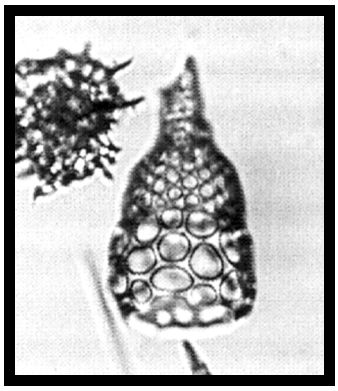
Lamprocyrtis heteroporos (Hays)



Lamprocyclas heteroporos Hays, 1965, p.179, pl.3, fig.1; Kling, 1971, p.1088, pl.1, fig.1

Lamprocyclas heteroporos ? Hays, 1970, p.214, pl.1, fig.3

Lamprocyrtis heteroporos (Hays), Kling, 1973, p.639, pl.5, figs.19-21, pl.15, fig.6

DESCRIPTION

Shell rough, campanulate, with indistinct collar stricture but distinct lumbar stricture; relative length of three joints 2.5:5:7, although in some specimens the thorax and abdomen are nearly equal. Cephalis [three-lobed,] hemispherical, pores circular to subcircular with diameter about equal to bar width. Cephalis bears a long three-bladed apical horn, as long as, to three times as long as, cephalis. Thorax campanulate, with pores similar in size and shape to those of cephalis, arranged in irregular longitudinal rows, 5-7 pores per row; pores increase in size distally. Abdomen cylindrical to slightly conical with maximum diameter just above mouth; pores large, irregular in size and shape, separated by thick bars; abdominal pores 2-3 times the size of thoracic pores. Aperture slightly constricted, 3-5 poorly developed short terminal teeth extend downward from a thick peristomal ring (Hays, 1965).

DIMENSIONS

Length of apical horn 22-60 µm, of cephalis 15-25 µm, of thorax 48-65 µm, of abdomen 55-70 µm. Maximum width of shell 88-100 µm, diameter of thoracic pores 4-9 µm, usually about 6, of abdominal pores 10-22 µm (Antarctic; Hays, 1965).

Length of apical horn 15-70 µm, of cephalis 21-35 µm, of thorax 41-82 µm, of abdomen 50-110 µm. Width of cephalis 26-44 µm, of abdomen 88-120 µm. Diameter of pores, thorax 3-12 µm, usually 6 µm, abdomen 3-50 µm, usually 24 µm (North Pacific; Hays, 1970).

DISTINGUISHING CHARACTERS

L. heteroporos is easily distinguished from other members of the genus by its cylindrical abdomen and the contrast between the large pores of the abdomen and the smaller pores of the thorax (Hays, 1965).

DISTRIBUTION

This species is essentially absent from tropical sediments. In middle latitudes its morphotypic first appearance lies within the *Sphaeropyle langii* Zone and its morphotypic last appearance lies within the *Eucyrtidium matuyamai* Zone.

PHYLOGENY

The genus *Lamprocyrtis* was erected by Kling (1973) to accommodate the lineage from *L. heteroporos* to *L. nigriniae*. The lineage initially includes three-segmented forms, but later forms are only two segmented. Members of the genus usually have an open, indistinctly three-lobed cephalis, which tends to be cylindrical. The cephalis bears one stout, three-bladed apical horn and commonly one or more accessory spines. Pores of the post-cephalic segment(s) usually increase in size distally, earlier species displaying a distinctive irregular row of axially to inwardly directed teeth that sometimes occupy a weakly developed peristome. Teeth occasionally occur outside the terminal row, but do not constitute a distinct second row as in *Lamprocyclas* Haeckel, 1881 (modified from Kling, 1973).

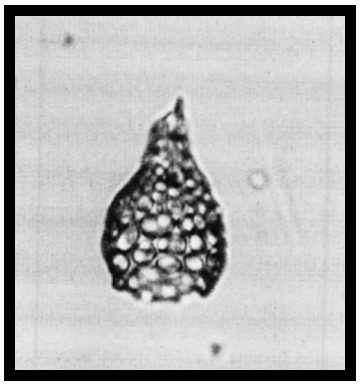
According to Kling (1973) *L. heteroporos* is the ancestor of *Lamprocyrtis neoheteroporos*, which in turn evolved into *L. nigriniae*; *Lamprocyrtis(?) hannai* (Campbell and Clark) is a likely ancestor of *L. heteroporos*. However, Caulet (1986, p.850, pl.3, figs.13-16) has described, from the lower part of the *Spongaster pentas* Zone, a morphotype, *Lamprocyrtis daniellae*, which is similar to *L. nigriniae*. He suggests that *L. daniellae* may be the ancestor of *L. nigriniae* and that the *L. heteroporos* -> *L. neoheteroporos* lineage may need to be revised.

Morphotypes similar to *Lamprocyrtis nigriniae* were found in samples from the *Spongaster pentas* Zone in DSDP Sites 77B, 157, 173 and 494. These forms appear to be closely related to *L. hannai* (Campbell and Clark) (Kling, 1973, p.638, pl.5, figs.12-14, pl.12, figs.10-14), and are below the earliest occurrence of *L. neoheteroporos* (Sanfilippo et al., 1985).

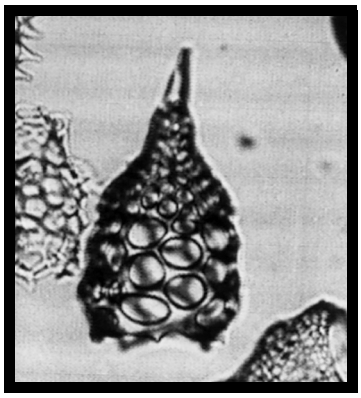
REMARKS

The individuals of this species from the North Pacific resemble in nearly all aspects the Antarctic individuals. They differ only in being on average larger than the Antarctic forms and some have a lateral oblique spine rising from the cephalis (Hays, 1970).

Lamprocyrtis neoheteroporos Kling



Middle-Latitude Form



Low-Latitude Form

Lamprocyrtis neoheteroporos Kling, 1973, p.639, pl.5, figs.17-18, pl.15, figs.4-5

DESCRIPTION

Two segmented forms with cephalis [three-lobed,] hemispherical to cylindrical, commonly open; with a stout three-bladed apical horn and usually one or more accessory spines; with circular to elliptical, irregularly arranged pores. Collar stricture indistinct. Thorax proximally conical, distally cylindrical to slightly inflated; circular to elliptical or irregular pores, longitudinally aligned, increasing in size distally, becoming two or more times as large along a horizontal discontinuity as in *L. heteroporos*. Smaller pores may again appear near mouth. Although early specimens show a slight, gentle indentation of the wall at this discontinuity, there is no internal stricture or septal ring separating two segments. Mouth, sometimes slightly constricted, surrounded by irregular row of small teeth; a weak peristome seldom developed. Later specimens become smaller and more inflated (Kling, 1973).

DIMENSIONS

Based on 15 specimens. Maximum width 74-90 μm, length from top of cephalis 100-130 μm, proximal pore diameter 2-14 μm, (average near upper value), distal pore diameter 6-28 μm (average near upper value) (Kling, 1973).

DISTINGUISHING CHARACTERS

The pores in the proximal part of the postcephalic shell are small, and distally they are two to three times as large, the change occurring abruptly as at an intersegmental boundary, which, however, is not marked by an internal stricture (Riedel and Sanfilippo, 1978a).

This species is distinguished from *L. heteroporos* by the absence of a lumbar constriction with an internal septal ring. It differs from *L. nigriniae* in having a transverse discontinuity across which the pore size differs by a factor of two or more (Sanfilippo et al., 1985).

VARIABILITY

The shell is two-segmented, but shows evidence of its three-segmented ancestor by an abrupt increase in pore size (by a factor of two or more) between the upper and lower parts of the present thorax. The species varies from a compact, small (100 µm in length) form with heavy bars between pores, to a larger form (140 µm in length) with more open lattice and lighter bars (Sanfilippo et al., 1985).

DISTRIBUTION

L. neoheteroporos occurs in late Pliocene early Quaternary assemblages in latitudes lower than 40°, but is rare in tropical sediments. Its morphotypic first appearance lies within the *Pterocanium prismatium* Zone and its morphotypic last appearance lies within the *Anthocyrtidium angulare* Zone in low-latitude sediments. In middle latitudes its morphotypic first appearance lies within the *Eucyrtidium matuyamai* Zone and its morphotypic last appearance lies within the *Stylatractus universus* Zone.

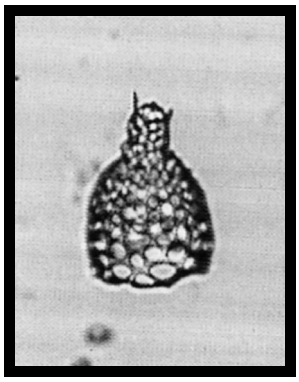
PHYLOGENY

L. neoheteroporos arose from *L. heteroporos*, and evolved into *L. nigriniae*. See also discussion under Phylogeny of *L. heteroporos*.

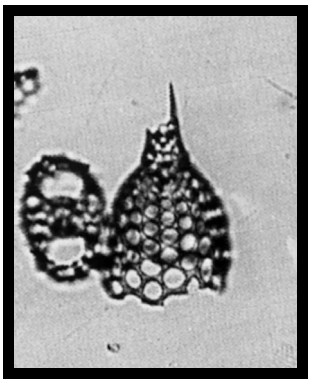
REMARKS

Additional illustrations can be found in Goll, 1980, pl.3, fig.11.

Lamprocyrtis nigriniae (Caulet)



Middle-Latitude Form



Low-Latitude Form

Conarachnium ? sp. Nigrini, 1968, p.56, pl.1, fig.5a (*partim*.)

?*Conarachnium*? sp. Nigrini, 1968, p.56, pl.1, fig.5b (*partim*.)

Conarachnium nigriniae Caulet, 1971, p.3, pl.3, figs.1-4, pl.4, figs.1-4

Lamprocyrtis haysi Kling, 1973, p.639, pl.5, figs.15-16, pl.15, figs.1-3

Lamprocyrtis nigriniae (Caulet), Kling, 1977, p.217, pl.1, fig.17

DESCRIPTION

Two-segmented forms with hemispherical to cylindrical [three-lobed] cephalis, commonly open, with irregularly arranged circular to elliptical pores and a three-bladed apical spine and usually one or more accessory spines. Collar stricture indistinct. Thorax inflated conical, thin-walled, smooth, with subcircular (rarely elliptical to irregular) pores generally aligned in longitudinal and transverse rows (rarely irregularly arranged) and gradually increasing in size distally. Thorax terminates, sometimes slightly constricted, with an irregular row of small teeth; a weak peristome is seldom developed (Kling, 1973).

See also Nigrini (1968) and Caulet (1971).

DIMENSIONS

Maximum width 80-90 µm; length from top of cephalis 100-150 µm; thoracic pores 2-20 µm (Kling, 1973).

The thoracic breadth given by both Nigrini (1968) and Caulet (1971) is greater than that found by Kling for North Pacific specimens. For this reason Kling only tentatively included the specimen figured by Nigrini (1968) on pl.1, fig.5b.

DISTINGUISHING CHARACTERS

A small form with only two segments, the pores of the second increasing in size gradually from collar stricture to distal margin. Distal margin has a differentiated peristome. There is no abrupt change in size between distal and proximal thoracic pores as in its ancestor *L. neoheteroporos* (Riedel and Sanfilippo, 1978a).

L. nigriniae is distinguished from *L. neoheteroporos* by the pores increasing regularly in size, rather than abruptly across a circumferential discontinuity. It differs from co-occurring *Anthocyrtidium* spp. in having a thicker shell with pore size increasing distally (Sanfilippo et al., 1985).

VARIABILITY

In this two-segmented pterocorythid, the pore size increases distally in a regular fashion. Like its ancestor, *L. neoheteroporos*, *L. nigriniae* varies from small, compact, heavy-shelled forms (100 μm in length) to longer (up to 160 μm), more broadly flared, open latticed forms with lighter bars. The latter variety is often broken before the termination, whereas the former usually terminates in a slightly constricted, weak peristome. Both extremes co-occur in low-latitude sites, but at DSDP Sites 173 and 310 only the smaller, more compact form occurs (Sanfilippo et al., 1985).

DISTRIBUTION

The species is not found in latitudes higher than 45°. It is relatively rare in tropical open ocean sediments, but more abundant in middle latitudes in areas of upwelling. *L. nigriniae* is restricted to the middle and late Quaternary. In low latitudes its morphotypic first appearance lies within the *Anthocyrtidium angulare* Zone. In middle latitudes its morphotypic first appearance lies within the *Eucyrtidium matuyamai* Zone. It is extant.

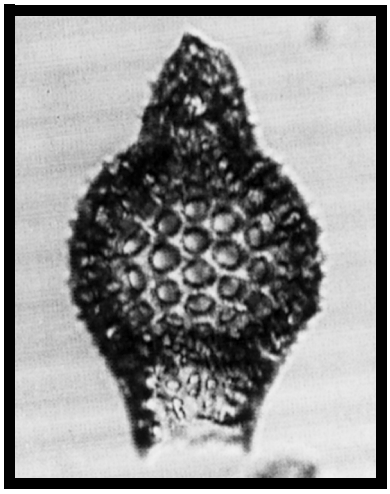
PHYLOGENY

L. nigriniae is an extant species that evolved from *L. neoheteroporos*. See also discussion under Phylogeny of *L. heteroporos*.

REMARKS

Additional illustrations can be found in Goll, 1980, pl.3, fig.10.

Lamptonium fabaeforme chaunothorax Riedel and Sanfilippo



Lamptonium(?) fabaeforme(?) chaunothorax Riedel and Sanfilippo, 1970, p.524, pl.5, figs.8-9

DESCRIPTION

Similar to the nominate subspecies, but with larger thoracic pores (Riedel and Sanfilippo, 1970) See Description of *L. fabaeforme fabaeforme* herein.

DIMENSIONS

Length excluding horn 195-285 µm, of cephalothorax 160-235 µm. Maximum breadth 120-175 µm.

DISTINGUISHING CHARACTERS

L. f. chaunothorax is distinguished from its ancestor *L. f. fabaeforme* by the larger thoracic pores, from its descendant *L. f. constrictum* by not having a distinct constriction in the upper part of the thorax, and from *L. sanfilippoae* by the horn not being covered by a massive layer of rough shell material (Sanfilippo et al., 1985).

VARIABILITY

The spherical cephalis, enclosed by the thick wall continuing upward from the thorax, bears a conical to bladed horn of variable length. The base of the horn also is sometimes obscured by this thickened wall. Thoracic pores are large, less than eleven pores (often as few as eight) around half the circumference, irregular in size, with small thorns projecting inward from the margin. Shell wall thick, and roughened by thorns. The subcylindrical to tapering abdomen is short, with irregularly scattered pores, distally hyaline, and with no differentiated margin (Sanfilippo et al., 1985).

DISTRIBUTION

This species is found in most low- to middle-latitude assemblages of early to middle middle Eocene age, and occurs sporadically. Its morphotypic first appearance lies within the *Bekoma bidartensis* Zone and its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

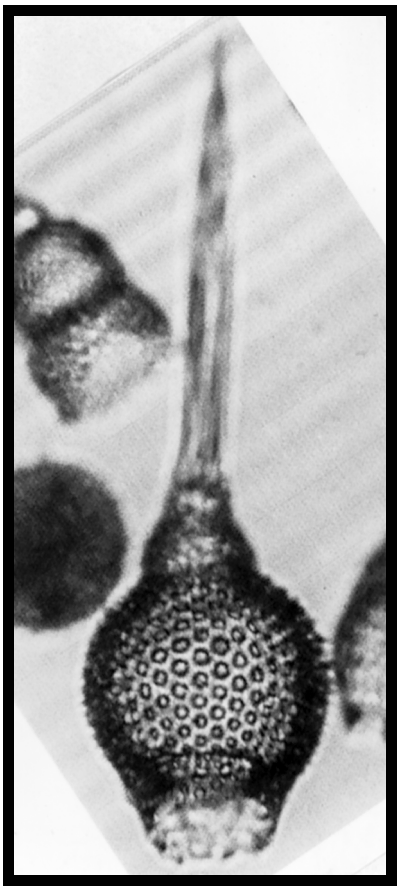
PHYLOGENY

L. f. chaunothorax is member of the lineage leading from *L. pennatum* to *L. f. constrictum*.

REMARKS

Additional illustrations can be found in Foreman, 1973, pl.6, figs.10-12.

Lamptonium fabaeforme constrictum Riedel and Sanfilippo



Lamptonium(?) fabaeforme(?) constrictum Riedel and Sanfilippo, 1970, p.523, pl.5, fig.7

DESCRIPTION

Generally similar to the nominate subspecies [see description herein], but differing in that at the base of the narrow part of the thorax is a constriction, which is, however, not accompanied by an internal septal ring. The horn is often long, and in some specimens, twisted spirally (Riedel and Sanfilippo, 1970).

DIMENSIONS

Length excluding horn 185-275 μm; of cephalothorax 160-235 μm. Maximum breadth 125-190 μm.

DISTINGUISHING CHARACTERS

L. f. constrictum is distinguished from other members of the lineage by its robust horn and the constricted upper part of the thorax, and from *L. sanfilippoae* by not being closed distally (Sanfilippo et al., 1985).

VARIABILITY

The cephalis is enclosed in the base of the very long (up to 210 μm), robust, bladed, sometimes twisted horn. The base of the narrow part of the thorax is constricted to a varying degree, but does not have an internal segmental division (Sanfilippo et al., 1985).

DISTRIBUTION

L. f. constrictum has been found in late early to middle Eocene assemblages from the Indian Ocean at DSDP Site 220, but not further south, at DSDP Sites 313 and 40 in the Pacific, and in the Gulf of Mexico,

but not in the open Atlantic Ocean. Its morphotypic first appearance is approximately synchronous with the lower limit of the *Phormocyrtis striata striata* Zone and its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

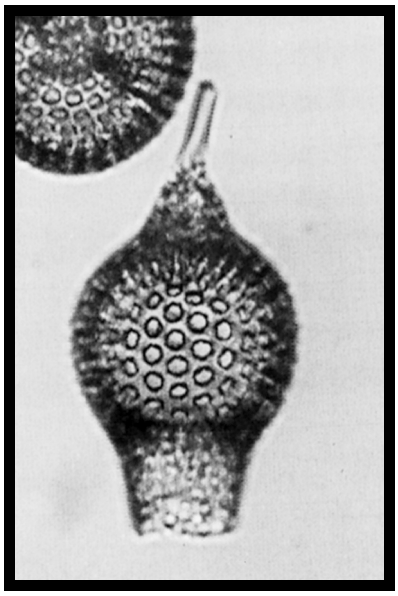
PHYLOGENY

L. f. constrictum terminates the lineage that began with *L. pennatum*.

REMARKS

Additional illustrations can be found in Foreman, 1973, pl.6, figs.13-14.

Lamptonium fabaeforme fabaeforme (Krasheninnikov)



[?] *Cyrtocalpis fabaeformis* Krasheninnikov, 1960, p.296, pl.3, fig.11

Lamptonium(?) fabaeforme fabaeforme (Krasheninnikov), Riedel and Sanfilippo, 1970, p.523, pl.5, fig.6; Foreman, 1973, p.436, pl.6, figs.6-9

DESCRIPTION

Cephalis spherical, surrounded by the thick wall continuing upward from the thorax, bearing a conical or bladed horn of variable length. Thorax inflated-pyriform, with rough or thorny surface, and with circular or subcircular pores that are largest in the midregion. Abdomen short, narrow, subcylindrical or tapering, with irregularly scattered pores and no differentiated termination (Foreman, 1973).

DIMENSIONS

Length excluding horn 150-285 µm; of cephalothorax 125-200 µm. Maximum breadth 100-170 µm.

DISTINGUISHING CHARACTERS

Thorax elongated, inflated pyriform without lateral spines. Abdomen much narrower than thorax, subcylindrical or tapering distally (Riedel and Sanfilippo, 1978a)

L. f. fabaeforme differs from its ancestor *L. pennatum* in lacking thoracic wings, and from *L. f. chaunothorax* in having smaller thoracic pores. *L. f. fabaeforme* has at least twelve pores across the half circumference of the thorax (Sanfilippo et al., 1985).

VARIABILITY

This three-segmented form has a spherical cephalis, enclosed in the thick wall continuing upward from the thorax, bearing a bladed or conical horn of variable length. In early forms the thorax is somewhat

smaller than in later ones, and nodose rather than thorny. The pores are circular to subcircular, largest in the mid-region, and frequently with an uneven margin. The subcylindrical to tapering abdomen has scattered, irregular pores and an undifferentiated margin (Sanfilippo et al., 1985).

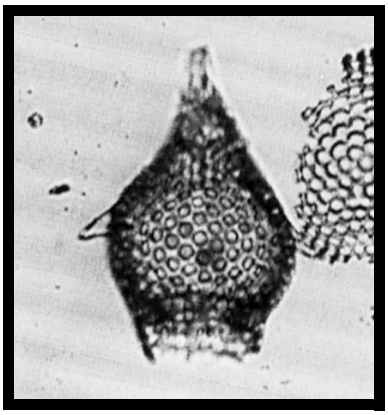
DISTRIBUTION

Lamptonium f. fabaeforme is found in early to early middle Eocene assemblages from 35°S to 35°N, except at DSDP Site 366 where the assemblages are sparse (other members of the genus occur there). It evolved from *Lamptonium pennatum* within the *Bekoma bidartensis* Zone. Its morphotypic last appearance lies within the *Dictyoprora mongolfieri* Zone.

PHYLOGENY

L. f. fabaeforme developed from *L. pennatum*, and gave rise to *L. f. chaunothorax*.

Lamptonium pennatum Foreman



Lamptonium pennatum Foreman, 1973, p.436, pl.6, figs.3-5, pl.11, fig.13

DESCRIPTION

Cephalis subhemispherical, with a few circular pores and pore-shaped depressions, and bearing a sturdy bladed horn. Collar stricture with six collar pores internally, not expressed externally, contour of cephalis merging with that of inflated thorax. Thoracic pores circular to subcircular, occasionally uneven or with prongs on their margin, generally regularly quincuncially arranged in longitudinal rows; surface roughened with pointed nodes. Three three-bladed wings extend outwards from the median thorax. Abdomen subcyclindrical, fragile, lamellar, with circular to elliptical pores; termination ragged (Foreman, 1973).

DIMENSIONS

Based on 20 specimens. Length of cephalis and thorax, excluding horn 125-150 µm; greatest width of thorax 100-140 µm, width of proximal abdomen 68-80 µm (Foreman, 1973).

Length excluding horn 140-215 µm; of cephalothorax 115-160 µm; maximum breadth 100-155 µm (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

L. pennatum differs from *L. f. fabaeforme* by the presence of wings, from *L.(?) colymbus* Foreman (1973) by possessing a third segment, being smaller in size, and having the wings more distally placed on the thorax (Sanfilippo et al., 1985).

VARIABILITY

The collar stricture is not expressed externally, so that the cephalis merges with the inflated thorax. The horn varies in degree of development, but is usually sturdy and bladed. The thoracic pores, generally in longitudinal rows, vary somewhat in size, as does the length

of the three-bladed wings originating from the median thorax. The thoracic surface is roughened by small thorns. The small abdomen is very fragile, with circular to elongate pores and a ragged termination. Very rare early forms have been observed to have a closed, inverted cap-like abdomen (Sanfilippo et al., 1985).

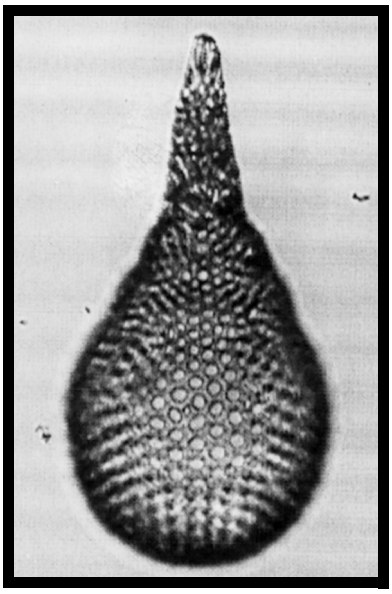
DISTRIBUTION

Lamptonium pennatum is found in Paleocene to earliest Eocene assemblages from the tropical Indian and Pacific Oceans, from the Caribbean and the Gulf of Mexico. Its morphotypic first appearance is below the oldest defined Paleocene zone, the *Bekoma campechensis* Zone. It evolved into *Lamptonium fabaeforme fabaeforme* within the *Bekoma bidartensis* Zone.

PHYLOGENY

L. pennatum is the precursor of *L. f. fabaeforme*. Its own ancestor is not known. However, intermediate forms have been observed in one Indian Ocean sample (DSDP 237-41-1) appearing to link *Sethochytris babylonis* (Clark and Campbell, 1942) to the *Lamptonium* lineage. The forms transitional to *Sethochytris babylonis* have a smaller thorax (length of cephalothorax 90-120 µm; maximum breadth 90-100 µm) than *Lamptonium pennatum* occurring in the same sample (length of cephalothorax 125-140 µm; maximum breadth 110-130 µm). The transitional forms show remnants of a very delicate third segment, and the three feet originating from the distal portion of the thorax in *Sethochytris babylonis* here extend outward from the median thorax (Sanfilippo et al., 1985).

Lamptonium sanfilippoae Foreman



Lamptonium sanfilippoae Foreman, 1973, p.436, pl.6, figs.15, 16, pl.11, figs.16-17

DESCRIPTION

Shell of two segments, pyriform, with collar stricture not expressed externally. Cephalis subhemispherical, with a massive layer of rough shell material apically from which extends a bladed horn frequently broken. Internally the collar stricture has five collar pores, the vertical spine rising so sharply that it does not divide the cervical pore. Thorax proximally with or without one or two slight constrictions, basally closed, and tending to be flattened. Circular to subcircular pores with or without prongs on their margin may be largest medianly at point of greatest expansion and distinctly smaller, less regularly arranged basally, or more regular in size, tending to longitudinal alignment; surface spiny (Foreman, 1973).

DIMENSIONS

Based on 15 specimens. Length overall, exclusive of horn, 210-325 µm; greatest width 130-205 µm (Foreman, 1973).

DISTINGUISHING CHARACTERS

Large pyriform test of two segments, closed distally. Cephalis enclosed in a rough layer of shell material continuing from the horn (Riedel and Sanfilippo, 1978a).

This species is distinguished from co-occurring members of the genus *Lamptonium* by being two-segmented, closed basally and possessing a bladed horn covered proximally by a porous layer of shell material (Sanfilippo et al., 1985).

VARIABILITY

This large, two-segmented pyriform species exhibits all its variation in the thorax. The thorax may have one or two constrictions proximally;

it is closed, and varies in shape from subspherical to terminally flattened. The thoracic pores are circular to subcircular, largest medially, with a tendency to longitudinal alignment (Sanfilippo et al., 1985).

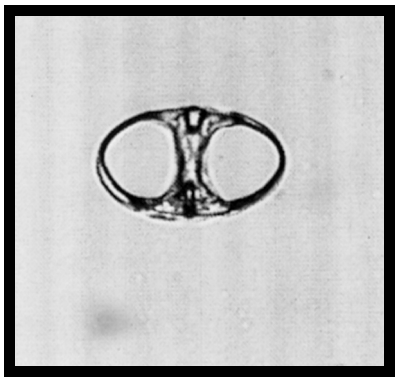
DISTRIBUTION

L. sanfilippoae occurs in early Eocene assemblages from the Gulf of Mexico and the tropical Pacific. Its morphotypic first appearance lies within the *Buryella clinata* Zone and its morphotypic last appearance lies within the *Phormocyrtis striata striata* Zone.

PHYLOGENY

L. sanfilippoae is obviously related to the lineage from *Lamptonium pennatum* to *L. fabaeforme constrictum*, but the details of the phylogeny are unknown. *L. sanfilippoae* left no descendants.

Liriospyris parkerae Riedel and Sanfilippo



Liriospyris parkerae Riedel and Sanfilippo, 1971, p.1590, pl.2C, fig.15, pl.5, fig.4

DESCRIPTION

Sagittal ring D-shaped, with a furrow on the anterior and posterior sides. Four collar pores, separated by the median and sternal (in the sense of Goll) bars and the primary lateral spines, are enclosed within the basal ring. The remainder of the skeleton is a simple longitudinally furrowed frontal ring, except that it is divided apically to join the upper part of the sagittal ring at two points. There is no apical spine, and the vertical spine is represented by a short thorn. At the base of the apical bar of the sagittal ring is a single small pore, near which can be distinguished two very small secondary lateral bars, and near the base of the vertical bar is a pair of small pores and near them a sternal bar (in the sense of Goll, 1968) (Riedel and Sanfilippo, 1971).

DIMENSIONS

Based on 25 specimens. Height of sagittal ring 50-70 µm, total width of skeleton 95-125 µm (Riedel and Sanfilippo, 1971).

DISTINGUISHING CHARACTERS

The lateral part of the shell consists of a simple longitudinally furrowed frontal ring, divided apically to join the upper part of the sagittal ring at two points (Riedel and Sanfilippo, 1978a).

The lack of pores on the narrow frontal ring distinguishes this species from the otherwise similar *Liriospyris stauropora*. The only other species with which it might be confused is the very much larger *Acrocubus octopylus* Haeckel (1887, p.993, pl.82, fig.9; Goll, 1972, p.961, pl.37, figs.1-3), which is commonly about 120 µm high at the sagittal ring and 250 µm wide, and has a pronouncedly knobby sagittal ring. In only one assemblage (DSDP 316-3-2) have we found some enigmatic specimens intermediate between *Liriospyris parkerae* and *Acrocubus octopylus*. Until a satisfactory taxonomic position for these intermediate forms can be

established, we exclude from *Liriospyris parkerae* any specimens larger than described in the "Variability" paragraph, or with knobby sagittal ring (Sanfilippo et al., 1985).

VARIABILITY

The skeleton of this spyrid, which consists essentially of two mutually perpendicular rings, shows little variability. Some early specimens are transitional to its ancestor (*L. stauropora*) in having a few small pores in the normally poreless, longitudinally furrowed frontal ring. The primary lateral bars are sometimes missing, or reduced to small remnants. Height of the skeleton at the sagittal ring is usually 60-70 µm, and its total width is usually 95-120 µm, but in two assemblages examined (from DSDP 79-5-1 and DSDP 369A-5-5) the height reached 75 µm and the width 130 µm (Sanfilippo et al., 1985).

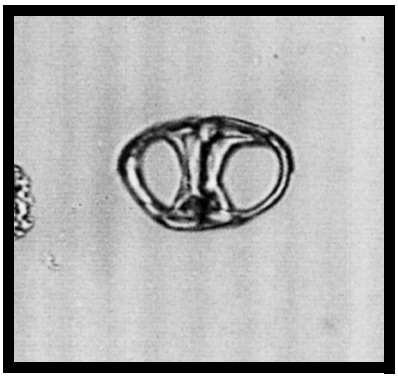
DISTRIBUTION

L. parkerae occurs in latest early to middle Miocene assemblages from the tropical zones of all major oceans, and almost as far north as Japan (DSDP Site 296). However, it apparently does not occur off northern California (DSDP Site 173). It evolved from *Liriospyris stauropora* within the *Calocycletta costata* Zone. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Diartus petterssoni* Zone.

PHYLOGENY

This species evolved from *L. stauropora* by loss of the pores on the frontal ring, and left no known descendants.

Liriospyris stauropora (Haeckel)



Trissocyclus stauroporus Haeckel, 1887, p.987. pl.83. fig.5

Liriospyris stauropora (Haeckel), Goll, 1968, p.1431, pl.175, figs.1-3, 7, text-fig.9; Riedel and Sanfilippo, 1971, p.1590-1591, pl.2C, figs.16-19

DESCRIPTION AND DIMENSIONS

Sagittal ring subpolygonal; 39 to 85 µm high; 31 to 74 µm thick; joined directly to apex of lattice shell. No frontal or axial spines; vertical spine very short, broad, projecting from approximate midpoint of sagittal ring. Some specimens have short knoblike apical spine; in other skeletons, apical spine is lacking. A median furrow extends from vertical spine to front-apex of sagittal ring; in some individuals, furrow present on front of sagittal ring. Other specimens have vertical median ridge on front of sagittal ring. Eight basal connector bars joined to basal ring.

Basal ring oval; 46 to 102 µm wide; 22 to 42 µm thick; encloses four basal pores. No basal or lattice spines. Lattice shell oval in front view; 62 to 170 µm wide; not constricted sagittally; restricted to narrow lateral band that does not extend below basal ring. Lattice bars narrow; subcircular in cross section; frame subcircular lattice pores 8 to 65 µm in diameter. Two lattice bars joined to each side of basal ring, and two to apex of sagittal ring. In some specimens, shallow depressions are at junctions of lattice bars or lattice bars and basal ring. Frontal and sternal pores; three pairs of sagittal-lattice pores; no vertical pore. Approximately nine-tenths of width of lattice shell is occupied by two pairs of sagittal-lattice pores adjacent to front and back of basal ring (Goll, 1968).

DISTINGUISHING CHARACTERS

The lateral part of the shell consists of a narrow, delicate ladderlike structure with a single row of pores (Riedel and Sanfilippo, 1978a).

The unnamed ancestor of *L. stauropora* has two pores (rather than one) across the width of the frontal ring throughout, and in particular where it joins the top of the sagittal ring. *L. stauropora* arises by reduction of the frontal ring to one pore in width. Another superficially similar

species with two pores in the frontal ring on either side of the top of the sagittal ring is *L. elevata* Goll (1968, p.1426-1427, pl.175, figs.4-5, 8-9, text-fig.9; 1972, pl.68, figs.3-4). That species occurs later than the termination of the *L. stauropora - L. parkerae* lineage, and its evolutionary relationships are not yet clear (Sanfilippo et al., 1985).

VARIABILITY

Although the frontal ring characteristically has a single row of pores throughout its length, in occasional specimens it has two pores across its width where it joins the basal ring. Primary lateral bars may be complete, or reduced to short remnants. Apart from these variations, the form is constant. Height of the skeleton at the sagittal ring is 60-75 μm and the total width is 90-115 μm (Sanfilippo et al., 1985).

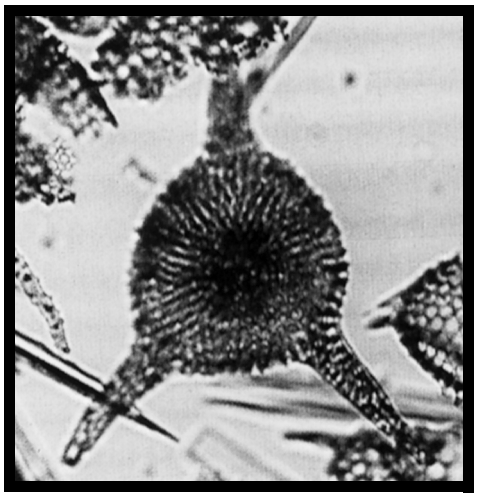
DISTRIBUTION

The distribution of this late early Miocene species is the same as that of *L. parkerae*. Its morphotypic first appearance lies within the *Stichocorys wolffii* Zone and it evolved into *Liriospyris parkerae* within the *Calocycletta costata* Zone.

PHYLOGENY

L. stauropora evolved from an unnamed ancestor by reduction of the frontal ring to one pore width, and into *L. parkerae* by eventual loss of the pores of the frontal ring.

Lithocyclia angusta (Riedel)



Trigonactura ? angusta Riedel, 1959, p.292, pl.1, fig.6

Lithocyclia angustum (Riedel), Riedel and Sanfilippo, 1970, p.522, pl.13, figs.1-2

DESCRIPTION

Phacoid cortical shell approximately three times as broad as the medullary shell (when the latter is distinct), with eight to eleven subcircular to circular pores on its radius. Cortical shell in some specimens filled with spongy meshwork. Three arms not strictly chambered, but rather subcylindrical spongy columns, broader at the base and tapered distally. In rare specimens a spongy patagium, its outline parallel to that of the cortical shell, connects the bases of the arms (Riedel, 1959).

DIMENSIONS

Based on 20 specimens. Diameter of cortical shell 108-145 µm; of medullary shell (shadowy outline seen through cortical shell) 35-50 µm. Length of arms 85-158 µm; median breadth 18-28 µm (Riedel, 1959).

Diameter of cortical shell 110-150 µm (to 185 µm in DSDP 78-24-1), width of arms medially 15-35 µm (usually 20-25 µm) (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

From the margin of the discoidal cortical shell arise three narrow spongy arms (forms with four arms being separated as *L. crux* Moore) (Riedel and Sanfilippo, 1978a).

L. angusta is distinguished from *L. crux* by having three spongy arms rather than four, and from *L. aristotelis* by the arms being narrower. When the arms are reduced to only spines, the species closely resembles *Periphaena tripyramis* (Haeckel, 1887), but that is an early to middle Eocene species with rather smaller pores on the cortical shell (Sanfilippo et al., 1985).

VARIABILITY

In early specimens the phacoid cortical shell is circular and the three spongy arms are of almost equal width throughout, while in late specimens the cortical shell tends to be slightly triangular and the arms are shorter, tapering, and merge into a solid terminal spine (reduced to only a spine in DSDP 78-24-1). The surface of the cortical shell is irregular, almost spongy, in some early specimens, but is a more regularly latticed lamella in late ones (Sanfilippo et al., 1985).

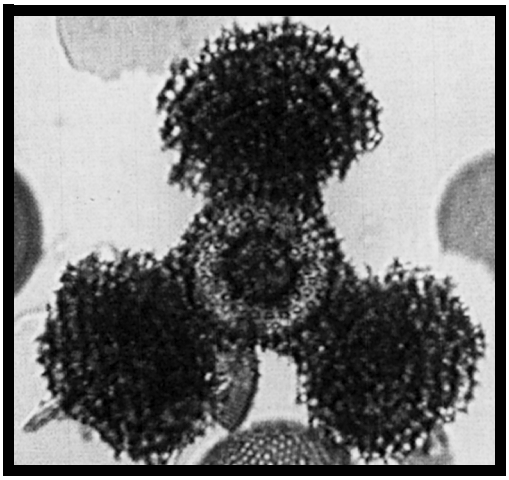
DISTRIBUTION

This species is found in practically all tropical assemblages of Oligocene age. The evolutionary transition of this species from the *Lithocyclia aristotelis* group defines the base of the *Theocyrtis tuberosa* Zone. Its morphotypic last appearance lies within the *Dorcadospyris ateuchus* Zone.

PHYLOGENY

This species developed from the *Lithocyclia aristotelis* group, and it (or *L. crux*) evolved into *Didymocyrtis prismatica*.

Lithocyclia aristotelis (Ehrenberg) group



Astromma aristotelis Ehrenberg, 1847b, p.55, fig.10

Lithocyclia aristotelis (Ehrenberg) group, Riedel and Sanfilippo, 1970, p.522, pl.13, figs.1-2

DESCRIPTION

This species-group name is used for a number of forms with skeletons similar to those of the *L. ocellus* group, but with separated spongy arms rather than a continuous spongy zone around the phacoid shell. In the group are included forms with three or four (or more?) arms, with or without terminal spines, and with or without a patagium (Riedel and Sanfilippo, 1970).

DIMENSIONS

See under Variability

DISTINGUISHING CHARACTERS

From the margin of the phacoid shell arise three or four wide spongy arms, with or without terminal spines (Riedel and Sanfilippo, 1978a).

Members of this group differ from their descendants, *Lithocyclia angusta* and *L. crux*, by the arms being generally wider, not tapering distally, and never exhibiting marked longitudinal structure. From co-occurring species of *Stephanastrum*, wherein the central structure to which the arms are attached has a diameter of only 55-70 μm. The *Lithocyclia aristotelis* group differs in having a larger cortical shell (Sanfilippo et al., 1985).

VARIABILITY

Under this name are grouped a great variety of forms with a distinct cortical shell enclosing a double medullary shell, and three or four arms with or without terminal spines and with or without a patagium. The cortical shell usually has a diameter of 90-120 μm (occasionally as small

as 75 μm), and the arms maintain the same breadth throughout their length or expand distally. The arms are sometimes irregularly spongy throughout, sometimes concentrically zoned in their proximal part or their entire length (Sanfilippo et al., 1985).

DISTRIBUTION

This species group is found in tropical assemblages of late middle Eocene to early Oligocene age. It has not been found at DSDP Site 283, near Tasmania. Its evolutionary transition from the *Lithocyclia ocellus* group is approximately synchronous with the lower limit of the *Podocyrtis goetheana* Zone. Its evolutionary transition to *Lithocyclia angusta* defines the base of the *Theocyrtis tuberosa* Zone.

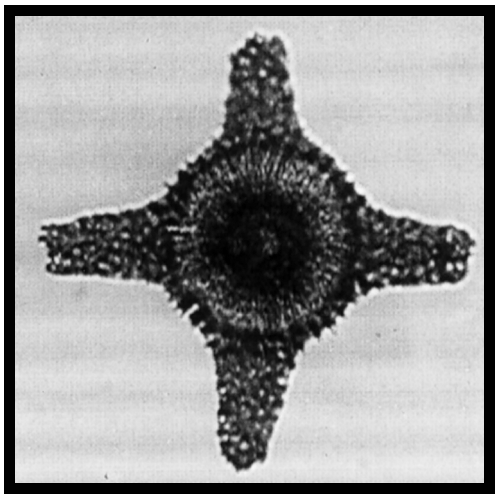
PHYLOGENY

The *L. ocellus* group evidently gave rise to the *Lithocyclia aristotelis* group, from which developed *L. angusta* and *L. crux*.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.3A, figs.2, 4-5.

Lithocyclia crux Moore



Lithocyclia crux Moore, 1971, p.737. pl.6, fig.4

DESCRIPTION

Phacoid cortical shell approximately two to three times as broad as medullary shell with subcircular to irregular pores. Cortical shell may be filled with spongy meshwork. Four arms, approximately perpendicular and in the same plane, are very irregularly pored to form spongy, subcylindrical columns. In rare specimens a spongy patagium is preserved. It connects the base of the arms and is formed parallel to the cortical shell. This species resembles *Lithocyclia angustum* (Riedel) in all respects except the number of arms (Moore, 1971).

DIMENSIONS

Based on 30 specimens. Diameter of cortical shell 113-132 µm; of medullary shell (shadowy outline seen through cortical shell) 37-66 µm; Length of arms 75-168 µm; median breadth 22-47 µm (Moore, 1971).

Diameter of cortical shell 125-150 µm, width of arms medially 20-30 µm (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

Four narrow spongy arms, approximately perpendicular to each other (Riedel and Sanfilippo, 1978a).

L. crux is distinguished from *L. angusta* by having four spongy arms rather than three, and from the *L. aristotelis* group by the arms being narrower (Sanfilippo et al., 1985).

VARIABILITY

This species varies in similar ways to *L. angusta*, but not to such a great extent. The meshwork of the cortical shell tends to be spongy in early specimens, and more regularly latticed in later ones. Arms vary in

width, but have not been observed to be reduced to spines (Sanfilippo et al., 1985).

DISTRIBUTION

This species is found in practically all tropical localities of early Oligocene to early late Oligocene age - the exceptions being attributable to its sparseness. Its morphotypic first appearance lies within the *Theocyrtis tuberosa* Zone and its morphotypic last occurrence is approximately synchronous with the base of the *Dorcadospyris ateuchus* Zone.

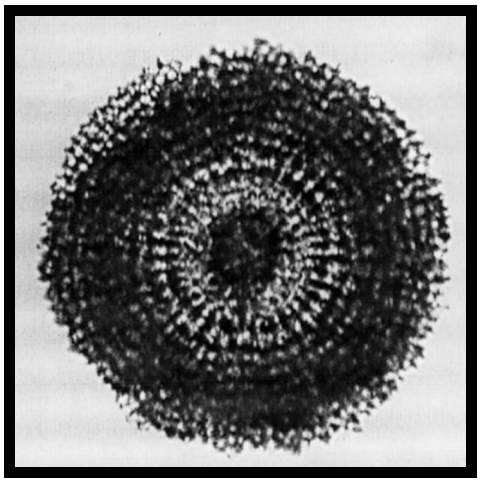
PHYLOGENY

This species developed from the *L. aristotelis* group, and it (or *L. angusta*) evolved into *Didymocyrtis prismatica*.

REMARKS

Additional illustrations can be found in Dinkelman, 1973, pl.5, fig.9; Johnson, 1974, pl.6, fig.5; Riedel and Sanfilippo, 1978a, pl.6, fig.7

Lithocyclia ocellus
Ehrenberg group



Lithocyclia ocellus Ehrenberg, 1854, pl.36, figs.30; 1873, p.240

Lithocyclia ocellus Ehrenberg, Riedel and Sanfilippo, 1970, p.522, pl.5, figs.1-2

DESCRIPTION

Medullary shell double. Phacoid cortical shell with circular to subcircular pores, 12 to 18 µm on a diameter, covered in some specimens by a thin spongy layer. Cortical shell surrounded by a continuous spongy zone, which, in late specimens especially, is usually concentrically zoned, the innermost zone commonly being the widest and most distinct. Spines of variable number (sometimes none), bladed, acute, originate within the spongy zone, or at the periphery of the cortical shell, or occasionally at the outer medullary shell (Riedel and Sanfilippo, 1970).

DIMENSIONS

Diameter of outer medullary shell 35-50 µm, of cortical shell 85-140 µm, of outer spongy zone 165-325 µm (Riedel and Sanfilippo, 1970).

DISTINGUISHING CHARACTERS

Surrounding the periphery of the phacoid cortical shell is a continuous spongy region that in late specimens is concentrically zoned and in very early specimens extends over the surface of the cortical shell. Marginal spines may or may not be present (Riedel and Sanfilippo, 1978a).

The *Lithocyclia aristotelis* group differs by the spongy girdle being interrupted to form arms, members of the genus *Periphaena* lack a spongy girdle, and *Stylocyclia dimidiata* Ehrenberg (1873, p.257; 1875, pl.29, fig.4) and related forms have two opposite spines that originate at the medullary shell, traverse the wide phacoid shell, and extend beyond the concentrically zoned girdle (Sanfilippo et al., 1985).

VARIABILITY

The only constant features of members of this species-group are the double medullary shell, phacoid cortical shell, and broad equatorial girdle of spongy material. Cortical shell has subcircular to circular pores, 12-18 on a diameter, and in some specimens is covered by a thin spongy layer. The equatorial flange is concentrically zoned in late specimens, the innermost zone being the widest. Many specimens have a variable number of bladed, acute spines which originate within the spongy zone or at the periphery of the cortical shell (Sanfilippo et al., 1985).

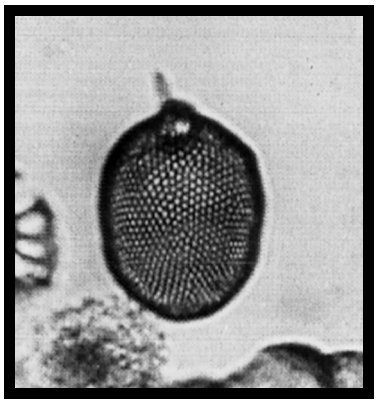
DISTRIBUTION

The *L. ocellus* group is common and widely distributed in sediments from late early Eocene through middle Eocene. Its morphotypic first appearance lies within the *Buryella clinata* Zone and its evolutionary transition to the *Lithocyclia aristotelis* group is approximately synchronous with the base of the *Podocyrtis goetheana* Zone.

PHYLOGENY

The origin of this earliest coccodiscid, which gave rise to the *L. ocellus* group, remains obscure.

Lithopera (Lithopera) bacca Ehrenberg



Lithopera bacca Ehrenberg, 1872a, p.314; 1872b, pl.8, fig.1; Nigrini, 1967, p.54, pl.6, fig.2 (with synonymy); Sanfilippo and Riedel, 1970, p.455, pl.1, fig.29

DESCRIPTION

Cephalis simple, spherical, thick-walled, surface rough with small subcircular pores; half to two-thirds of cephalis depressed into thorax. Apical horn cylindrical, needle-like, less than or equal to length of cephalis; apical spine free. Dorsal and primary lateral spines extend beyond collar structure. In the region of the collar structure they lie entirely within the thoracic cavity, but very often become incorporated distally into the thoracic wall and may even project beyond it to form small wings about a third of the way down the thorax. Rarely, one of these spines forks within the thoracic cavity.

Thorax rather thick-walled, rough, ellipsoidal to subspherical, closed distally. Thoracic pores small, circular to subcircular, sometimes hexagonally framed, arranged in transverse rows (Nigrini, 1967).

DIMENSIONS

Total length (excluding apical horn) 119-136 μm. Diameter of cephalis 18-27 μm. Length of thorax 100-128 μm; breadth 90-109 μm (Nigrini, 1967).

Total length 100-150 μm; maximum breadth 100-140 μm (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

Closed postcephalic segment smoothly ellipsoidal, with numerous circular pores very regularly arranged in diagonal intersecting rows (Riedel and Sanfilippo, 1978a).

This species differs from *L. neotera* by the smoothness of its shape and regularity of its pore pattern (Sanfilippo et al., 1985).

VARIABILITY

The cephalis is half-buried in a closed spherical to ellipsoidal thorax with numerous circular pores very regularly arranged in diagonal intersecting rows. Most specimens are perfectly smooth in outline, and the pore arrangement is so regular that a small change in focus produces a characteristic optical interference pattern. Some specimens have an irregularity in the shell wall, where the pore pattern is interrupted, but the major part of the shell is always regular (Sanfilippo et al., 1985).

DISTRIBUTION

L. bacca is found in all middle late Miocene to Quaternary assemblages from latitudes lower than 40°. Its evolutionary transition from *Lithopera neotera* lies within the *Diartus petterssoni* Zone. It is extant.

PHYLOGENY

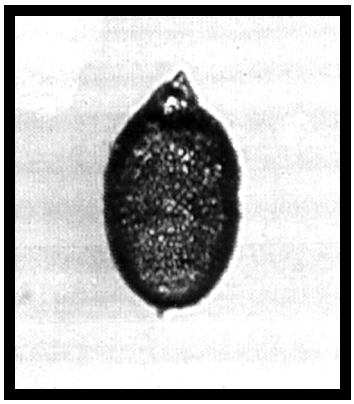
L. bacca is an extant species that evolved from *L. neotera*.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.1F, figs.11-13; 1978a, pl.6, fig.9.

For further taxonomic discussion, see Nigrini (1967) and Sanfilippo and Riedel (1970).

Lithopera (Lithopera) neotera Sanfilippo and Riedel



Lithopera (Lithopera) neotera Sanfilippo and Riedel, 1970, p.454, pl.1, figs.24-26, 28

DESCRIPTION

Subellipsoidal shell, of which the thorax forms the major part. Cephalis spherical, usually poreless, half or more of it sunken into the thorax, with a small apical horn. Collar structure generally not pronounced externally. From the base of the cephalis, primary lateral and dorsal spines extend in the thoracic wall or within the thoracic cavity to join the inner surface of the upper wall. Remainder of shell subellipsoidal with subregular pores not arranged in rows, and with practically no tendency to form a spongy meshwork in some specimens, a line in the shell wall (with no change in contour) distally separates a short, flattened area, which may be regarded as an abdomen, from the remainder, which may be regarded as the thorax (Sanfilippo and Riedel, 1970).

DIMENSIONS

Based on 35 specimens. Total length 95-150 µm. Maximum breadth 75-130 µm (Sanfilippo and Riedel, 1970).

DISTINGUISHING CHARACTERS

Closed postcephalic shell rather irregularly ellipsoidal, sometimes with a line in the shell wall (with no change in contour) demarcating an abdomen. Pores less regular than in *L. bacca*, and shell not spongy (Riedel and Sanfilippo, 1978a).

This species is distinguished form *L. bacca* by at least the major part of its shell wall being composed of irregularly spaced pores, and by its less regular contour. It differs from *L. baueri* Sanfilippo and Riedel (1970, p.455, pl.2, figs.1-2) in its smaller dimensions and in not having a spongy wall, and from *L. renzae* in not having a spongy wall and in its less pronounced third segment (Sanfilippo et al., 1985).

VARIABILITY

The shell is usually a two-segmented ellipsoid, but rare specimens show a line in the shell wall (with no change in contour) demarcating an abdomen. Early forms may have subdivided pores, reflecting the spongy character of the ancestor *L. renzae*. More commonly the pores are simple and irregularly arranged. In the upper part of the range, specimens transitional to *L. bacca* have some portion of shell wall in which the pores are very regular in arrangement (Sanfilippo et al., 1985).

DISTRIBUTION

L. neotera is found in all middle Miocene assemblages from latitudes lower than 40°. Its evolutionary transition from *Lithopera renzae* lies within the *Dorcadospyris alata* Zone and its evolutionary transition to *Lithopera bacca* lies within the *Diartus petterssoni* Zone.

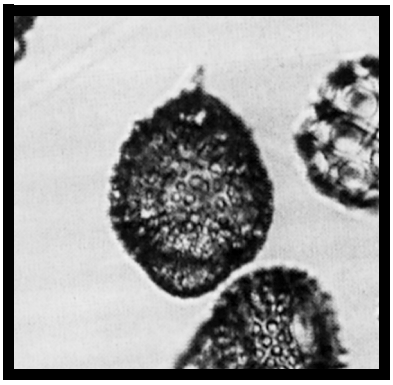
PHYLOGENY

L. neotera descended from *L. renzae* and is the ancestor of *L. bacca*.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.1F, figs.14-15, pl.2E, fig.19; 1978a, pl.6, fig.10.

Lithopera (Lithopera) renzae Sanfilippo and Riedel



Lithopera (Lithopera) renzae Sanfilippo and Riedel, 1970, p.454, pl.1, figs.21-23, 27

DESCRIPTION

Subellipsoidal shell, of which the thorax forms the major part. Cephalis spherical, usually with small circular pores, half or more of it enclosed in the thoracic wall, with a small apical horn. Collar stricture not usually pronounced externally. From the base of the cephalis, primary lateral and dorsal spines extend in the thoracic wall or within the thoracic cavity to join the inner surface of the upper wall. Remainder of shell subellipsoidal, with pores very irregular in size and arrangement, tending to form a spongy meshwork especially in the upper part of the thorax. In some specimens the thoracic wall is not actually spongy, but the pores are divided by secondary bars. Inverted-hemispherical or inverted-conical abdomen usually separated from the larger thorax by a distinct stricture and change in contour (Sanfilippo and Riedel, 1970).

DIMENSIONS

Based on 30 specimens. Total length (excluding horn) 100-165 μm. Maximum breadth 80-110 μm. Ratio of length of abdomen to length of thorax (measured from base of cephalis) (0.01-1.3):1, usually (0.3-0.7):1 (Sanfilippo and Riedel, 1970).

Total length 100-180 μm; maximum breadth 80-120 μm (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

Closed subellipsoidal shell, of which the thorax forms the major part. Pores irregular, tending to be spongy (especially proximally). Lumbar stricture distinct (Riedel and Sanfilippo, 1978a).

L. renzae is distinguished from the other members of its genus by having a third segment delineated by a lumbar stricture usually accompanied by a change in contour. Co-occurring *Cyrtocapsella japonica* (Nakaseko, 1963, p.143, text-figs.20-21, pl.4, figs.1-3) is three-segmented

and similar in shape, but its pores are more regularly arranged, never spongy, and its abdomen is usually larger than the thorax (Sanfilippo et al., 1985).

VARIABILITY

The thorax forms the major part of the three-segmented ellipsoidal shell. In some specimens the cephalis may be free, but more often it is half or more enclosed in the thoracic wall. The shell wall varies from irregularly spaced pores to subdivided pores to a spongy meshwork. The abdomen is inverted-conical or inverted hemispherical and as little as 0.01, to as much as 1.5 times the length of the thorax (Sanfilippo et al., 1985).

DISTRIBUTION

This species is found in most middle Miocene assemblages from latitudes lower than 40°. Its morphotypic first appearance and its evolutionary transition to *Lithopera neotera* both lie within the *Dorcadospyris alata* Zone.

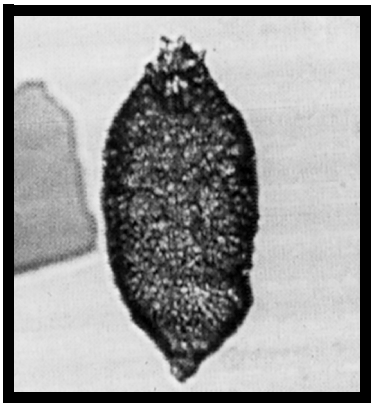
PHYLOGENY

Lithopera renzae may be a descendant of the four-segmented *Stichocorys diploconus* Haeckel (1887, p.1513, pl.78, fig.6), and gives rise to *Lithopera neotera* by loss of the lumbar stricture.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.2E, figs.17-18, pl.7, fig.14; 1978a, pl.6, fig.11.

Lithopera (Glomaria) thornburgi Sanfilippo and Riedel



Lithopera (Glomaria) thornburgi Sanfilippo and Riedel, 1970, p.455, pl.2, figs.4-6

DESCRIPTION

Spindle-shaped shell, tapering equally at both ends. Cephalis spherical, apparently poreless, completely enclosed in the spongy thoracic wall. Thorax spindle-shaped, tapering and closing distally, sometimes with a short terminal spine or acute cone. No third segment distinguished. Thoracic wall thick, of spongy meshwork, especially in the proximal half. The thoracic wall adjacent to the cephalis is of spongy mesh-work and has some straight, rodlike elements developed within and projecting from it, which are probably the primary spines (Sanfilippo and Riedel, 1970).

DIMENSIONS

Based on 35 specimens. Total length 140-285 µm. Maximum breadth usually 85-135 µm, but rarely to 150 µm (Sanfilippo and Riedel, 1970).

DISTINGUISHING CHARACTERS

Shell elongate, spindle-shaped, pointed at both ends. Cephalis enclosed in spongy thoracic wall (Riedel and Sanfilippo, 1978a).

L. thornburgi is distinguished from *L. baueri* Sanfilippo and Riedel (1970, p.455, pl.2, figs.1-2) in that both ends are tapered and pointed, and the cephalis is enclosed in the spongy thoracic wall (Sanfilippo et al., 1985).

VARIABILITY

This spongy, spindle-shaped theoperid, tapered at both ends, has the cephalis completely enclosed in the thoracic wall. In some specimens, the distal part of the shell is composed of small irregularly spaced pores, rather than spongy material, and there is sometimes a contour change, though this is not accompanied by an internal ring (Sanfilippo et al., 1985).

DISTRIBUTION

This species is found in late middle Miocene samples from latitudes lower than 40° in the Indian and Pacific Oceans and the Mediterranean and Caribbean Seas. Its morphotypic first appearance lies within the *Dorcadospyris alata* Zone and its morphotypic last appearance lies within the *Diartus petterssoni* Zone.

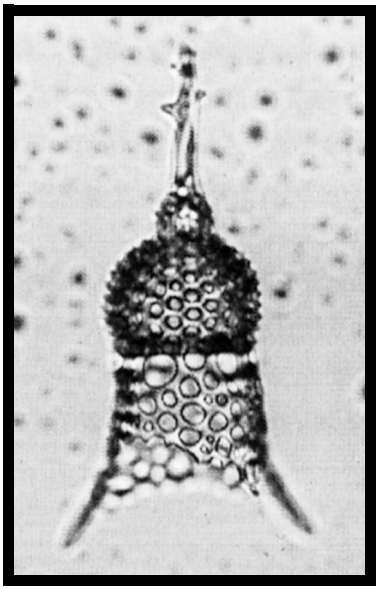
PHYLOGENY

L. thornburgi appears to have evolved from *L. renzae*, and to have left no descendants.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1978a, pl.6, fig.12.

Lophocyrtis (Lophocyrtis) jacchia (Ehrenberg)



Thyrsocyrtis jacchia Ehrenberg, 1873, p.261; 1875, pl.12, fig.7

Lophocyrtis(?) jacchia (Ehrenberg), Riedel and Sanfilippo, 1970, p.530; Riedel and Sanfilippo, 1971, p.1594, pl.3C, figs.4-5, pl.7, fig.16; Sanfilippo, 1990, p.302, pl.I, figs.5-10, pl.III, fig.6

DESCRIPTION

Three-segmented theoperid with a porous subspherical cephalis bearing a well-developed conical horn that is distally thorned and has arches at the base where it joins the cephalis. Cephalic wall perforated by 20-30 small circular to subcircular pores. Collar stricture marked by a distinct change in contour. Some specimens have a single row of larger pores just below the collar stricture. Thorax inflated hemispherical with a rough sometimes thorny surface, and 18-25 pores around the greatest circumference. Abdomen subcylindrical with three short subcylindrical, subterminal or terminal, strongly divergent feet. The abdominal pores are irregularly arranged, and vary in size from half to twice the size of the thoracic pores. Some specimens have a single row of larger pores just below the lumbar stricture, similar to the row of pores at the collar stricture (Sanfilippo, unpubl. data).

DIMENSIONS

Total length (excluding horn and feet) 135-215 µm; length of thorax 45-80 µm, its maximum width 65-110 µm, number of pores around its circumference 18-25; length of abdomen 45-90 µm, its maximum width 75-100 µm and the number of pores around its circumference 12-20. (Sanfilippo, 1990).

DISTINGUISHING CHARACTERS

The apical horn is supported by three (possibly four) arches. Abdomen subcylindrical, with undifferentiated termination; except in

late specimens, there are three or four terminal or subterminal feet (Riedel and Sanfilippo, 1978a).

L. (L.) jacchia is distinguished from its descendant *L. (L.) exitelus* (Sanfilippo, 1990, p.300) by the greater number of pores around the abdominal circumference (usually 16-20 vs. 6-12) and from *L. (Cyclampterium) hadra* (Sanfilippo, 1990, p.304) by having a narrow, terminally open abdomen (Sanfilippo, 1990).

VARIABILITY

Middle-latitude forms range from typical low-latitude *Lophocyrtis* morphotypes of *L. jacchia* to what appear to be middle-latitude morphotypes. These forms have a slender conical horn with almost non-existent arches near the base, smaller abdominal pores (24-30 vs. 16-20 pores around the circumference) and the short feet commonly distort the cylindrical shape of the abdomen. High-latitude forms are quite similar with the exception of a more robust, thicker shell (modified from Sanfilippo, 1990).

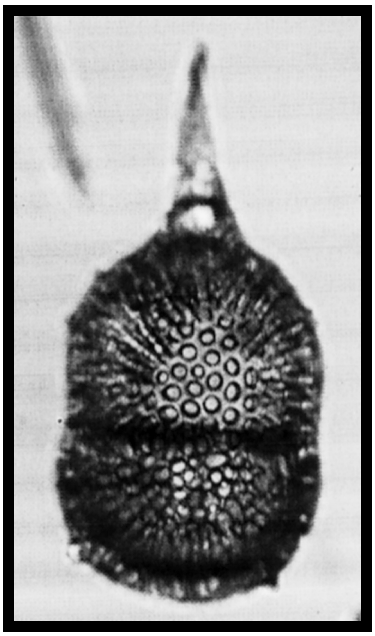
DISTRIBUTION

This cosmopolitan species occurs from the late Paleocene *Bekoma bidartensis* Zone into the upper part of the *Cryptocarpium ornatum* Zone straddling the Eocene/Oligocene boundary. *L. jacchia* occurs rarely and sporadically in the early part of its range and becomes more consistent and moderately abundant later in its range.

PHYLOGENY

The earliest occurrence of *L. (L.) jacchia* is in the late Paleocene, and its ancestry is not yet known. It persists with little morphologic change until the latest Eocene where it gives rise to the subgenus *Cyclampterium* and subsequently evolves into the short-lived *L. (L.) exitelus*.

Lychnocanoma amphitrite Foreman



Lychnocanoma amphitrite Foreman, 1973, p.437, pl.11, fig.10

DESCRIPTION

Cephalis and thorax similar to *L. bellum*. Differs in larger size and more massive wall of thorax and relatively shorter feet. Third segment triangular in cross-section, inverted subhemispherical to pyramidal, with very irregular pores. Hollow feet incorporated in shell wall except distally where they protrude outwardly, solid, short, stubby, and bladed (Foreman, 1973).

DIMENSIONS

Based on 20 specimens. Length overall, exclusive of horn 190-280 µm, length of cephalis and thorax 140-175 µm, of abdomen 40-110 µm; greatest width of thorax 150-190 µm (Foreman, 1973).

DISTINGUISHING CHARACTERS

Thorax large, hemispherical. Abdomen inverted-hemispherical, with very irregular pores. Three hollow feet mostly incorporated in abdominal wall, distally usually free (Riedel and Sanfilippo, 1978a).

VARIABILITY

Later specimens tend to have the horn become slightly bladed, and very late specimens...have a less robust abdomen with the feet less integrated into the shell wall. Sometimes only a fragment of the third segment is present at the base of the feet (Foreman, 1973).

Specimens have been found where the spongy-walled abdomen is so dense that the hollow feet incorporated in the wall are difficult to discern. A spongy layer may cover the thorax as well (Sanfilippo, unpubl. data).

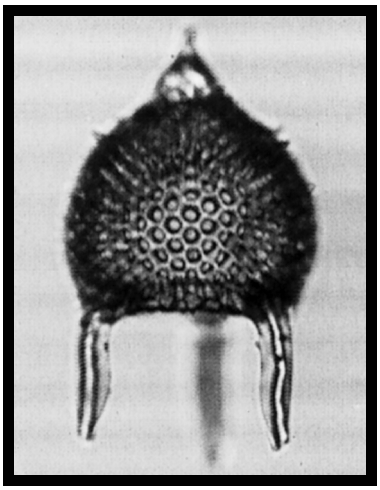
DISTRIBUTION

This species is found in late Eocene sediments from all oceans. In low latitudes its morphotypic first appearance lies within the *Cryptocarpium azyx* Zone, but in high latitudes its first occurrence is earlier, in the early Eocene. Its morphotypic last appearance lies within the *Theocyrtis tuberosa* Zone.

PHYLOGENY

L. amphitrite evolved from *L. bellum*.

Lychnocanoma bellum (Clark and Campbell)



Lychnocanium bellum Clark and Campbell, 1942, p.72, pl.9, figs.35, 39; Riedel and Sanfilippo, 1970, p.529, pl.10, fig.5; Riedel and Sanfilippo, 1971, p.1595

Lychnocanoma bellum (Clark and Campbell), Foreman, 1973, p.437, pl.1, fig.17, pl.11, fig.9

DESCRIPTION

Shell broadly conical, trim, and with sharp collar stricture; apical horn, short, conical, base as wide as length; cephalis subhemispherical, very short (not over 0.3 length of shell), generally slightly asymmetrical with swollen sides, its basal diameter greater than its altitude, collar distinctly set off from thorax below it; thorax dome-shaped with greatly swollen sides, its greatest diameter reached at or near its middle, symmetrical, and very neat and trim; legs three, equal, equidistant, strong, divergent, curved inwardly and hollowed out... with expanded bases; wall relatively thick, uniform, with depressed areas whose elevated edges appear in edge view as surface projections; surface of apical horn, hyaline; of cephalis, without pores; of thorax, with numerous well-spaced, subcircular, elongate-oval, squarish or even subhexagonal pores, these pores double-contoured, generally uniform in size except for a very few, odd scattered small ones; framework around the aperture not dense and connecting the bases of the feet with a narrow, hyaline collar with a basal row of reticulations at the thoracic margin (Clark and Campbell, 1942).

In addition the collar stricture has four collar pores internally, and occasional specimens possess fragments of a partially developed third segment between the feet (Foreman, 1973).

DIMENSIONS

Length of shell 150 μm; of horn 10 μm; of cephalis 21 μm; breadth of base of cephalis 32 μm; maximum of thorax 140 μm; diameter of pores 8.8 μm (Clark and Campbell, 1942).

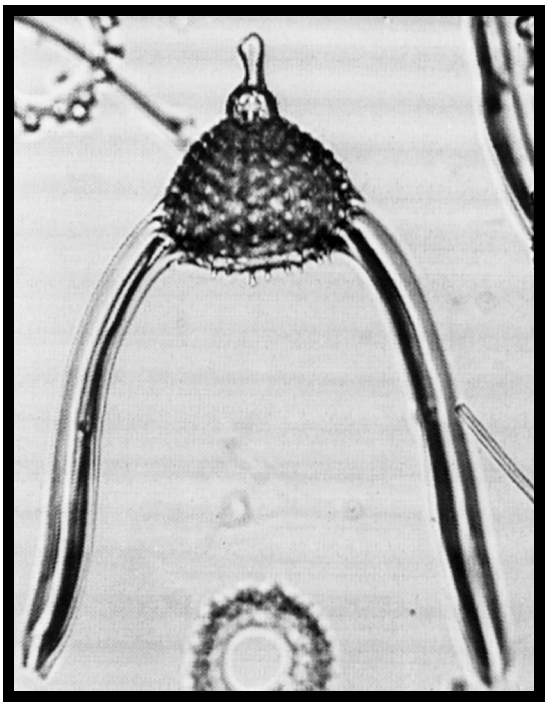
DISTINGUISHING CHARACTERS

The hollow legs of this species are unique.

DISTRIBUTION

This species is found in both low and middle latitudes and possibly extends even into high latitudes. Its morphotypic first appearance is approximately synchronous with the boundary between the *Buryella clinata* and *Phormocyrtis striata striata* Zones. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Cryptocarpium ornatum* Zone.

Lychnocanoma elongata (Vinassa de Regny)



Tetrahedrina elongata Vinassa de Regny, 1900, p.243, pl.2, fig.31

Lychnocanium bipes Riedel, 1959, p.294, pl.2, figs.5-6

Lychnocanoma elongata (Vinassa de Regny), Sanfilippo et al., 1973, p.221, pl.5, figs.19-20 (with synonymy)

DESCRIPTION

Cephalis globular, hyaline or with a few reduced pores, and bearing a conical or weakly clavate apical horn. Thorax inflated hemispherical, with thick wall, slightly rough surface, and circular pores quincuncially arranged. From the base of the thorax arise two heavy, generally divergent, three-bladed feet, which are to a greater or lesser extent curved, with convexity outward. Mouth somewhat narrower than widest part of thorax. In some specimens, a rudimentary subcylindrical abdomen is developed between the feet. This species is distinguished from all others of the genus by having only two feet (Riedel, 1959).

DIMENSIONS

Based on 30 specimens. Length of apical horn 8-55 µm; of cephalis 23-33 µm; of thorax 76-115 µm; of feet 125-275 µm. Maximum breadth of thorax 100-145 µm (Riedel, 1959).

DISTINGUISHING CHARACTERS

From the base of the thorax arise two large, robust, bladed feet, slightly curved proximally with convexity outward (Riedel and Sanfi1ippo, 1978a).

No other two- or three-segmented theoperid is known, which possesses only two feet (Sanfilippo et al., 1985).

VARIABILITY

This species is rather constant in most of its features - inflated-conical to slightly more than hemispherical thorax, with uniform circular pores and surface roughened by minute thorns, and two feet generally 150-275 µm in length, robust, bladed, subparallel to moderately divergent, curved at least proximally with convexity outward. In most assemblages, the thorax is about 110-135 µm wide and 85-105 µm long, but toward the end of the range of the species it is 135-165 µm wide and 105-130 µm long and has concomitantly more numerous pores. The apical horn varies from absent to long and cylindrical, widened distally, but is usually conical, half to twice as long as the cephalis. When post thoracic skeletal structure is preserved, it consists of a delicate, irregularly latticed lamella forming a kind of abdomen joined only to the thorax, never to the feet (Sanfilippo et al., 1985).

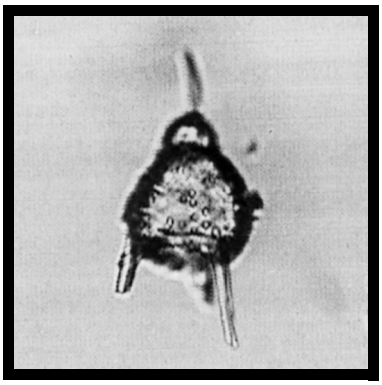
DISTRIBUTION

This species occurs in most assemblages of early Miocene age between 56°S (DSDP Site 278), and the Mediterranean region. Its morphotypic first appearance defines the base of the *Lychnocanoma elongata* Zone. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Calocycletta costata* Zone.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1971, pl.2F, figs.1-2; Moore, 1971, pl.9, fig.8.

Lychnocanoma trifolium (Riedel and Sanfilippo)



Lychnocanium trifolium Riedel and Sanfilippo, 1971, p.1595, p.l.3B, fig.12, pl.8, figs.2-3

Lychnocanoma trifolium (Riedel and Sanfilippo), by implication in Sanfilippo et al., 1973, p.221

DESCRIPTION

Cephalis spherical, poreless, bearing a conical or three-bladed apical horn. Collar stricture pronounced. Thorax campanulate, with smooth surface and subcircular pores generally arranged in groups of three separated by wide poreless areas. Three feet three-bladed, approximately straight, longer than the thorax (Riedel and Sanfilippo, 1971).

DIMENSIONS

Based on 20 specimens. Length excluding horn and feet 75-90 μm. Maximum breadth of thorax 75-90 μm (Riedel and Sanfilippo, 1971).

DISTINGUISHING CHARACTERS

This species differs from all other members of the genus in the characteristic grouping of thoracic pores in threes (Riedel and Sanfilippo, 1971).

Although some specimens admitted to this species have more pores than does the holotype, all have part of the shell wall (usually the upper part of the thorax) poreless except for scattered groups of three pores (Sanfilippo et al., 1985).

VARIABILITY

Some specimens have a rougher surface than those forming the basis for the original description, as a result of their having a larger number of pores, either still open or secondarily closed. Sometimes the pores in each group of three are fused into one, while retaining their 3-lobed outline, possibly as a result of dissolution (Sanfilippo et al., 1985).

DISTRIBUTION

Lychnocanoma trifolium is a rare, short-ranging species so far recorded only in late late Oligocene assemblages from tropical Pacific and Indian Ocean sequences. Its morphotypic first and last appearances both lie within the *Dorcadospyris ateuchus* Zone.

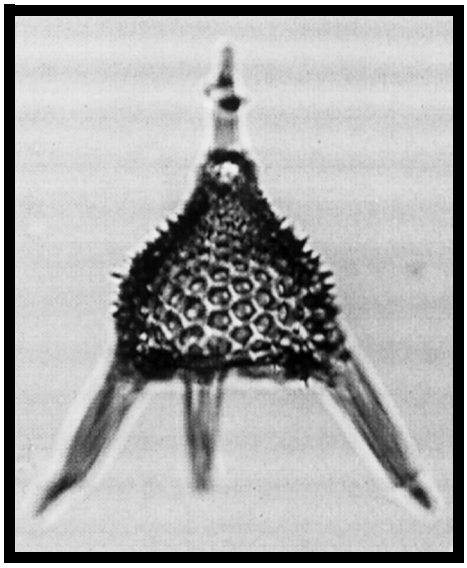
PHYLOGENY

Unknown.

REMARKS

Additional illustrations can be found in Ling, 1975, pl.10, fig.12.

Lychnodictyum audax Riedel



Lychnodictyum audax Riedel, 1953, p.810, pl.85, fig.9; Sanfilippo and Riedel, 1974, p.1022, pl.2, fig.8

DESCRIPTION

Shell campanulate, with rough surface and distinct collar stricture. Length of the two joints 1:4, breadth 1:5. Cephalis subspherical, with rather few, subcircular, well-separated pores, bearing a conical horn of the same to twice the length, which has short, obtusely conical protuberances in its distal portion. Thorax subglobular, with rough ridges between the large rounded pores, which are 2-5 times as broad as the intervening bars. Peristome constricted, the feet arising slightly above the margin. Feet of approximately the same length as the thorax, triangular pyramidal with pronounced blades, fenestrated in the proximal portion, almost straight, divergent. Small spines are often present on the lower edge of the thorax as if remnants from a reduced abdomen (Riedel, 1953).

DIMENSIONS

Length of the apical horn 35-50 µm; of the cephalis 24-28 µm; of the thorax 90-105 µm; of the feet 75-110 µm. Breadth of the cephalis 25-30 µm; of the thorax 110-130 µm; of the thoracic pores 4-12 µm (Riedel, 1953).

Thorax plus cephalis 85-130 µm long; thorax 95 (rarely 80)-130 µm wide (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

The three feet arising from the base of the thorax are almost straight, widely divergent, and latticed proximally. Horn prominent, thorny distally (Riedel and Sanfilippo, 1978a).

This species differs from *Pterocanium trilobum* (Haeckel, 1860, p.839; Nigrini, 1967, p.71, pl.7, figs.3a-3b) by the thorns on the horn (Sanfilippo et al., 1985).

VARIABILITY

This two-segmented theoperid has a campanulate, rough-surfaced shell, three divergent, bladed legs that are fenestrated proximally, and a stout horn, which is thorny distally. Occasionally, remnants of a skirt of meshwork hangs from the peristome. Some specimens from high-latitude sites have thorns on the surface of the thorax, and poorly developed protuberances on the horn (Sanfilippo et al. 1985).

DISTRIBUTION

L. audax is found in all oceans, in middle Oligocene through early Pliocene samples from latitudes lower than 40°. Its morphotypic first appearance lies within the *Theocyrtis tuberosa* Zone. Its morphotypic last appearance lies within the *Spongaster pentas* Zone.

PHYLOGENY

Lychnodictyum audax extends as far back in time (to the middle Oligocene) as any of the other two-segmented theoperids with three feet latticed proximally (members of the genera *Lychnodictyum* and *Pterocanium* in the sense of Haeckel, 1887). In the early part of its range, all members of this group are rare and sporadic in their occurrence, so that it is difficult to determine their ancestry. Very rare specimens in DSDP 77B-46-6 and -47-2 have an outwardly-directed thorn proximally on each foot, suggesting a relationship to the late Eocene *Lychnocanium tridentatum* Ehrenberg (1873, p.244; 1875, pl.7, fig.4), but on the other hand *Lychnodictyum audax* and the other members of the *Lychnodictyum - Pterocanium* group may equally well have originated from one of the abundant late Eocene or early Oligocene species of *Lychnocanium* with imperforate feet (Sanfilippo et al., 1985).

REMARKS

Although this species is evidently closely related to stratigraphically useful forms such as *Pterocanium prismatium*, it is not now transferred to that genus because of uncertainty regarding the nature of the figured type species of *Pterocanium* (*Lithocampe aculeata* Ehrenberg, according to Foreman and Riedel, 1972) (Sanfilippo and Riedel, 1974).

We agree in principle with Lazarus et al., 1985 that *Lychnodictyum audax* and its probably descendant, *Pterocanium trilobum* (see Nigrini,

1967, p.71, pl.7, figs.3a-3b) belong in the same genus. However, since *L. audax* may well be the ancestral stock, we hesitate to use their synonym until the entire lineage has been examined (Caulet et al., 1993).