Theocorys anaclasta Riedel and Sanfilippo

Theocorys anaclasta Riedel and Sanfilippo, 1970, p.530, pl.10, figs.2-3; Riedel and Sanfilippo, 1978a, p.76, pl.1, figs.6-8

DESCRIPTION

Cephalis spherical, poreless or with few small pores bearing a stout conical horn of variable length. Collar and lumbar strictures distinct. Thorax conical to hemispherical, with small subcircular pores. Abdomen broader than thorax, with thick wall (less robust in late



specimens) and large rounded pores. Abdomen inflated in its main part, then constricting distally and expanded terminally, lacking distinct terminal ring. Proximal part of abdomen often thorny, and thorax less so (Riedel and Sanfilippo, 1970).

DIMENSIONS

Based on 20 specimens. Length (excluding horn) 225-390 μ m, maximum breadth 135-235 μ m (Riedel and Sanfilippo, 1970).

DISTINGUISHING CHARACTERS

Three-segmented form with stout conical horn and distinct collar and lumbar strictures. Abdomen inflated in its main part, then constricting distally and expanded to terminate in an undifferentiated margin.

The portion of the abdomen above its constriction is generally more voluminous than the thorax. Early specimens have abdominal pores, small and rather uniform in size; this serves to distinguish them from some late specimens of *T. acroria* Foreman with abdominal constriction (Foreman, 1973, p.439) (Riedel and Sanfilippo, 1978a).

T. anaclasta is distinguished from *T. acroria* Foreman (1973, p.439, pl.5, figs.11-13, pl.12, fig.2) by its more marked abdominal constriction (Sanfilippo et al., 1985).

VARIABILITY

Abdomen is inflated in its proximal part, then constricts distally and expands to terminate in an undifferentiated margin. The portion of the abdomen above its constriction is generally more voluminous than the thorax. Early forms have small abdominal pores, and late ones have large, irregularly rounded pores. Proximal part of abdomen is often thorny (Sanfilippo et al., 1985).

DISTRIBUTION

T. anaclasta is found in moderate abundance in tropical localities of early middle Eocene age. It does not occur at DSDP Site 248, south of Madagascar. Its morphotypic first appearance defines the base of the *Phormocyrtis striata striata* Zone. Its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

PHYLOGENY

T. acroria, T. anapographa Riedel and Sanfilippo (1970, p.530, pl.10, fig.4) and *T. anaclasta* are apparently related to each other, but the details are not yet understood.

Theocorys redondoensis (Campbell and Clark)

- *Theocyrtis redondoensis* Campbell and Clark, 1944, p.49, pl.7, fig.4; Nakaseko, 1963, p.179, pl.2, fig.4
- *Theocorys redondoensis* (Campbell and Clark) Kling, 1973, p.638, pl.11, figs.26-28

DESCRIPTION



Shell large, with two sharp strictures, one of most beautiful species in this collection (its length four apertural, or two maximum diameters); apical horn occipital in origin but arising freely from cephalic vertex, gracefully curved, and distally pointed; cephalis distinctly globular and knoblike, set off sharply by distinct cervical suture from thorax below it, relatively large (0.3 maximum diameter of shell, and with its neck about a third of that diameter); thorax greatly exceeding other shell segments in prominence, very nearly perfectly hemispherical, greatest diameter, at its middle (0.5 total length), widely open at oral end, there squarely truncated, and outside, around thick rim that encircles base of abdomen, a row of short downwardly directed spines; abdomen taperingly subcylindrical with two sides unlike with local bulges and rather general asymmetry (its origin 0.32, and its opening 0.25 total length of shell), and distal end widely open but with a short, flared, entire lip, squarely truncated; wall of thorax thick, of cephalis a little thinner, and of abdomen membrane-like, latter readily torn cleanly off from remainder of shell so that majority of specimens appear formed of but two joints rather than three, and, in addition, horn is often torn off; surface of cephalis and of thorax roughened, latter much more so, otherwise shell glass-clear; pores of cephalis numerous, and very tiny, almost dotlike circles, very well separated, and in rather shallow depressions, freely scattered between surface tubercles, pores of thorax subuniformly circular, comparatively small for so large a species, perhaps as many as 75 around transverse axis, deeply sunken into hexagonal concavities or pits with blunt sepaloid points arising from frames; pores of abdomen subelliptical to subrectangular with rounded corners, freely scattered, not uniform in size but generally larger than those of thorax,

perhaps a dozen in a vertical line and 20 around circumference, strikingly different from those of thorax (Campbell and Clark, 1944).

DIMENSIONS

Length, total, 240 μ m, of horn, 30 μ m, of cephalis, 50 μ m, of thorax 100 μ m; diameter of thoracic maximum, 120 μ m, of shell-aperture, 60 μ m, of thoracic pores, 6.6 μ m (Campbell and Clark, 1944).

DISTINGUISHING CHARACTERS

T. redondoensis differs greatly in form, especially in large knoblike cephalis and inflated thorax from other described species (Campbell and Clark, 1944).

Prominent spherical, hyaline cephalis with sharp collar stricture. Thorax thick-walled and perfectly hemispherical.

DISTRIBUTION

According to Reynolds (1980) this species ranges from his early Miocene *Cannartus violina* Zone, which may be approximately equivalent to part of the tropical *Cyrtocapsella tetrapera* Zone to the lower part of the early Pliocene *Sphaeropyle langii* Zone of Foreman (1975).

REMARKS

Kling (1973) correctly pointed out that this species belongs in the family Theoperidae and not in the family Pterocorythidae.

Theocorythium trachelium trachelium (Ehrenberg)

Eucyrtidium trachelius Ehrenberg, 1872a, p.312

Theocorythium trachelium trachelium (Ehrenberg), Nigrini, 1967, p.79, pl.8, fig.2, pl.9, fig.2

DESCRIPTION

Shell rather rough and thick-walled. Cephalis in 2 parts: (1) spherical portion, with circular to subcircular pores, bearing a 3-bladed



apical horn, 1 or 2 times its length; and (2) "neck", separated from the first part by an internal ringlike ledge, pores similar but larger and in 2 transverse rows, shell a little heavier. This "neck" is apparently homologous with the paired lobes of a trilocular cephalis in which the lobes are directly beneath the larger unpaired lobe. Collar structure at the base of the "neck". Apical spine incorporated in the cephalic wall (both spherical and "neck" parts). Primary lateral and dorsal spines continue as ribs in the thoracic wall for about half its length; sometimes these project, or are external, forming small wings.

Thorax large, distinctly cupola-shaped (conical above, expanded below) with hexagonally framed, circular to subcircular pores, closely spaced, quincuncially arranged and aligned longitudinally, 12-15 on a half-equator, 8-10 in a vertical series. Pronounced lumbar stricture.

Abdomen usually elongate, cylindrical or with a slight medial constriction. Pores similar in size, shape, and arrangement to those of the thorax, 12-15 on a half-equator, 8-14 in a vertical series.

Slight terminal constriction usually with 4-6 triangular lamellar teeth. Some specimens have similar subterminal teeth near the mouth or scattered irregularly over the distal half of the abdomen. In most specimens a peristome is either absent or only poorly developed, but a few have a well-differentiated poreless peristome (Nigrini, 1967).

DIMENSIONS

Based on 20 specimens. Total length (excluding apical horn and terminal teeth) 146-209 μ m. Length of cephalis 27-36 μ m; of thorax 45-72 μ m; of abdomen (excluding terminal teeth) 54-109 μ m. Maximum

breadth of cephalis 27-36 μ m; of thorax 81-100 μ m; of abdomen 72-100 μ m (Nigrini, 1967).

DISTINGUISHING CHARACTERS

Lower part of the cephalis forms a "neck" to the inflated conical or cupola-shaped thorax. Abdomen subcylindrical or slightly expanding distally, with small triangular teeth terminally and sometimes also on distal part of abdomen. A poorly developed poreless peristome is associated with the slight terminal constriction (Riedel and Sanfilippo, 1978a).

T. t. trachelium is distinguished from *T. vetulum* and from *T. trachelium dianae* (Nigrini, 1967, p.77, pl.8, figs.1a-1b, pl.9, figs.1a-1b) by its cylindrical abdomen. *T. t. dianae* is restricted to middle latitudes (higher than 30°).

VARIABILITY

The character that varies the most is the length of the abdomen. Rare specimens have an abdomen shorter than the thorax, and in some it may be as much as three times the length of the thorax. Also, the terminal teeth range from quite large to barely noticeable or even absent (Sanfilippo et al., 1985).

There is a undescribed form similar to *T. trachelium*, but with a much shorter abdomen, with a range well before the first appearance of *T. trachelium*.

DISTRIBUTION

Common in low-latitude Quaternary sediments from the Pacific and Indian Oceans. Absent in samples south of 35°S in the Indian Ocean, but present as far north as 40-45°N in the Pacific Ocean. Its morphotypic first appearance lies within the *Pterocanium prismatium* Zone, but is a diachronous event by approximately 1 m.y. (older in the tropical Indian Ocean than in the tropical Pacific Ocean). It is extant.

PHYLOGENY

It has been assumed in some of the literature (Riedel and Sanfilippo, 1978a; Baker, 1983; Johnson et al., 1989) that *T. vetulum* evolved into *T. trachelium*. We think now that there may be a more complex relationship

between *T. trachelium*, *T. vetulum* and an undescribed form, similar to *T. trachelium*, but with a much shorter abdomen (Caulet et al., 1993).

Theocorythium vetulum Nigrini

Theocorythium vetulum Nigrini, 1971, p.447, pl.34.1, figs.6a-6b

DESCRIPTION

Shell quite smooth and usually thin-walled. Cephalis trilocular, the paired lobes beneath and only slightly lateral to the larger unpaired lobe; pores small, subcircular. Stout, three-bladed



apical horn, between equal to and twice the cephalic length. Primary lateral and dorsal spines continue as ribs in the thoracic wall for about half its length, but have not been observed to project externally.

Thorax cupola-shaped with circular to subcircular pores arranged longitudinally, 7-10 in a vertical series, 12-15 on a half-equator. Pronounced lumbar stricture.

Abdomen inflated conical. Pores similar in size, shape and arrangement to those of thorax, 5-12 in a vertical series, 12-17 on a halfequator. Distally, a row of three-bladed subterminal teeth is usually present. Slight terminal constriction to termination at a poreless peristome and up to eleven triangular terminal teeth, which may or may not be well-developed (Nigrini, 1971).

DIMENSIONS

Based on 20 specimens. Total length (excluding apical horn and terminal teeth) 137-182 μ m. Length of cephalis 27-36 μ m; of thorax 45-63 μ m; of abdomen (excluding terminal teeth) 45-90 μ m. Maximum breadth of cephalis 27-36 μ m; of thorax 81-90 μ m; of abdomen 90-123 μ m (Nigrini, 1971).

DISTINGUISHING CHARACTERS

Similar to *T. trachelium*, but with the abdomen inflated conical rather than subcylindrical (Riedel and Sanfilippo, 1978a).

T. vetulum is distinguished from *T. trachelium dianae* (Nigrini, 1967, p.77, pl.8, figs.1a-1b, pl.9, figs.1a-1b) by its more flared abdomen (abdominal breadth of *T. vetulum* 90-128 μm, of *T. t. dianae* 72-109 μm). It is distinguished from *Lamprocyclas maritalis polypora* Nigrini (1967,

p.76, pl.7, fig.6) in that the paired cephalic lobes of *Theocorythium* are beneath or only slightly lateral to the unpaired lobe, whereas in *Lamprocyclas* they are decidedly lateral. This is not always easily recognizable, and a more obvious difference is that *Theocorythium vetulum* has a longer, narrower abdomen with a finer pore pattern (Sanfilippo et al., 1985).

VARIABILITY

T. vetulum is a three-segmented pterocorythid with an inflatedconical abdomen. The most variable character is the size of the abdomen, which ranges from 40-120 μ m in length. This measurement may be as little as 1/3 to greater than half the total length of the specimen. The large specimens often, but not always, have large terminal and subterminal teeth. The teeth on the smaller variety may be rudimentary or absent. In the Indian Ocean ... specimens often have no peristome. When a peristome is present, it is very weak (Sanfilippo et al., 1985).

DISTRIBUTION

T. vetulum is not found above 40° in the North Pacific, or above 50° in the South Pacific. It is also absent between 140°W and 175°W in the Tropical Pacific. Its occurrence is rare and sporadic in late Pliocene sediments of the Indian Ocean, and it is also rare in the North Atlantic. Its morphotypic first appearance lies within the *Spongaster pentas* Zone and its morphotypic last appearance lies within the *Pterocanium prismatium* Zone.

PHYLOGENY

See Phylogeny of *Theocorythium trachelium trachelium* herein.

REMARKS

Additional illustrations can be found in Sanfilippo and Riedel, 1974, pl.4, figs.6-7.

Theocotyle conica Foreman

Theocotyle (Theocotyle) cryptocephala(?) conica Foreman, 1973, p.440, pl.4, fig.11, pl.12, figs.19-20

Theocotyle conica Sanfilippo and Riedel, 1982, p.177, pl.2, fig.13 (with synonymy)

DESCRIPTION



Similar in all respects to *T. cryptocephala* except abdomen has greatest width distally rather than medially (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 25 specimens. Maximum length excluding horn 130-175 μ m, of abdomen 65-105 μ m. Maximum width 105-135 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. conica is distinguished from its ancestor *T. cryptocephala*, which it accompanies through part of its range, by having its greatest width distally, and from *T. ficus* by its smaller size. Early forms of *T. ficus* whose size might coincide with that of *T. conica* are ovate in general form, rather than distinctly conical. It is distinguished from *T. venezuelensis* by having a campanulate thorax and not such a distinct change of contour at the lumbar stricture (Sanfilippo et al., 1985).

VARIABILITY

The abdomen is always distinctly conical, with pores varying in size to twice as large as those on the thorax. Some early specimens have vestigial wings (Sanfilippo et al., 1985).

DISTRIBUTION

T. conica has a short range in the middle middle Eocene. Its evolutionary transition from *Theocotyle cryptocephala* lies within the *Dictyoprora mongolfieri* Zone. Its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

PHYLOGENY

T. conica terminates the lineage *T. nigriniae* - *T. conica*. The intermediate form is *T. cryptocephala*.

Theocotyle cryptocephala (Ehrenberg)

[?] Eucyrtidium cryptocephalum Ehrenberg, 1873, p.227; 1875, pl.11, fig.11

Theocotyle cryptocephala (Ehrenberg), Sanfilippo and Riedel, 1982, p.178, pl.2, figs.4-7 (with synonymy)



DESCRIPTION

Subcylindrical to ovate in general form. Cephalis hemispherical, with few small pores, bearing horn of about same length. Thorax campanulate, with regular, circular pores. Lumbar stricture usually distinct. Abdomen subcylindrical to inflated, with greatest width medially, and regular pores consistently larger than those of thorax. Poreless peristome distinct, thick, with external contour tapered distally, and smooth margin (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 30 specimens. Maximum length excluding horn 130-190 $\mu m,$ of abdomen 70-125 $\mu m.$ Maximum width 100-145 μm (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. cryptocephala differs from *T. nigriniae* in its inflated abdomen with regularly arranged, consistently larger pores, and thick, tapering peristome, and from *T. conica* in the abdomen having its greatest width medially rather than distally (Sanfilippo et al., 1985).

VARIABILITY

The abdomen varies somewhat in length, and from subcylindrical in early forms to inflated, with greatest width medially in later forms. The abdominal pores are regular and consistently larger than those of the thorax. Early forms have a campanulate thorax often with short vestigial wings; later forms have a more conical thorax, without wings, and the

shell wall becomes thicker, obscuring the lumbar stricture (Sanfilippo et al., 1985).

DISTRIBUTION

T. cryptocephala is found in tropical assemblages of early middle Eocene age. Its evolutionary transition from *Theocotyle nigriniae* defines the base of the *Theocotyle cryptocephala* Zone. Its evolutionary transition to *Theocotyle conica* lies within the *Dictyoprora mongolfieri* Zone.

PHYLOGENY

T. cryptocephala evolved from *T. nigriniae*, which accompanies it for much of its range, and gave rise to *T. conica*.

Theocotyle nigriniae Riedel and Sanfilippo

Theocotyle cryptocephala(?) nigriniae Riedel and Sanfilippo, 1970, p.525, pl.6, fig.5 (*non* 6); Sanfilippo and Riedel, 1982, p.178, pl.2, figs.1-3 (with synonymy)

DESCRIPTION

Subcylindrical in general form. Cephalis large for a theoperid, moderately porous, bearing conical horn of usually 2-3 times its length.



Thorax campanulate, approximately as wide as abdomen, usually with three short wings. Lumbar stricture distinct. Abdomen subcylindrical, often puckered medially, with pores of approximately same size as those of thorax, and showing some irregularity in size and some tendency to longitudinal alignment. Peristome long and usually not pronouncedly thickened, with external contour not strongly tapering distally. In many specimens, abdominal pores irregularly transgress onto proximal part of peristome. Peristomial margin usually with tiny, irregular thorns terminally, and some early specimens with three short, broad, footlike extensions (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 25 specimens. Maximum length excluding horn 140-210 $\mu m,$ of abdomen 65-140 $\mu m.$ Maximum width 80-115 μm (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

Theocotylissa auctor differs from *Theocotyle nigriniae* by its more robust horn and three distinct feet. *T. cryptocephala* differs by having an inflated, rather than subcylindrical, abdomen, with larger pores tending to be more regularly arranged (Sanfilippo et al., 1985).

VARIABILITY

The thorax is constantly campanulate, and usually bears three short wings. The subcylindrical abdomen is much more variable, usually longer

than the thorax but commonly shorter in early specimens. When the abdomen is long, it is commonly slightly puckered medially and the pores there tend to be less regular. The hyaline, bandlike peristome is a little thickened in some specimens, and usually bears tiny, irregular thorns terminally. There is no marked change in contour where the peristome joins the abdomen, and the abdominal pores irregularly transgress onto the proximal part of the peristome. The typical forms [length (excluding horn) 110-205 μ m; of abdomen 65-140 μ m; maximum breadth 70-125 μ m] are accompanied in many assemblages by markedly smaller ones [length (excluding horn) 85-140 μ m; length of abdomen 25-70 μ m; maximum breadth 60-90 μ m]. These small forms are often closed basally by a transverse lattice-plate, and range higher stratigraphically than forms with the typical morphology (which become sparse in and above the *Theocotyle cryptocephala* Zone) (Sanfilippo et al., 1985).

DISTRIBUTION

This species is found in considerable numbers in samples of middle early to early middle Eocene age from the tropics. Its morphotypic first appearance is approximately synchronous with the lower limit of the *Buryella clinata* Zone. Its evolutionary transition to *Theocotyle cryptocephala* defines the base of the *Theocotyle cryptocephala* Zone, but its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

PHYLOGENY

T. nigriniae possibly originated from *Theocotylissa auctor* by loss of the three feet, and evolved into *Theocotyle cryptocephala* by the peristome becoming thick, thornless and marked off from the abdomen by a change in contour.

REMARKS

Additional illustrations can be found in Cita et al., 1970, pl.2, fig.L.

Theocotyle venezuelensis Riedel and Sanfilippo

Theocotyle venezuelensis Riedel and Sanfilippo, 1970, p.525, pl.6, figs.9-10, pl.7, figs.1-2; Sanfilippo and Riedel, 1982, p.179, pl.2, figs.8-12 (with synonymy)

DESCRIPTION

General form subconical to inflated, with distinct collar and lumbar strictures (see



illustrations accompanying original description for range of morphologies). Cephalis subspherical, its wall often including arches directed toward primary laterals from apical bar, with few small pores and apical horn of approximately same length. Thorax hemispherical, with circular pores. Abdomen inflated, with larger circular pores, much wider than thorax and with constricted mouth, terminated by distinct peristome. Late specimens considerably larger than earlier ones, with thorax relatively smaller. Surface of thorax and abdomen rough (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 40 specimens. Total length excluding horn 155-285 μ m, of thorax 40-45 μ m, of abdomen 115-200 μ m. Maximum width 125-245 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. venezuelensis is distinguished from *T. cryptocephala* and *T. conica* by a more pronounced lumbar stricture and more inflated abdomen, and from *Theocotylissa ficus* by its larger abdominal pores, generally thinner wall and hemispherical rather than conical thorax. A very similar, earlier form of uncertain affinity, but with less regularly arranged abdominal pores and larger mouth, occurs in DSDP 40-14-3 (*Buryella clinata* Zone). Late specimens of *Theocotyle venezuelensis* with large inflated abdomen and relatively smaller thorax, resemble *Theocotylissa ficus* (Sanfilippo et al., 1985). This causes some problems of identification particularly in the tropical Pacific (DSDP Sites 40 and 162), where *T. ficus* becomes extremely

rare near the base of the *Thyrsocyrtis triacantha* Zone, and at the same time large specimens of *Theocotyle venezuelensis* are particularly abundant (Sanfilippo and Riedel, 1982).

VARIABILITY

Subconical to inflated, three-segmented form, with distinct collar and lumbar strictures. The wall of the cephalis often includes arches directed toward the primary laterals from the apical bar. The thorax varies from hemispherical to inflated-conical, and the abdomen from inflatedannular to inflated-conical. Through time, the thorax decreases in size and the abdomen increases. Late specimens are much larger (maximum length excluding horn 255-285 μ m, maximum width 215-245 μ m) than early ones (maximum length excluding horn 155-215 μ m, maximum width 125-195 μ m) (Sanfilippo et al., 1985).

DISTRIBUTION

Although this form is found in most tropical assemblages of early middle Eocene age, the Indian Ocean samples contain only forms with thicker than normal shell walls obscuring the characteristic lumbar stricture. Its morphotypic first appearance lies within the *Theocotyle cryptocephala* Zone. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Podocyrtis ampla* Zone.

PHYLOGENY

Theocotyle venezuelensis appears to be an evolutionary offshoot from *T. cryptocephala*, and it left no descendants.

REMARKS

Additional illustrations can be found in Moore, 1971, pl.1, fig.11.

Theocotylissa alpha Foreman

Theocotyle (Theocotylissa) alpha Foreman, 1973, p.441, pl.4, figs.13-15 (*non* 14), pl.12, fig.16; Foreman, 1975, p.621; Sanfilippo and Riedel, 1982, p.179, pl.2, figs.16-17 (with synonymy)

DESCRIPTION

Cephalis subspherical, with no or few small pores, and bearing stout conical horn of about the same length to twice the length. Thorax conical. Lumbar stricture indistinct or not



expressed externally. Abdomen longer than thorax, barrel-shaped or subcylindrical. Wall of abdomen and thorax thick, with regularly arranged pores (longitudinally aligned on abdomen) only slightly smaller on thorax. Flat peristome (thicker than in *T. auctor*) bears three undulations or short, triangular feet, blunt or in some specimens bearing an outward thorn (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 20 specimens. Maximum length excluding horn 135-225 μ m, of abdomen including feet 85-160 μ m. Maximum width 110-145 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. alpha differs from *T. auctor* (Foreman, 1973, p.441, pl.4, fig.8, *non* 9-10), pl.12, fig.13) in not having a distinct lumbar stricture and in the abdomen usually more inflated, and from *T. ficus* in possessing feet and a less conical shape (Sanfilippo et al., 1985).

VARIABILITY

This barrel-shaped or subcylindrical species has a thick wall, with the lumbar stricture indistinct or only slightly expressed externally. The pores tend to be longitudinally aligned on the abdomen. The thick poreless peristome bears three undulations or short, triangular feet, blunt or in some specimens bearing an outward thorn (Sanfilippo et al., 1985).

DISTRIBUTION

T. alpha is found in the tropical Indian and Pacific Oceans, in the Gulf of Mexico and the Caribbean, in middle early Eocene assemblages. Its evolutionary transition from *Theocotylissa auctor* lies within the *Bekoma bidartensis* Zone. Its evolutionary transition to *Theocotylissa ficus* lies within the *Buryella clinata* Zone.

PHYLOGENY

T. alpha is the intermediate form in the lineage leading from *T. auctor* to *T. ficus*.

REMARKS

Additional illustrations can be found in Foreman, 1973, pl.4, figs.9-10 (as *T. auctor*).

The definition of this species [has been] modified in that the distinction from *T. auctor* is now based on the outer expression of the lumbar stricture, rather than on abdominal length and size of horn. This change has caused some re-identification of figured specimens (Sanfilippo and Riedel, 1982).

Theocotylissa ficus (Ehrenberg)

Eucyrtidium ficus Ehrenberg 1873, p.228; 1875, pl.11, fig.19

Theocotylissa ficus (Ehrenberg), Sanfilippo and Riedel, 1982, p.180, pl.2, figs.19-20 (with synonymy)

DESCRIPTION

Thick shell, subovate to broadly conical in overall form. Cephalis subspherical, with few or



no pores, bearing bladed or conical horn of about same length or shorter. Thick shell wall obscures collar stricture, and through it cephalic pores pass obliquely in such a way that the shell material between them projects as supplementary cephalic thorns. Thorax conical, with small circular pores. Lumbar stricture indistinct externally (and completely lost both internally and externally in some late specimens). Abdomen large, inflated (sometimes with straight sides), with circular pores arranged quincuncially in apparent longitudinal rows, and with somewhat constricted, greatly thickened peristome (Sanfilippo and Riedel, 1982).

DIMENSIONS

Maximum length (excluding horn) 155-250 μm , of thorax 35-45 μm , of abdomen 120-195 μm . Maximum breadth 140-235 μm (Sanfilippo et al., 1985).

DISTINGUISHING CHARACTERS

T. ficus is distinguished from *T. alpha* by the lack of feet, from *T. fimbria* by being thicker-walled and having a smooth apertural rim, and from *Theocotyle venezuelensis* by not having a marked lumbar change in contour externally (Sanfilippo et al., 1985).

VARIABILITY

The subspherical cephalis, sometimes obscured by the thick shell wall, bears a short conical horn often associated with a cluster of minute thorns. The collar and lumbar strictures are vaguely expressed externally in some specimens, in others not at all. Early forms are ovate in general

form and have a thick smooth rim that becomes less prominent and turned inward in later forms. With time, the conical thorax becomes smaller, and the inflated abdomen becomes truncate conical, sometimes with straight sides. The abdominal circular to subcircular pores are arranged quincuncially and show vertical alignment (Sanfilippo et al., 1985).

DISTRIBUTION

Theocotylissa ficus occurs in late early and middle Eocene samples from tropical to northern mid-latitudes. Its evolutionary transition from *Theocotylissa alpha* lies within the *Buryella clinata* Zone. Its morphotypic last appearance lies within the *Podocyrtis chalara* Zone.

PHYLOGENY

Theocotylissa ficus is the last member of the lineage leading from *Theocotylissa auctor* through *T. alpha*.

REMARKS

Additional illustrations can be found in Foreman, 1973, pl.4, figs.16-20.

Theocyrtis annosa (Riedel)

Phormocyrtis annosa Riedel, 1959, p.295, pl.2, fig.7

Calocycletta annosa (Riedel) Petrushevskaya and Kozlova, 1972, p.544

Theocyrtis annosa (Riedel), Riedel and Sanfilippo, 1970, p.535

DESCRIPTION

Cephalis elongate, lobate, with a few small pores, surmounted by a stout three-bladed horn. Thorax inflated-campanulate, with regular circular pores.

Thoracic wall pronouncedly plicate longitudinally, the plicae being separated by three to five longitudinal rows of pores. Abdomen



subcylindrical, with a thinner wall than the thorax, and sub-circular to circular pores usually less regularly arranged than in the thorax. In most specimens the thoracic plicae extend into the abdomen, where they become less distinct. Termination of the abdomen usually ragged, but in some specimens with approximately eight to fifteen parallel, triangular lamellar feet or teeth. This species differs from all others of the genus in having a thick-walled, pronouncedly plicate thorax (Riedel, 1959).

DIMENSIONS

See under Variability

DISTINGUISHING CHARACTERS

The thorax of this species is not tuberose, but has pronounced longitudinal plicae spaced in such a way that each separates several longitudinal rows of pores. This species is not to be confused with the superficially similar form that is evidently ancestral to *T. tuberosa*. Throughout and beyond the ranges of both *T. tuberosa* and *T. annosa*, occurs a generalized type of *Theocyrtis* with unornamented shell wall (Riedel and Sanfilippo, 1978a).

Longitudinal plicae in the wall of the thorax (and often also of the abdomen), which separate 2-6 rows of pores, distinguish this species from

practically all other pterocorythids. The only exception, with which *Theocyrtis annosa* may be confused, is an early form of *T. tuberosa*, prior to the development of pronounced tubercles on the thorax of that species. These two forms are so similar that they can be confidently identified only when the age of the assemblage is known (Sanfilippo et al., 1985).

VARIABILITY

The most notable variation in this smoothly contoured, broadly spindle-shaped form is a marked increase in size from early to late specimens. Near the beginning of its stratigraphic range the total length of cephalis plus thorax is usually 115-135 μ m and the maximum width of the thorax is 110-125 μ m, while near the end of its range these dimensions are about 180-210 μ m and 170-185 μ m, respectively. Throughout its range, the length of the stout, bladed apical horn is commonly 35-75 μ m, and the length of the abdomen 25-90 μ m. The thorax varies in degree of inflation, from campanulate to inflated-conical. The abdomen in late specimens often terminates in 8-15 small triangular teeth, and it is not known whether their absence in early specimens is a result of poor preservation (Sanfilippo et al., 1985)

DISTRIBUTION

This species is a common member of assemblages of late late Oligocene to early early Miocene age in low and middle latitudes, including the Mediterranean region. Its morphotypic first appearance lies within the *Dorcadospyris ateuchus* Zone. Its morphotypic last appearance defines the base of the *Stichocorys delmontensis* Zone.

PHYLOGENY

It seems clear that *Theocyrtis annosa* evolved from *T. tuberosa*, though there appears to be a short gap between their stratigraphic ranges at some localities (Riedel and Sanfilippo, 1973).

REMARKS

The [earliest occurrence] of this species may have been recorded at Site 289 at a level that is relatively lower than that previously recorded. Three variants are tabulated: *Theocyrtis annosa* Form A. The earliest *T. tuberosa* Zone specimens: very delicately ribbed, usually rare and often represented by only fragmentary specimens.

Theocyrtis annosa Form B. Specimens with more pronounced ribbing and a suggestion that the shell is molded into broad, raised, longitudinal segments--identical with Riedel and Sanfilippo, 1971, pl.3D, fig.13. The first appearance is higher than the morphotypic base of Form A.

Theocyrtis annosa Form C. Larger specimens, lacking the suggestions of longitudinal segmentation, identical with Riedel and Sanfilippo, 1971, pl.2H, fig.4; pl.3D, fig.12. The first appearance is higher again than that of Form B, and it is probable that only Form C persists to the extinction level of *T. annosa* group. In the highest part of its range Form C shows a tendency to reduction in rib strength and reversion to a morphotype somewhat similar to Form A (Holdsworth, 1975).

Theocyrtis tuberosa Riedel, *emend*. Sanfilippo et al.

Theocyrtis tuberosa Riedel, 1959, p.298, pl.2, figs.10-11; Sanfilippo et al., 1985, p.701, figs.32.1a-d

DESCRIPTION

Cephalis elongate, subdivided into three(?) indistinct loculi, with rough surface and subcircular to circular pores. Apical horn short, stout, three-bladed, often irregular in form or forked. Thorax subhemispherical, with pronouncedly tuberose surface due to low irregular protuberances, and subcircular to circular pores showing a tendency to longitudinal



alignment. Lumbar stricture indistinct externally. Abdomen subcylindrical, somewhat contracted distally, usually with ragged termination, and having a plicate wall in which adjacent plicae are separated by two to four longitudinal rows of subcircular to circular pores (Riedel, 1959).

DIMENSIONS

Based on 30 specimens. Length of apical horn 13-50 μ m; of cephalis 28-50 μ m; of thorax 83-133 μ m; of abdomen 38-168 μ m. Breadth of cephalis 35-45 μ m; of thorax 120-175 μ m (Riedel, 1959).

DISTINGUISHING CHARACTERS

T. tuberosa is distinguished from other pterocorythids by the tuberculate surface of the thorax, but for further discussion of the distinction of early forms from *T. annosa*, and phylogenetic relationships, see discussion under that heading (Sanfilippo et al., 1985).

VARIABILITY

Overall form cylindro-conical, with the bladed vertical horn as long to about twice as long as the cephalis, and the thorax campanulate to inflated. Thoracic surface pronouncedly tuberculate in late specimens,

less so (and often indistinctly longitudinally ribbed) in early ones. Abdomen of very variable length, with no differentiated peristome, and in many specimens having longitudinal plicae in its wall. Thorax 85-135 μ m long, 120-175 μ m broad. Until now early forms lacking pronounced tubercles on the thorax have been excluded from this species, but they are now included because of the difficulty of satisfactorily separating "pronounced" from less pronounced tubercles, and in order to provide a taxonomic home for co-occurring, obviously related, longitudinally plicate forms superficially resembling *T. annosa* (Sanfilippo et al., 1985).

PHYLOGENY

T. tuberosa evolved from a small, unnamed *Theocyrtis* sp. (Sanfilippo and Riedel, 1992, p.20, pl.1, figs.20-23) in the late Eocene/early Oligocene.

DISTRIBUTION

This species is common in late late Eocene to early late Oligocene assemblages from low and middle latitudes of all ocean basins. Its morphotypic first appearance lies within the *Calocyclas bandyca* Zone. Its morphotypic last appearance lies within the *Dorcadospyris ateuchus* Zone.

REMARKS

Additional illustrations can be found in Riedel and Sanfilippo, 1970, pl.13, figs.8-10; 1971, pl.3D, figs.14-18; 1978a, pl.1, figs.10-11.

Thyrsocyrtis (Thyrsocyrtis) bromia Ehrenberg

Thyrsocyrtis bromia Ehrenberg, 1873, p.260; 1875, pl.12, fig.2; Sanfilippo and Riedel, 1982, p.172, pl.1, figs.17-20 (with synonymy)

DESCRIPTION

Inflated form with somewhat constricted mouth. Cephalis subspherical with moderate number of small pores, and with conical



(sometimes fluted) horn several times its length, which in many specimens is roughened or thorny distally. Thorax campanulate, in some assemblages tending to be cylindrical distally and conical proximally, with thorny to tuberculate surface and rounded pores of varying size. Lumbar stricture distinct. Abdomen subcylindrical to inflated, with 12 pores on half-circumference in early specimens and 5-8 in late ones. Differentiated peristome (thicker and wider than a pore bar) about two thirds as broad as abdomen, often with three short, triangular feet (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 20 specimens. Total length excluding horn 145-215 μ m, of thorax 40-70 μ m, of abdomen 65-110 μ m. Maximum width 105-160 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

Differs from *Thyrsocyrtis rhizodon* in having large abdominal pores. From *T. tetracantha* it differs in possessing a distinct peristome, and from *T. triacantha* in having shorter feet or none -- in addition, both of these species have a simple, conical thorax (Sanfilippo and Riedel, 1982).

T. bromia is distinguished from its ancestor *T. rhizodon* by the larger pores on the abdomen, and from *T. tetracantha* by a distinct peristome, which is thicker and wider than a pore-bar, three feet much shorter when present, and by the porous cephalis (Sanfilippo et al., 1985).

VARIABILITY

Early forms of *T. bromia* have a thorax that is cylindrical below and conical above, usually thorny, abdomen annular with small circular to subcircular pores, twice as many as later specimens (12 pores on a half-circumference of the abdomen), and a narrow peristome surrounding the wide aperture. In later forms the thorax becomes campanulate with a rough and thorny, sometimes tuberculate, surface. The abdomen varies in shape from cylindrical to inflated, with 5-8 pores across its half-circumference. A peristome of varying width is always present, sometimes with three short triangular feet. The aperture is less constricted in earlier forms (Sanfilippo et al., 1985).

DISTRIBUTION

T. bromia is widespread in late Eocene assemblages from the tropics. Its morphotypic first appearance lies within the *Podocyrtis goetheana* Zone. Its morphotypic last appearance lies within the *Cryptocarpium ornatum* Zone.

PHYLOGENY

Although only rare transitional forms have been found, it appears that *T. bromia* arose from *T. rhizodon* and left no descendants.

Thyrsocyrtis (Thyrsocyrtis) hirsuta (Krasheninnikov)

Podocyrtis hirsutus Krasheninnikov, 1960, p.300, pl.3, fig.16 *Thyrsocyrtis (Thyrsocyrtis) hirsuta* (Krasheninnikov), Sanfilippo and Riedel, 1982, p.173, pl.1, figs.3-4 (with synonymy)

DESCRIPTION

Subcylindrical form. Hemispherical to subspherical cephalis, poreless or with a few small pores, bearing cylindro-conical horn of extremely



variable length (from shorter than cephalis to as long as entire shell). Thorax campanulate, of approximately same width as abdomen or slightly narrower, with circular, close-packed pores. Lumbar stricture distinct. Abdomen subcylindrical to slightly inflated, with pores equal to or slightly larger than those of thorax. Feet tapering from peristome, often as long as abdomen, usually slightly curved with convexity inward, tapered terminally and typically thickened medially. Shell surface slightly thorny (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 20 specimens. Length excluding horn 120-220 μ m, of cephalothorax 65-95 μ m, of abdomen 35-70 μ m. Maximum breadth 75-140 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. hirsuta differs from *T. tarsipes* in lacking perforations on the feet, from *T. rhizodon* in the feet not being thorned or divided terminally, from *T. tensa* in having smaller abdominal pores, and from *T. robusta* in the less rough thorax, less pronounced lumbar stricture and smaller size (Sanfilippo et al., 1985).

VARIABILITY

The cylindro-conical horn is extremely variable in length, from shorter than the cephalis to as long as the entire shell. The thorax is

campanulate to somewhat inflated, and the subcylindrical to slightly inflated abdomen is of approximately the same length and breadth as the thorax. The pores of the abdomen are 1.0-1.5 times as large as those of the thorax (Sanfilippo et al., 1985).

DISTRIBUTION

T. hirsuta is found in tropical localities of early to early middle Eocene age. Its morphotypic first appearance is approximately synchronous with the lower limit of the *Buryella clinata* Zone. Its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

PHYLOGENY

T. hirsuta evolved from *T. tarsipes* or from an ancestor common to both, and gave rise to *T. tensa*.

Thyrsocyrtis (*Pentalacorys*) *lochites* Sanfilippo and Riedel

Thyrsocyrtis (Pentalacorys) lochites Sanfilippo and Riedel, 1982, p.175, pl.1, fig.13, pl.3, figs. 5-9 (with synonymy)

DESCRIPTION

General form broadly conical. Cephalis subspherical, with few small pores, bearing horn of the same length to several times the length. Thorax campanulate, with rather small pores. Lumbar stricture distinct. Abdomen inflated-annular, with pores similar to those of early representatives of *T*. *triacantha* -- 1.5-3 pore centers in 50 μ m, 10-15 on a half-circumference. Peristome distinct. Feet bladed (at least proximally), originating above peristome, usually widely divergent but in some specimens subparallel (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 30 specimens. Total length excluding feet and horn 170-230 μ m, of cephalothorax 65-90 μ m, of abdomen 75-130 μ m. Maximum width 155-220 μ m (Sanfilippo and Riedel, 1982).



x 130



x 215

DISTINGUISHING CHARACTERS

The bladed nature of the proximal part of the feet is associated with a ridge that extends between nearby abdominal pores, and subparallel to the peristome. The pores adjacent to the peristome are smaller than the other abdominal pores, which are smaller than those of co-occurring (late) *T. triacantha*.

A tendency for the feet to originate slightly above the peristome is observed also in some specimens of *T. tensa* and early *T. triacantha* (in individuals with relatively small abdominal pores), but these are included within the morphological variation of those species. Some of the earliest specimens with features resembling *T. lochites* (treated as variants of *T. tensa*) have feet partly porous in the manner of *T. tarsipes*. Three of these early variants of *T. tensa* were noted by Foreman (1973, pl.3, figs.18-19; pl.12, fig.7), who identified them simply as *Thyrsocyrtis* sp. (Sanfilippo and Riedel, 1982).

T. lochites accompanies *T. triacantha*, which it closely resembles, in the later part of its range, and then accompanies *T. tetracantha*. It differs from *T. tensa* and *T. triacantha* in the feet being bladed, at least proximally, and originating above the peristome (Sanfilippo et al., 1985).

VARIABILITY

A robust species, with inflated abdomen and large abdominal pores (10-12 pores across the half circumference). The peristome is distinct, sometimes with remnants of a fourth, very weak segment. Prominent bladed feet are widely divergent, in some specimens subparallel (Sanfilippo et al., 1985).

DISTRIBUTION

T. lochites occurs in late middle through late Eocene tropical assemblages. Its morphotypic first appearance lies within the *Podocyrtis mitra* Zone. Its morphotypic last appearance is approximately synchronous with the lower limit of the *Cryptocarpium ornatum* Zone.

PHYLOGENY

T. lochites is an evolutionary offshoot from *T. triacantha* from which it arose by the origin of the feet becoming separated from the peristome. It did not leave any known descendants.

Thyrsocyrtis (Thyrsocyrtis) rhizodon Ehrenberg

Thyrsocyrtis rhizodon Ehrenberg, 1873, p.262; 1875, p.94, pl.12, fig.1; Sanfilippo and Riedel, 1982, p.173, pl.1, figs.14-16, pl.3, figs.12-17 (with synonymy)



DESCRIPTION

General form barrel-shaped to somewhat conical. Cephalis subspherical with few, small pores, bearing conical horn, usually short but in some specimens up to half length of shell. Thorax campanulate to hemispherical, with pores commonly about as wide as intervening bars. Lumbar stricture usually distinct. Abdomen longer than thorax, subcylindrical to somewhat inflated, with pores larger than thoracic and usually quincuncially arranged. Feet tapering from peristome then cylindrical, and terminally stubbily branched or with outwardly directed thorn (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 25 specimens. Length excluding horn 140-225 μ m, of cephalothorax 55-85 μ m, of abdomen 55-100 μ m. Maximum breadth 95-130 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. rhizodon differs from *T. hirsuta* and *Theocotyle nigriniae* in the terminally branched or thorned feet, and from *Thyrsocyrtis bromia* in smaller abdominal pores, and from *T. robusta* in the less rough thorax, less pronounced lumbar stricture and smaller size (Sanfilippo et al., 1985).

VARIABILITY

This species gradually changes its general shape, through time, from conical to barrel-shaped, the shell wall becoming thicker in later specimens, which causes the collar and lumbar strictures to become less pronounced. The abdomen is usually longer (length of cephalothorax 55-85 μ m; of abdomen 55-100 μ m) than the thorax, and the pores are 2 to 3 times as large, in later specimens arranged quincuncially. Early forms

have a more inflated abdomen, three slender cylindrical feet arising from a poreless abdominal rim, terminally truncate or bluntly pointed, sometimes with an outwardly directed thorn, or occasionally more complicatedly branched. In later specimens the feet are short triangular extensions of the abdominal rim and not branched (Sanfilippo et al., 1985).

DISTRIBUTION

This rather long-ranging species occurs in moderate numbers in all oceans from 15°S to 20°N during the middle and late Eocene. Its morphotypic first appearance lies within the *Phormocyrtis striata striata* Zone. Its morphotypic last appearance lies within the *Cryptocarpium ornatum* Zone.

PHYLOGENY

T. rhizodon evolved from *T. hirsuta* and gave rise to *T. bromia*. *T. rhizodon* co-occurs with its descendant through the late Eocene.

Thyrsocyrtis (Thyrsocyrtis) robusta Riedel and Sanfilippo

Thyrsocyrtis hirsuta robusta Riedel and Sanfilippo, 1970, p.526, pl.8, fig.1

Thyrsocyrtis (Thyrsocyrtis) robusta Riedel and Sanfilippo, Sanfilippo and Riedel, 1982, p.174, pl.1, fig.5

DESCRIPTION

Similar in general form to *T. hirsuta*, but larger, and differing also in the following respects: shell surface pronouncedly roughened



by thorns arising mainly from the junctions of intervening bars; horn usually long; both abdomen and thorax conspicuously inflated, and lumbar stricture consequently deep; feet straight, or slightly curved inward or outward, and often terminally fluted and perforated (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 20 specimens. Length (excluding horn and feet) 160-250 μ m, maximum breadth 115-160 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. robusta differs from *T. hirsuta* and *T. tarsipes* in larger size, more pronounced lumbar stricture and thorny surface (Sanfilippo et al., 1985).

VARIABILITY

T. robusta has a hemispherical thorax, inflated abdomen, well defined lumbar stricture and a very rough surface. The feet are straight, or curved with convexity inward or outward, pointed or ragged terminally. Through its short stratigraphic range the only variation observed is in the degree of inflation of the thorax and the abdomen, and the development of the horn and thorns on the shell (Sanfilippo et al., 1985).

DISTRIBUTION

T. robusta is restricted to the early part of the early middle Eocene in middle to low paleolatitudes (Indian, Pacific, Atlantic, Gulf of Mexico and the Caribbean). Its morphotypic first appearance lies within the *Theocotyle cryptocephala* Zone. Its morphotypic last appearance lies within the *Thyrsocyrtis triacantha* Zone.

PHYLOGENY

T. robusta appears to be an evolutionary offshoot from the lineage connecting *T. hirsuta* and *T. tensa*.

Thyrsocyrtis (Thyrsocyrtis) tarsipes Foreman

Thyrsocyrtis tarsipes Foreman, 1973, p.442, pl.3, fig.9, pl.12, fig.14; Sanfilippo and Riedel, 1982, p.174, pl.1, figs.1-2

DESCRIPTION

Subcylindrical form. Small, spherical cephalis



with moderate number of small pores and cylindro-conical horn of usually 2-3 times its length. Thorax campanulate to inflated, usually as wide as, or wider than abdomen, with circular, close-packed pores. Vestigial wings commonly present halfway down the segment. Lumbar stricture usually distinct. Abdomen annular to short cylindrical, with pores generally less regular than those of thorax. Feet tapering from peristome, subcylindrical, irregularly and finely perforate, usually divergent (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 10 specimens. Length excluding horn 180-230 μ m, of cephalothorax 75-95 μ m, of abdomen 35-55 μ m. Maximum breadth 80-105 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. tarsipes is distinguished from its descendant, *T. hirsuta*, in its generally smaller size and porous feet (Sanfilippo et al., 1985).

VARIABILITY

The campanulate to inflated thorax commonly bears three vestigial wings. The cylindrical to slightly inflated abdomen is rounded-triangular in cross-section, shorter than, and of approximately the same width as the thorax. Abdominal pores are generally irregular in size and shape, as large to twice as large as those of the thorax, and more widely spaced. The three feet vary in length, and are irregularly perforated (Sanfilippo et al., 1985).

DISTRIBUTION

T. tarsipes occurs in Paleocene to early early Eocene sediments from the Atlantic (DSDP 384), the Caribbean and the Gulf of Mexico from 15°S to 30°N. Its morphotypic first appearance has not been determined. Its morphotypic last appearance lies within the *Buryella clinata* Zone.

PHYLOGENY

T. tarsipes, or an ancestor common to both, apparently gave rise to *T. hirsuta*.

Thyrsocyrtis (Pentalacorys) tensa Foreman

Thyrsocyrtis hirsuta tensa Foreman, 1973, p.442, pl.3, figs.13-16, pl.12, fig.8; Sanfilippo and Riedel, 1982, p.176, pl.1, figs.6-7, pl.3, figs.1-2 (with synonymy)

DESCRIPTION

Similar in general form to *T. hirsuta*, except that the pores of the abdomen are markedly larger



than those of the thorax (at least 1.5 times as large, with 5-6 pore centers in 50 μ m on thorax and 3-4 in 50 μ m on abdomen), and the abdomen is inflated. Feet are slightly curved with convexity inward, or straight, and usually do not show the medial thickening that is characteristic of those of *T. hirsuta*. Rare specimens have feet porous in the manner of *T. tarsipes*, or bladed in the manner of *T. lochites*. In both of these, the abdomen tends to be more inflated than usual (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 15 specimens. Length excluding horn 190-265 μ m, of cephalothorax 70-105 μ m, of abdomen 55-80 μ m. Maximum breadth 100-135 μ m (85-140 μ m according to Foreman, 1973) (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. tensa differs from *T. hirsuta* in larger abdominal pores, and from its descendant *T. triacantha* in having feet descending straight down or with convexity inward (Sanfilippo et al., 1985).

VARIABILITY

T. tensa varies greatly, some forms being robust and others more delicate with thin shells and spindly legs. Rare specimens have feet porous in the manner of *T. tarsipes*, or bladed in the manner of *T. lochites*. The abdominal pores are markedly larger than those of the thorax (5-6 pore centers in 50 μ m on the thorax, and 3-4 in 50 μ m on the abdomen), increasing slightly in size as the abdomen becomes more inflated in later

forms. Feet are slightly curved with convexity inward; towards the end of its range becoming straight and without the medial thickening characteristic of *T. hirsuta* (Sanfilippo et al., 1985).

DISTRIBUTION

T. tensa is found in all tropical oceans in middle early to early middle Eocene assemblages. Its evolutionary transition to *Thyrsocyrtis triacantha* is approximately synchronous with the lower limit of the *Thyrsocyrtis triacantha* Zone. Its morphotypic first appearance lies within the *Buryella clinata* Zone.

PHYLOGENY

T. tensa is part of the *Pentalacorys* evolutionary lineage leading from *T. hirsuta* via *T. triacantha* to *T. tetracantha*.

Thyrsocyrtis (Pentalacorys) tetracantha (Ehrenberg)

Podocyrtis tetracantha Ehrenberg, 1873, p.254; 1875, pl.13, fig.2; Sanfilippo and Riedel, 1982, p.176, pl.1, figs.11-12, pl.3, fig.10 (with synonymy)

DESCRIPTION

Similar in general form to *T. triacantha*, but abdomen with very large pores, no differentiated peristome (here resembling pore bars), and 3-6 (most commonly 4) short to long feet, circular in



section. Some populations, mainly from the early part of the stratigraphic range, with feet so short as to be practically absent (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 25 specimens. Maximum length excluding horn 205-320 μ m, of cephalothorax 60-80 μ m, of abdomen 50-100 μ m. Maximum width 120-155 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

Differs from *T. triacantha* and *T. bromia* in the absence of a differentiated peristome and usually more than three feet, and from *T. bromia* also in the cephalis not being porous and the horn not tending to have spinules distally (Sanfilippo et al., 1985).

VARIABILITY

The delicate to robust abdomen has very large pores (1-4 along its length), no differentiated peristome, and feet varying in number from 3-6 (commonly 4). Around the time of transition from *T. triacantha* to *T. tetracantha*, the feet in many specimens are reduced to short spikes projecting from the distal margin of some of the pores (Sanfilippo et al., 1985).

DISTRIBUTION

T. tetracantha is found in all tropical assemblages of latest middle to late Eocene age. Its morphotypic first appearance lies within the *Podocyrtis goetheana* Zone. Its morphotypic last appearance defines the base of the *Cryptocarpium ornatum* Zone.

PHYLOGENY

T. tetracantha evolved from *T. triacantha* and left no known descendants.

Thyrsocyrtis (Pentalacorys) triacantha (Ehrenberg)

Podocyrtis triacantha Ehrenberg, 1873, p.254; 1875, pl.13, fig.4; Sanfilippo and Riedel, 1982, p.176, pl.1, figs.8-10, pl.3, figs.3-4 (with synonymy)

DESCRIPTION

General form conical. Cephalis subspherical,



with few small pores, bearing cylindrical horn several times its length. Collar stricture distinct. Thorax considerably shorter than abdomen, broadly conical or slightly inflated, with small subcircular pores. Lumbar stricture usually slight. Abdomen broadest segment, robust, with large subcircular pores, distinct peristome, and occasionally thorny surface. Three feet cylindrical, of variable length (often longer than abdomen), arising from peristome, curved with convexity outward, with terminations simple or ragged, rarely forked, and rarely bladed proximally (Sanfilippo and Riedel, 1982).

DIMENSIONS

Based on 25 specimens. Length excluding horn 240-370 μ m, of cephalothorax 65-85 μ m, of abdomen 85-125 μ m; maximum breadth 130-195 μ m (Sanfilippo and Riedel, 1982).

DISTINGUISHING CHARACTERS

T. triacantha differs from its ancestor *T. tensa* in the feet being convex outward, from *T. tetracantha* in having a differentiated peristome and constantly three feet, and from *T. lochites* in the feet originating from the peristome rather than slightly above it (Sanfilippo et al., 1985).

VARIABILITY

Cephalis with a variable cylindrical or elongate-conical horn. Thorax broadly conical to slightly inflated, decreasing in size in late forms (from 102 μ m wide in early specimens to 83 in late forms, and in length from 80 μ m to 62 μ m). The thick-walled abdomen is broader than the thorax, occasionally thorny, with large subcircular pores (10-13 on a half-circumference in early forms and 5-7 on a half circumference in late

forms). From a distinct peristome [originate] three cylindrical feet of variable length, (often longer than the abdomen), curved with the convexity outward, with terminations simple or ragged, rarely forked (Sanfilippo et al., 1985).

DISTRIBUTION

T. triacantha occurs commonly in tropical assemblages from middle middle through late Eocene. Its morphotypic last appearance lies within the *Calocyclas bandyca* Zone. Its evolutionary transition from *Thyrsocyrtis tensa* is approximately synchronous with the lower limit of the *Thyrsocyrtis triacantha* Zone.

PHYLOGENY

This species evolved from *T. tensa* and into *T. tetracantha*. *T. lochites* is an evolutionary offshoot from this lineage.

Tristylospyris triceros (Ehrenberg)

Ceratospyris triceros Ehrenberg, 1873, p.220; 1875, pl.21, fig.5

Tristylospyris triceros (Ehrenberg), Haeckel, 1887, p.1033; Riedel, 1959, p.292, pl.1, figs.7-8

DESCRIPTION

Shell nut-shaped, tuberculate, thick-



walled, with indistinct sagittal stricture, and with subcircular to circular pores without regular arrangement. Three primary feet robust, circular in section, curved, with convexity outward. Secondary feet, which are not developed in all specimens, are one to seven in number (usually three), of the same general form as the primary feet but smaller. Rarely a small apical horn is present. The few specimens that could be observed from the base were found to have three large and six small collar pores such as Bütschli (1882) described for *Petalospyris argiscus* Ehrenberg, and the three primary feet correspond in position with the bars separating the three large pores (Riedel, 1959).

DIMENSIONS

Based on 30 specimens. Length of shell 68-88 μ m; of primary feet 155-415 μ m; of secondary feet 18-105 μ m. Breadth of shell 88-105 μ m (Riedel, 1959).

DISTINGUISHING CHARACTERS

Cephalis without horn. Three equally large, divergent, slightly curved cylindro-conical feet, alternating with (usually three) shorter ones that may be tabular (Riedel and Sanfilippo, 1978a).

This species differs from its descendant *Dorcadospyris ateuchus* by having three primary feet rather than two (Sanfilippo et al., 1985).

VARIABILITY

The nut-shaped lattice-shell bears three strong, cylindrical primary feet, varying from slightly divergent with most of the curvature

proximally and almost straight distally, to semicircularly curved. The three (or occasionally more) secondary feet are shorter, varying in form from cylindro-conical to lamellar. Rare specimens have a small apical horn (Sanfilippo et al., 1985).

DISTRIBUTION

Tristylospyris triceros is common in assemblages of late middle Eocene through early Oligocene age from low and middle latitudes of all ocean basins. Its morphotypic first appearance is approximately synchronous with the lower limit of the *Podocyrtis chalara* Zone. Its evolutionary transition to *Dorcadospyris ateuchus* defines the base of the *Dorcadospyris ateuchus* Zone.

PHYLOGENY

Tristylospyris triceros appears to have evolved from a middle Eocene ancestor having six similar primary feet. It is the ancestor of *Dorcadospyris ateuchus*.

REMARKS

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