# *Diartus hughesi* (Campbell and Clark)

*Ommatocampe hughesi* Campbell and Clark, 1944, p.23, pl.3, fig.12

- *Ommatartus hughesi* (Campbell and Clark), Riedel and Sanfilippo, 1970, p.521
- *Diartus hughesi* (Campbell and Clark), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Shell generally robust with thick walls and a rough surface. Cortical twin shell approximately cylindrical or with slightly concave sides, bearing numerous circular to



subcircular pores of variable size and arrangement. Inner and outer medullary shells spherical, attached to the mid-section of the cortical shell by radial beams. Two to 6 rounded polar caps, which fit against each other, are attached to each end of the cortical shell. Caps may be the same width as the cortical shell or broaden distally. When the distal caps become spongy, however, they are narrower than the cortical shell. In many specimens solid tubercules project laterally from the sides the cortical shell near the polar caps and from the polar caps themselves (Nigrini, unpubl. data).

#### DIMENSIONS

Length, total, 280  $\mu$ m, of central section, 48  $\mu$ m; greatest width (across peripheral arm), 90  $\mu$ m (Campbell and Clark, 1944).

#### DISTINGUISHING CHARACTERS

The cortical shell is approximately cylindrical and the outer medullary shell approximately spherical. The polar caps are multiple (*Ommatartus hughesi* in Riedel and Sanfilippo, 1978a).

It is distinguished from *D. petterssoni* by more than half of the skeletal structure at each end of the cortical shell being composed of discrete caps, rather than spongy material (even though the latter may

be transversely zoned). It differs from those occasional specimens of *Didymocyrtis antepenultima* [and *D. penultima*] that have more than one cap on each pole by the cortical shell being subcylindrical rather than equatorially constricted. It differs from such two-armed porodiscids as *Ommatocampe polyarthra* Ehrenberg (1872a, p.317; 1872b, pl.6, 3, fig.9) and the form identified as belonging to the "*Amphymenium splendiarmatum* Clark and Campbell group" by Petrushevskaya (1975, pl.7, fig.1) by having a cortical shell distinct from the medullary shell(s) and caps (Sanfilippo et al., 1985).

#### VARIABILITY

The sub-cylindrical cortical shell has a single ring of protuberances at each pole, surmounted by 2-6 polar caps. As in *D. petterssoni*, the tubercles on the cortical shell are variably developed - in some specimens, practically absent. Also as in *D. petterssoni*, the cortical shell in some specimens tends to be subspherical (particularly in the early part of the range of *D. hughesi*).

#### DISTRIBUTION

This species occurs widely in middle late Miocene assemblages. The evolutionary transition to this species from *Diartus petterssoni* defines the boundary between the *Diartus petterssoni* Zone and the *Didymocyrtis antepenultima* Zone. Its morphotypic last appearance marks the top of the *Didymocyrtis antepenultima* Zone.

#### PHYLOGENY

This species evolved from *Diartus petterssoni* and terminates the *Diartus* lineage.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.1C, figs.17-18; Johnson, 1974, pl.7, figs.8-10; Holdsworth, 1975, pl.1, figs.3-5.

# *Diartus petterssoni* (Riedel and Sanfilippo)

*Cannartus(?) petterssoni* conditional manuscript name proposed in Riedel and Funnell, 1964, p.310; Riedel and Sanfilippo, 1970, p.520, pl.14, fig.3

*Diartus petterssoni* (Riedel and Sanfilippo), Sanfilippo and Riedel, 1980, p.1010





Cortical shell rather thick-walled, approximately cylindrical (sometimes bulged at the equator), with pronounced protuberances surrounding each end of the cortical shell. Pores of the cortical shell circular or subcircular, smaller near the equator. Two medullary shells, of which the outer is commonly spherical, sometimes lenticular. Very broad spongy columns (in some specimens divided into narrow parallel zones) are separated from the cortical shell by a narrow clearer zone: the distal margin of this clearer zone is commonly at the end of the protuberances (Riedel and Sanfilippo, 1970).

#### DIMENSIONS

Length of spongy columns 25-100  $\mu$ m (commonly about 50  $\mu$ m); their median breadth 50-85  $\mu$ m. Length of cortical shell 80-100  $\mu$ m; its maximum breadth (including protuberances) 75-95  $\mu$ m. Breadth of outer medullary shell 25-40  $\mu$ m (Riedel and Sanfilippo, 1970).

#### DISTINGUISHING CHARACTERS

The most characteristic features are the broad, spongy columns at the ends of the subcylindrical to subspherical cortical shell, medullary shell tending to be spherical, and, in most specimens, pronounced tubercles in a single row at each end of the cortical shell. Closely related species are *Didymocyrtis laticonus*, which has tubercles more evenly distributed over the cortical shell, and *Diartus hughesi*, in which the skeletal structures at each end of the cortical shell are multiple concentric caps rather than spongy columns (Sanfilippo et al., 1985).

#### VARIABILITY

The tubercles on the cortical shel1 are variably developed--in some specimens, practically absent. The cortical shell is usually elongate, but, especially in the later part of the range of the species, it is subspherical in some specimens (*Cannartus* sp. aff. *C. petterssoni* in Holdsworth, 1975, p.519): the fact that the cortical shell varies continuously in length from 115 to 80 µm leads us not to separate the two as separate taxa. Some specimens show concentric zonation (like the caps of *Diartus hughesi*) in the proximal parts of their spongy columns. The medullary shell typically presents a circular outline, but in some specimens it is compressed as in most other artiscins (Sanfilippo et al., 1985).

#### DISTRIBUTION

A late middle Miocene species. Specimens from different parts of its geographic range (DSDP Sites 66, 71, 77, 206, 214, 216 and 223, and Experimental Mohole) show no noticeable morphologic differences. None were found at latitudes higher than about 45° (DSDP Sites 281 and 341). The record of this species at Site 139 (Petrushevskaya and Kozlova, 1972, pl.12, fig.5) is based on specimens that we would identify as *Didymocyrtis laticonus* (Sanfilippo et al., 1985).

The morphotypic first appearance of this species defines the lower limit of the *Diartus petterssoni* Zone. The evolutionary transition of this species to *Diartus hughesi* marks the boundary between the *Diartus petterssoni* Zone and the *Didymocyrtis antepenultima* Zone.

#### PHYLOGENY

This species originated from *Didymocyrtis laticonus*, and evolved into *Diartus hughesi*.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.1C, figs.15-16, 19-20; Johnson, 1974, pl.7, figs.6-7.

### *Dictyocoryne ontongensis* Riedel and Sanfilippo

*Dictyocoryne ontongensis* Riedel and Sanfilippo, 1971, p.1588, pl.1E, figs.1, 2, pl.4, figs.9-11

#### DESCRIPTION

Central disc small, with usually 5 concentric rings. Three arms arranged usually in a Y-shape, with one angle smaller than the others, but in some early specimens at equal angles. Arms rarely with slight transverse zonation, parallel-sided or slightly expanding distally; one or



more of them forked distally at a very obtuse angle, each branch being approximately the same width as the distal part of the arm or wider, and with a bluntly rounded termination. Rarely, the terminations of the arms are doubly bifurcated. Some specimens have a patagium that occupies practically all of the space outlined by the arms and their bifurcations (Riedel and Sanfilippo, 1971).

#### DIMENSIONS

Based on 30 specimens. Maximum radius 116-215  $\mu m$  (Riedel and Sanfilippo, 1971).

#### DISTINGUISHING CHARACTERS

This species is the only one known to have three spongy arms in which one or more of the arms bifurcates distally.

#### VARIABILITY

Angle between arms varies from being equal (in early specimens) to having one angle smaller than the other two. Length of arms may also vary.

#### DISTRIBUTION

This low-latitude species has its morphotypic first appearance within the *Dorcadospyris alata* Zone. Its morphotypic last appearance lies within the *Didymocyrtis antepenultima* Zone.

## *Dictyoprora armadillo* (Ehrenberg)

*Eucyrtidium armadillo* Ehrenberg, 1873, p.225; 1875, p.70, pl.9, fig.10

*Theocampe armadillo* (Ehrenberg) group, Riedel and Sanfilippo, 1971, p.1601, pl.3E, figs.3-5 (*partim*.)

*Dictyoprora armadillo* (Ehrenberg), Nigrini, 1977, p.250, pl.4, fig.4



#### DESCRIPTION

Shell rather smooth, thick-walled, cephalis small, subspherical with few large pores and well-developed, three-bladed apical horn. Vertical tube short, cylindrical, upwardly directed. Thorax relatively small, inflated with large circular pores, irregularly arranged. Abdomen large, bulbous with 12 to 15 closely spaced transverse rows of circular pores, downwardly directed arches framing distal pores. Shell narrows sharply to well-developed, poreless peristome with smooth, even termination; transverse section circular (Nigrini, 1977).

#### DIMENSIONS

Based on four specimens. Total length (excluding apical horn) 177-225  $\mu m$ ; maximum breadth 95-105  $\mu m$  (Nigrini, 1977).

#### DISTINGUISHING CHARACTERS

*D. armadillo* is distinguished from other artostrobiids by having a three-bladed horn and a large, bulbous abdomen with closely spaced transverse rows of circular pores, that are framed by downwardly directed arches (Sanfilippo, unpubl. data).

#### VARIABILITY

It is rather constant during its short range.

#### DISTRIBUTION

This species is found in low-latitude sediment samples from all oceans. Its morphotypic first appearance lies within the *Podocyrtis goetheana* Zone and its morphotypic last appearance is at the top of the *Cryptocarpium ornatum* Zone.

PHYLOGENY Uncertain.

## *Dictyoprora mongolfieri* (Ehrenberg)

*Eucyrtidium mongolfieri* Ehrenberg, 1854, pl.36, fig.18, B lower; 1873, p.230

*Dictyoprora mongolfieri* (Ehrenberg), Nigrini, 1977, p.250, pl.4, fig.7

#### DESCRIPTION



Cephalis hemispherical, with circular pores, and with an inconspicuous lateral tubule lying against the upper part of the thoracic wall. Collar stricture indistinct. Thorax slightly inflated annular, with circular pores inclined obliquely upwards and inward as they traverse the thick wall. Lumbar stricture distinct. Abdomen inflated barrel-shaped, constricted distally to a short cylindrical, hyaline peristome. Abdominal pores strictly in longitudinal and transverse rows, the longitudinal rows separated by ridges (Riedel and Sanfilippo, 1970).

#### DIMENSIONS

Total length of shell 125-160  $\mu m$ ; maximum breadth 75-100  $\mu m$  (Nigrini, 1977).

#### DISTINGUISHING CHARACTERS

*D. mongolfieri* is distinguished from all other species of *Dictyoprora* by the abdominal pores being in strict longitudinal and transverse rows. It differs from *D. armadillo* (Ehrenberg, 1873, p.225) in lacking an apical horn and having an ellipsoidal rather than pyriform abdomen. This species has been widely used in stratigraphy because it is relatively easily recognized, occurs fairly abundantly throughout its range, and can be recognized in assemblages that are not very well preserved. Its [distinction] from other artostrobiid species [of the *D. amphora* (Haeckel) group Foreman, 1973] is not completely satisfactory in some assemblages, where specimens with abdominal pores strictly aligned longitudinally [co-occur with transitional forms] having abdominal pores quincuncially arranged. Uncertainties are best avoided by not admitting specimens departing to any degree from strictly longitudinal and transverse

alignment of the pores. Even so, there is a problem in recognizing the [lowermost] limit of occurrence of *D. mongolfieri*. Because it is a morphotypic rather than an evolutionary limit, single specimens justify its being recorded as present, and their detection in [the earliest] assemblages depends on the amount of effort spent in searching. This difficulty cannot be avoided until the evolutionary origin of the species is satisfactorily determined (Sanfilippo et al., 1985)

#### VARIABILITY

Throughout its stratigraphic range, *D. mongolfieri* varies only slightly in the lumbar stricture being more or less distinct, depending on the degree of inflation of the abdomen. The abdominal pores are always strictly aligned rectangularly in longitudinal and transverse rows, with the longitudinal rows separated by ridges. Late forms tend to be a little wider than earlier forms (75-100  $\mu$ m as compared to 65-90  $\mu$ m), with somewhat more pores on a half-diameter of the abdomen (9-11 as compared to 7-9). The simple, short, hyaline peristome also undergoes a change toward the end of the range, to an undulating margin or three smooth shovel-shaped feet in some specimens (Sanfilippo et al., 1985).

#### DISTRIBUTION

*D. mongolfieri* is common at all tropical (30°S-30°N) localities from which sediments of middle middle Eocene to early early Oligocene age are available. The morphotypic first appearance of this species defines the base of the *Dictyoprora mongolfieri* Zone. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Theocyrtis tuberosa* Zone.

#### PHYLOGENY

*D. mongolfieri* might have arisen from the *D. amphora* group, but this group is very varied and has a similar stratigraphic range to *D. mongolfieri*. It left no known descendants.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.3E, fig.13; Nigrini, 1974, pl.IM, figs.7-10, pl.2E, fig.9.

## Dictyoprora pirum (Ehrenberg)

*Eucyrtidium pirum* Ehrenberg, 1873, p.232; 1875, pl.10, fig.14

*Dictyoprora pirum* (Ehrenberg), Nigrini, 1977, p.251, pl.4, fig.8

#### DESCRIPTION

Shell three-segmented, smooth, hyaline.



Cephalis small, spherical with few circular pores; no apical horn. Vertical tube short, cylindrical, laterally directed. Collar stricture indistinct. Thorax inflated with two or three transverse rows of circular pores. Lumbar stricture distinct. Abdomen much inflated in normal view, but laterally compressed: four to seven widely spaced, transverse rows of circular pores. Pores also widely spaced. Distal opening relatively small with well-differentiated, but short, poreless peristome and smooth termination (Nigrini, 1977).

#### DIMENSIONS

Based on 10 specimens. Total length 88-120  $\mu m$ ; maximum breadth 65-83  $\mu m$  (Nigrini, 1977).

#### DISTINGUISHING CHARACTERS

A three-segmented form with the last segment having sparse, transversely aligned pores, and being compressed in the [lateral] plane (Riedel and Sanfilippo, 1978a).

*D. pirum* is distinguished by its sparsely pored, inflated, laterally compressed abdomen (Sanfilippo et al., 1985).

#### VARIABILITY

This three-segmented, smooth, hyaline form constantly possesses an inflated abdomen that is laterally compressed, four to seven widely spaced transverse rows of small circular pores, and terminally a welldifferentiated, short, poreless peristome (Sanfilippo et al., 1985).

#### DISTRIBUTION

*D. pirum* is found in all tropical localities of latest middle Eocene to early early Oligocene age. Its morphotypic first appearance lies within the *Podocyrtis goetheana* Zone and its morphotypic last appearance lies within the *Theocyrtis tuberosa* Zone.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.3E, figs.10-11.

## *Didymocyrtis antepenultima* (Riedel and Sanfilippo)

- *Panarium antepenultimum* conditional manuscript name proposed by Riedel and Funnell, 1964, p.311
- *Ommatartus antepenultimus* Riedel and Sanfilippo, 1970, p.521, pl.14, fig.4
- *Didymocyrtis antepenultima* (Riedel and Sanfilippo), Sanfilippo and Riedel, 1980, p.1010



#### DESCRIPTION

Cortical and medullary shells similar to those of [*Didymocyrtis laticonus*] and [*Didymocyrtis penultima*]. [*D.laticonus*] has no polar caps (the distal boundary of the narrow clearer zone between the cortical twin-shell and spongy column is parallel to the distal wall of the cortical shell...) whereas [*D. penultima*] s.s. has caps at least as well developed as its holotype (Riedel, 1957, pl.1, fig.1). [*D. antepenultima*] includes all forms in which the development of the caps and spongy columns is intermediate between these two (Riedel and Sanfilippo, 1970).

#### DIMENSIONS

Length of spongy columns 20-90  $\mu$ m; their median breadth 20-55  $\mu$ m. Height of polar caps 15-35  $\mu$ m. Length of cortical shell 90-115  $\mu$ m; its maximum breadth (including protuberances) 75-115  $\mu$ m. Breadth of outer medullary shell 25-40  $\mu$ m (Riedel and Sanfilippo, 1970).

#### DISTINGUISHING CHARACTERS

Between the equatorially constricted cortical shell and each polar spongy column is a cap varying in its state of development, between those of its immediate ancestor and descendant, [*Didymocyrtis laticonus*] and [*Didymocyrtis penultima*], respectively (*Ommatartus antepenultimus* in Riedel and Sanfilippo, 1978a). Westberg and Riedel (1978) restricted the use of this name to "specimens in which the proportion of the height of the polar cap to the length of the cortical shell is > 0.20 and < 0.25."

#### VARIABILITY

The variably tuberculate, equatorially constricted cortical shell bears at each end a polar cap surmounted by a spongy column. The most obvious variable within the species is the size of the polar caps. The proportion of the height of the polar cap to the length of the cortical shell increases from 0.20 in early specimens to (but not including) 0.25 in late ones. The spongy column may be nearly as broad at the base as the polar cap, or as narrow as 0.1 times the width of the cap - this extreme is probably a result of dissolution (Sanfilippo et al., 1985).

#### DISTRIBUTION

This species is found in material of middle late Miocene age in latitudes lower than 40°. Specimens with more than one polar cap have been observed in the Indian Ocean and off W. Africa (DSDP Sites 217, 223, 238 and 362). At DSDP Sites 281 and 223, south of Tasmania and in the NW Indian Ocean, respectively, forms with multiple caps and a medullary shell that is circular in outline have been observed.

The evolutionary transition of this species from *Didymocyrtis laticonus* is approximately synchronous with the lower limit of the *Didymocyrtis antepenultima* Zone. The evolutionary transition of this species to *Didymocyrtis penultima* is approximately synchronous with the lower limit of the *Didymocyrtis penultima* Zone.

#### PHYLOGENY

*D. antepenultima* evolved from *D. laticonus* by an increase in the height of the polar caps, and developed into *D. penultima* by a continuation of this tendency.

#### REMARKS

Additional illustrations can be found in Westberg and Riedel, 1978, pl.2, figs.4-5.

# Didymocyrtis avita (Riedel)

Panartus avitus Riedel, 1953, p.808, pl.84, fig.7

*Ommatartus avitus* (Riedel), Riedel and Sanfilippo, 1971, p.1588, pl.4, fig.6

*Didymocyrtis avita* (Riedel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION



Cortical shell and polar caps of similar general form, kidney-shaped (as in [*Didymocyrtis*] *tetrathalamus* (Haeckel)), except that the two polar caps are somewhat narrower than the cortical shell. Pores of the cortical shell subcircular, 3-6 times as broad as the intervening bars, 13-15 on a half equator, 7-9 on the length of a chamber. Walls of the cortical shell bearing large, obtuse protuberances, 1.5-2 times as broad as the pores and half as long, usually concentrated on the widest part of the shell. Pores of the polar caps similar to those of the cortical shell, except for a row of larger pores at the junction with the latter. Surface of the polar caps usually covered with short, acute, conical spines, approximately as long as the diameter of the pores. External medullary shell compressed, its greatest diameter half the equatorial diameter of the cortical shell; the inner medullary shell not clearly visible (modified from Riedel, 1953).

#### DIMENSIONS

Total length of the shell 162-180  $\mu$ m; of the apical spines 2-6  $\mu$ m. Maximum breadth of the cortical shell 80-85  $\mu$ m; of polar caps 65-75  $\mu$ m; of the equatorial constriction 70-75  $\mu$ m; of the external medullary shell 32-35  $\mu$ m (Riedel, 1953).

#### DISTINGUISHING CHARACTERS

*D. avita* is distinguished from *D. penultima* [and from all others of the genus] by the absence of spongy columns [and by the heavy protuberances on the cortical shell]. In poorly preserved material, it is often difficult to tell whether specimens are actually columnless, or eroded. Furthermore, the remnants of bars that attached a veil, or a second cap, often resemble the framework of a spongy column. However,

if the assemblage is examined as a whole, it can usually be determined whether the species is present.

At the upper end of its range, *D. avita* loses the tubercles on its cortical shell and evolves to *D. tetrathalamus*. In some assemblages, broadbased spines on the cortical shell of *D. tetrathalamus* give the appearance of tubercles (Sanfilippo et al., 1985).

#### VARIABILITY

*D. avita* has a tuberculate, equatorially constricted cortical shell with large caps at each pole, and no spongy columns. The tubercules are prominent in the early part of the range, and become less pronounced with time. Polar caps are sometimes multiple, and a veil may enclose the shell (Sanfilippo et al., 1985).

#### DISTRIBUTION

*D. avita* is found in all localities of middle Pliocene age from latitudes lower than 40°. It evolved from *Didymocyrtis penultima* and into *Didymocyrtis tetrathalamus* within the *Spongaster pentas* Zone.

#### PHYLOGENY

*D. avita* arose from *D. penultima* and evolved into *D. tetrathalamus*.

#### REMARKS

Additional illustrations may be found in Riedel and Sanfilippo, 1971, pl.4, fig.6; 1978b, pl.2, fig.9.

# Didymocyrtis laticonus (Riedel)

Cannartus laticonus Riedel, 1959, p.291, pl.1, fig.5

*Didymocyrtis laticonus* (Riedel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Cortical twin-shell rather thick-walled, with pores subcircular or circular, ten to thirteen on the half-equator. On the broader parts of the shell, on either side of the equatorial constriction, are pronounced obtuse moundlike protuberances, at which the shell wall is



thickened; there is a tendency in some specimens for these protuberances to be so arranged that two girdles of them encircle each half of the twinshell. At each pole of the shell arises a broadly subconical, densely spongy column, which is almost as broad at its base as the polar surface of the twin-shell. Medullary shells two (or perhaps only one in some specimens), of which the inner is spherical and the outer spherical or lenticularly compressed. This species is distinguished from all others of the genus by the broadly subconical polar columns (Riedel, 1959).

#### DIMENSIONS

Based on 20 specimens. Length of polar columns 45-70  $\mu$ m; median breadth 28-40  $\mu$ m. Length of cortical shell 93-125  $\mu$ m; maximum breadth 68-113  $\mu$ m. Breadth of outer medullary shell 30-35  $\mu$ m (Riedel, 1959).

#### DISTINGUISHING CHARACTERS

The equatorially constricted cortical shell has a tuberculate surface, and bears wide, spongy polar columns. There are no pronounced caps, but a parallel-sided clear zone, no wider than the height of the tubercules, separates the cortical shell from the columns (*Cannartus laticonus* in Riedel and Sanfilippo, 1978a).

Westberg and Riedel (1978) used this name only for specimens "in which the height of the clear zone below the spongy column is less than 0.2 the length of the cortical shell."

*D. laticonus* is distinguished from its ancestor, *D. mammifera*, by having "clear zones" parallel to the cortical shell. In addition, the spongy columns tend to be wider than those of *D. mammifera*. It differs from its descendant *D. antepenultima* in that the proportion of the length of the clear zone (cap) to the length of the cortical shell is less than 0.20 (Sanfilippo et al., 1985).

#### VARIABILITY

*D. laticonus* has a tuberculate, equatorially constricted cortical shell with a clear zone at the base of each broad spongy column, parallel to the end of the cortical shell. Tubercles vary from 0.2 the length of the cortical shell to very minor protuberances. In the early part of the range, where *D. laticonus* has just evolved from *D. mammifera*, some specimens have spongy columns somewhat narrower and less robust than the very wide co]umns (at least 0.6 times the greatest width of the cortical shell) characteristic of the species (Sanfilippo et al., 1985).

#### DISTRIBUTION

*D. laticonus* is found in all assemblages of late middle Miocene age from latitudes lower than 40°. It evolved from *Didymocyrtis mammifera* within the *Dorcadospyris alata* Zone and evolved into *Didymocyrtis antepenultima* within the *Didymocyrtis antepenultima* Zone.

#### PHYLOGENY

*D. laticonus* evolved from *D. mammifera* and developed into *D. antepenultima*.

#### REMARKS

Additional illustrations can be found in Westberg and Riedel, 1978, pl.2, figs.1-3.

## *Didymocyrtis mammifera* (Haeckel)

*Cannartidium mammiferum* Haeckel, 1887, p.375, pl.39, fig.16

*Cannartus mammiferus* (Haeckel), Riedel, 1959, p.291, pl.1, fig.4

*Cannartus mammifer* (Haeckel), Sanfilippo et al., 1973, p.216, pl.1, fig.7



Didymocyrtis mammifera (Haeckel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Cortical shell ellipsoidal, with an equatorial constriction and with pores subcircular or circular, twelve to fifteen on the half-equator. On the broader parts of the shell, on either side of the equatorial constriction, there are pronounced obtuse moundlike protuberances, at which the shell wall is thickened. At each pole of the cortical shell arises a subcylindrical spongy column with meshes much smaller than those of the cortical shell. Medullary shells two, of which the inner is spherical and the outer spherical or lenticularly compressed. This species differs from [*Didymocyrtis violina*] in that the protuberances on the cortical shell are mammilliform rather than pliciform (Riedel, 1959).

#### DIMENSIONS

Based on 20 specimens. Length of polar columns 43-75  $\mu$ m; median breadth 20-30  $\mu$ m. Length of cortical shell 110-145  $\mu$ m; maximum breadth 93-115  $\mu$ m. Breadth of outer medullary shell 33-43  $\mu$ m (Riedel, 1959).

#### DISTINGUISHING CHARACTERS

This species is distinguished by its mammilliform protuberances on the cortical shell and its subcylindrical spongy columns that cover about one third of the polar ends of the cortical shell (Moore, pers. comm., 1992). *Didymocyrtis violina* has thickenings of the cortical shell in the form of coarse plicae rather than tubercles, and *D. laticonus* has broader polar columns (Sanfilippo et al., 1985).

#### VARIABILITY

This form is rarely found well preserved, but even corroded specimens are recognizable on the basis of the cortical shell with distinct tubercular thickenings on its broader parts (not transversely aligned as in *Diartus petterssoni*) and narrow, spongy polar columns (Sanfilippo et al., 1985).

#### DISTRIBUTION

*Didymocyrtis mammifera* occurs in late early to middle Miocene assemblages from all oceans in low and middle latitudes, including the Mediterranean region. Its morphotypic first appearance lies within the *Stichocorys wolffii* Zone and it evolved into *Didymocyrtis laticonus* within the *Dorcadospyris alata* Zone.

#### PHYLOGENY

*Didymocyrtis mammifera* evolved from *D. violina* by increased localization of the thickenings on the shell surface.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.2C, figs.1-3; Sanfilippo et al., 1973, pl.1, fig.7.

## Didymocyrtis penultima (Riedel)

*Panarium penultimum* Riedel, 1957, p.76, pl.1, fig.1; Riedel and Funnell, 1964, p.311

- *Ommatartus penultimus* (Riedel) *sensu stricto,* Riedel and Sanfilippo, 1970, p.521
- *Didymocyrtis penultima* (Riedel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Cortical twin-shell constricted equatorially, with circular to irregularly rounded pores: its surface bearing prominent, obtuse



protuberances. Distal chambers hemispherical, as caps on either end of cortical twin-shell, their length usually 0.2-0.3 that of twin-shell, somewhat narrower than twin-shell. Each cap surmounted by a spongy tube or tongue-shaped column, of which the width is approximately half that of the maximum breadth of twin-shell, or less. Outer medullary shell lenticular, inner one spherical (Riedel, 1957).

... Restricted to those forms in which the polar caps are at least as large, and as well separated from the cortical shell, as those of the holotype (Riedel and Funnell, 1964).

The proportion of the height of the polar caps to length of cortical shell in the holotype is 0.25 (Westberg and Riedel, 1978).

#### DIMENSIONS

Length of cortical twin-shell usually 100-120  $\mu$ m; its maximum breadth 80-105  $\mu$ m. Length of polar caps 25-40  $\mu$ m, of spongy polar columns 25-80  $\mu$ m (Riedel, 1957).

#### DISTINGUISHING CHARACTERS

The equatorially constricted cortical shell has a tuberculate surface, and the polar caps (at least as large and well developed as those of the holotype) bear narrow spongy columns (*Ommatartus penultimus* in Riedel and Sanfilippo, 1978a).

*D. penultima* is distinguished from its ancestor, *D. antepenultima*, by its larger polar caps (ratio of the polar cap to cortical shell 0.25 or greater). It is distinguished from its descendant, *D. avita*, by the presence of spongy columns. The multi-capped form is distinguished from *D. hughesi* by its equatorially constricted cortical shell and presence of spongy columns (Sanfilippo et al., 1985).

#### VARIABILITY

The tuberculate, equatorially constricted, cortical shell bears at each end a polar cap that is 0.25 or more times the length of the cortical shell, and a spongy column.

In the upper part of the range (*Stichocorys peregrina* Zone - *Spongaster pentas* Zone), many specimens have multiple polar caps. In the early part of the range, when the caps are multiple, the second one is very small. Though the species has been defined as having narrow spongy columns, the bases of the columns in some specimens are as much as 0.8 the width of the polar caps. In well preserved samples, a veil sometimes surrounds the entire skeleton or sometimes only the cortical shell and caps (Sanfilippo et al., 1985).

#### DISTRIBUTION

*D. penultima* is found in sediments of late late Miocene to early Pliocene ages from latitudes lower than 40°. Its evolutionary transition from *Didymocyrtis antepenultima* is approximately synchronous with the lower limit of the *Didymocyrtis penultima* Zone and its evolutionary transition to *Didymocyrtis avita* lies within the *Spongaster pentas* Zone.

#### PHYLOGENY

This species arose from *D. antepenultima* and evolved into *D. avita*.

#### REMARKS

Additional illustrations can be found in Westberg and Riedel, 1978, pl.2, figs.6-8.

# *Didymocyrtis prismatica* (Haeckel)

*Pipettella prismatica* Haeckel, 1887, p.305, pl.39, fig.6; Riedel, 1959, p.287, pl.1, fig.1

- Pipettella tuba Haeckel, 1887, p.337, pl.39, fig.7
- *Cannartus prismaticus* (Haeckel), Riedel and Sanfilippo, 1970, pl.15, fig.1
- *Didymocyrtis prismatica* (Haeckel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Cortical shell ellipsoidal, with the major axis generally 1.1-1.2 times the length of the



minor axis, and with the wall somewhat thicker at the equatorial band than at the poles. Pores of the cortical shell circular, regularly arranged and usually hexagonally framed, ten to fifteen on the half-equator, separated by rather narrow intervening bars. Surface of the cortical shell slightly rough. Medullary shell almost invariably present, spherical or slightly lenticularly compressed, thin-walled and with subcircular pores, joined to the cortical shell by an equatorial series of [supporting bars]. Subcylindrical spongy polar columns arise rather abruptly from the cortical shell, and have meshes much smaller than those of the cortical shell. In some specimens the meshes of the polar columns are longitudinally aligned, and four to six longitudinal ridges extend along their surface (Riedel, 1959).

#### DIMENSIONS

Based on 30 specimens. Major axis of cortical shell 115-163  $\mu$ m, minor axis 108-148  $\mu$ m. Diameter of medullary shell 28-38  $\mu$ m. Length of polar columns 50-240  $\mu$ m; median breadth 12-35  $\mu$ m (Riedel, 1959).

Length of cortical shell 115-175  $\mu$ m, its maximum breadth 105-150  $\mu$ m (Sanfilippo et al., 1985).

#### DISTINGUISHING CHARACTERS

*Didymocyrtis prismatica* similar to *D. tubaria* and *D. violina* and other *Didymocyrtis* species of the upper Oligocene to lowermost Miocene, but with the absence of any equatorial constriction, or plicae evident on the cortical shell. Similar also to other unnamed *Didymocyrtis* species, especially in subtropical to subpolar latitudes, but with spongy polar columns that are only up to one quarter the width of the cortical shell (Moore, pers. comm., 1992).

*Didymocyrtis prismatica* differs from *D. tubaria* by the equator of the cortical shell not being puckered (Sanfilippo et al., 1985).

#### VARIABILITY

The ellipsoidal cortical shell with a narrow spongy column at each pole is usually thick-walled, rarely thinned by dissolution. Presence of a single or double medullary shell is characteristic of the genus *Didymocyrtis*, but many specimens of *D. prismatica* show no trace of it, nor of its supporting bars. It is not yet clear whether this is a result of dissolution of a very delicate structure (Sanfilippo et al., 1985).

#### DISTRIBUTION

This species occurs in substantial numbers in assemblages of late Oligocene to early Miocene age in all oceans, including the Mediterranean region. Its morphotypic first appearance lies within the *Theocyrtis tuberosa* Zone and its morphotypic last appearance lies within the *Calocycletta costata* Zone.

#### PHYLOGENY

This species developed from *Lithocyclia angusta* by reduction of the number of spongy arms from three to two, and by the axis of rotational symmetry becoming aligned with the spongy columns, rather than being at right angles to their plane. *Didymocyrtis prismatica* apparently gave rise to *D. tubaria* and to *D*(?) *bassanii* (Carnevale) (Sanfilippo et al., 1973, p.216, pl.l, figs.1-3): it accompanies both of these species through a major part of their stratigraphic ranges (Sanfilippo et al., 1985).

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.2C, figs.11-13, pl.4, fig.5; Moore, 1971, pl.12, figs.1-2; Sanfilippo et al., 1973, pl.1, fig.8.

See Holdsworth (1975) for a discussion of the development of the medullary shell.

# *Didymocyrtis tetrathalamus tetrathalamus* (Haeckel)

*Panartus tetrathalamus* Haeckel, 1887, p.378, pl.40, fig.3; Nigrini, 1967, p.30, pl.2, figs.4a-4d (with synonymy)

*Panartus tetrathalamus tetrathalamus* Haeckel, Nigrini, 1970, p.168, pl.1, fig.12

*Didymocyrtis tetrathalamus* (Haeckel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Terminology is that proposed by Riedel



(1957, p.76). Cortical twin-shell constricted equatorially, with subcircular to subangular pores, having no definite arrangement, sometimes hexagonally framed; surface usually rough, spiny. Polar caps, when present, hemispherical to conical, approximately the same breadth as cortical twin-shell, supported by about 12 spines. Caps generally more delicate than twin-shell, with smaller pores and smoother surface. There are approximately equal numbers of specimens with and without single polar caps; rarely, completely or incipiently double-capped specimens are found. A few specimens have a delicate lateral meshwork supported by numerous rods, usually around the twin-shell, but sometimes extending around the caps. There is a tendency for middle-latitude forms to develop rather stout unbranched spines, either on the distal ends of the cortical twin-shell or on the polar caps. Such forms are rare in low latitudes.

Outer medullary shell lenticular, inner one spherical; radial beams connect outer medullary to twin-shell at the equatorial constriction (Nigrini, 1967).

#### DIMENSIONS

Length of cortical twin-shell 90-136  $\mu$ m; of polar caps 36-63  $\mu$ m. Maximum breadth of cortical twin-shell 72-109  $\mu$ m (Nigrini, 1967).

#### DISTINGUISHING CHARACTERS

*D. tetrathalamus* differs from *D. avita* in the absence of tubercles on the cortical shell.

#### VARIABILITY

This species has a non-tuberculate, equatorially constricted cortical shell with two large polar caps. It varies in that the surface of the cortical shell may be very smooth, or quite spiny, even to the extent that broad based spines may give the appearance of a tuberculate surface. Polar caps may be absent, small, well developed and sometimes double. They are frequently supported well away from the cortical shell by about twelve spines creating a row of large arches between cap and shell. In other specimens caps are attached closely, the pores between the cap and the cortical shell being about the same size as those of the latter. The shell in some specimens is surrounded by a veil, which may enclose the cortical shell only or cortical shell and caps (Sanfilippo et al., 1985).

#### DISTRIBUTION

*D. tetrathalamus* is found in assemblages of late Pliocene to Quaternary age from latitudes lower than 40°. Its evolutionary transition from *Didymocyrtis avita* lies within the *Spongaster pentas* Zone. It is extant.

#### PHYLOGENY

*D. tetrathalamus* is the extant representative of the *Didymocyrtis* lineage, having evolved from *D. avita*.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.1C, figs.5-7.

The nominate subspecies permits distinction from *D. tetrathalamus coronatus* (Haeckel) in Nigrini, 1970, p.168, pl.1, figs.13-14 (as *Panartus tetrathalamus coronatus*).

# *Didymocyrtis tubaria* (Haeckel)

- *Pipettaria tubaria* Haeckel, 1887, p.339, pl.39, fig.15
- *Cannartus tubarius* (Haeckel) Riedel, 1959, p.289, pl.l, fig.2
- *Didymocyrtis tubaria* (Haeckel) Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Cortical shell usually rather thick-walled,



ellipsoidal with an equatorial constriction, with pores subcircular, irregular in size and arrangement, eleven to eighteen on the half-equator. At the equatorial constriction the shell wall is puckered to form coarse plicae, which Haeckel called "short conical protuberances." At each pole arises a subcylindrical spongy column with meshes much smaller than those of the cortical shell. Medullary shells two (perhaps only one in some specimens), of which the outer is spherical or lenticularly compressed (Riedel, 1959).

#### DIMENSIONS

Based on 30 specimens. Length of polar columns 63-125  $\mu$ m; median breadth 15-30  $\mu$ m. Length of cortical shell 108-145  $\mu$ m; maximum breadth 80-123  $\mu$ m. Breadth of outer medullary shell 33-40  $\mu$ m (Riedel, 1959).

#### DISTINGUISHING CHARACTERS

In the region of the indistinct equatorial constriction, the shell wall is puckered to form coarse plicae. The spongy polar columns are narrow (*Cannartus tubarius* in Riedel and Sanfilippo, 1978a).

This species lacks the thickenings of the bulged part of the cortical shell on either side of the equator, which characterize *Didymocyrtis violina*. *D*(?) *bassanii* (Carnevale) (1908, p.21, pl.3, fig.12) lacks the longitudinal equatorial plicae, and usually has a longer, more dumbbell-shaped cortical shell and more inflated medullary shell (Sanfilippo et al., 1985).

#### VARIABILITY

The equatorial region of the cortical shell is puckered to a variable degree, forming coarse longitudinal plicae. The single or double medullary shell varies from moderately compressed (discoidal) to subspherical (Sanfilippo et al., 1985).

#### DISTRIBUTION

*Didymocyrtis tubaria* occurs in substantial numbers in assemblages of middle early to early middle Miocene age from low and middle latitudes of all oceans, including the Mediterranean region. Its morphotypic first appearance lies within the *Stichocorys delmontensis* Zone and its morphotypic last appearance lies within the *Dorcadospyris alata* Zone.

#### PHYLOGENY

*Didymocyrtis tubaria* evidently evolved from early *D. prismatica*, by development of the pronounced, longitudinally puckered equatorial constriction.

#### REMARKS

Additional illustrations may be found in Riedel and Sanfilippo, 1970, pl.15, fig.2; Sanfilippo et al., 1973, pl.1, figs.9-10.

## Didymocyrtis violina (Haeckel)

*Cannartus violina* Haeckel, 1887, p.358, pl.39, fig.10; Riedel 1959, p.290, pl.1, fig.3 (with synonymy)

*Didymocyrtis violina* (Haeckel), Sanfilippo and Riedel, 1980, p.1010

#### DESCRIPTION

Cortical shell ellipsoidal, with an equatorial constriction and with pores



subcircular or circular, twelve to eighteen on the half-equator. On the broader parts of the shell on either side of the equatorial constriction, the shell wall is somewhat thickened and puckered to form short, coarse plicae. At each pole arises a subcylindrical spongy column with meshes much smaller than those of the cortical shell. Medullary shells two, of which the inner is spherical and the outer spherical or lenticularly compressed. The thickened plicae, which are equatorial in [*Didymocyrtis tubaria*] are situated on the two broad zones of the cortical twin-shell of [*Didymocyrtis violina*] (Riedel, 1959).

#### DIMENSIONS

Based on 17 specimens. Length of polar columns 70-130  $\mu$ m; median breadth 15-33  $\mu$ m. Length of cortical shell 113-143  $\mu$ m; maximum breadth 85-108  $\mu$ m. Breadth of outer medullary shell 33-88  $\mu$ m (Riedel, 1959).

#### DISTINGUISHING CHARACTERS

The equatorial constriction is distinct, and on either side of it the wall of the broader parts of the cortical shell is somewhat thickened and puckered to form short, coarse plicae. The spongy polar columns are narrow (*Cannartus violina* in Riedel and Sanfilippo, 1978a).

In this species the puckering is confined to the equatorial zone, and in *D. mammifera* the thickenings of the cortical shell form distinct tubercles rather than plicae (Sanfilippo et al., 1985).

#### VARIABILITY

This species is narrowly defined, to include only individuals in which the equatorial constriction is distinct, and on either side of it the wall of the broader parts of the cortical shell is thickened and puckered to form short, coarse plicae. The medullary shell is compressed, lenticular (Sanfilippo et al., 1985).

#### DISTRIBUTION

*Didymocyrtis violina* is widespread in sediments of middle early to early middle Miocene age in low and middle latitudes of all oceans, including the Mediterranean region. Its morphotypic first appearance lies within the *Stichocorys delmontensis* Zone and its morphotypic last appearance lies within the *Dorcadospyris alata* Zone.

#### PHYLOGENY

*D. violina* evolved from *D. tubaria* by poleward migration of the equatorial plicae, becoming more abundant than its ancestor within the *Calocycletta costata* Zone.

#### REMARKS

Additional illustrations can be found in Sanfilippo et al., 1973, pl.1, figs.11-12.

## Dorcadospyris alata (Riedel)

*Brachiospyris alata* Riedel, 1959, p.293, pl.1, figs.11-12

*Dorcadospyris alata* (Riedel), Riedel and Sanfilippo, 1970, p.523, pl.14, fig.5

#### DESCRIPTION

Shell thick-walled, nut-shaped, tuberculate, with slight sagittal stricture externally and subcircular to circular pores irregularly arranged and separated by wide intervening bars. Two feet, circular in section, widely divergent, proximally at 180° or sometimes more, subsequently curved downward to a greater or lesser extent, in occasional

3, x 130



x 215

specimens approximately semicircular. The outer edges of the feet of most specimens bear short conical spinules. This species is distinguished from all other members of the genus by the pronounced divergence of the feet and the tendency to the development of accessory spinules on the feet (Riedel, 1959).

#### DIMENSIONS

Length of shell 50-68  $\mu$ m; of feet 285-930  $\mu$ m; of accessory spinules 3-13  $\mu$ m; breadth of shell 55-78  $\mu$ m. The maximum width, across the semicircularly curved feet, is 565-775  $\mu$ m (Riedel, 1959; Sanfilippo et al., 1985).

#### DISTINGUISHING CHARACTERS

Shell small and thick-walled, with two very widely divergent feet bearing short thorns (Riedel and Sanfilippo, 1978a).

See also Dorcadospyris dentata herein.

#### VARIABILITY

The angle between the proximal parts of the widely divergent feet is frequently slightly more than 180°. Thorns on the feet are variably developed (Sanfilippo et al., 1985).

#### DISTRIBUTION

A middle Miocene species. There are no noticeable morphologic differences in various parts of its geographic range, which extends throughout the low latitudes, but not to latitudes higher than about 30° except in the Mediterranean region (absent at DSDP Sites 173, 206, 281, 338) (Sanfilippo et al., 1985).

The evolutionary transition of this species from *Dorcadospyris dentata* defines the base of the *Dorcadospyris alata* Zone and its morphotypic last appearance is approximately synchronous with the upper limit of the same zone.

#### PHYLOGENY

See Dorcadospyris dentata.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.2D, fig.l; Riedel and Sanfilippo, 1978a, pl.5, fig.2; Goll, 1972, pl.4, figs.1-3, pl.41, figs.1-3.

## Dorcadospyris ateuchus (Ehrenberg)

- *Ceratospyris ateuchus* Ehrenberg 1873, p.218; 1875, pl.21, fig.4D
- *Cantharospyris ateuchus* (Ehrenberg), Haeckel, 1887, p.1051; Riedel, 1959, p.294, pl.22, figs.3-4
- *Dorcadospyris ateuchus* (Ehrenberg), Riedel and Sanfilippo, 1970, p.523, pl.15, fig.4
- *Dorcadospyris*(?) or *Petalospyris*(?) *ateuchus* (Ehrenberg), Petrushevskaya and Kozlova, 1972, p.532

#### DESCRIPTION

Shell nut-shaped, tuberculate, thick-walled, with indistinct sagittal







x 215

stricture and with subcircular to circular pores without regular arrangement. Two primary feet robust, circular in section, usually tending to be straight, though in some specimens curved, with convexity outward. Secondary feet not present in all specimens, one to four in number, much smaller than the primary feet. In some specimens a small amount of irregular lamellar meshwork is developed in place of the secondary feet. In many specimens a small apical horn is present. The one specimen that could be observed from the base was found to have three large and six small collar pores, similar to those of *Tristylospyris triceros*, and the primary spines correspond in position with the bars that Bütschli (1882) designated as *e* in his figure of the collar structures of *Petalospyris argiscus* Ehrenberg (Riedel, 1959).

#### DIMENSIONS

Based on 30 specimens. Length of shell 63-98  $\mu$ m; of primary feet 190-720  $\mu$ m; of secondary feet 20-188  $\mu$ m. Breadth of shell 78-120  $\mu$ m (Riedel, 1959).

#### DISTINGUISHING CHARACTERS AND PHYLOGENY

Two primary feet robust, circular in section, tending to be straight and divergent. In some specimens there are one to four small secondary feet, sometimes replaced by irregular meshwork (Riedel and Sanfilippo, 1978a).

*Dorcadospyris ateuchus* differs from its ancestor *Tristylospyris triceros* by the number of primary feet being reduced from three to two, and from its descendant *Dorcadospyris praeforcipata* Moore (1971, p.738, pl.9, figs.4-7) by the feet being straight rather than semicircularly curved, and in the apical horn being less well developed (Sanfilippo et al., 1985).

#### VARIABILITY

The nut-shaped lattice-shell bears two strong, obliquely downwardly directed primary feet, which are straight or slightly reflexed, and shorter, variably developed secondary feet which are cylindroconical or lamellar. Apical horn weakly developed or absent (Sanfilippo et al., 1985).

#### DISTRIBUTION

This species is common in assemblages of late Oligocene to early early Miocene age from low and middle latitudes of all oceans. The evolutionary transition of this species from *Tristylospyris triceros* defines the base of the *Dorcadospyris ateuchus* Zone. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Stichocorys wolffii* Zone.

#### REMARKS

Additional illustrations can be found in Moore, 1971, pl.8, figs.1-2; Ling, 1975, pl.5, figs.3-6.

Holdsworth (1975) noted a number of specimens, n. aff. *ateuchus*, "possessing a third, weak foot of circular cross-section and/or lacking the symmetry of *D. ateuchus*."

### *Dorcadospyris dentata* Haeckel

*Dorcadospyris dentata* Haeckel, 1887, p.1040, pl.85, fig.6; Riedel, 1957, p.79, pl.1, fig.4; Holdsworth, 1975, p.528

Dorcadospyris decussata Haeckel, 1887, p.1041, pl.85, fig.7

#### DESCRIPTION

Shell subspherical, smooth to tuberculate, with circular or subcircular pores separated by thick intervening bars, bearing a smooth, cylindro-conical apical horn, which is as long to four times as long as shell. Two basal-lateral feet thick, subcylindrical, curved, almost semicircular or sometimes somewhat S-shaped, departing from the shell approximately at right angles, with distal ends approaching, crossing, or fused with one another. Convex side of each foot having a series of usually 4-10 simple conical spines, which vary considerably in their state of development (Riedel, 1957).

#### DIMENSIONS

Length of apical horn usually 70-230  $\mu m,$  of shell 60-75  $\mu m,$  of feet (straight-line distance from

x 130





proximal to distal end) 250-450  $\mu m$  , of spines on feet 5-125  $\mu m$  . Breadth of shell 80-95  $\mu m$  (Riedel, 1957)

#### DISTINGUISHING CHARACTERS AND PHYLOGENY

Long, stout conical horn. Feet also stout, curved with convexity outward, and bearing thorns on the outer edge (Riedel and Sanfi1ippo, 1978a).

There is a clear evolutionary lineage from *Dorcadospyris forcipata* to *D. alata*, with *D. dentata* as the intermediate form, but the lineage includes a wide range of variation. Through the entire range of these species, the feet vary from semicircular to lyre-shaped (except in the latest part of the lineage, where the lyre-shaped form disappears). In the early part of the lineage there are no thorns on the outer sides of the feet, and these thorns become more prevalent and better developed as time progresses, though toward the end of the lineage they become smaller but persist on almost all specimens. In this present concept of the phylogeny, *Dorcadospyris simplex* Riedel (1959, p.293, pl.1, fig.10) becomes merged with *D. forcipata*. The portion of the lineage before the majority of specimens have thorns on the feet is referred to *D. forcipata*, the middle part of the lineage is *D. dentata*, and the terminal part, when the majority of forms have lost the apical horn and the lyre shape of the feet, is *D. alata* (Sanfilippo et al., 1985).

#### VARIABILITY

The general shape of the feet varies from semicircular to distally reflexed (in the form of a lyre). Thorns on the outer side of the feet are short in early specimens, long in late specimens. The horn is usually long and robust, but occasionally less developed (Sanfilippo et al., 1985).

#### DISTRIBUTION

This species is more common than *Dorcadospyris alata*, and has a similar geographic distribution, but in late early Miocene assemblages. Its morphotypic first appearance lies within the *Stichocorys wolffii* Zone. Its evolutionary transition to *Dorcadospyris alata* defines the base of the *Dorcadospyris alata* Zone.

#### REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.2D, figs.2-3.

Holdsworth (1975) records several morphotypes of this species and of *D. alata*.

## *Dorcadospyris forcipata* (Haeckel)

- *Dipodospyris forcipata* Haeckel, 1887, p.1037, pl.85, fig.1
- *Dipodospyris forcipata* Haeckel, Riedel, 1957, p.79, pl.1, fig.3
- *Dorcadospyris forcipata* (Haeckel), Riedel and Sanfilippo, 1970, p.523, pl.15, fig.7

#### DESCRIPTION

Shell subspherical to nut-shaped, tuberculate, with circular to subcircular pores separated by thick intervening bars. Horn thick, cylindrical, tapering to a point, approximately as long to 3 times as long as shell. Feet long, thick, cylindrical, almost semicircular or sometimes slightly recurved distally, with their convergent ends often separated, sometimes crossed (Riedel, 1957).

#### DIMENSIONS

Length of apical horn usually 100-200  $\mu$ m, of shell 75-85  $\mu$ m, of feet (straight-line distance from origin to tip) 230-350  $\mu$ m. Breadth of shell 95-115  $\mu$ m (Riedel, 1957).

Breadth of lattice-shell 70-115  $\mu$ m; length of feet 230-620  $\mu$ m (Sanfilippo et al., 1985).







x 215

#### DISTINGUISHING CHARACTERS

*Dorcadospyris forcipata* similar to *D. praeforcipata*, but without secondary feet, often seen on the latter form only as a ragged edge on the basal ring in poorly preserved specimens. Similar also to *D. simplex*, but with a strong apical horn and legs that often recurve distally (Moore, pers. comm., 1992).

*Dorcadospyris forcipata* differs from *D. dentata* and *D. alata* in lacking marginal spines on the feet, and from *D. praeforcipata* Moore (1971, p.738, pl.9, figs.4-7) in lacking secondary feet (Sanfilippo et al., 1985).

#### VARIABILITY

This broadly defined species is characterized by two strong, curved primary feet and no secondary feet. A robust, cylindro-conical horn is usually present, but may be weakly developed or absent. The feet are commonly reflexed (lyre-shaped), but may also be simply semicircular (Sanfilippo et al., 1985).

#### DISTRIBUTION

This species is widely distributed in early Miocene samples in low and middle latitudes of all oceans. Its morphotypic first appearance lies within the *Dorcadospyris ateuchus* Zone and its morphotypic last appearance is approximately synchronous with the base of the *Dorcadospyris alata* Zone.

#### PHYLOGENY

This species apparently evolved from *D. ateuchus*, and to *D. dentata*.

#### REMARKS

Additional illustrations can be found in Riedel, 1959, pl.1, figs.9-10; Riedel and Sanfilippo, 1971, pl.2C, figs.20-23, pl.3A, fig.8.

Holdsworth (1975) uses "*D. forcipata* Group" for this species, *D. simplex, D. praeforcipata* and intermediate forms.

# *Dorcadospyris papilio* (Riedel)

- *Hexaspyris papilio* Riedel, 1959, p.294, pl.2, figs.1-2
- *Dorcadospyris papilio* (Riedel), Riedel and Sanfilippo, 1970, p.523, pl.15, fig.5

#### DESCRIPTION

Shell nut-shaped, tuberculate, thick-walled, with no sagittal stricture externally and with subcircular to circular pores without regular arrangement. Two primary feet more strongly developed than the others, circular in section, initially divergent at approximately 180° or more, then curved semicircularly and thus convergent terminally. Secondary feet three to eight in number (often four), lamellar or subcylindrical, varying in form and disposition. A stout, conical apical horn is present in most specimens. This species is distinguished from all others of the genus by the two primary feet, which are extremely divergent (Riedel, 1959).

#### DIMENSIONS

Based on 25 specimens. Length of apical horn 65-245  $\mu$ m; of shell 63-88  $\mu$ m; of primary feet 260-880  $\mu$ m; of secondary feet 25-34  $\mu$ m. Breadth of shell 33-100  $\mu$ m (Riedel, 1959).









Lattice shell 80-100  $\mu m$  broad; primary feet 250-900  $\mu m$  long (Sanfilippo et al., 1985).

#### DISTINGUISHING CHARACTERS

*Dorcadospyris papilio* similar to *D. riedeli* (Moore, 1971, p.739, pl.9, figs.1-3), but with only one pair of primary feet. Similar also to *D. pseudopapilio*, but with consistently widely divergent primary feet, more than one pair of simple (non-branching) secondary feet, and with no indication of irregular, fine meshwork attached to the secondary feet (Moore, pers. comm., 1992)

At many of its occurrences, this species is accompanied by *Dorcadospyris riedeli* Moore (1971, p.739, pl.9, figs.1-3), which has four, rather than two, highly arching primary feet (Sanfilippo et al., 1985).

#### VARIABILITY

A considerable variety of morphotypes are admitted into this species, which is characterized by the two strong feet initially diverging at 180° or more, thus arching high before curving downward. The small lattice-shell bears also a small to large, conical apical spine, and usually 3-8 secondary feet, which vary from small and subcylindrical to large and lamellar. In some late specimens the lamellar secondary feet are only two in number, distally bifurcate (sometimes doubly) (Sanfilippo et al., 1985).

#### DISTRIBUTION

*Dorcadospyris papilio* has so far been found only in latest Oligocene and earliest Miocene sediments from low latitudes of the Pacific and Indian Oceans, and in the Caribbean region. Its morphotypic first appearance lies within the *Dorcadospyris ateuchus* Zone and its morphotypic last appearance lies within the *Lychnocanoma elongata* Zone.

#### PHYLOGENY

During the stratigraphic range of this species (latest Oligocene to earliest Miocene) there are many spectacular species of *Dorcadospyris*, the inter-relationships of which are not yet worked out.

#### REMARKS

Additional illustrations can be found in Moore, 1971, pl.8, figs.6-7.

### *Dorcadospyris pseudopapilio* Moore

*Dorcadospyris pseudopapilio* Moore, 1971, p.738, pl.6, figs.7-8

#### DESCRIPTION

Shell nut-shaped, tuberculate, thick-walled with a slight external indication of a sagittal stricture. A conical apical horn is present in most specimens. Two primary feet, circular in section and divergent at approximately 180°. These feet curve semicircularly and in some specimens cross or join. Two secondary feet, tabular in section, located at joint of the sagittal and basal rings. Along the lateral edges of these secondary feet, remnants of an irregular lamellar meshwork can usually be detected. This species is distinguished from Dorcadospyris papilio by the difference in their secondary feet (Moore, 1971).



x 130



x 215

#### DIMENSIONS

Based on 30 specimens. Length of apical horn 19-134  $\mu$ m; of shell 56-95  $\mu$ m; of primary feet 416-1002  $\mu$ m; of secondary feet 19-77  $\mu$ m. Breadth of shell 19-117  $\mu$ m (Moore, 1971).

#### DISTINGUISHING CHARACTERS

*D. pseudopapilio* differs from all other species of *Dorcadospyris* by the two lamellar, distinctively laterally fringed secondary feet. This fringe has been described as resembling the irregular remnants of a latticed meshwork, but it is more reminiscent of the form of the margin of some lichens (Sanfilippo et al., 1985).

#### VARIABILITY

The nut-shaped lattice-shell usually bears a well developed apical horn, but this is absent in some specimens. The two strong primary feet diverge initially at 180° or slightly more or less, curve semicircularly, often cross and occasionally join. Secondary feet are only two in number, laterally fringed (Sanfilippo et al., 1985).

#### DISTRIBUTION

Probably because sediments from its short stratigraphic range have seldom been encountered, this species has been found only in the Oligocene of the tropical Pacific and the Caribbean. Its morphotypic first and last appearances both lie within the *Theocyrtis tuberosa* Zone.

#### PHYLOGENY

This short-ranging species (middle early Oligocene) originated at the very beginning of the genus *Dorcadospyris* - some specimens transitional from *Tristylospyris triceros* to *Dorcadospyris ateuchus* have the secondary feet lamellar, fringed laterally.

#### REMARKS

Additional illustrations can be found in Dinkelman, 1973, pl.4, figs.2-3.

The consistent and unique nature of the secondary feet distinguish this species. Although the primary feet are usually strongly divergent (equal to or greater than 180°) as in *Dorcadospyris papilio*, some specimens have primary feet that diverge at an angle somewhat less than 180° (Moore, 1971).