the basal rib and reflexed columellar lip, ×3.

one present at a site. The relative placement and development of these spiral elements affects the shape of the whorl profile and hence the entire shell shape. Sutural placement on the whorl is another theme of species variation, although we can recognize interspecific variation patterns; we have hardly any understanding of intraspecific variation owing to the small size of population samples. However, this current study allows us to examine several patterns that do occur with populations, such as the intensity of spiral element development, changes in the shape of the growth lines, and the nature of secondary ornamentation discussed below.

The Malaysian species are much more abundant than at any other known locality. For example, at the richest known Permian locality (AMNH no. 512, Getaway Limestone, Guadalupe Mountains, Texas), *Orthonema* is represented by 10 specimens while other genera are known by thousands of specimens. Schindel (oral commun.) reports that in the Yale collections from the Pennsylvanian of North Central Texas, one kilogram of shale will yield one or two specimens where hundreds of other gastropod specimens are recovered.

The morphotypes of *Orthonema* in the Malaysian Permian duplicate rather closely the range of variation noted by Knight (1934) in the North American Pennsylvanian, as discussed in the Introduction. There appears to be a species of *Orthonema* in the Permian of the Crimea of the *O. salteri* morphotype which is undescribed. Other than that occurrence, I have not found any other reports of the genus in the Tethyan Permian. The illustration of *O.* cf. *salteri* in Delpey (1941, fig. 63, p. 67) is so generalized that I am unable to place it even in a suborder.

IMPORTANT NOTE ON MEASUREMENTS: All of the specimens of *Orthonema* have the early whorls missing; no complete specimens were recovered. Therefore, I have omitted the total height measurement since it is meaningless. Only the whorl height (WhH) and whorl width (WhW) of the penultimate whorl are given and these have been made on the last complete whorl preserved.

Orthonema rectimurum, new species

Figure 25

DIAGNOSIS: Two dominant spiral ribs mark an outer whorl face that is flat or slightly concave and inclined toward the axis; it is ornamented by one to ten spiral threads; if by a single thread, it is medially located and prominent. An upper rib or thread marks the upper margin of the outer whorl face; it is separated from the suture by an additional thread. The sutures are sharp and deep. The lower rib defining the outer whorl face is more strongly developed and it also is separated from the suture by a thread. The base is flattened with one or two ribs as ornament. The columellar lip is straight and the lower lip forms an acute angle with the columellar lip bearing a sharply defined groove.

DISCUSSION: This species differs from the North American *O. salteri* by having a less well-developed upper rib and by having a flat almost vertical outer whorl face as contrasted to the concave face of *O. salteri.* That species has a rounded, unornamented base. I have found no other species that has many of the features noted in these two. **Eighteen specimens.**

MEASUREMENTS: Holotype AMNH 42822, WhH 1.9 mm, WhW 1.6 mm; paratype (largest) AMNH 42823, WhH 8.3 mm, WhW 8.8 mm.

ETYMOLOGY: *Rectus,* Lat. straight or upright; *murus,* Lat. wall.

Orthonema nakazawai, new species

Figure 26

DIAGNOSIS: The outer whorl face is concave with one or more threads unevenly distributed; the upper rib defines the outer whorl face and has several threads above it near the suture. The lower rib is much more developed and is rounded; one or two threads underlie the lower rib on the concave base where it forms interference nodes with basal threads. Some collabral ornament is noted on the upper whorl face as well. Sutures embrace at the point where the base flattens out from a concave region at the edge of the lower whorl face.

DISCUSSION: *O. nakazawai* differs from *O. rectimurum* n. sp. in that the outer whorl face is concave and the lower and upper ribs are more centrally located. The ribs of the latter species are much closer to the sutures, forming a wider outer whorl face. The two species are similar in having the outer whorl face defined by an upper and lower rib. *O. rectimurum* differs from *O. salteri* in having a concave outer whorl face with the suture embracing farther down the base. In addition, the ribs are not as well developed in *O. salteri,* so that the shell shape is less steplike. It differs from the North American *O. marvinwelleri* in having the lower rib more fully developed, and with collabral ornament (this is an autapomorphic feature). Also, the spiral threads adjacent to the sutures are weaker in the Malaysian species and the main ribs are closer to the sutures. It is similar to the North American populations in having the outer whorl face occupy over one-half of the whorl; the visible upper whorl face has one or two threads and an exposed base which also may have one or more threads.

The most notable variation within this species is the relative development of the upper and lower spiral ribs that delineate the whorl face. In the holotype they are about equally well developed and the outer whorl face between them is nearly flat. In one variant, the upper rib complex is more developed than the lower and in still others the lower rib is more fully formed. A number of specimens show the latter condition which causes the outer whorl face to appear concave, thus giving the shell a more turriculate shape. Other variations include changes in the numbers and development of the basal spiral ornament and in the relative height of the whorl (reflecting the placement of the sutures).

Some specimens show some collabral ornament in the form of faint nodes on the spiral ornament only—not observed on the whorl face itself. **Seventeen specimens.**

MEASUREMENTS: Holotype AMNH 42824, WhH 3.0 mm, WhW 5.3 mm; paratype AMNH 42825, WhH 2.0 mm, WhW 4.0 mm; paratype AMNH 42826, WhH 1.3 mm, WhW 2.9 mm.

ETYMOLOGY: Named for Professor Keiji Nakazawa.

Orthonema tirusum, new species

Figures 27a, b

DIAGNOSIS: Moderately small shells with two subsutural carinae, the lower one forming the shoulder of the outer whorl face. The outer whorl face occupies about one-third of the whorl. The upper subsutural carinae or thread is located in the central portion of the upper whorl face. The outer whorl face may be flat, gently convex, or somewhat concave depending on the relative development of the carinae. The lower whorl face–outer whorl face boundary is marked by a large rib. The whorl profile, on the whole, slopes gently outward giving the shell a rather smooth cone shape. Growth lines form a sinus resulting in the formation of a pseudoselenizone located between the upper suture and the shoulder. From the shoulder, the growth lines swing strongly opisthocline on the outer whorl face. The base is flat and the columellar lip is reflexed forming a callus or funicle.

DISCUSSION: The sinus is the deepest and most sharply defined of any of the genera of the Turritellidae. The only other genus that shows a slight sinus is the Pennsylvanian *Callispira* Nelson, 1947 which has a broad sinus in the middle of the whorl. The sinus of *O. tirusum* is somewhat closer to the suture than the selenizone of the murchisoniid *Stegocoelia* which it resembles in several features.

This species differs from *O. rectimurum* by having the lower subsutural carina placed lower on the whorl and in being more weakly developed so that the outer whorl face is sloping rather than being nearly vertical; this results in a shell shape that is more conical compared to the turriculate *O. rectimurum.* It differs from *O. nakazawai* in lacking the full rib development of the upper and lower ribs, the lack of the basal carinae, and with a flattened base.

Variation between specimens is noted in the relative development of the spiral carinae and lower rib. If these are well developed, the outer whorl face tends to be flat or concave and the base more flattened. If the spiral ornament is less well formed, then the outer whorl face will appear convex and the base more rounded, giving the shell a more conical shape. **Five specimens.**

MEASUREMENTS: Holotype AMNH 42827, WhH 2.7 mm, WhW 7.6 mm; paratype AMNH 42828, WhH 4.5 mm, WhW 2.0 mm; paratype AMNH 42829 WhH 3.2 mm, WhW 5.8 mm. *Note:* only whorl heights and widths were measured on the last whorl preserved because all specimens are fragments; also, the spiral angle could not be taken.

ETYMOLOGY: *Tirus,* Malayan for conical.

Orthonema knighti, new species

Figure 28

DIAGNOSIS: High-spired many-whorled shell with flat to rounded whorls. The suture is sharply defined but shallow. There is a faint spiral thread which marks the lower margin of the very narrow, concave upper whorl face. The outer whorl face is flat to slightly convex. Whorls embrace on the basal spiral thread which marks the lower margin of the outer whorl face. In some forms there is a basal rib marking the lower margin of the outer whorl face. The base is somewhat rounded with a spiral thread in the middle portion.

DISCUSSION: Because of poor preservation of most specimens, it is not possible to observe the details of ornament or any other feature. However, the whorl profiles are well defined and strongly suggest that there was no ribbing to begin with. Therefore, I am reasonably confident that these specimens constitute a distinct species. Again, this species appears to have an iterative counterpart in *O. inornatum* Knight, 1934, which also lacks typical spiral ribbing but has more convex whorl profiles.

There is some variation in the shape of the whorl profile ranging from slightly convex, flat-sided to convexoconcave with the outer face either parallel or inclined to the axis forming a conical shell. The specimens having convex-sided whorls are an enigma since no species of *Orthonema* possess smooth, unornamented convex whorls. However, there are gradations between those specimens and others that have flattened whorl profiles. The growth lines (see fig. 28a) that are preserved are typical of the genus in being essentially vertical with a sharp turn immediately adjacent to the suture, marking a shallow anal notch. The only other group to which these forms could be assigned would be some genus of loxonematids, but they all have a well developed, broad sinus. **Forty-one specimens.**

MEASUREMENTS: Holotype AMNH 42830, WhH 3.0 mm, WhW 5.2 mm; paratype AMNH 42831, WhH 1.6 mm, WhW 2.7 mm.

ETYMOLOGY: Named for J. Brookes Knight.

FAMILY PROCERITHIIDAE COSSMANN, 1905

DISCUSSION: Delpey (1942, p. 69) placed the genus *Paleostylus* Mansuy, 1914 in the family Terebrellidae, an imperfectly known Mesozoic group. *Paleostylus* shares a number of features with *Knishbia* Winters, 1963, particularly transverse nodes confined to the upper portion of the whorls, a basal rib forming the periphery, a high-spired shell, and an incipient siphonal notch. Hence, I will assume that this family should be the proper place for this genus.

The procerithids are common elements of the Triassic and Jurassic faunas, but are known only by *Spanionema* from the Devonian and *Knishbia, Paleostylus,* and the new genus *Sinozyga* from the Permian.

Genus *Paleostylus* Mansuy, 1914

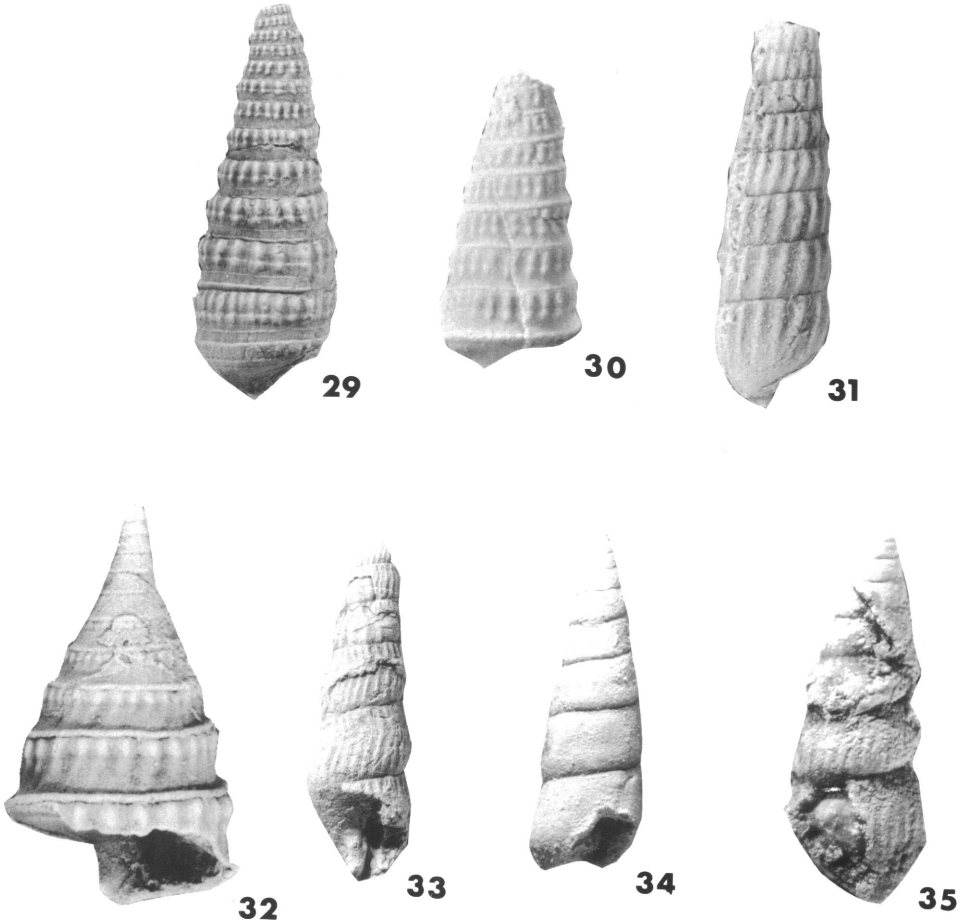
TYPE SPECIES: *Paleostylus pupoides* Mansuy, 1914a, p. 48, pl. 7, fig. 16.

DISCUSSION: *Paleostylus* is known from three species which were described from the Carboniferous and Permian of Southeast Asia by Mansuy (1914a) and Delpey (1942). The species are moderately variable with the variation involving ornament and, more importantly, axial translation. This latter variation alters shell shape; in *P. pupoides* the rate of axial translation in some individuals slows down relative to whorl expansion causing the pupoid (beehive) shape. In *P. delpeyi,* new species, the axial growth speeds up relative to whorl expansion causing a coeloconoid shape to the shell (fig. 31). Ornament ranges from well-developed axial ribs which are straight and evenly formed from suture to suture in *P. dussaulti* Mansuy, 1914a to a reduced ornament with collabral ornament restricted to the upper portion of the whorl in *P. pupoides.*

In the Treatise, Knight et al. (1960) placed this group as a subgenus of *Pseudozygopleura* based on several homologies. However, the range of variation, as in the Malaysian fauna, clearly demonstrates a generic separation—indeed, I suggest that *Paleostylus* is not a loxonematid at all but rather a cerithiid based on the fundamental apertural characters. Delpey (1942) placed it in the Terebrellidae and suggested that it might be a campanilid, but I find few features that are shared with those groups and such a placement appears quite farfetched.

The pseudozygopleurid relationship does have merit; the strong collabral ribs found in *Paleostylus* are nearly identical to those found in several species of the pseudozygopleurids, such as *P. tenuivirga* Knight, 1930. In *Helminthozyga* the last several whorls become uncoiled, thus resembling the cerithiid *Vermicularia* which displays a change in the relationship between axial translation and whorl expansion as seen in *Paleostylus* but not to the degree seen in those other genera. The most striking example of the convergence of *Paleostylus* and *Pseudozygopleura* is in *Paleostylus pseudozyga,* new species, which would be described as a species of *Pseudozygopleura* if the apertural features were missing.

A feature which separates *Paleostylus* from the pseudozygopleurids is the presence of an umbilicus. This feature was used by Hoare and Sturgeon (1981, p. 572) to reject the use of *Paleostylus* for North American pseudozygopleurids and to point out the similarity



FIGS. 29–35. **29.** *Paleostylus pupoides* Mansuy, 1914, AMNH 42832, side view of specimen with a weak basal rib, ×3. **30.** *P. pupoides,* AMNH 42833, side view of a specimen with a low outer whorl face and a well-developed basal rib, ×7.5. **31.** *P. dussaulti* Mansuy, 1914, AMNH 42836, side view, 1914. **32.** *P. delpeyae,* holotype, AMNH 42839, apertural view, ×7. **33.** *P. pseudozyga,* holotype, AMNH 42840, apertural view, note the well-developed siphonal trough and subsutural nodes on the second whorl, ×2. **34.** *Protostylus lantenoisi* Mansuy, 1914, AMNH 42843, side view, ×5. **35.** *Sinuozyga ajoka,* holotype, AMNH 42844, apertural view, ×7.5.

of *Spiromphalus* Hayaska, 1939 to *Paleostylus.*

The most important feature which separates *Paleostylus* from the pseudozygopleurids is the presence of a siphonal notch at the junction of the columellar lip and the lower lip. Looking over the Mesozoic faunas, I note the presence of a large number of species described as "*Cerithium*" in the Inferior Oolite (Jurassic) by Huddleston (1889). Such species as *C. subglabrum* Huddleston, 1889, *C. beanii* Huddleston, 1889, or *C. wansfordiae* Huddleston, 1889 all have ornament which is similar to *Paleostylus* and the siphonal notches are all shallow. In addition, *C. wansfordiae* is shown to have a coeloconoid shell. I am uncertain as to the systematics of the Huddleston species and it is beyond the scope of this study to assess their taxonomic position; suffice it to say that I am convinced that *Paleostylus* should be considered a cerithiacean rather than a loxonematid. I find nothing in the Triassic faunas that I can associate *Paleostylus* with. Finally, this genus is apparently restricted to the Tethyan Permian. I am certain that all of the species from the

North American Upper Paleozoic currently identified as belonging to *Paleostylus* and having holostomous apertures should probably be considered pseudozygopleurids as suggested by Hoare and Sturgeon (1981).

Paleostylus does occur in the North American Permian. I have examined some of the specimens in the type lot of *P. giganticus* Winters, 1963 from the Permian Supai Formation of eastern Arizona which have collabral ornament concentrated near the upper suture, steplike whorls, spiral ornament confined to the upper whorl face where it forms interference nodes with collabral ornament, and a narrow umbilicus. They differ from species of *Knishbia* (also described from the Supai Formation by Winters) which has rounded whorls and a different ornament pattern. However, judging from the suite of specimens in the type lots of the species of both genera in the Supai material, I am of the opinion that *Knishbia* should also be considered closely related to *Paleostylus* if not a synonym. This conclusion could reinforce my belief that *Paleostylus* is a cerithiid, since *Knishbia* was placed in the Procerithiidae by Knight et al. (1960) near *Orthonema.*

Paleostylus pupoides Mansuy, 1914
Figures 29–30

Paleostylus pupoides Mansuy, 1914, p. 49, pl. 7, fig. 16.

DESCRIPTION: High-spired forms with axial growth which may become progressively slower relative to whorl expansion causing the shell to be pupaeform. The whorls are flattened to somewhat convex with a sharply defined spiral rib at the base of the outer whorl face which forms the boundary of the flattened base. Whorls embrace just below this spiral rib. There are three spiral threads evenly spaced on the outer whorl face. Collabral ribs occupy the upper half of the whorl and form interference nodes at the intersection of the upper two spiral threads. The third spiral thread is centrally located on the lower half of the whorl face. Cryptomphalus.

DISCUSSION: There is some variation in axial growth; in several specimens the shells are pupaeform, but most shells appear to be normally orthostrophic. There is a considerable amount of variation in the height of the outer whorl face; figure 30 shows a relatively low whorl face; in figure 29 the whorl face is high causing a more turriculate shell shape. The unornamented lower half of the outer whorl face may be concave so that the upper half and the basal spiral rib of the preceding whorl form a rectangular unit producing a more tabulate shell. In some specimens, the spiral rib at the base of the outer whorl face may be absent. The base is variable in being flat to rounded. **Thirty-seven specimens.**

MEASUREMENTS: AMNH 42832, WhH 2.8 mm, WhW 7.2 mm; AMNH 42833, WhH 2.0 mm, WhW 5.8 mm; AMNH 42834, WhH 1.3 mm, WhW 2.5 mm; AMNH 42835, WhH 2.2 mm, WhW 4.0 mm.

Paleostylus dussaulti Mansuy, 1914
Figure 31

P. dussaulti Mansuy, 1914, p. 49, pl. 4, fig. 21.
P. inosinicus Mansuy, 1914, p. 49, pl. 4, fig. 20.

DISCUSSION: The most significant feature of this species is the full development of collabral ribs, which are spread uniformly across the whorl surface, rather than restricted as in other species. Furthermore, in contrast to most species of pseudozygopleurids, these ribs are vertical (or slightly opisthocline) and straight. The whorls embrace above the base. As in other species, the inner lip is reflexed to form a cryptomphalid condition of the umbilicus. The chief features separating this species from the pseudozygopleurids are the siphonal notch and an umbilicus. Also the slope of the whorl profile is rectangular rather than inflated. **Eight specimens.**

MEASUREMENTS: AMNH 42836, WhH 1.5 mm, WhW 3.2 mm; AMNH 42837, WhH 1.3 mm, WhW 2.6 mm; AMNH 42838, WhH 0.9 mm, WhW 2.4 mm.

Paleostylus delpeyae, new species
Figure 32

Paleostylus pupoides Delpey, 1942, fig. 66.

DIAGNOSIS: Coeloconoid shells with collabral ornament restricted to the upper quarter of the whorl. There is a single spiral rib just below the suture which causes larger interference nodes to form at the intersection of collabral ribs which extend to just below a spiral thread just below the nodes. Faint traces of these collabral ribs can be found on the lower whorl face. There are 10 or more fine spiral threads just barely visible on the lower whorl face. Sutures embrace just below a very prominent flange marking the lower margin of the outer whorl face. The base is flat. Narrowly phaneromphalus.

DISCUSSION: There are but two known specimens representing this species. The morphological discontinuity from other species is sufficient to cause me no hesitation in recognizing this species as being distinct. Delpey (1942, p. 71) was of the opinion that the specimen she illustrated (fig. 66, p. 71) represents one end of a range of variation in the rate of axial growth causing a coeloconoid shell shape, the rate of axial growth slowed in relation to whorl expansion rate. She illustrated (an ink sketch) the specimen as having uniform collabral ribs as in *P. dussaulti,* but she also illustrated a specimen of a pupoid type of *P. pupoides* as having the same uniform development. In both cases, the Malaysian specimens have the collabral ribs restricted to the upper portion of the whorl, and the presence of spiral ornament not illustrated by Delpey. The types illustrated by Mansuy (1914a, pl. 6, fig. 16) have identical ornament patterns to those of the Malaysian specimens, so that again I suspect that Delpey's renditions may not be accurate.

In any event, the flange demarking the base is quite distinct from the relatively weak spiral rib in the same position in *P. pupoides* and is lacking altogether in *P. dussaulti.* The flange emphasizes the very flat base not seen in the other species. The most important distinction (quite apart from the distinct shell shape) is the presence of a single spiral rib at the top of the whorl compared to two or more spiral ribs consistently found in *P. pupoides.* The outer whorl face over the lower three-quarters of the surface is devoid of ornament other than very faint spiral threads. **Two specimens.**

MEASUREMENTS: Holotype AMNH 42839, H 6.0 mm, W 5.0 mm, WhH 1.4 mm, WhW 5.0 mm, SpAng 22°. The other species average about 10°.

ETYMOLOGY: Named for Genevieve Delpey.

***Paleostylus pseudozyga*, new species**
Figure 33

DIAGNOSIS: Moderately large, turriculate shells with inflated, convex whorls with sinuous to straight collabral ribs which are fully developed from suture to suture across the whorl face. Sutures are shallow, but sharply defined. The upper whorl face is flat to slightly concave and the outer whorl face is convex. Subsutural nodes are present on early whorls. Whorls embrace just beneath a periphery which is low on the whorl. The columellar lip is reflexed and forms an angle with the inner lip which has a well-developed siphon. There is no spiral ornament and the rounded base has diminished collabral ornament. Cryptomphalus.

DISCUSSION: This species is highly convergent on the pseudozygopleurids in shell shape, whorl profile, and dominant collabral ribbing. Without the presence of subsutural nodes on the early whorls and the complete aperture and base, this species would be considered a species of *Pseudozygopleura.* There is some variation in the shape of the whorl from evenly convex with a medial periphery to a flattened whorl face near the upper suture becoming convex to a low periphery. The development of the ribs ranges from fine to coarse. The shell shape also varies from high-spired to an almost trochoid shape. **Seven specimens.**

MEASUREMENTS: Holotype AMNH 42840, H 20.6 mm, W 6.1 mm, WhH 3.7 mm, WhW 5.0 mm, SpAng 13°; paratype AMNH 42841, H 10.9 mm, W 4.1 mm, WhH 2.3 mm, WhW 3.1 mm, SpAng 14.5°; paratype AMNH 42842, H 3.2 mm, W 2.1 mm, WhH 0.9 mm, WhW 1.7 mm, SpAng 40°.

ETYMOLOGY: *Pseudos,* Gk. lie; *zygon,* Gk. yoke.

Genus *Protostylus* Mansuy, 1914

TYPE SPECIES: *P. lantenoisi,* Mansuy, 1914a, SD, Batten, 1956.

DISCUSSION: Knight et al. (1960) placed this genus in Loxonematacea, genus *Inquirendum* because details of the aperture were unknown. The specimens from this Malaysian fauna clearly show a reflexed columellar lip and a siphonal trough indicating that the genus should be placed in the cerithiids.

Protostylus lantenoisi Mansuy, 1914a
Figure 34

Protostylus lantenoisi Mansuy, 1914a, p. 11, pl. 1, fig. 17.

DISCUSSION: I have identified five shells as belonging to this species. The shells are nearly identical to that illustrated by Mansuy (1914a, pl. 1, fig. i), but there are some variations in the whorl profile. Three specimens have slightly inflated and evenly rounded profiles. The other two specimens have less inflated whorls with a flattened upper whorl surface and a rounded periphery just below the midwhorl. The columellar lip is reflexed and the lower lip shows a siphonal trough. All specimens are cryptomphalus.

Mansuy also described *P. dussaulti* and his illustration (1914b, pl. 1, fig. 18) is of a shell with a more flattened whorl profile. Based on the variation I have noted above, I suspect that *P. dussaulti* is synonymous with the type species. Delpey (1941a) does not report this genus from the Cambodian Permian, but it is possible that her illustration of *Trypanostylus* cf. *cerithiformis* (p. 51, fig. 44) could be of *Protostylus*. **Five specimens.**

MEASUREMENTS: (of illustration specimen) AMNH 42843, H 8.2 mm, W 2.8 mm, SpAng 29°.

Sinuozyga, New Genus

DIAGNOSIS: Moderately high-spired siphonate forms with a reflexed columellar lip, presumably cryptomphalus. The first several whorls have very faint spiral ornament; the next several have relatively straight, nearly vertical collabral ribs. The last two or three whorls have a slightly depressed trough just beneath the suture on the upper whorl face. Collabral ribs and growth lines abruptly bend backward into the trough forming a shallow asymmetrical sinus. In the trough the ribbing disappears. The whorl profile is evenly convex except at the trough region in the adult whorls where there is an indentation. Some specimens have a poorly defined periphery low on the whorl; most specimens have a periphery in midwhorl. The base is rounded.

DISCUSSION: Because of the presence of an umbilicus, reflexed columellar lip, shallow siphonal trough, and sinus, this genus cannot be placed in the pseudozygopleurids in spite of its close resemblance in shell shape, whorl profile, and collabral ribbing. The ornament, in contrast to most species of *Pseudozygopleura,* becomes progressively stronger with growth.

There is no other genus to which comparisons can be made. It bears a resemblance to *Loxosonia zygopleuroides* in having a sinus on the upper whorl face; however in that genus the sinus is quite deep and narrow and closer to the suture. The closest genus may be *Paleostylus* based on the presence of a reflexed columellar lip, a siphonal notch, dominant collabral ornament, and the cryptomphalus condition. Therefore, I consider it to be a member of the procerithiids. The function of the sinus that appears on the adult whorls is a puzzle. It may be an anal notch, but it is not at the suture where it is always located in siphonate forms and why is it found only in the adults? In almost every group that possesses a sinus beneath the suture, such as the pleurotomarians, there are paired organs associated with a holostomous aperture. This genus is unknown elsewhere.

ETYMOLOGY: *Sinus,* Lat. curve; *zygon,* Gk. yoke.

Sinuozyga ajoka, new species
Figure 35

DIAGNOSIS: Moderately high-spired forms with at least nine whorls. The whorl profile is rounded with an ill-defined periphery either at midwhorl or low on the whorl. The collabral ribbing is well developed, becoming stronger with growth. The base is rounded.

DISCUSSION: The six specimens available for study show some degree of variability permitting a study of interspecific variation. The whorl profile is variably shaped from an evenly rounded, convex profile to one which has a recognizable periphery low on the whorl; also the profile may be less inflated. Ribbing shows a range from relatively fine ribs to coarse ribs fewer in number on the whorl. **Six specimens.**

MEASUREMENTS: Holotype AMNH 42844, H 6.7 mm, W 2.5 mm, WhH 1.7 mm, WhW 2.5 mm, SpAng 62°; paratype AMNH 42845, H 5.9 mm, W 3.1 mm, WhH 2.1 mm, WhW 3.1 mm, SpAng 60°.

ETYMOLOGY: *Ajoka* means mimic in Malayan.

FAMILY COELOSTYLINIDAE COSSMANN, 1909

Wenz (1938, p. 39) included a number of genera in this family which are highly divergent in many basic features and by today's criteria are clearly unrelated. A revision of the family is long overdue. Because Wenz included *Omphaloptychia* Ammon, 1892 in the family, I will retain Wenz's scheme. Since there are three species in the Malaysian fauna I do not believe it is warranted to undertake a revision. Wenz placed this family in the Loxonematacea but because of the importance I have placed on the siphonate condition, I would suggest that this family be placed near the Procerthiidae in the Cerithiacea.

Genus *Omphaloptychia* Ammon, 1892

TYPE SPECIES: *O. nota* Ammon, 1892, p. 199.

DISCUSSION: There has been much discussion about the relationship and the status of *Omphaloptychia* and *Coelostylina* (see Haas, 1953, pp. 131–132, 137). Haas decided to recognize both genera, placing the lower-spired more robust species in the former genus and the higher-spired forms in the latter. The problem with recognition lies in the fact that these species are very conservative and are almost featureless with smooth, rounded whorls like beans. I have only used the literature for a survey of the species and conclude that all species should be placed in a single genus. Since *Omphaloptychia* is the prior name, I shall use that.

The genus is characterized by having a smooth shell with sigmoid growth lines but without ornamentation, and medium high-spired turbiniform shells which may be phaneromphalus or anomphalus and with a siphonal trough. In addition, I have found ornament in the two described species. *O. cingulata* has subsutural nodes and *O. paleozoica* has faint basal collabral ornament. It is widely distributed and one of the most abundant snails found in the Triassic. Wenz reported that it is found in the Permian, but I have not seen it in the literature or in collections except for this one occurrence.

Omphaloptychia paleozoica, new species

Figures 36a, b, c

DIAGNOSIS: Moderately high-spired turbiniform shells with convex to somewhat inflated whorls with or without weak subsutural nodes. The suture is deeply recessed. The whorls embrace just below a broad, low-lying periphery. The base is flatly rounded. There is very faint ornament in the form of broad collabral raised areas more fully developed on the base (see fig. 36c). Phaneromphalus to cryptomphalus. The columellar lip is reflexed and the parietal inductura is thin. A broad shallow sinus in the lower lip is located adjacent to the columella.

DISCUSSION: These very conservative shells, as in other species, lack general ornament except for some of the specimens which have very faint subsutural nodes. The whorls are more inflated and the sutures embrace lower on the whorl than those without the nodes, giving a more steplike shell shape; these resemble the St. Cassian *Coelostylina crassa* Kittl, 1894. The others in this sample resemble *C. conica* Kittl, 1894. Both of these Permian forms differ from the Triassic species by having a more developed siphonal notch. **Seventy-four specimens.**

MEASUREMENTS: Holotype AMNH 42846; H 9.1 mm, W 4.8 mm, SpAng 34°; paratype AMNH 42847, H 9.4 mm, W 5.2 mm, SpAng 32°; paratype AMNH 42848, H 9.6 mm, W 5.2 mm, SpAng 43°.

ETYMOLOGY: Named for the Paleozoic Era.

Omphaloptychia cingulata, new species

Figure 37

DIAGNOSIS: Moderately high-spired turbiniform shells with a well-developed row of nodes adjacent to the suture. Whorls are gently rounded and sutures embrace at or just below a low, ill-defined periphery. Growth lines are sigmoid but nearly vertical at the suture where elongated nodes occur. The columellar lip is reflexed, forming a narrow, arcuate parietal inductura. The lower lip has a broad, shallow siphonal trough. Cryptomphalus.

DISCUSSION: This species resembles *O. paleozoica* but has stronger subsutural nodes and less inflated whorls. It sharply differs from all other known species by the presence of subsutural nodes. *Anozyga* Hoare, 1980, classified as a pseudozygopleurid, is moderately high-spired with a very similar shell shape and a row of subsutural nodes. It differs in being holostomous and having flattened embryonic whorls. An undescribed specimen in the Molengraaff Collection (housed in the

Geological Museum of the Delft Technical Institute) from the Permian of Nefalassi, Timor, has flattened whorls which are slightly concave in the upper half of the whorl and has a raised subsutural rib with nodes, the whorls embracing higher on the whorls. It should be included with this species. **Seventeen specimens.**

MEASUREMENTS: Holotype AMNH 42849, H 4.4 mm, W 2.6 mm, SpAng 38°; paratype AMNH 42850, H 5.2 mm, W 2.6 mm, SpAng 38°; paratype AMNH 42851, H 5.0 mm, W 3.8 mm, SpAng 47°.

ETYMOLOGY: *Cingulum,* Lat. belt or zone.

Omphaloptychia sp.
Figure 38

DISCUSSION: A group of quite variable specimens belongs to a separate species but is not sufficiently well preserved to warrant formalization. They are characterized by a distinct angulate periphery very low on the whorl. Figure 38 illustrates a lower-spired form. **Fifteen specimens.**

MEASUREMENTS: AMNH 42852, H 6.8 mm, W 4.9 mm, SpAng 32°.

Genus *Trypanostylus* Cossmann, 1895

TYPE SPECIES: *Eustylus militaris* Kittl, 1894.

DISCUSSION: Cossmann erected this genus name to replace *Eustylus* Kittl, 1894, which is a homonym of *Eustylus* Schornherr, 1843.

Trypanostylus triadicus Kittl, 1894
Figure 39

Eustylus triadicus Kittl, 1894, p. 195, pl. 8, figs. 26–27.

DISCUSSION: Two specimens in the fauna are so morphologically similar to this St. Cassian species that I can find no way of recognizing differences. The whorl profile is flat with a deeply incised suture, but, importantly, there is a narrow siphonal trough on the outer margin of the base. The columellar lip is reflexed and a siphonal notch is incised at the junction of the columellar lip and the lower lip. These are apomorphic features of the St. Cassian population. **Two specimens.**

MEASUREMENTS: AMNH 42853, H 5.4 (e) mm, W 2.1 mm, WhH 0.9 mm, WhW 0.8 mm, SpAng 19°.

SUPERFAMILY SUBULITACEA LINDSTROM, 1884
FAMILY MEEKOSPIRIDAE KNIGHT, 1956

Genus *Meekospira* Ulrich, in Ulrich and Scofield, 1897

TYPE SPECIES: *Eulima? peracuta* Meek and Worthen, 1861 (Ulrich, p. 1079).

DISCUSSION: As far as I am aware, *Meekospira* has not been reported previously from Asia. A specimen identified as *Holopella* cf. *trimorpha* Waagen by Grabau (1931) from the Permian of Mongolia quite possibly is a member of the genus, but it is a fragment. The illustration in Waagen (1880, pl. 10) is apparently a steinkern of a murchisoniid from the Productus Limestone of the Salt Range.

Meekospira melanoides, new species
Figure 40

DIAGNOSIS: Many-whorled high-spired *Melania*-like shells with sutures at an acute angle to the axis. The whorl profile is flattened or very gently convex, giving the shell an evenly fusiform shape. The aperture is narrow, teardrop shaped, and holostomous. The columellar lip is reflexed. The base tapers to a narrow point at the bottom of the lower lip. Anomphalus.

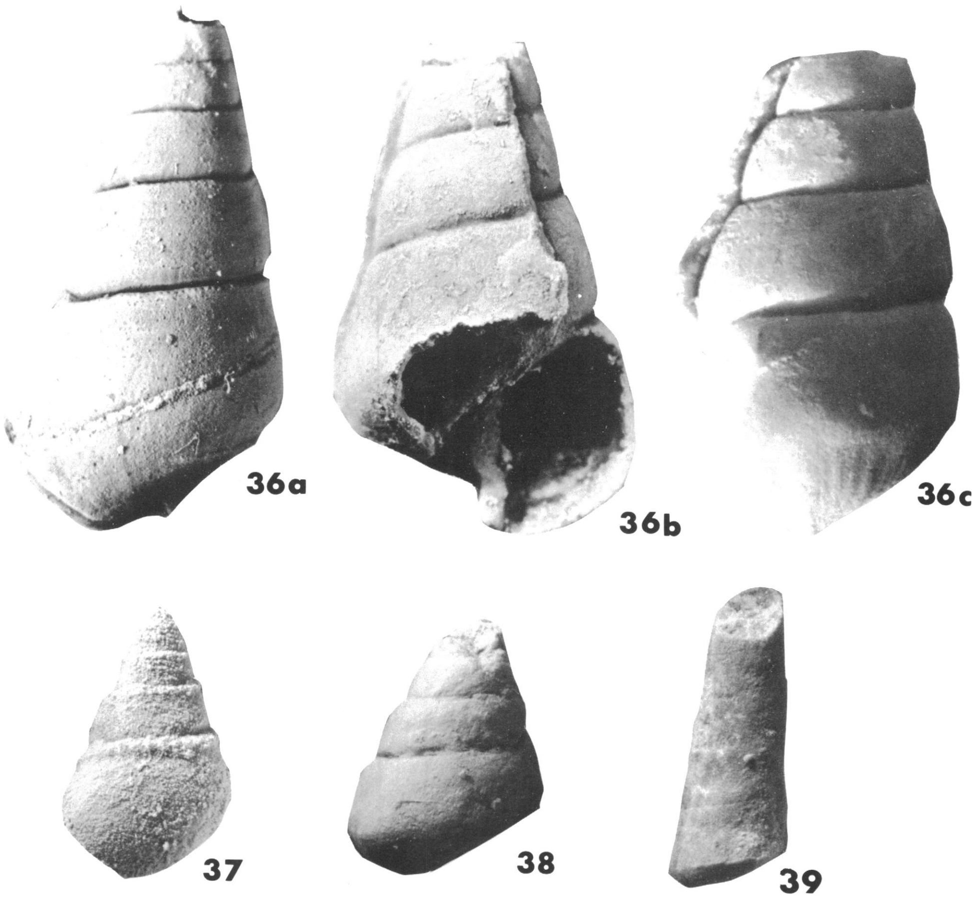
DISCUSSION: Most species of the genus have fewer whorls (usually 6–8) than does *M. melanoides* (with at least 10). The rate of axial translation is much greater than for other known species and this is reflected in the sharply acute suture lines. This rapid rate also results in the more flattened whorls and the narrow aperture. No other species is remotely similar to this one, which represents an extreme variant for an elongated species within this genus. **Eighteen specimens.**

MEASUREMENTS: Holotype AMNH 42854, H 4.55 mm, W 1.28 mm, SpAng 6°; paratype AMNH 42855, H 3.91 mm, W 1.19 mm, SpAng 7°.

ETYMOLOGY: Like the genus *Melania.*

Meekospira ligoni, new species
Figure 41

DIAGNOSIS: Inflated, fusiform shells with suture lines normal to the coiling axis. The whorl profile is broadly convex with a rounded periphery at midwhorl. Whorls embrace



FIGS. 36–39. **36.** *Omphaloptychia paleozoica*; (**a**) holotype, AMNH 42846, side view, ×8; (**b**) paratype, AMNH 42848, apertural view, ×8; (**c**) side view, ×8. **37.** *Omphaloptychia cingulata,* holotype, AMNH 42849, side view, ×6. **38.** *Omphaloptychia* sp., AMNH 42852, side view, ×8. **39.** *Trypanostylus* cf. *triadicus* Kittl, 1894, AMNH 42853, side view, ×8.

well below the periphery. Whorl expansion rate is moderate. Aperture oval shaped and the columellar lip is straight.

DISCUSSION: This species, like *M. melanoides,* has a rather high axial translation rate compared to other species. It differs from the type species in having a higher whorl expansion rate with the same number of whorls (eight). As a result, the shell shape is more fusiform than in the type. I have not found this species in other faunas. **Seventeen specimens.**

MEASUREMENTS: Holotype AMNH 42856, H 4.27 mm, W 1.37 mm, SpAng 11°; paratype AMNH 42857, H 1.65 mm, W 0.65 mm, SpAng 20°.

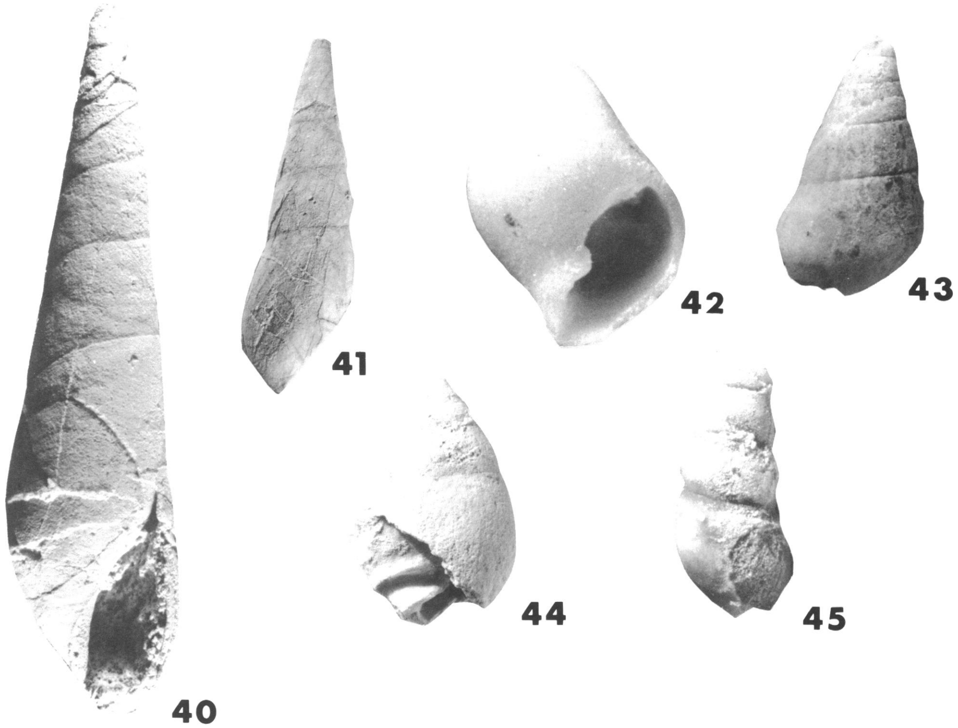
ETYMOLOGY: Named for William Ligon, Jr.

FAMILY SUBULITIDAE LINDSTROM, 1884
SUBFAMILY SOLENISCINAE, WENZ, 1938

Genus *Strobeus* deKoninck, 1881

TYPE SPECIES: *S. ventricosus* deKoninck, 1881, pl. 3, figs. 26–27.

DISCUSSION: The Treatise on Invertebrate Paleontology, Part I, recognized *Ianthinopsis* Meek and Worthen, 1866, as the valid name for this group. This was not a wise decision since the type is missing and the original description and illustrations prevent firm recognition of the taxon. *Strobeus ventricosus* is



FIGS. 40–45. **40.** *Meekospira melanoides,* holotype, AMNH 42854, apertural view with low side lighting to bring out details of the reflexed columellar lip, ×2. **41.** *Meekospira ligonensis,* holotype, AMNH 42856, side view, ×10. **42.** *Strobeus* sp., AMNH 42858, apertural view, ×10. **43.** *Soleniscus elegans* Gemmellaro, 1889, AMNH 42859, side view, ×6. **44.** *Cylindritopsis* sp., AMNH 42860, side view with the aperture broken to reveal the columellar folds, ×1.75. **45.** *Ceraunocochlis* sp., AMNH 42861, side view, ×7.

well known in Europe and the type is preserved in Brussels, and hence should serve well as the name bearer, as discussed by Harper (1981).

Strobeus sp.
Figure 42

DISCUSSION: Six very small and not well preserved specimens can be referred to this genus. Delpey described three specimens of what she called *Soleniscus* from Cambodia. The Malaysian specimens most closely resemble the illustrations she labeled *Soleniscus welleri* Knight, 1931. They are low-spired whorls that are evenly inflated but with a rounded periphery centrally located. Broken specimens reveal a columellar fold low on the columella, the distinctive generic feature. **Six specimens.**

MEASUREMENTS: (of illustrated specimen) AMNH 42858, H 3.2 mm, W 3.0 mm, SpAng 84°.

Genus *Soleniscus* Meek and Worthen, 1861

TYPE SPECIES: *S. typicus* Meek and Worthen, 1861, p. 467

Soleniscus elegans Gemmellaro, 1889
Figure 43

DISCUSSION: Twelve tiny specimens of subulitids in this fauna lack columellar folds or apertural teeth. They vary considerably in shell shape, whorl convexity, and whorl expansion rate but lack of other significant features precludes further taxonomic assessment. The specimen illustrated comes closest to a described species of *Girtyspira* with a deeply set suture suggesting a ramp, similar to that of *Girtyspira fusiformis* deKoninck (1881). The whorls are evenly convex and whorls embrace just below the broad periphery. However, *S. elegans* of Gemmellaro also has deeply set sutures but lacks the ramp so that, to be conservative, I shall assign these specimens to that taxon. **Thirteen specimens.**

MEASUREMENTS: AMNH 42859, H 4.7 mm, W 2.5 mm, SpAng 39°.

Genus *Cylindritopsis* Gemmellaro, 1889

TYPE SPECIES: *C. oovalis* Gemmellaro, 1889.

Cylindritopsis sp.
Figure 44

DISCUSSION: Three specimens can safely be assigned to this genus. They are relatively high-spired and clearly have two distinct columellar folds low on the columella. Most species have an ovoid shell shape with the exception of *C. inflata* Gemmellaro, 1889, from the Permian Sosio beds of Sicily. Specimens are rare in most faunas and spotty in distribution in the Upper Paleozoic.

Delpey described a new genus, *Angkorella,* in 1942 from Cambodia and it clearly is synonymous with this genus. The type species *A. sisophonensis* is very low-spired and ovoid but unrelated to the Lee Mine forms. Since the three Malaysian specimens are not particularly well preserved, I have refrained from formalizing a species name. **Three specimens.**

MEASUREMENTS: (of illustrated specimen) AMNH 42860, H 1.79 mm, W 1.22 mm.

SUBFAMILY SUBULITINAE LINDSTROM, 1884

Genus *Ceraunocochlis* Knight, 1931

Ceraunocochlis sp.
Figure 45

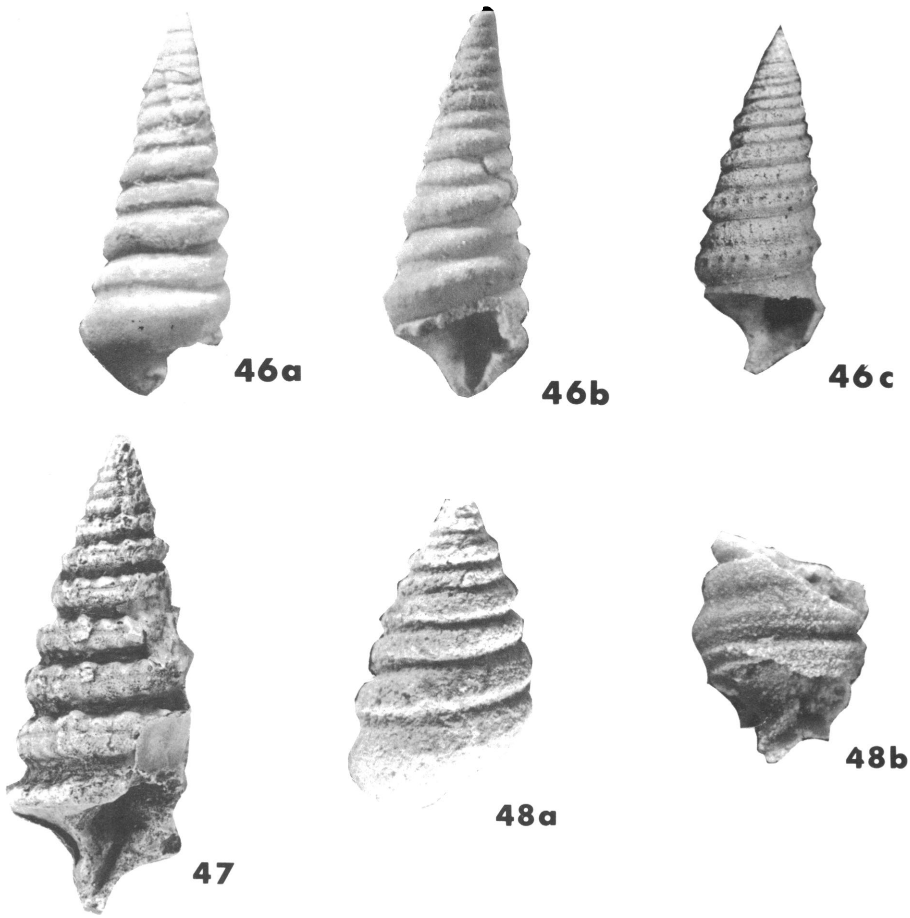
DISCUSSION: A single sinistral specimen clearly should be assigned to this genus. Its axis of coiling is curved and the shell is fusiform, typical of the genus. The genus is found sporadically in the Upper Paleozoic, usually a single specimen at each locality. The whorls are evenly convex; the sutures are deeply indented, forming a weak subsutural ramp. Whorls embrace beneath a broad periphery. The base is evenly convex and the siphonal notch is well developed. **One specimen.**

MEASUREMENTS: (of illustrated specimen) AMNH 42861, H 5.3 mm, W 2.1 mm, SpAng 15°.

?SUPERFAMILY NERINEACEA ZITTEL, 1873
FAMILY NERINEIDAE ZITTEL, 1873

DISCUSSION: I provisionally place the new genus *Prodiozoptyxis* in the nerineids as discussed below. The nerineids are a prominent Jurassic and Cretaceous group which have not been firmly related to any other group. According to Cossmann (1909, vol. 21, p. 209), two genera, *Pseudonerinea* (Ceritellidae) and *Iturvia* (Itieriidae) have heterostrophic nuclear whorls and, in consequence, he erected an opisthobranch suborder, the Entomotaeniata, for the superfamily. Knight et al. (1960, p. I145) point out that the group possesses features not present in most of the opisthobranchs, namely the short siphonal canal and a narrow anal emargination of the outer lip (as in the conidae), which gives rise to an anal fasciole. Yochelson (1956) suggested that the columellar folds resemble those of the subulitacean *Labridens* but the absence of an anal fasciole, the relatively low whorl translation rate, and shell thickening in that genus suggest convergence rather than a relationship. However, I lean toward a subulitid derivation. Houbrick (1981, p. 282) states that there is some doubt regarding the placement of the Cretaceous genus *Diopzoptyxis* in the nerineidae. This is based, in part, on the study of the campanilids by Delpey (1941b) in which she discussed the features of *Diozoptyxis* she considered to be campanilid in nature. The most important were a heterostrophic nucleus and an anal fasciole. However, the campanilids lack the complex internal folds that characterize the nerineids and for this reason I will place *Prodiozoptyxis* along with *Diozoptyxis* in that group.

The most improbable assignment of the nerineaceans was made by V. F. Pchelintsev (1968) who placed them into the order Murchisoniata (Mesogastropoda) along with the murchisoniids (Archeogastropoda), cerithiids, turritellids, caecids, and ianthiniids (all Mesogastropoda) along with many other groups. The lack of a selenizone is a clear



FIGS. 46–48. **46.** *Prodiozoptyxis permiana*; (**a**) holotype, AMNH 42862, side view, ×8.5; (**b**) apertural view, ×8.5; (**c**) paratype, AMNH 42863, apertural view with some of the whiting removed from the spiral ribs to show collabral nodes, ×7.5. **47.** *Diozoptyxis monilifera* (d'Orbigny), AMNH 42865, apertural view showing siphonal trough, ×0.75. **48.** *Prodiozoptyxis* sp., from the Permian Colina Formation, Warren, Ariz. (AMNH Loc. 2019); (**a**) AMNH 42866, side view, note pupoid shape, ×6; (**b**) AMNH 42867; (**b**) an apertural view of a fragment showing the deep siphonal trough, ×8.

indication that they are not related to the murchisoniids.

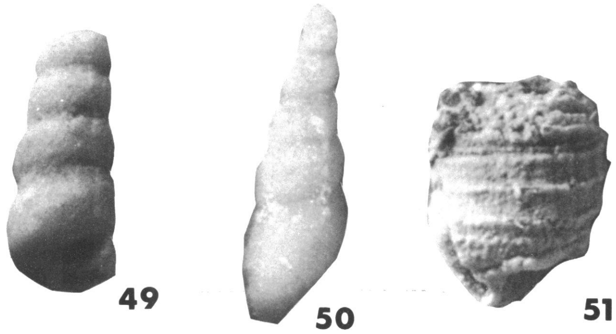
Prodiozoptyxis, New Genus

TYPE SPECIES: *Prodiozoptyxis permiana*, new species.

DIAGNOSIS: High-spired, turriculate shells with spiral angles less than 30°, two spiral ribs forming most of the external whorl surface, two internal folds located on the upper and lower internal whorl surfaces, phaneromphalus or cryptomphalus.

DISCUSSION: This genus is highly convergent on the Cretaceous nerineid species *Diozoptyxis monilifera* (d'Orbigny) which has two spiral ribs occupying most of the whorl surface except for a narrow trough separating them in the midwhorl, and in bearing elongate axial costae or nodes. The height and shape of the shell, the phaneromphalus, flattened base, and the quadratic aperture are the same in both genera.

The principal difference is in the internal fold pattern, which is the characteristic of most importance for generic recognition within the family. In *Diozoptyxis* there is a strong upper internal surface fold and a lower internal fold as in *Prodiozoptyxis*. But, in ad-



FIGS. 49–51. **49.** *Donaldina* sp., AMNH 42868, apertural view, ×17. **50.** *Streptacis* sp., AMNH 42869, side view, ×17.5. **51.** *Spirocyclina* sp., AMNH 42870, side view of fragment, ×15.

dition, *Diozoptyxis* has two axial folds and a low parietal fold. Since the Permian genus is the earliest appearing member of the family, it would be reasonable to assume that the internal fold system should be the simplest, as is the case with the earliest Jurassic nerineans. No function has yet been assigned to this system.

Prodiozoptyxis permiana, new species
Figures 46–48

DIAGNOSIS: Turriculate shells with coiled, rope-like whorl profiles, with eight or more whorls; elongate axial costae or nodes on two large spiral ribs are weakly developed and have faintly developed collabral nodes. Phaneromphalus. Base flattened, two internal folds present.

DISCUSSION: This is the only species known; therefore most of the generic diagnosis applies to it. A sample of *Diozoptyxis monilifera* (d'Orbigny) (AMNH #2894/1) from the Cretaceous Naaman beds of Syria, figure 47, shows a high degree of variability particularly in the shape of the whorls. Shape changes are due to the relative development of the spiral ribs, the development of the upper rib at the suture, and the development of the lower rib at the basal margin. In some specimens, the two ribs are weakly formed so that the whorl face between them is broad and flat, with a flat base. In other specimens the two spiral ribs are massive and occupy all of the whorl face so that only a narrow trough separates them. The result is that the whorl profile is inflated as in the Permian genus.

There is an undescribed species in the Permian Colina Limestone in the Mule Mountains of S.E. Arizona (AMNH Loc. 2019), figure 48. It has two large spiral ribs separated by a relatively narrow trough much like *P. permiana* but differs from that species in having a deeper trough and lower spires. The axial translation rate appears to slow down with growth, causing a somewhat pupoid shell shape.

There is some variation in *P. permiana* in the whorl translation rate, which causes the shell shape to be more or less turriculate. The ornament varies from a faint axial threading on the spiral ribs to moderately well-developed costae. **Thirty-seven specimens.**

MEASUREMENTS: Holotype AMNH 42862, H 11.0 mm, W 4.3 mm, WhH 2.2 mm, WhW 4.3 mm, SpAng 25°; paratype AMNH 42863, H 5.7 mm, W 3.6 mm, WhH 1.6 mm, SpAng 23°; paratype AMNH 42864, H 4.3 mm, W 2.4 mm, SpAng 28°; *Diozoptyxis monilifera* AMNH 42865, H 12.6 mm, W 6.0 mm, SpAng 28°.

Prodiozoptyxis sp.
Figures 48a, b

DISCUSSION: This is an undescribed species from the Permian Colina Limestone, in the Mule Mountains, one mile north of Warren, Arizona, U.S.A. (AMNH Loc. 2019). **Ten specimens.**

MEASUREMENTS: AMNH 42866, H 6.8 mm, W 4.2 mm, SpAng 41°; AMNH 42867, WhH 1.9 mm, WhW 3.4 mm.

ORDER OPISTHOBRANCHIA

SUPERFAMILY PYRAMIDELLACEA D'ORBIGNY, 1840

FAMILY STREPTACIDIDAE KNIGHT, 1931

Genus *Donaldina* Knight, 1931

TYPE SPECIES: *Aclisina grantonensis* Donald, 1898, p. 60.

Donaldina sp.
Figure 49

DISCUSSION: Three fragments appear to belong to this genus. The whorl profiles are evenly convex and there are spiral threads ornamenting the lower half of the whorl. The growth lines are sinuous and the apertures are holostomous. Their size also suggests that they are members of the genus. The embryonic whorls are missing, as are the diagnostic heterostrophic nuclear whorls. **Three specimens.**

MEASUREMENTS: AMNH 42868, WhH 0.5 mm, WhW 0.7 mm.

Genus *Streptacis* Meek, 1872

TYPE SPECIES: *S. whitfieldi* Meek, 1872, p. 173.

Streptacis sp.
Figure 50

DISCUSSION: A single specimen clearly belongs to this genus. It has the diagnostic heterostrophic nuclear whorls and the typical elongate, somewhat flattened whorl profiles. The growth lines are sinuous and the aperture is holostomous. As is typical, the shell lacks ornament. This is the first report of either *Donaldina* or this genus in the Tethyan Permian. **One specimen.**

MEASUREMENTS: AMNH 42869, H 2.4 mm, W 0.8 mm, SpAng 20°.

Genus *Spirocyclina* Kittl, 1894

TYPE SPECIES: *Turritella eucycla* Laube, 1869, p. 14, pl. 30.

Spirocyclina sp.
Figure 51

DISCUSSION: A fragment of a single whorl is sufficient to place it in this genus. The very distinctive spiral threads are unevenly spaced on the whorl with the most prominent thread forming a low-lying periphery on the inflated whorl. The columellar lip is reflexed and obscures a narrow umbilicus. Laube and Kittl defined the genus and type species from the Middle Triassic St. Cassian beds of Cortina, Italy, and Wenz (1938) placed the genus in the streptacids, a conclusion with which I concur. **One specimen.**

MEASUREMENTS: AMNH 42870, WhH 1.4 mm, WhW 1.5 mm.

?SUBORDER TROCHINA

SUPERFAMILY TROCHACEA RAFINESQUE, 1815

FAMILY TURBINIDAE RAFINESQUE, 1815

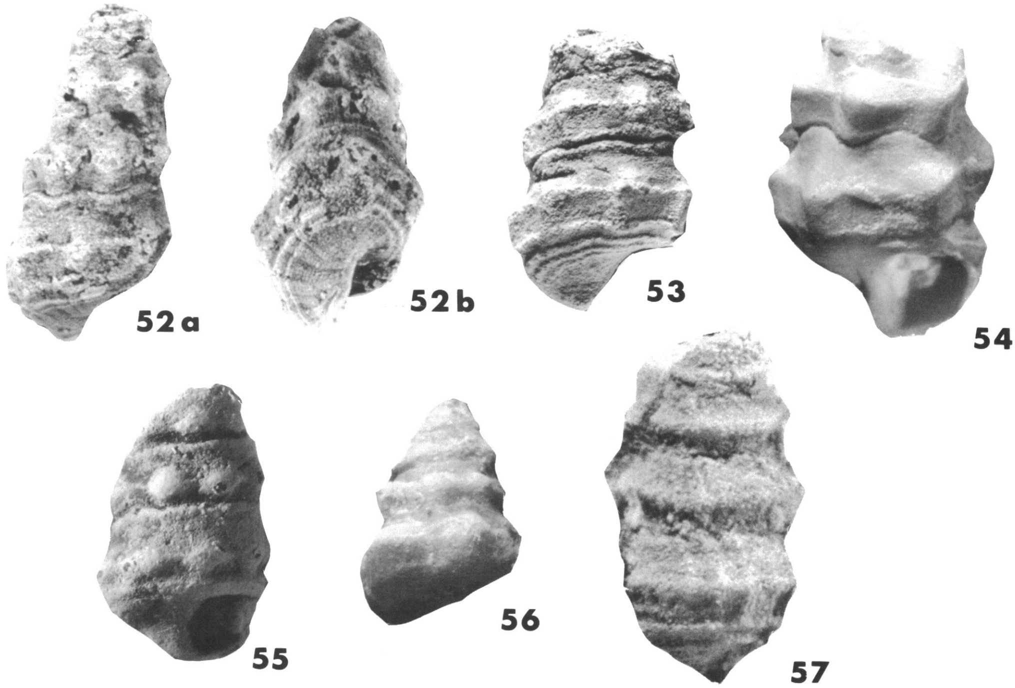
This family ranges from the Triassic to Recent and is worldwide in distribution. Most genera have strong ornament dominantly axial or collabral and there is a considerable range of shell shapes from almost planispiral to high-spired and uncoiled like *Vermicularia*.

SUBFAMILY LIOTIINAE ADAMS AND ADAMS, 1854

Genus *Eucycloscala* Cossmann, 1893

TYPE SPECIES: *Trochus binodosus* Munster, SD, Cox, 1960.

DISCUSSION: When I first observed the specimens I am now identifying as *Eucycloscala,* I believed them to be promathildid cerithiaceans based on the presence of a siphonal trough, the shell shape, varices, and other distinctive ornament features. These specimens are convergent on *Promathilda tyrsoecus* (Kittl), 1894, or *P. decorata* (Klipstein) Kittl, 1893. But there is a dilemma which I cannot resolve at this point. The Permian specimens even more closely resemble many species of Triassic *Eucycloscala* such as the type species. The problem is that the Malaysian shells all have siphonal troughs and reflexed columellar lips that are never found in the trochids. However, they also have orthostrophic nuclear whorls, whereas the promathildids have markedly heterostrophic nuclear whorls. Since there are more elements in common with *Eucycloscala,* I will assume that the Permian specimens should be assigned to that genus. The illustrations



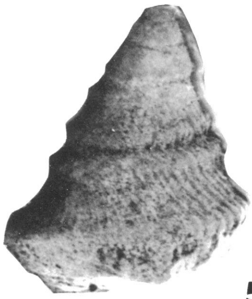
FIGS. 52–57. **52-54. 52(a)** *Eucycloscala asiatica,* holotype, AMNH 42871, side view, ×8; **(b)** oblique basal view, ×8. **53.** Paratype, AMNH 42871, side view showing well-developed collabral ribs on outer whorl face, ×8; **54.** Paratype, AMNH 42873, apertural view showing varixlike ribs, ×7.5. **55-57.** *Eucycloscala medionodosa.* **55.** Holotype, AMNH 42874, apertural view, ×6. **56.** Paratype, AMNH 42875, side view, ×8.5. **57.** Paratype, AMNH 42876, side view, ×12.5.

of the Triassic species do not indicate the presence of a siphonal trough and this is the principal difference between the Permian and the Triassic species.

Eucycloscala asiatica, new species
Figures 52–54

DIAGNOSIS: Relative high-spired, turriculate shells with concave profiles on the upper third of the whorls. The outer whorl face is flat to somewhat convex and slopes inward toward the base. The base is flat to somewhat concave. The sutures may be wavy, reflecting the whorl embracement at the sites of varices. Whorls embrace at the lower margin of the outer whorl face. The periphery is the shoulder marking the junction of the upper and outer whorl faces. Five to seven varices are developed mostly on the outer whorl face at the shoulder. There are usually four spiral costae; one adjacent to the suture, on the upper whorl face, at the shoulder, and on the basal margin. There are several additional threads on the base that become progressively weaker on the base. The columellar lip is reflexed. Cryptomphalus. The junction of the columellar and lower lips is the site of a siphonal trough.

DISCUSSION: There is considerable variation in the development of the varices. In one specimen, the varices are sharply delineated and evenly developed on the outer whorl face. On another, the varices are more diffused with the upper portion rounded almost into a boss; in other specimens, the varices are uniformly rounded to form an elongate node on the outer whorl face. In some specimens the outer whorl face is flat and the upper whorl face is concave giving an angulate, turreted appearance; in others, the upper and outer whorl face may be convex giving the whorl a globose profile and a more trochoid shell shape. **Nine specimens.**



58

59

FIGS. 58–59. **58.** *Glyptospira* sp., AMNH 42918, side view, ×16. **59.** *Phymatopleura* sp., AMNH 42919, side view, ×24.

MEASUREMENTS: Holotype AMNH 42871, H 5.8 mm, W 3.2 mm, SpAng 23°; paratype AMNH 42872, WhH 1.7 mm, WhW 3.2 mm.

Eucycloscala medionodosa, new species
Figures 55–57

DIAGNOSIS: Variable shells, medium to high-spired with dominant spiral ribs located midwhorl to somewhat lower, forming the periphery. Spiral ornament consists of a prominent thread adjacent to the suture, a central spiral rib, and a spiral thread at the basal margin. The upper whorl surface is concave, flat, or convex. The lower whorl face is short and usually flat. Whorls embrace just below the basal spiral thread. The rounded or flat base has several spiral threads. Collabral ornament is either threads, nodes, or varices confined to the periphery and lower whorl surface. Crytomphalus.

DISCUSSION: This is one of the most variable species encountered in the Malaysian Permian. The width and shape of the upper whorl face, the strength of the collabral ornament, and the base greatly alter the shell shape. The region between the periphery and the basal thread is the same as the outer whorl face in *E. asiatica* and is occupied by ornament, in contrast to the well-developed and usually flat outer whorl face of the other species. Ornament tends not to be as well developed in this species. There are from 10 to 15 nodes per whorl compared to 5 to 7 varices in *E. asiatica.* The spiral thread next to the suture is much more strongly formed and is consistently present. The height of the spire is also variable, ranging from almost turbiniform to a high cerithid appearing shell. The predominant shell shape, however, is high turbiniform with a row of nodes on a periphery low on the whorl. **Thirty-one specimens.**

MEASUREMENTS: Holotype AMNH 42874, H 7.2 mm, W 4.0 mm, WhH 1.7 mm, WhW 4.0 mm; paratype AMNH 42875, H 2.7 mm, W 3.6 mm, WhH 2.7 mm, WhW 3.6 mm, SpAng 46°.

ETYMOLOGY: *Medius,* Lat. middle; *nodosus,* Lat. knot.

GENERAL CONCLUSIONS

Now that this Tethyan fauna is known, it is clear that the southeastern Asian gastropod fauna is the probable source for the Mesozoic faunas that spread from that region to all of the seas by Jurassic time. The elusive lower Triassic refugia were undoubtedly concentrated in the center of the eastern Tethys and should be looked for in eastern Tibet to eastern Sichuan (Wang, 1978). The western Tethyan fauna, while having many common elements with the eastern, is related in a fundamental way with faunas of the Western Hemisphere, particularly the southwestern United States and western South America. The presence of the nerineid *Prodiozoptyxis,* the trochid *Eucycloscala,* the neritid *Trachydomia,* the murchisoniid *Loxosonia,* the loxonematids *Sinozyga* and *Acrospira,* and the coelostylinids *Omphaloptychia* and *Trypanostylus* are all on phyletic lines leading to major elements of the Jurassic and Cretaceous cosmopolitan fauna.

There are two aspects of the Permian faunas as they relate to Mesozoic faunas: (1) the presence of long-ranging, conservative Permian genera in the Middle to Upper Triassic and (2) "precursor" genera in the Permian of higher categories that become important and diverse groups in the Mesozoic. These aspects give the Triassic faunas a distinct Paleozoic appearance that I have discussed previously (Batten, 1973). At that time, I observed that the last of the diverse marine gastropod faunas in most of the world occurred at the end of Guadalupian (Kazanian) time. Since then, two localities have been discovered which have diverse gastropod assemblages in the Late Permian. A fauna collected by Richard Grant in the highest Permian (Dzulfian) of Greece contains a normal marine fauna but with numerous species of zygopleurids and other mesogastropods which have a distinct Triassic appearance. In several places in south China in the latest Changxingian there are diverse gastropod faunas (Wang, 1978; Pan, 1983). Thus the gap between the Middle Permian and Middle Triassic normal marine faunas has been greatly reduced.

My conclusions are basically the same as in 1973. While there are extinctions at the end of the Permian (such as most of the bellerophontids), many Paleozoic families survived into the Triassic, finally becoming extinct at the end of the Triassic when a major extinction occurred in the Mollusca. I would amend my view that most of the extinction took place at the end of the Middle Permian.

The presence of diverse faunas in China right at the boundary of the Triassic means that the extinction that took place at the close of the Permian was a sudden event. This is reinforced by the presence at many localities in China of an iridium "spike" in a boundary clay, recently discovered by a Beijing research group. The extinction of gastropods was not, however, as profound at the Permo–Triassic boundary as it was at the Triassic–Jurassic boundary when most of the families were replaced by the cosmopolitan families that dominate today's seas. Thus again we have the quandry of many groups that survived the meteoritic holocaust that the Alvarez theory pictures.

Some of the new species described herein have convergent counterparts in the Western Hemisphere Pennsylvanian of Lower Carboniferous. Delpey (1941) alluded to this convergence by identifying the Cambodian Permian species as those of Western Europe or North America. However, in such groups as the pseudozygopleurids and in *Orthonema,* a cladistic analysis shows that apomorphic characters group East Asian Tethyan species more closely, thus providing sufficient evidence to warrant recognition of the Malaysian species as being distinct.

Another aspect of this Malaysian fauna is the presence of a number of species (18) that are siphonate; usually only one or two species of the siphonate *Orthonema* would be found in a normal Upper Paleozoic fauna. There has been discussion that gastropods began invading the infaunal realm by Jurassic time (Signor, 1982). It has been suggested that this was in response to the evolution of predators. The development of siphons was an important factor in allowing migration into infaunal niches. I am suggesting that the movement into the infauna was in response to the origin of predators in the Permian rather than the Jurassic. Probably later in the Mesozoic there was a secondary migration of some siphonate groups into the epifaunal realm to account for the epifaunal siphonate forms found today. *Prodiozoptyxis,* to illustrate, has by far the deepest siphon of any known Paleozoic genus and even the trochid *Eucycloscala* has an incipient siphon and varices suggesting an infaunal habitat.

ADDENDUM

Several taxa of importance were discovered in processing bulk loaned material for return: (1) A low-spired trochiform species with a single spiral rib near the suture, a spiral rib on the periphery, and a concave outer whorl face was recognized as a species of *Glyptospira* Chronic, 1952, which is a microdomatid trochid, figure 58. (2) A new species of *phymatopleura* Girty, 1939, which is distinguished by having dominant spiral ornament with subdued collabral ornament, figure 59, and *Worthenia* deKoninck, 1883, a low-spired form quite distinct from other described species, figure 60; both of these pleurotomarians were reported in Part 1 of this series (Batten, 1972). (3) A new species of *Mourlonia* deKoninck, 1883 (Pleurotomariina), figure 61, has a shape much like *M.*

FIGS. 60–61. **60.** *Worthenia* sp., AMNH 42920, oblique side view, ×17. **61.** *Mourlonia* sp., AMNH 42922, side view, ×10.

talboti (Dickens), 1963 (reported in Part 1, Batten, 1972, p. 14) but with the collabral ornament greatly subdued and with strong spiral costae on the upper whorl surface and base. (4) A new species of *Glabrocingulum*, a flat, tabulate form with a strikingly wide umbilicus, is so unique that it is described below:

Glabrocingulum (*Glabrocingulum*) *umbilicatus*, new species

Figures 62a, b

DIAGNOSIS: Very low-spired trochiform shells with a very wide umbilicus revealing internal sutures and ornament to the early whorls. Whorls embrace at the lower margin of the selenizone. Sutural trough is narrow and deep. The upper whorl face is convexo-concave with collabral nodes on the upper convex portion. Fourteen equally developed spiral threads intersect the collabral nodes with weakly formed interference development. The slightly concave outer whorl face (here the same as the alveozone) is marked by the lower margin of the selenizone and a lower spiral thread that marks the boundary of the base. The base is convex with numerous evenly developed spiral threads. The collabral elements are very faint. The umbilicus occupies about one-third the area of the base and the spiral threads continue along the sides. The umbilical sutures are sharply defined. There is a slight thickening of the columellar lip.

DISCUSSION: The fine spiral threads which dominate the ornament pattern are similar to those found in *G.* (*Stenozone*) *brennensis* (Reed) but the more important features such as the presence of an alveozone, subsutural trough, and well-defined selenizone margins clearly indicate its affinities with *G.* (*Glabrocingulum*). Many species have an umbilicus. For example, several undescribed species from West Texas and Greece have a modest umbilical opening, but none are broad enough to reveal the earliest whorls as in this species; also, no other known species has dominant spiral ornament. **One specimen.**

MEASUREMENTS: Holotype AMNH 42921, H 10.1 mm, W 6.0 mm, SpAng 120°

ETYMOLOGY: *Umbilicus,* Lat. navel.

FIG. 62. *Glabrocingulum* (*Glabrocingulum*) *umbilicatus,* holotype, AMNH 42921; (**a**) side view, ×3; (**b**) oblique basal view, ×3.5.

LITERATURE CITED

Batten, R. L.

1966. The lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. Pts. 1 and 2. Palaeont. Soc. Monographs, Publ. 509 and 513, 109 pp., 10 pls.

1972. Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. Bull. Amer. Mus. Nat.

Hist., vol. 147, art. 2, pp. 1–44, figs. 1–52.
1973. The vicissitudes of the gastropods during the interval of Guadalupian-Ladinian time. *In* Logan, A (ed.), The Permian and Triassic systems and their mutual boundary, Can. Soc. Pet. Geol., Sp. Pap., pp. 596–607, 5 figs.
1979. Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids and neritids. Amer. Mus. Novitates, no. 2685, pp. 1–26, figs. 1–33.
1984. The calcitic wall in the Paleozoic families Euomphalidae and Platyceratidae, (Archeogastropoda). Jour. Paleont., vol. 58, no. 5, pp. 1185–1192, 2 figs.

Bayer, F. L., and G. McGhee
1984. Iterative evolution in the middle Jurassic ammonite faunas of wesern Germany. Lethaia, vol. 54, no. 2, pp. 544–566.

Cossmann, M.
1909. Essais de paléoconchologie comparée. Livr. 8, pp. 1–287, pls. 8.

Cox, L. R., and J. B. Knight
1960. Suborders of Archeogastropods. Jour. Malac. Soc. London, vol. 33, pp. 17–18.

Delpey, G.
1941a. Les Gastéropodes Permiens de Cambodge. Jour. de Conch., vol. 84, pp. 255–278 and 346–369.
1941b. Histoire du genre *Camapanile.* Ann. de Paléont., vol. 24, pp. 3–25.
1942. Les Gastéropodes Permiens de Cambodge. *Ibid.,* vol. 85, pp. 50–83.

Gemmellaro, G. G.
1889. La fauna dei calcari con Fusulina della valle del fiume Sosio nella provincia de Palermo. Fasc. 2, Nautiloidea–Gastropoda, pp. 97–182, pls. 11–19.

Grabau, A. W.
1931. The Permian of Mongolia. Nat. Hist. of Mongolia, Amer. Mus. Nat Hist., vol. 4, pp. 1–665, 35 pls.

Haas, O.
1953. Mesozoic invertebrate faunas of Peru. Bull. Amer. Mus. Nat. Hist., vol. 101, pp. 1–321, 18 pls.

Harper, J. A.
1981. The use–misuse of *Ianthinopsis* Meek and Worthen, 1866 (Mollusca: Gastropoda). Jour. Paleont., vol. 59, pp. 180–185.

Hoare, R. D.
1980. New Pennsylvanian gastropods from Ohio. Jour. Paleont., vol. 54, no. 5, pp. 1035–1040, 1 pl.

Hoare, R. D., and M. T. Sturgeon
1978. The Pennsylvanian genera *Cyclozyga* and *Helminthozyga* and the classification of the Pseudozygopleuridae. Jour. Paleont., vol. 52, no. 4, pp. 850–858, 2 pls.
1981. Pennsylvanian pseudozygopleurid gastropods from the Appalachian Basin. Jour. Paleont., vol. 55, no. 6, 3 pls.

Horný, R.
1955. Palaeozygopleuridae nov. fam. (Gastropoda), Ze středoceského siluru. Uštřed Ústavu Geol. Sborn., odd. Paleont., vol. 21, pp. 17–143, pls. 2–11.

Houbrick, R.
1979. Classification and systematic relationships of the abyssochrysidae, a relict family of bathyal snails (Prosobranchia: Gastropoda). Smithson. Contr. to Zool., no. 290, 21 pp., 11 figs.
1981. Anatomy, biology and systematics of *Campanile symbolicum* (Gastropoda: Prosobranchia). Malacologia, vol. 21 (1), pp. 263–289.

Huddleston, W.
1889. British Jurassic Gasteropoda, Part 1, no. 3. Gasteropoda of the Inferior Oolite, pp. 137–192, pls. 7–11.

Jones, C. R., D. J. Gobbett, and T. Kobayashi
1966. Summary of fossil record in Malaya and Singapore, 1900–1965. Geology and Palaeontology of Southeast Asia, vol. 2, pp. 309–359.

Kittl, E.
1893. Die Gastropoden des Schichten von St. Cassian der Südalpinen Triassic. Ann. der K. K. Naturhistorischen Hofmuseums, Bd. 7, pp. 35–97, pls. 5–9.
1894. Die Gastropoden des Schichten von St. Cassian der Südalpinen Triassic. Ann. der K. K. Naturhistorischen Hofmuseums, Bd. 9, pp. 143–275, pls. 4–12.

Knight, J. B.
1930. The gastropods of the St. Louis, Missouri Pennsylvanian outlier: the pseudozygopleurinae. Jour. Paleont., vol. 4 (suppl. 1), 89 pp., 5 pls.
1934. *Ibid.,* vol. 8, no. 4, pp. 433–447, pls. 56–57.

Knight, J. B., R. L. Batten, and E. L. Yochelson
1960. Part I. Mollusca. *In* Moore, R. C. (ed.), Treatise on invertebrate paleontology. Geol. Soc. Amer., Univ. Kansas Press, pp. I1–I351, figs. 89–216.

Koken, E.
1892. Uber die Gastropoden der Rothen Schlernschichten nebst bemerkungen uber verbreitung und herkunft einiger

triassischen Gattungen. Neus. Jahrb. Min., Bd. 2, pp. 25–36.

Koninck, L. G. de
1883. Faune du calcaire Carbonifère de la Belgique. Gasteropodes. Ann. Mus. Roy. d'Hist. Nat. Belg., vol. 8, pp. 1–240, pls. 22–54.

Laube, G. C.
1869. Die Fauna der Schichten von St. Cassian. K. Akad. Wiss., Denkschr., Abt. 2, Bd. 28, pp. 29–94, pls. 21–28.

Mansuy, H.
1912. Étude géologie du Yunnan oriental. 2e partie. Paléont. Indochina, Service Géologique. Mém. 1, fasc. 2, pp. 1–146, 25 pls.
1914a. Faunas des calcaire a *Productus* de l'Indo-chine. 2e ser.: Indo-china. *Ibid.,* fasc. 2, pp. 1–190, 10 pls.
1914b. Nouvelle contributions a la Paléontologie du Yun-nan. *Ibid.,* Mem. 1, vol. 3, fasc. 2, pp. 1–12, 1 pl.

Pan, Yin Tang
1983. The character of the geologic and geographic distribution of gastropods in the Yangtze district. Acta Paleont. Sinica, vol. 22, pp. 1441–1447.

Pchelintsev, V. F.
1968. Mesozoic Murchisoniata of the Crimean Highlands. Internatl. Geol. Rev., vol. 10, no. 11, 46 pp., 8 pls.

Signor, P. W.
1982. Resolution of life habits using multiple morphological criteria. Paleobiol., vol. 8, no. 4, pp. 378–388.

Taylor, D. W., and N. F. Sohl
1962. An outline of gastropod classification. Malacol., vol. 1, no. 1, pp. 7–32.

Thiele, J.
1931. Handbuch der Systematischen Weichtierkunde, Bd. 1, 778 pp. Jena, Gustav Fischer.

Tomlin, J. R.
1927. Reports on the marine Mollusca in the collections of the South African Museum: families Abysochysidea, Ocorythidae, Haliotidae and Tonnidae. Ann. South Afr. Mus., vol. 25, no. 1, pp. 77–83, 4 pls.

Waagen, W.
1880. Productus limestone fossils. Palaeont. Indica, Mem. Geol. Surv. India, ser. 13, vol. 1, pt. 2, pp. 73–183, pls. 7–16.

Wang, G. G.
1978. Gastropods. *In* Atlas of fossils of southwest China, Guizhou Volume, Pt. 2. Carboniferous to Recent, Guizhou Working Team (eds.), pp. 394–413, pls. 108–129.

Wang, H. J., and Y. Xi
1980. Late Permian and early Triassic gastropods of western Guizhou. *In* Stratigraphy and Paleontology of Upper Permian coal-bearing formations in western Guizhou, Nanking Instit. of Geol. and Paleont. (eds.). Beijing, China Science Press.

Wenz, W.
1938. Gastropoda, Allgemeiner Teil, und Prosobranchia. *In* Schindewolf, O. (ed.), Handbuch der Palaozoologie, Bd. 6, Teil 1, pp. 1–240.

Winters, S. S.
1963. Supai Formation (Permian) of eastern Arizona. Geol. Soc. Amer., Mem. 89, pp. 1–99, 9 pls.

Yin, H. F.
1983. Uppermost Permian Pectinacea from South China. Riv. Ital. Paleont., vol. 88, no. 3, pp. 337–386.

Yochelson, E. L.
1956. Permian gastropods of the southwestern United States, pt. 1. Bull. Amer. Mus. Nat. Hist., vol. 110, art. 3, pp. 173–260, pls. 9–24.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Bulletin, Novitates,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.