

The Gregarines: A generic level review

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PHYLUM APICOMPLEXA Levine, 1970

ORDER EUGREGARINORIDA LÉGER, 1900

Merogony absent; gamogony and sporogony present; typically parasites of annelids and arthropods but some species in other nonvertebrates; locomotion progressive, by gliding or undulation of longitudinal ridges, or nonprogressive.

Among the Apicomplexa, the diversity of the gregarines is surpassed only by the coccidia. Eugregarinorida are all parasitic and are restricted to non-vertebrates, largely invertebrates. A few species have been reported from tunicates. Eugregarinorida contains ~1656 species divided among ~244 genera; however, these figures are at best a cursory survey of the group's total biodiversity. Gregarines have been reported from only about 3,124 invertebrate species, less than one-third of one percent of the named invertebrate fauna (Levine, 1988). The majority of eugregarine species are reported from insects, which are the most speciose invertebrate group. Yet again, gregarines have been reported from less than 0.32% of named insect species (Levine, 1988). For example, gregarines have been reported from only about 850 (<0.31%) of the over 277,000 named beetle species, (Borror et al., 1981; Levine, 1988). Thus, the potential gregarine fauna from over 99% of the known invertebrate world remains to be discovered.

Grassé (1953) provides the only modern revision of the group. Significant reviews include Reichnow (1953) and Kudo (1966). Useful keys and photomicrographs of many European species are provided by Geus (1969) and Lipa (1967), respectively. Uniform terms for ontogenetic stages and morphological structures of Eugregarinorida are provided by Levine (1971). Levine (1988) provides the most complete checklist of named species and his systematic arrangement is used as a starting point for this work. The arrangement presented

here is congruent with the macrotaxonomic arrangement of Vivier and Desportes (1990). No modern phylogenetic arrangement exists for members of Eugregarinorida; however, the group is assumed monophyletic and has been used as an outgroup in other cladistic studies of the Apicomplexa (e.g. Barta, 1989). The systematic arrangement within Eugregarinorida presents some challenges for systematists: many, if not most taxa are diagnosed by unique combinations of non-unique characters. This arrangement facilitates information storage and retrieval, but it does not provide an inclusive evolutionary hypothesis.

SUBORDER BLASTOGREGARINORINA CHATTON & VILLENEUVE, 1936

Gamogony by gamonts while still attached to the intestine, gametes budding off of gamonts; anisogamy present; syzygy absent; gametocysts absent; oocysts with 10 to 16 naked sporozoites; gamont composed of a single compartment without definite protomerite and deutomerite, but with mucron; in marine polychaetes.

This suborder contains a single monotypic family.

SUBORDER ASEPTATORINA CHAKRAVARTY, 1960

Gamont composed of a single compartment, without definite protomerite and deutomerite, but with an epimerite or mucron in some species; syzygy present.

This suborder contains ~489 named species constituting 72 genera. These animals lack a septum differentiating the body into compartments. This character distinguishes the aseptate gregarines from the septate gregarines. One of the major hinderances to work within the group is the scattered and incomplete state of the taxonomic literature on Aseptatorina and gregarines in general. Although there is no recent complete review of Aseptatorina, substantial progress has been made in the group revisions and species checklists of Levine (1971a, 1976, 1977a, 1977b, 1977c, 1977d, 1988). These references provide the current systematic framework and a clear foundation for additional systematic review and revision within the group.

SUBORDER SEPTATORINA LANKESTER, 1885

Gamont or trophozoite divided into protomerite and deutomerite by a septum; with epimerite, in invertebrates, especially arthropods.

This suborder contains ~1,166 named species constituting 151 genera. The septate gregarines possess a septum differentiating the protomerite from the

deutomerite. This character distinguishes the septate gregarines from the aseptate gregarines. Although this septum is usually apparent under light microscopy, it does not always appear complete under electron microscopy. Important reviews of Septatorina include Watson (1916b), Kamm (1922), Levine (1988), Geus (1969) and Grassé (1953).

Although Levine (1971b) reviewed the terminology of the group, gregarine ontogenic terminology remains unresolved (e.g., Margulis et al., 1993). Terminology used here is consistent with Levine (1971b), except that I have distinguished "syzygy" and "association". Association is primarily a developmental event marked by the assortment and union of haploid individuals prior to the onset of gametogony. Syzygy is primarily a reproductive event marked by the initiation of gametocyst formation. It is the functional onset of gamete formation. Syzygy has been used as a general term to encompass both events; however, the distinction is important: association is developmental while syzygy is reproductive. For example, association occurs early in growth of individuals of Gregarinicae and syzygy is delayed until growth and development are complete. In contrast, members of Stenophoricae remain isolated until mature, only forming associations at the onset of syzygy. Individuals in association are often called gamonts without reference to the onset of gamete formation. This usage makes taxonomic comparison within Septatorina difficult because of the disparity in the timing of association and syzygy among superfamilies. Levine (1971b) noted that "gamonts" and "trophozoites" are both modified sporozoites; the terms simply differentiate developmental phases of the same life cycle stage. I have used "trophozoite" to refer to the motile, vegetative stage, reserving "gamont" for individuals that have entered syzygy to begin the gametogenic cycle. The primary distinction is between a growth phase and a reproductive phase: individuals in association are functional trophozoites until the onset of gametogony.

The terms "endosome", "karyosome", and "nucleolus" have all been used to describe condensed chromatin bodies in septatorian nuclei. In most gregarines, chromosomal association and Feulgen reactivity have not been demonstrated. I have followed the usage of individual workers in the original literature rather than choose a single unified term because such unification would entail the risk of confounding the following descriptions.

The species descriptions that follow often include data from several sources. The intent is to provide information for species identification and clarification. The keys that follow are incomplete; they will help you identify common genera but always refer to the generic diagnoses to confirm your identifications. No exhaustive keys to new world species within the septate gregarines have been assembled since those of Ellis (1913a). Geus

(1969) provides a more recent set of keys for the septate species of central Europe.

Key to the superfamilies of Septatorina

1. Life cycle monogenic.....2
- 1'. Life cycle digenic Porosporicae
2. (1) Nucleus and endocyte of satellite injected into primate during syzygy..... Fusionicae
- 2'. (2) Nucleus and endocyte of primate and satellite remain isolated until gametocyst formation3
3. (2') Association precocious (associations formed before trophozoites mature and enter syzygy) Gregarinicae
- 3'. (3) Trophozoites solitary (associations are not formed until the onset of syzygy)..... Stenophoricae

SUPERFAMILY POROSPORICAE CHAKRAVARTY, 1960

Heteroxenous; two host species involved, one crustacean and the other molluscan.

This superfamily contains a single family with 3 genera and 37 named species. Its members are differentiated from other septate gregarines by a digenic or two host life cycle.

FAMILY POROSPORIDAE LABBÉ, 1899

Vegetative development in digestive tract of a decapod crustacean and sporogony in the connective tissue of lamellibranch molluscs.

The validity and relationships of taxa within Porosporidae should be considered unstable. These taxa are characterized by a digenic life cycle; however, no porosporid life cycle has been experimentally completed. Prytherch (1940) ostensibly completed the life cycle of *Nematopsis ostrearum* by cycling vegetative stages through a mud crab, *Panopeus herbsti*, using infective, monozoic oocysts obtained from an oyster, *Crassostrea virginica*. However, all of the animals used in his work were collected from the field: there is no evidence (e.g. time zero or concomitant control post-mortem examinations) to suggest that the work was not confounded by existing infections. Théodoridès (1961, 1962) has suggested that *Nematopsis* and *Caridohabitans* are junior synonyms of *Porospora* and our current view of porosporid life cycles reflects the combination of a gregarine life cycle with that of an undescribed coccidian. This observation is reasonable

given the coccidians reported from crustacea (e.g. Théodoridès and Desportes [1975]). (Thus the life cycle in Figure 39 would be reduced, passing from the release of oocysts [k] to the the establishment of trophozoites [c].) If this view is correct, *Nematopsis* and *Caridohabitans* are junior synonyms of *Porospora*. Additional field surveys and careful experimental study of porosporid life cycles will be required to stabilize this group; but I hesitate to make any changes without such information.

protomerite deutomerite septum sometimes lost in satellite(s) which fuse to form a multinucleate compartment; protomerite of primate with a muscular collar. Thirty - two named species.

Nematopsis are distinguished from *Porospora* by the production of a resistant oocyst in the molluscan host.

Key to the genera of Porosporicae

- 1. Gamonts with a single nucleus.....2
- 1'. Gamonts with 2–3 nuclei *Pachyporospora*
- 2. (1) Naked sporozoites produced in molluscan host..*Porospora*
- 2'. (2) Sporozoites with a resistant oocyst produced in molluscan host *Nematopsis*

Genus *Porospora*
Schneider, 1875

Oocysts absent, the sporozoites occurring in the host leukocytes; gymnosporozoites develop into naked sporozoites rather than resistant oocysts in molluscan host; mature trophozoites relatively long, with a tendency to remain isolated. Two named species.

Porospora are distinguished from *Nematopsis* by production of naked sporozoites rather than a resistant oocyst in the molluscan host. (For additional information regarding the systematic placement and validity of *Porospora*, see discussion under "Family Porosporidae".)

Porospora gigantea (van Beneden, 1869) Schneider, 1875 (= *Gregarina gigantea* van Beneden, 1869). TYPE SPECIES.

TYPE HOST: Crustacea, *Homarus gammarus*, *Homarus americanus*; Mollusca, *Trochocochelea mutabilis*.

Notes: This is the only species in *Porospora* for which the complete life cycle, (which is similar to *Nematopsis*), has been demonstrated. Ref. Levine (1988), Prytherch (1940), Sprague & Couch (1971).

Genus *Nematopsis*
Schneider, 1892

Oocysts with a single sporozoite (monozoic); sporozoites in a doubled envelope; gymnosporozoites develop into monozoic resistant oocysts in molluscan host; pre - reproductive associations present, typically with several individuals in straight or forked chains, intermittent; in reproductive associations primate and satellite may be enclosed in a common epicyte,

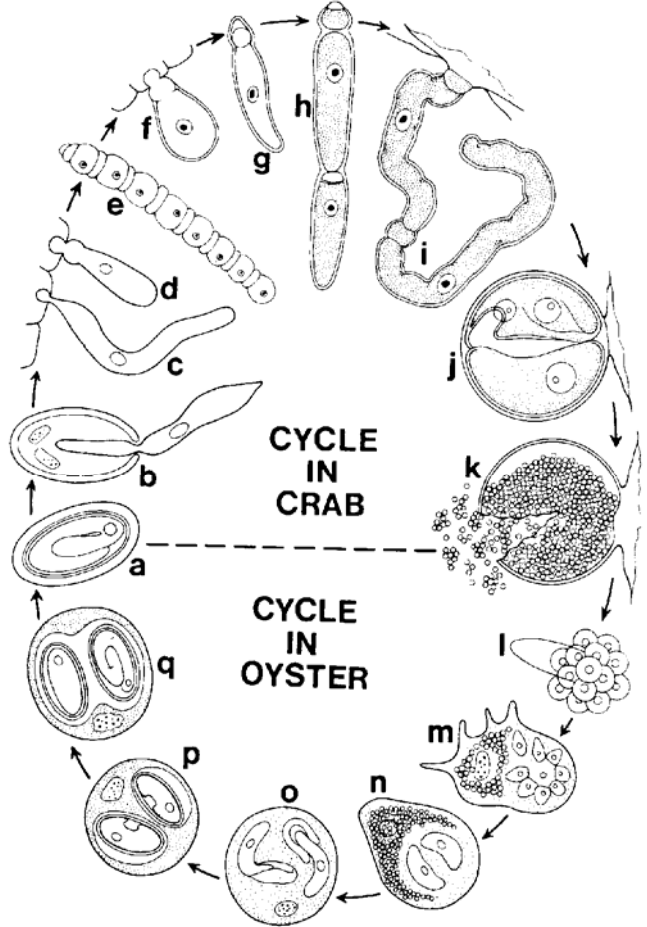


Fig. 1. *Nematopsis ostrearum*. Life cycle: a. Sporocyst containing a sporozoite; b. Sporozoite escaping from sporocyst; c–g. Formations of gamonts; h. Association; i. Syzygy; j. Gametocyst; k. Gametocyst releasing oocysts; l. Single gymnosporozoite; m. Engulfment of gymnosporozoite by oyster phagocyte and separation of sporozoites; n–q. Sporogony. (Based on Prytherch, 1940.)

The literature reflects some differences in the life cycle (or at least in its interpretation) among species of this genus. (For additional information regarding the systematic placement and validity of *Nematopsis*, see discussion under "Family Porosporidae".) Prytherch (1940) reported that individuals of *Nematopsis ostrearum* undergo normal growth, gametogenesis, sexual recombination, zygote formation, and sporogony within the decapod host, producing gymnosporozoites that are infective to the molluscan host. Gymnosporozoites are transmitted to the molluscan host, and engulfed by host leukocytes where they form resistant oocysts. However, Hatt (1931) suggested that individuals of *Nematopsis*

legeri undergo normal growth and gametogenesis within the decapod crustacean host and form bundles of male and female gametes or "heliospores". Heliospores are transmitted to the molluscan host where the parasites complete sexual recombination and zygote formation to produce infective, naked sporozoites.

Nematopsis ostrearum Prytherch, 1938 (Fig. 1). Crustacean hosts are infected by ingesting infective, monozygotic oocysts; either in discharged oyster leukocytes or infected oyster tissues. Free sporozoites (length 26.0 µm, width 6.0 µm) migrate to the intestinal epithelium, attach to epithelial cells with a globular epimerite, assume a globular shape, and grow. Trophozoites detach from the epithelium approximately 15–20 hours postinfection, and form prereproductive associations, typically of 2–10 individuals in straight or forked chains. Prereproductive associations disassemble and individual trophozoites undergo a 14–21 days period of extracellular growth, attaining a mature length of 220.0–342.0 µm. Biassociative, caudofrontal, reproductive associations are formed and migrate to the rectum of the crab, where the parasite attaches to the rectal wall with a muscular collar or adhesive disk. Syzygy, gametocyst formation, gamete formation, gametogony and sexual recombination occur in the host's rectum. Within the gametocyst, zygotes form thin oocyst walls and divide to form a clump of 8–16 sporozoites called a gymnospor. Oocyst and gametocyst walls rupture to release these gymnosporozoites through the crab's anus into the surrounding sea. Molluscan hosts are infected when gymnosporozoites are carried into the shell with the feeding current. Gymnosporozoites attach to the gill or mantle and penetrate the epithelium with a pseudopod projected from the central sporozoite. Gymnosporozoites are engulfed by oyster leukocytes and undergo a period of presporogonic growth. When mature, each sporozoite forms a resistant, double-walled sporocyst, length 20.0 µm, width 11.0 µm. TYPE HOST: Crustacea, *Panopeus herbsti*, *Eurypanopeus depressus*; Mollusca, *Crassostrea virginica*. Ref. Prytherch (1938a, 1938b, 1940).

Genus ***Pachyporospora***
Théodoridès, 1961

Gamonts with multiple nuclei, but without functional or vestigial septa. Three named species.

TYPE SPECIES: ***Pachyporospora laubieri***
Théodoridès, 1961.

TYPE HOST: *Atelecyclus septemdentatus* and *Atelecyclus rotundatus*.

Notes: Levine (1988) suspected that this genus was based on individuals in syzygy and doubted the validity of the genus. Théodoridès (1961) based the description on associated individuals that had begun syzygy, and he noted the initial loss of septa differentiating the protomerites and deutomerites of

gamonts. I have examined Théodoridès' type and paratype specimens, as well as specimens of *Pachyporospora retorta* Ormieres, 1968 collected from *Cancer productus* in British Columbia. The characters of the genus are clearly demonstrated in these specimens, and I conclude that the taxon is both valid and based on firm intrinsic characters. However, all 3 named species are described from gamonts in the intestines of crabs and no other life cycle stage is known. Additional information will be required to make unambiguous systematic decisions regarding the member genera of Porosporidae. (See discussion under "Family Porosporidae".) Ref. Ormieres (1968), Théodoridès (1961, 1962, 1977)

SUPERFAMILY GREGARINICAE
CHAKARAVARTY, 1960

Homoxenous, association early.

This superfamily contains 7 families with ~45 genera and ~561 named species. Its members are differentiated from Porosporidae by a monogenic (one host) life cycle in which sporogony is completed in the gametocyst. Members of Gregarinicae characteristically form associations prior to syzygy. This distinguishes them from Stenophoricae, members of which characteristically remain solitary until mature, forming associations only at the onset of syzygy.

Key to the families of Gregarinicae

1. Mature trophozoite with primary segmentation only (distinguishing the protomerite and deutomerite); no secondary segmentation present.....2
- 1'. Mature trophozoite with secondary segmentation of the protomerite and deutomerite.....Metameridae
2. (1) Holdfast or epimerite simple, not dilated into a lobate sucker.....3
- 2'. (2) Holdfast or epimerite dilated into a lobate sucker.....7
3. (2) Gametocysts dehisce by simple rupture.....4
- 3'. (3) Gametocysts dehisce through one or more sporocysts.....6
4. (3) Oocysts with equatorial ridge or radial processes.....5
- 4'. (4) Oocysts smooth, without equatorial ridge or radial processes.....Hirmocystidae (in part)
5. (4) Early trophozoite development intracellular.....
.....Cephaloidophoridae
- 5'. (5) Early trophozoite development extracellular.....
.....Uradiophoridae

- 6. (3') Gametocyst with more than 1 sporoduct
.....Gregarinidae
- 6'. (6) Gametocyst with a single sporoduct
.....Didymophyidae
- 7. (2') Epimerite apparently an extension of protomerite,
without distinct neck or stalk; parasitic in crustacea
..... Cephalolobidae
- 7'. (7) Epimerite with four distinct cup - like suckers and a
distinct neck; parasitic in insects
..... Hirmocystidae (in part)
..... *Quadruhyalodiscus*



Fig. 3. *Cephaloidophora duboscqi*. Association. (Based on Poisson, 1924.)

FAMILY CEPHALOIDOPHORIDAE
KAMM, 1922

Epimerite present; early development intracellular; association head to tail (caudofrontal), early, with primitive different from satellite; marked anisogamy; gametocysts open by simple rupture; oocysts ovoid or spherical, with protruding equatorial ridge; no distinct episporic; in intestine of crustacea and other relatively primitive arthropods.

This family contains 3 genera and 70 species, primarily intestinal parasites of decapods, amphipods, and cirripedes.

Genus *Cephaloidophora*
Mavrodiadi, 1908

Epimerite small, lenticular; oocysts ellipsoidal or spherical, with inconspicuous equatorial ring, expelled in chains or singly; in intestine of cirripedes, decapods, and amphipods. Sixty - two named species. Figs. 2-5.

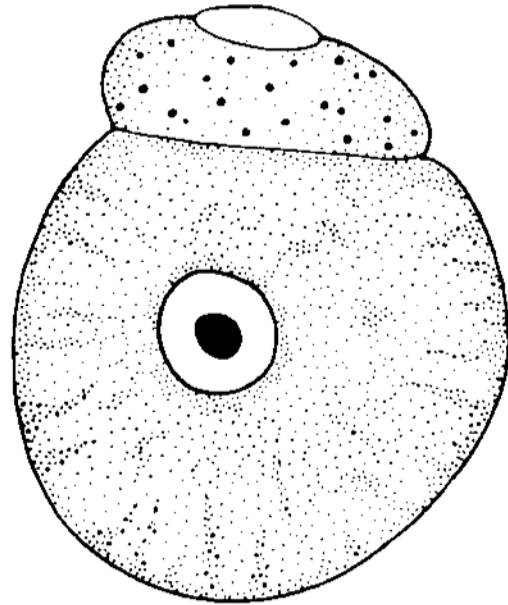


Fig. 4. *Cephaloidophora duboscqi*. Trophozoite. (Based on Poisson, 1924.)

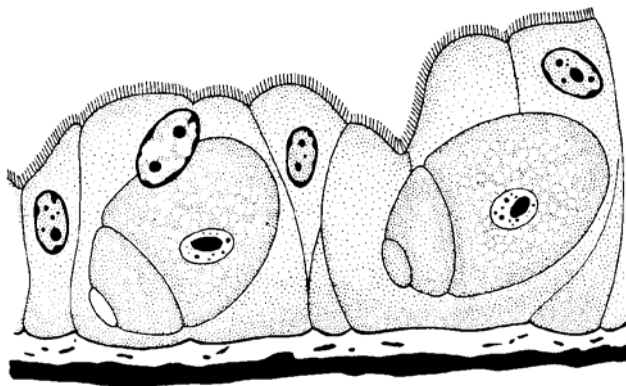


Fig. 2. *Cephaloidophora duboscqi*. Trophozoites inside host cells. (Based on Poisson, 1924.)



Fig. 5. *Cephaloidophora communis*. Oocysts. (Based on Tuzet and Ormieres, 1964 [1965].)

Cephaloidophora communis Mavrodiadi, 1908 (= *Pyxinioides chthamali* Tuzet and Ormieres, 1956. (Fig. 5). TYPE SPECIES. Initial development intracellular, trophozoites released from host cells measure 20.0-40.0 μ m. Epimerite small, lenticular, appearing as a thickened hyaline zone at the anterior end of the protomerite; protomerite hemispherical, length 10.0-24.0 μ m (primitive), 10.0-20.0 μ m (satellite), width 14.0-27.0 μ m (primitive), 14.0-24.0 μ m (satellite); with distinct constriction at protomerite deutomerite septum; deutomerite elongate ellipsoidal, blunt posteriad, length 31.0-58.0 μ m (primitive), 31.0-54.0 μ m (satellite), width 17.0-37.0 μ m (primitive), 15.0-27.0 μ m (satellite); nucleus spherical. Association precocious, caudofrontal, protomerite of satellite forming a depression in the

posterior end of the deutomerite of primate. Oocyst: Spherical, diameter 4.5–5.0 µm; with equatorial ridge or ring; expelled in chains, liberated from the gametocyst by simple rupture. **Notes:** Measurements taken from Henry (1938). Trégouboff (1912) states that mature primites are rarely greater than 80.0 µm and satellites are usually much shorter, rarely exceeding 65.0 µm in length.

TYPE HOST: *Balanus improvisus*, *Balanus eburneus*, *Balanus amphitrite*. Ref. Henry (1938), Kamm (1922), Sprague & Couch (1971), Trégouboff (1912), Tuzet & Ormières (1964).

Notes: Six species within *Cephaloidophora* have recently been described from the Antarctic (Avdeev and Avdeeva, 1989). These species illustrate the habitat extremes of the eugregarines.

(For additional information regarding the systematic affinities of *Cephaloidophora*, see discussion under "Genus *Gregarina* Dufour, 1828".)

Genus ***Caridohabitans***
Ball, 1959

Epimerite functional, transparent, crescent - shaped, concave anteriad; epicyte thick; nucleus with granules distributed irregularly along membrane, without endosome; gametocysts and oocysts unknown; in digestive tract of crustacea. Four named species.

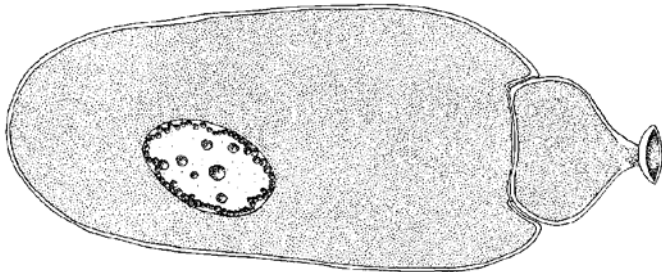


Fig. 6. *Caridohabitans setnai*. Trophozoite. (Based on Ball, 1959.)

Caridohabitans setnai Ball, 1959 (Fig. 6).

TYPE SPECIES. Trophozoite: Initial development intracellular, length 7.0–10.0 µm, width 5.0–7.0 µm; growth and maturation extracellular, epimerite functional, transparent, crescent - shaped, concave anteriad; protomerite spherical, often retracted into deutomerite in mature individuals; deutomerite elongate ellipsoidal; total length 110.0 µm, width 55.0 µm; nucleus spherical to slightly ovoid, with irregularly distributed peripheral layer of dark granules (chromatin ?), without endosome. Association caudofrontal, satellites 1.3 times larger than primites. Oocyst: Unknown.

TYPE HOST: *Peneus semisulcatus*. Ref. Ball (1959), Janardanan & Ramachandran (1980), Sprague & Couch (1971).

Notes: (For additional information regarding the systematic placement and validity of *Caridohabitans*, see discussion under "Family Porosporidae".)

Genus ***Rotundula***
Goodrich, 1949

Epimerite button - like, persistent; trophozoite round; oocysts small, spherical or subspherical, with equatorial suture; in amphipods. Four named species.

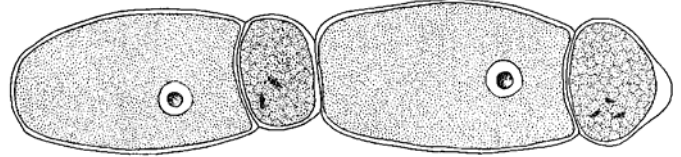


Fig. 7. *Rotundula gammari*. Association. (Based on Goodrich, 1949.)

Rotundula gammari (Diesing, 1859) Goodrich, 1949 (= *Gregarina gammari* von Siebold, 1839; *G. gammari* Diesing, 1859; *Cephaloidophora echinogammari* Poisson, 1921; *G. gammari* Georgévitch, 1951; *C. gammari* [von Frantzius - Seibold, 1848] Théodoridès, 1967) (Fig. 7). Epimerite a round button, persistent in primate; protomerite spherical, with slight tapering anteriad, vacuolated, with 2 or 3 chromatic granules, length 11.0–13.2–15.0 µm (primites), 10.0–12.2–21.0 µm (satellites), width 10.0–18.8–25.0 µm (primites), 10.0–13.6–21.0 µm (satellites); deutomerite ellipsoidal, blunt posteriad, becoming almost spherical with maturity, length 33.0–42.2–58.0 µm (primites), 27.0–33.0–38.0 µm (satellites), width 14.0–27.6–42.0 µm (primites), 12.0–19.2–31.0 µm (satellites); nucleus spherical, diameter 5.0–7.6–9.0 µm; with large central karyosome. Oocyst: Spherical to slightly oval, length 5.0–6.0 µm (Goodrich, 1949); with equatorial suture; liberated from the gametocyst by simple rupture. **Notes:** Narasimhamurti (1964) described the oocysts of *Rotundula gammari* as follows: oval, length 5.5 µm, width 5.0 µm. TYPE HOST: *Gammarus pulex*. Ref. Geus (1967, 1969), Goodrich (1949), Narasimhamurti (1964).

FAMILY CEPHALOLOBIDAE
THÉODORIDÈS & DESPORTES, 1975

Mature trophozoites fixed to stomach epithelium by a differentiation from the protomerite; this protoepimerite is dilated into a sucker and forms lobes which adhere closely to the microvillosities of the stomach epithelium; association precocious, composed of a primate and one or two satellites, these last being placed side by side; in amphipod and decapod crustaceans.

This family contains 2 genera and 5 species, primarily intestinal parasites of crustacea.

Genus ***Cephalolobus***

Kruse, 1959

Development extracellular; association caudofrontal, occurring while attached to host gut, with one, two, or three satellites, satellites smaller than primite; protomerite of satellite without specialized holdfast; in gut of crustacea. Four named species.

Cephalolobus penaeus Kruse, 1959 (Fig. 8).

TYPE SPECIES. Trophozoite: No true epimerite observed; protomerite a subcylindrical cone, length 46.0 µm, width 45.0 µm; modified anteriad to form an adhesive holdfast, with apical margin of 15–40 irregular digitiform lobes; holdfast region set off from remainder of protomerite by a constriction; deutomerite elongate ellipsoidal, length 125.0 µm, width 45.0 µm; with blunt point posteriad; nucleus spherical, diameter 33.0–56.0 µm; with 3–12 spherical endosomes. Association caudofrontal; forming associations with one, two, or three satellites; protomerite length 33.0–85.0 µm (primite), 26.0–52.0 µm (satellite), width 66.0–158.0 µm (primite), 33.0–188.0 µm (satellite); satellite without modified holdfast; deutomerite becoming broadly elliptical in primite, length 99.0–198.0 µm, width 66.0–158.0 µm; remaining elongate ellipsoidal in satellites, length 211.0–376.0 µm, width 33.0–188.0 µm. Oocyst: Unknown. TYPE HOST: *Penaeus aztecus* and *Penaeus duorarum*. Ref. Kruse (1959).

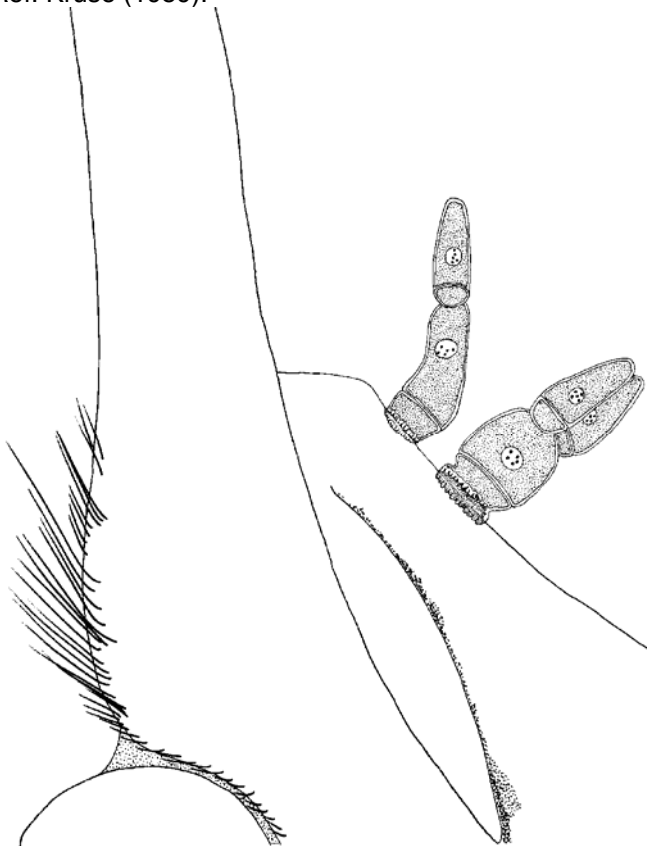


Fig. 8. *Cephalolobus penaeus*. Associations attached to the

thin chitinous sheet between base of host lappet and filter. (Based on Kruse, 1959.)

Genus ***Callynthrochlamys***
Frenzel, 1885

Trophozoite with tubules radiating out into the cytoplasm from the nucleus; syzygy caudofrontal; gametocyst oval; oocyst spherical, liberated in chains; in intestine of amphipods. Monotypic.

Callynthrochlamys phronimae Frenzel, 1885.

TYPE SPECIES. Notes: The genus is poorly described and the exact body form of this species is not well known. However, cytoplasmic, nuclear, and ultrastructural studies do exist. The taxon is based on the unique structure of the nucleus and associated structures. The oocysts are spherical and measure 3.0 µm in diameter (Théodoridès & Desportes, 1975). TYPE HOST: *Phronima sedentaria*. Ref. Desportes & Théodoridès (1969), Dogiel (1910), Frenzel (1885), Grassé (1953), Minchin (1903), Théodoridès & Desportes (1975).

FAMILY URADIOPHORIDAE
GRASSÉ, 1953

Epimerite simple and cylindrical; development extracellular; association caudofrontal (head to tail), precocious; with protomerite of satellite compressing deutomerite of primite; anisogamous; gametocyst opens by simple rupture; oocysts spherical, isolated, with fine equatorial ridge or radial processes.

This family contains 5 genera and 21 species, primarily intestinal parasites of crustacea.

**Key to the genera of Uradiophoridae
(In part)**

- 1. Oocysts spherical2
- 1'. Oocysts ellipsoidal or cylindrical.....3
- 2. (1) Oocysts with a fine equatorial backbone or ridge *Uradiophora*
- 2'. (2) Oocysts with equatorial ray - like processes formed by episore, giving oocyst a star - like appearance *Heliospora*
- 3. (1') Oocysts ellipsoidal, with single polar filament or appendage, emitted in clumps; epimerite a ribbed button *Pyxinioides*
- 3'. (3) Oocysts cylindrical, with polar filaments uniting oocysts into a long chain..... *Bifilida*

Genus ***Uradiophora***

Mercier, 1912

Epimerite simple; development extracellular; satellite with posterior appendix; gametocysts ovoid; oocysts spherical or subspherical, with a fine equatorial backbone or ridge; gametocysts dehisce by simple rupture, oocysts not emitted in chains; in crustacea. Six named species.

Uradiophora cuenoti (Mercier, 1911) Mercier, 1912 (= *Cephaloidophora cuenoti* Mercier, 1911).

TYPE SPECIES. Development extracellular. Young trophozoites (length <80.0 µm) without protomerite deutomerite septum; attached to host epithelium by a simple undifferentiated epimerite. Older trophozoites (length >100.0 µm) with distinct protomerite deutomerite septum; epimerite simple, cylindrical with apical taper, hyaline, length 6.0 µm; with basal tumidus, finely granulated, embedded 1.0–2.0 µm within the host epithelial cells; protomerite hemispherical; deutomerite elongate cylindrical, rounded posteriad; total length 80.0–150.0 µm; nucleus spherical, diameter 4.0–5.0 µm. Association early, precocious, caudofrontal; protomerite of satellite attaching within a depression on the posterior end of the primite deutomerite; satellite with a distinct posterior appendix, marked by a constriction between appendix and deutomerite; total length 300.0–700.0 µm. Oocysts spherical to subspherical, diameter 4.0 µm; with a fine equatorial backbone or ridge; gametocysts dehisce by simple rupture, oocysts not emitted in chains.

TYPE HOST: *Atyaephyra desmaresti*. **Notes:** the oocysts of *Uradiophora cuenoti* are similar in size and shaped to those of *Cephaloidophora communis*; however, the oocysts of *Uradiophora* are released individually and oocysts of *Cephaloidophora* are released in chains. Ref. Mercier (1911, 1912).

Genus ***Heliospora***
Goodrich, 1949

Epimerite simple; mature trophozoites elongate; oocysts roughly spherical, with equatorial ray - like processes formed by the episporic; in amphipods. Three named species.

Heliospora longissima (von Siebold in von Kölliker, 1848) Goodrich, 1949 (= *Gregarina gammari* von Kölliker, 1847; *Didymophes longissima* [von Siebold, 1839] von Frantzius, 1848; *Gregarina longissima* von Siebold in von Kölliker, 1848; *Gregarina millaria* [Zenker] Diesing, 1851); *Gregarina pediepiscolalis* von Wasielewski, 1896; *Uradiophora longissima* [von Siebold in von Kölliker, 1848] Poisson, 1921; *Uradiophora gammari* [von Kölliker, 1847] Poisson, 1924; *Monocystis gammari* Georgévitch, 1951; (Figs. 9–11).

TYPE SPECIES. Epimerite small, button - like, persistant until syzygy; protomerite spherical, length 5.0–6.4–7.0 µm (primite), 4.0–5.0–6.0 µm (satellite), width

7.0–7.2–8.0 µm (primite), 6.0–7.4–10.0 µm (satellite); deutomerite filiform, length 116.0–159.6–191.0 µm (primite), 119.0–135.6–152.0 µm (satellite); nucleus elliptical, length 6.0–8.0–10.0 µm, width 10.0–10.5–12.0 µm; equatorial, with central endosome. Total length up to 228.0 µm, width 8.0–16.0 µm. Association caudofronal, precocious, associations normally binary, but tertiary associations not uncommon. Oocyst: Spherical, slightly flattened at poles, diameter 7.0–8.0 µm; with 6 equatorial ray - like processes, length 10.0 µm; processes formed by the episporic; liberated from the gametocyst by simple rupture. TYPE HOST: *Gammarus pulex*. Ref. Geus (1967, 1969), Goodrich (1949), Kamm (1922), von Kölliker (1848), Lipa (1968).

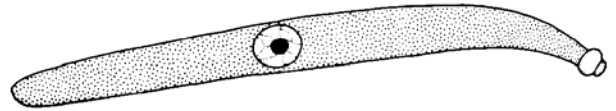


Fig. 9. *Heliospora gammari*. Trophozoite. (Based on Poisson, 1924.)

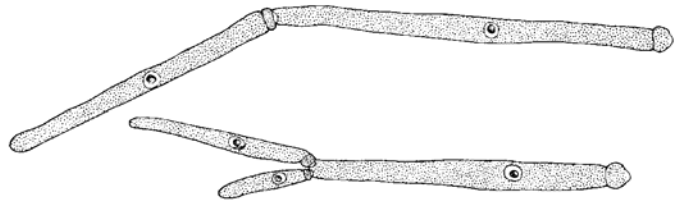


Fig. 10. *Heliospora longissima*. Associations. (Based on Goodrich, 1949.)

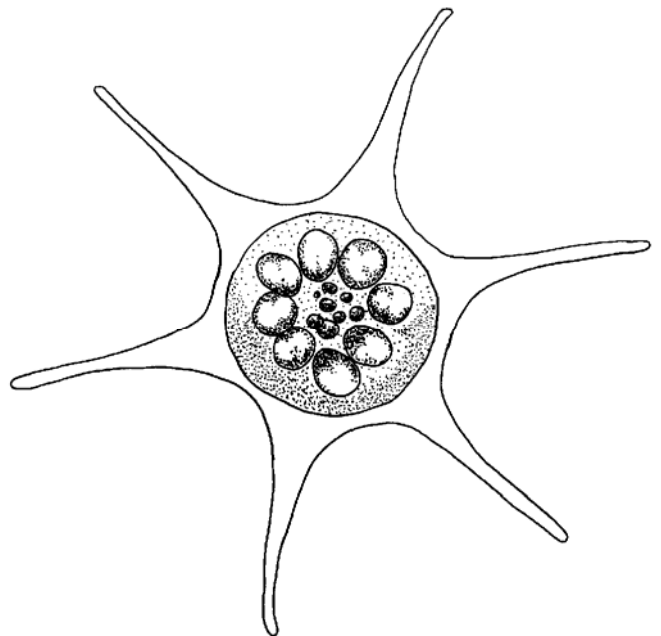


Fig. 11. *Heliospora longissima*. Oocyst. (Based on Goodrich, 1949.)

Genus ***Pyxinioides***
Trégouboff, 1912

Epimerite a ribbed button with 16 longitudinal furrows and a small apical cone, or a cupule with a central trunk; gametocysts dehisce by simple rupture; oocysts unknown or ellipsoidal, with a large appendage at one end, often united in packets; in barnacles. Ten named species.

Pyxinioides balani (Kölliker, 1848) Trégouboff, 1912 (= *Gregarina balani* von Kölliker, 1848) (Figs. 12 - 14).

TYPE SPECIES. Epimerite ribbed button with 16 longitudinal ribs or furrows, with a small apical cone, borne on a neck of varying length; protomerite dome-shaped with anterior taper, with posterior dilation; becoming cylindrical in satellites; deutomerite ellipsoidal, blunt posteriad, with deep constriction at protomerite deutomerite septum; nucleus spherical, large, with a single karyosome. Total length 130.0 µm (primites), 60.0 µm (satellites). Oocyst: unknown. TYPE HOST: *Balanus eburneus*. Ref. Grassé (1953), Henry (1938), Kamm (1922), Théodoridès & Laird (1970), Trégouboff (1912).

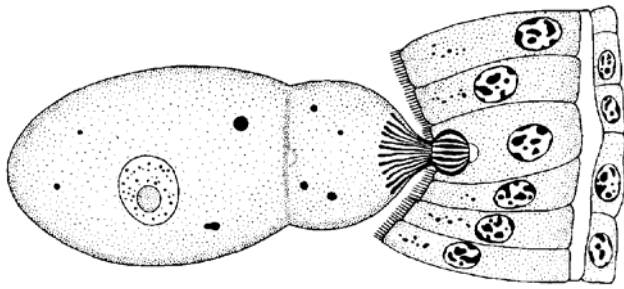


Fig. 12. *Pyxinioides balani*. Trophozoite attached to host intestinal cell. (Based on Trégouboff, 1912.)

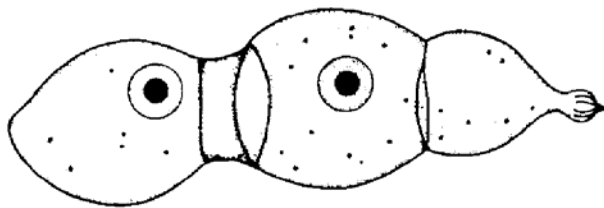


Fig. 13. *Pyxinioides balani*. Syzygy. (Based on Trégouboff, 1912.)

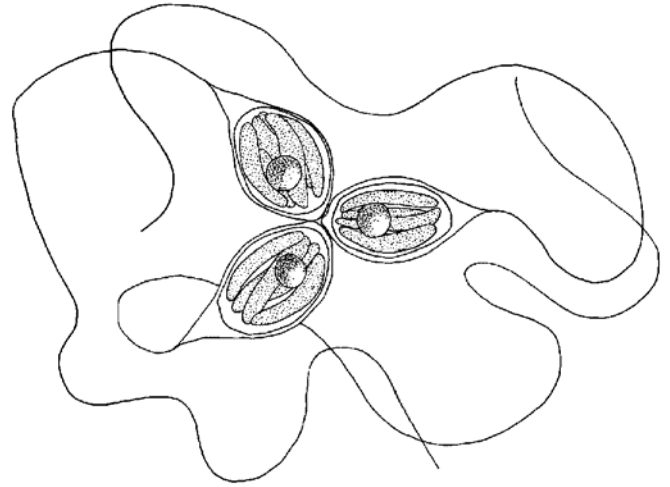


Fig. 14. *Pyxinioides balani*. Oocysts. (Based on Tuzet and Ormières, 1956.)

Genus ***Nematoides***
Mingazzini, 1891

Mature trophozoites vermiform; without septum; epimerite in form of a fork or pincers, on an elongate neck; in barnacles. Monotypic.

Nematoides fusiformis Mingazzini, 1891.

TYPE SPECIES. **Notes:** The genus is poorly described, and to the best of my knowledge, has not been reported since its original description almost a century ago. The validity and position of this genus is speculative. Placement is largely a function of the type host. Additional research is required to ascertain validity. Kamm (1922) includes a transcription of the original description. TYPE HOST: *Balanus perforatus*. Ref. Kamm (1922), Labbé (1899).

Genus ***Bifilida***
Tuzet & Ormières, 1964

Epimerite unknown; oocysts cylindrical, with a long filament at each end, emitted in chains; in barnacles. Monotypic.

Bifilida rara Tuzet & Ormières, 1964 (Fig. 15).

TYPE SPECIES. **Notes:** The description, (especially figure 7, reproduced here in part) of Tuzet & Ormières (1964) is sufficient to diagnose the genus; unfortunately, the type species is not fully described. TYPE HOST: *Chthamalus stellatus*. Ref. Tuzet & Ormières (1964).

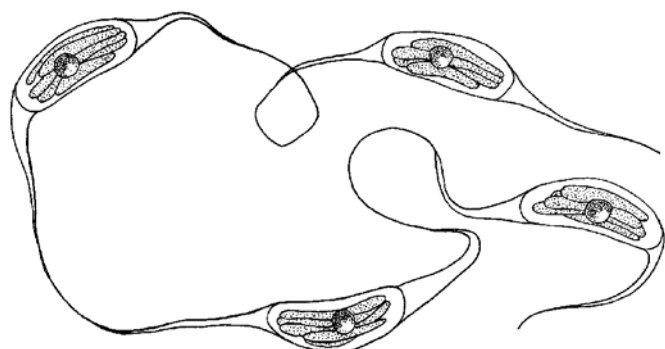


Fig. 15. *Bifilida rara*. Oocysts. (Based on Tuzet and Ormières, 1956.)

FAMILY GREGARINIDAE
LABBÉ, 1899

Epimerite simple; early development intracellular; association caudofrontal, ordinarily early, even very precocious; anisogamy moderately marked; gametocysts with sporoducts; oocysts clearly elongate or cylindrical, symmetrical.

This family contains 15 genera and 352 species, primarily intestinal parasites of insects. Several genera were erected by Levine (1979) to distinguish members of the family that are not parasites of insects.

Key to the genera of Gregarinidae
(In part)

- 1. Protomerite deutomerite septum apparent.....3
- 1'. Protomerite deutomerite septum transitory, vestigial or absent in mature trophozoites and gamonts.....2
- 2. (1') Epimerite absent; oocysts cylindrical -*Gamocystis*
- 2'. (2) Epimerite present; papillate or acicular; oocysts ovoid.....*Garnhamia*
- 3. (1) Epimerite apparent..... *Gregarina* (in part)
- 3'. (3) Epimerite apparently absent.....4
- 4. (3') Protomerite rounded anteriorly, not forming an adhesive disk5
- 4'. (4) Anterior margin of protomerite modified to form a strong adhesive disk*Anisolobus*
- 5. (4) Protomerite with equatorial toroid ring; deutomerite ellipsoidal.....*Torogregarina*
- 5'. (5) Protomerite without equatorial toroid ring; deutomerite filiform.....*Bolivia*

Genus *Gregarina*

Dufour, 1828

(= *Degiustia* Levine, 1979 [in part])

(= *Erhardovina* Levine, 1985 [in part])

Epimerite conical, button - shaped, globular, or cylindrical; association precocious; oocysts doliform, navicular, or spherical; in intestine of insects. Three hundred and seventeen named species.

Notes: Member taxa of *Gregarina* are often problematic and additional study will probably lead to a split of *Gregarina* into several less - inclusive taxa, and/or a shift of many member species to other existing genera. Unfortunately, many taxa within *Gregarina* have been distinguished largely on extrinsic characters (e.g., based on the notion that "a new host species implies a new gregarine species". Reciprocal cross - infections can and should be used to demonstrate host - specificity as an intrinsic character, but such experiments are rarely undertaken.). This practice, while convenient, undermines a fundamental taxonomic imperative: taxa must be based on intrinsic characters. The tendency to base protist systematics on host association has been extended to the generic level. Levine (1979, 1985a) split *Gregarina* and erected four new genera based on host association. The genera *Molluskocystis*, *Erhardovina*, and *Degiustia* all share the intrinsic characters of *Gregarina*. They were established solely on host associations. The fourth genus, *Cirrigregarina*, shares the intrinsic characters of *Gregarina* but also appears to have a unique set of intrinsic characters. The difficulties of this arrangement are addressed below.

Cirrigregarina is monotypic but the placement of its only species has been problematic since the taxon was first described as *Gregarina spissa* Henry, 1938. Henry (1938) provisionally placed the species within *Gregarina*, but was not confident of the affinities. Tuzet and Ormières (1964) were confident that *Gregarina spissa* possessed intrinsic characters differentiating it from *Gregarina*, but could not place it within any existing genus. Levine (1979) established the genus *Cirrigregarina* based on host associations, although other intrinsic characters may justify this arrangement. Thus *Cirrigregarina* is likely a valid genus, although it is poorly studied and ill - defined.

The genus *Molluskocystis* is in dispute. The genus is founded on *Molluskocystis pterotracheae* (Stuart, 1871) Levine, 1979 (= *Gregarina pterotracheae* [Stuart, 1871] Labbé, 1899; *Zygocystis pterotracheae* Stuart, 1871) and is also monotypic. Théodoridès and Desportes (1975) recovered gregarines specimens from Mediterranean pelagic copepods (*Phromia sedentaria*) and larvacean tunicates (*Oikopleura ablicans*) that appear to belong to the same species as those described by Stuart (1871). These specimens also strongly resemble

Cephaloidophora clausii (Frenzel, 1885) Kamm, 1922 (= *Gregarina clausi* Frenzel, 1885; *Gregarina clausii* [Frenzel, 1885] Labbé, 1899). Théodoridès and Desportes (1975) stated that *Gregarina pterotracheae* was synonymous with *Cephaloidophora clausii*, in which case the genus *Molluskocystis* is a *nomen nudum* and invalid. However, the nature of solitary encystation reported for *Cephaloidophora clausii* has not been observed in *Molluskocystis pterotracheae*. Although I favor the interpretation of Théodoridès and Desportes (1975), *Molluskocystis* should stand until additional evidence confirms the synonymy of *Cephaloidophora clausii* and *Molluskocystis pterotracheae*.

The remaining two genera, *Erhardovina* and *Degiustia*, are based solely on extrinsic characters: there is no additional support for their diagnosis as distinct genera. These genera are rejected and declared junior synonymns of *Gregarina*. Their member species are returned to the genus *Gregarina* as follows: *Gregarina scutovertexi* Erhardová, 1955 (= *Erhardovina scutovertexi* [Erhardová, 1955] Levine, 1985); *Gregarina euzeti* Lipa, 1982 (= *Erhardovina euzeti* [Lipa, 1982] Levine, 1985); and, *Gregarina hyalella* Batten and DeGiusti, 1949 (= *Degiustia hyalella* [Batten and DeGiusti, 1949] Levine, 1979). Ref. Batten & DeGiusti (1949), DeGiusti & Delidow (1956), Erhardová (1955), Frenzel (1885), Henry (1938), Kamm (1922), Levine (1979, 1985a), Stuart (1871), Théodoridès & Desportes (1975), Tuzet and Ormières (1964).

Gregarina ovata Dufour, 1828 (= *Clepsidrina conoidea* Hammerschmidt, 1838; *Clepsidrina ovata* [Dufour, 1826] Schneider, 1873;) (Fig. 16).

TYPE SPECIES. Epimerite a simple hyaline knob; protomerite hemispherical, length 24.0–38.7–60.0 µm, width 42.0–80.8–114.0 µm; flattened anteriorly in satellite; with constriction marking protomerite deutomerite septum; deutomerite broadly ellipsoidal, length 186.0–313.0–422.0 µm, width 68.0–150.1–264.0 µm; with blunt point posteriorly; nucleus spherical, diameter 24.0–65.0 µm. Oocyst: Cylindro-elliptic, length 16.0 µm, width 8.0 µm, depth 3.7 µm, with polar truncation; emitted in chains, liberated from the gametocyst through sporoducts. TYPE HOST: *Forficula auricularia*. Ref. Dufour (1828), von Frantzius (1848), Geus (1969), Watson (1916b).

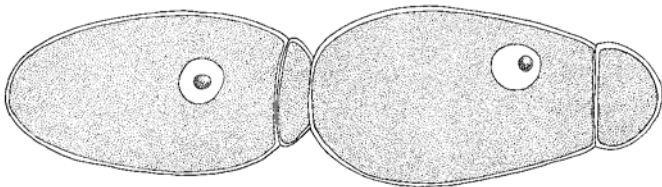


Fig. 16. *Gregarina ovata*. Association. (Based on von Frantzius, 1848.)

Gregarina munieri (Schneider, 1875) Labbé, 1899 (= *Clepsidrina munieri* Schneider, 1875; *Clepsidrina chrysomelae* von Wasielewski, 1896; *Gregarina*

diabrotica Kamm, 1918) (Figs. 17 & 18). Epimerite a small spherical papilla, length 20.0–25.0 µm; borne on a short conical neck; protomerite cylindrical, rounded with slight taper anteriorly, length 96.0–118.6–145.0 µm, width 102.0–129.7–157.0 µm; protomerite deutomerite septum with constriction; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriorly, length 378.0–447.2–602.0 µm, width 179.0–199.9–238.0 µm; nucleus spherical, diameter 48.0–60.0 µm; with spherical karyosome, diameter 20.0 µm, central. Biassociative, caudofrontal, precocious. Gametocyst with 3–6 spore ducts. Oocyst: Doliform, emitted in chains, liberated from the gametocyst through spore ducts.

TYPE HOST: *Timarcha tenebricosa*. Ref. Geus (1969), Labbé (1899), Théodoridès (1988), Watson (1916b).

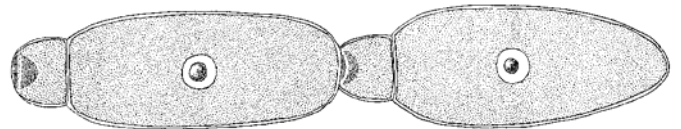


Fig. 17. *Gregarina munieri*. Association. (Based on Schneider, 1875.)

Gregarina cuneata von Stein, 1848 (= *Clepsidrina polymorpha* Hammerschmidt, 1838, in part; *Gregarina*

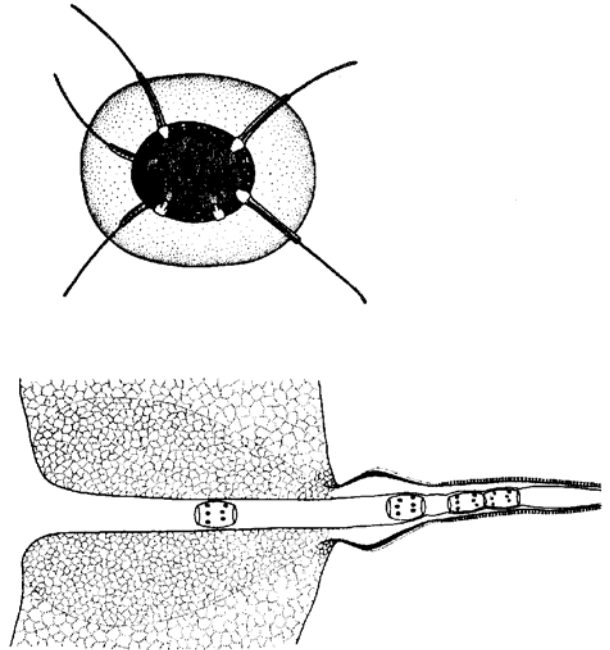


Fig. 18. *Gregarina munieri*. Top, cross-section through a gametocyst showing sporoducts through which oocysts emerge; below, cross-section through a sporoduct containing oocysts. (Top, based on Schneider, 1875; below, based on Schnitzler, 1905.)

polymorpha [Hammerschmidt, 1838] of Lankester, 1863, in part; *Gregarina polymorpha* var. *cuneata* [Hammerschmidt, 1838] Schneider, 1875; *Clepsidrina*

trimosa Schneider, 1875; *Clepsidrina cuneata* [von Stein, 1848] Pfeffer, 1910; *Gregarina xylopi* Crawley, 1903) (Figs. 19 - 22). Epimerite a simple hyaline knob; protomerite spatulate, length 38.4–63.39–115.2 μm , width 24.0–76.1–76.8 μm ; tapering posteriad to protomerite deutomerite septum; dome - shaped in satellites, length 19.2–40.9–86.4 μm , width 28.8–46.7–67.2 μm ; deutomerite elongate cylindrical, primitive length 86.4–189.0–278.4 μm , width 38.4–50.5–105.6 μm ; satellite length 38.4–132.7–211.2 μm , width 43.2–76.1–105.6 μm ; bluntly rounded posteriad; nucleus spherical, with large central endosome. Biassociative, caudofrontal, association precocious. Oocyst: In dorsal aspect doliform with angles roughly squared by enclosing sheath, length 4.9 μm , width 3.9 μm ; rectangular concavity apparent; in pleural aspect dorsum deeply concave, pleuron height 2.9 μm ; emitted in chains; liberated from the gametocyst through sporoducts.

TYPE HOST: *Tenebrio molitor*. Ref. Clopton et al. (1991), von Stein (1848), Watson (1916b).

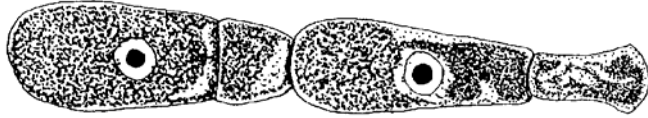


Fig. 19. *Gregarina cuneata*. Association. (Clopton, Percival and Janovy, 1991.)

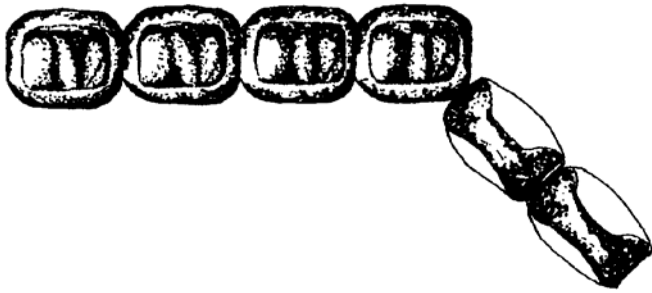


Fig. 20. *Gregarina cuneata*. Dorsal and lateral views of oocysts. (Clopton, Percival and Janovy, 1991.)

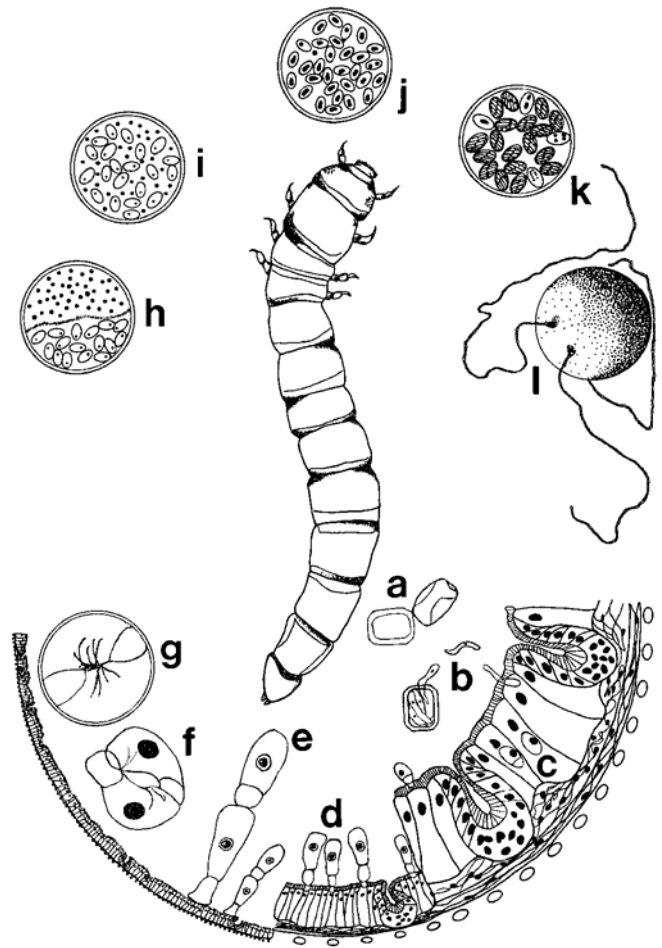


Fig. 21. Life cycle of *Gregarina cuneata* in *Tenebrio molitor*. (a) Oocysts in the environment are consumed by a suitable host; (b) sporozoites activate and excyst in the host gut where they migrate to the intestinal epithelium and undergo; (c) intracellular growth within the epithelium; and, (d) extracellular growth while attached to the epithelium. (e) Trophozoites form reproductive associations; and when mature, (f) undergo syzygy; (g) forming a reproductive gametocyst that is shed to the environment in the host's feces. (h) Gametogony; (i) fertilization; (j) zygote and oocyst formation; and, (k) sporogony occur within the gametocyst. (l) Mature gametocysts dehiscent, releasing infective oocysts into the environment to continue the infection cycle.

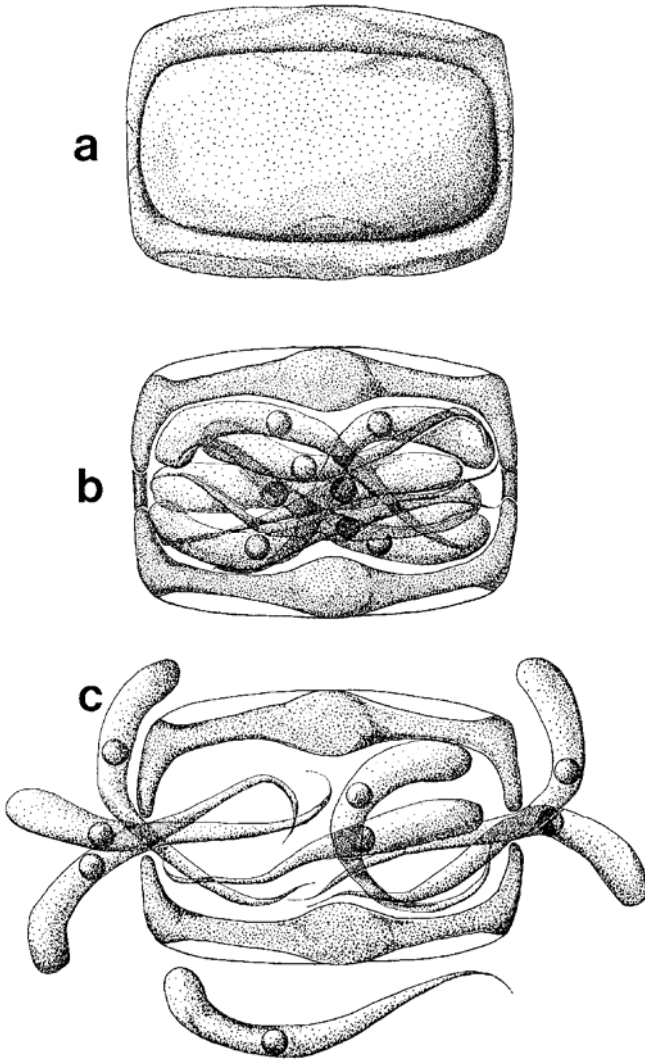


Fig. 22. Excystation of *Gregarina cuneata*: (a) dormant oocyst; (b) activated oocyst with defined lateral walls, polar plugs, and activated sporozoites; (c) excystation of sporozoites through polar canals.

Gregarina steini Berndt, 1902 (Fig. 23). Epimerite a simple globular papilla; protomerite spherical, length 13.2–19.9–33.0 μm , width 22.0–29.37–39.6 μm ; offset, strongly constricted at protomerite deutomerite septum; flattened anteriorly in satellites length 11.0–15.1–22.0 μm , width 15.4–29.6–41.8 μm ; deutomerite elongate obvoid, broadly tapering from the protomerite deutomerite septum to a blunt point posteriorly, primitive length 94.6–126.7–154.0 μm , width 37.4–49.9–63.8 μm ; satellite length 72.6–98.3–121.0 μm , width 36.3–46.8–55.0 μm ; nucleus spherical, with large central endosome. Biassociative, caudofrontal, association precocious. Oocyst: In dorsal aspect spherical with enclosing sheath, diameter 4.9 μm ; elliptical concavity apparent; in pleural aspect elliptical with dorsal scallop, pleuron height 2.9 μm ; emitted in chains; liberated from the gametocyst through sporoducts.

TYPE HOST: *Tenebrio molitor*. Ref. Berndt (1902), Clopton et al. (1991), Watson (1916b).

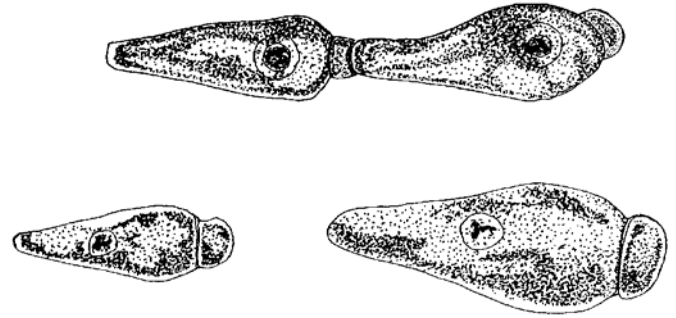


Fig. 23. *Gregarina steini*. Trophozoites and association. (Clopton, Percival and Janovy, 1991.)

Genus ***Gymnospora***
Moniez, 1886

Gametocyst with up to 8 spore ducts; with spherical oocysts. Monotypic.

Gymnospora nigra Moniez, 1886. TYPE SPECIES. With the characters of the genus. Trophozoite: Unknown. TYPE HOST: *Vanessa urticae*. Refs. Levine (1988), Moniez (1886).

Genus ***Triseptata***
H. Hoshide, 1958

Trophozoites biassociative, cylindrical, with body composed of three segments separated by septa; epimerite a simple ovoid knob; oocysts ellipsoidal, extruded in chains. Monotypic.

TYPE SPECIES: *Triseptata fungicola* H. Hoshide, 1958. TYPE HOST: Elotylidae gen. sp. Ref. Levine (1988).

Genus ***Gamocystis***
Schneider, 1875

Epimerite absent; protomerite transitory, lost in mature trophozoites; association precocious; trophozoite body cylindrical, round, or tongue-shaped; oocysts cylindrical; in intestine of insects. Seven named species.

Only very early trophozoites of this genus are septate. This character distinguishes this group from *Gregarina*.

Gamocystis tenax Schneider, 1875 (Fig. 24).

TYPE SPECIES. Epimerite absent; protomerite spherical, transitory; deutomerite variable, round to cylindrical, length 162.0 - 226.75 - 260.0 μm , width 124.0 - 155.5 - 186.0 μm ; often broadly tapering to a sharp point posteriorly; nucleus spherical, diameter 36.0 - 37.5 - 40.0 μm ; with a single elliptical karyosome, length 12.0 -

15.0 μm ; eccentric. Association precocious, frontal, protomerite absent in association. Gametocyst round, with thick outer layer, gelatinous; 15 or more spore ducts present, not extending beyond gelatinous layer. Oocyst: Elongate cylindrical, with rounded poles, length 10.1 μm , width 3.8 μm ; liberated from the gametocyst through spore ducts.

TYPE HOST: *Ectobius lapponicus* (syn. = *Blatella lapponicus*). Ref. Geus (1969), Levine (1988), Schneider (1875), Watson (1916b).

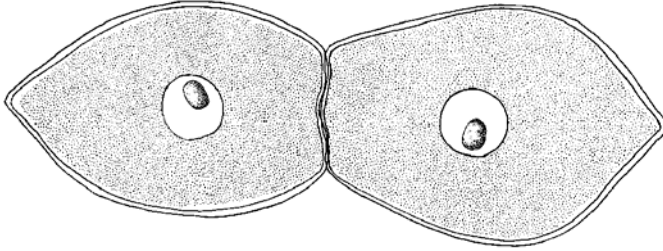


Fig. 24. *Gamocystis tenax*. Frontal syzygy. (Based on Schneider, 1875.)

Genus **Anisolobus**
Vincent, 1924

Epimerite apparently absent, even in youngest stages; anterior margins of protomerite forming a strong adhesive disk; association very early, precocious; gametocysts ellipsoidal, with thick wall; 6 - 8 sporoducts present; oocysts doliform, emitted in chains; in insects. Four named species.

Anisolobus dacnecola Vincent, 1924 (Fig. 25).

TYPE SPECIES. Trophozoite: Epimerite absent; protomerite broadly hemispherical, anterior margin expanding with maturity, forming a large adhesive disk, with multiple lobes; protomerite deutomerite septum present; deutomerite cylindrical, rounded posteriad; nucleus spherical; with a single spherical karyosome. Total length 50.0 - 150.0 μm , width 20.0 - 50.0 μm . Association precocious, adhesive disk lost in satellite, protomerite becoming quadrate. Oocyst: Doliform, length 6.0 μm , width 4.0 μm ; emitted in chains, liberated from the gametocyst through 6 - 8 sporoducts. TYPE HOST: *Dacne rufifrons*. Ref. Levine (1988), Vincent (1924).

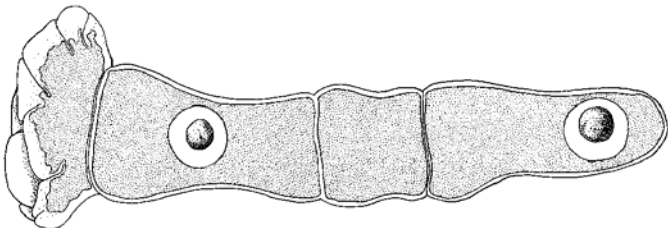


Fig. 25. *Anisolobus dacnecola*. Syzygy. (Based on Vincent, 1924.)

Genus **Anisoloboides**
Théodoridès, 1992

Similar to *Anisolobus*. Eugregarines with bi - associative trophozoites, with globular shape, globular shape conspicuous in primitive; protomerite with 15-20 well - differentiated lobes. Gametocysts spherical; oocysts unknown. Four named species.

Anisoloboides joliveti Théodoridès, 1992.

(Based on Cruz, 1957.)

TYPE SPECIES. Trophozoite: Proto - epimerite (fused protomerite and epimerite) roughly spherical, anterior margin expanding with maturity to form lobes with well - rounded ends, resembling the petals of a flower, lobe number increasing with maturity; cytoplasm of protomerite and deutomerite markedly more opaque than that of lobes; protomerite deutomerite septum present; deutomerite hemispherical, rounded posteriad; nucleus spherical, diameter 10-18 μm . Total length 100.0 μm , lobes undifferentiated; 100.0-150.0 μm , 5-10 lobes; 200.0 μm , 20 lobes present. Association precocious, epimerite lost in satellite, protomerite reduced to a thin transverse band; deutomerite becoming hemispherical. Oocyst: Unknown. TYPE HOST: *Brachyomus histro*. Ref. Théodoridès (1992).

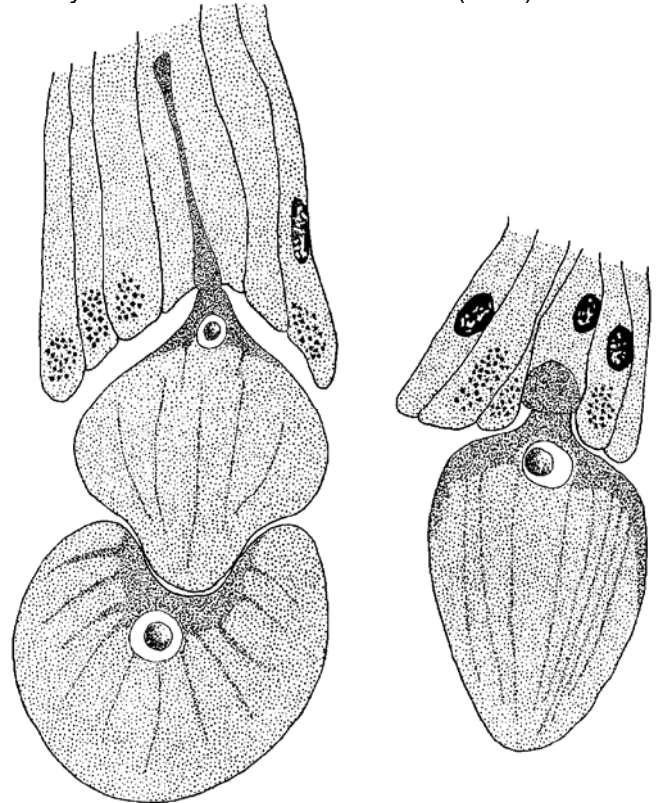


Fig. 26. *Garnhamia aciculata* attached to host epithelium. Left, association; Right, gamont.

Genus **Garnhamia**
Crusz, 1957

Epimerite papillate to acicular; without septum between protomerite and deutomerite (weak hyaline septum?); association takes place while the primite is still attached to midgut epithelium of host; gametocysts with sporoducts; oocysts ovoid, extruded in chains; in silverfish. Monotypic.

Garnhamia aciculata (Bhatia, 1938) Crusz, 1957 (= *Gregarina aciculata* Bhatia, 1938; *Gregarina ctenolepismae* Lindsay, 1939) (Fig. 26).

TYPE SPECIES. TYPE HOST: *Lepisma saccharina*. Ref. Crusz (1957), Levine (1988).

Genus **Amoebogregarina**
Kula & Clopton, 1998

Epimerite amoeboid, constricted at base, retained and structurally incorporated into the protomerite after detachment from host gut epithelium; association precocious, caudofrontal, biassociative; gametocysts ellipsoid, with sporoducts; oocysts dolioform, dehiscing in chains. Monotypic.

Amoebogregarina nigra (Watson, 1915) Kula & Clopton, 1998 (= *Gregarina nigra* Watson, 1915) (Fig. 27).

TYPE SPECIES. Trophozoite: Attached to host ventricular epithelium, solitary or in precocious association. Epimerite amoeboid, offset from the protomerite by a distinct hyaline zone, often constricted basally at junction with protomerite, retained and structurally incorporated into the protomerite after detachment from host gut epithelium length 20.0 - 50.5 μm ; width 54.9 - 105.1 μm . Protomerite oblong to transversely oblong, slightly constricted at protomerite - deutomerite septum; PL 4.5 - 123.7 μm ; PW 2.0 - 126.4 μm . Deutomerite narrowly ovate to roughly square; DL 90.6 - 458.9 μm ; DW .8 - 393.7 μm . TL 7.8 - 570.6 μm . Gamont: Free in midgut, located between host ventricular peritrophic membrane and ventricular epithelium, solitary or in association. Epimerite structurally incorporated into protomerite with maturation. Protomerite oblong to transversely widely oblong; PL 79.8 - 223.4 μm ; PW 57.2 - 240.7 μm ; slightly constricted at protomerite - deutomerite septum. Deutomerite narrowly ovate to oblong; DL 174.2 - 598.5 μm ; DW 66.5 - 320.5 μm . Total length 252.7 - 814.0 μm . Associations: caudofrontal, biassociative; between host ventricular peritrophic membrane and ventricular epithelium. Primite epimerite as in gamont, structurally incorporated into protomerite. Gametocysts: Oblate to transversely elliptic; length 318.7 - 488.0 μm ; width 216.0 - 348.0 μm ; dehiscing through sporoducts 48 - 72 hr after removal from host alimentary canal. Yellow under dissecting microscope. Oocysts: Dolioform. TYPE HOST: *Melanoplus differentialis* (Acrididae: Melanoplinae).

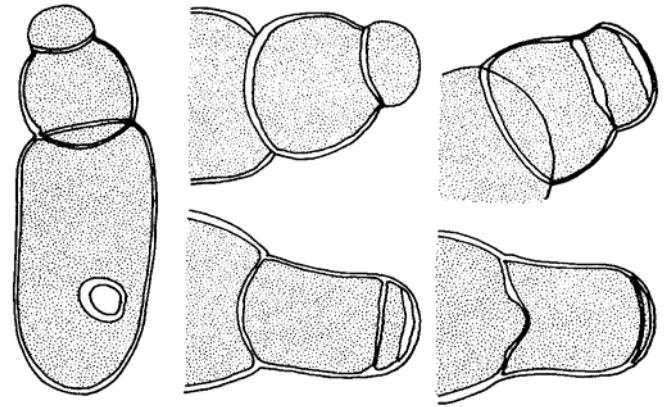


Fig. 27. *Amoebogregarina nigra*. Developmental incorporation of epimerite into protomerite complex.

Genus **Torogregarina**
Geus, 1969

Biassociative; protomerite with a broad swelling around its base; gametocysts round; oocysts ovoid. Monotypic. (Fig. 28, 29)

Torogregarina stammeri Rauchalles in Geus 1969 (Fig. 28).

TYPE SPECIES. Trophozoite: protomerite dome-shaped, length 17.0–20.1–25.0 μm , width 32.0–38.8–45.0 μm ; with a ring-shaped, basal tumidus, width 8.0–10.0 μm ; tumidus set directly anterior to protomerite deutomerite septum; protomerite deutomerite septum strongly constricted; deutomerite elongate ellipsoidal, length 93.0–101.5–112.0 μm , width 60.0–74.9–86.0 μm ; blunt posteriad; nucleus spherical, diameter 16.0–16.9–18.0 μm . Oocyst: Ovoid, length 7.0 μm , width 3.0 μm ; dehiscence not observed. TYPE HOST: *Nosodendron fasciculare*. Ref. Geus (1969), Levine (1988).

Genus **Faucispora**
Baudoin, 1967

Oocysts with ellipsoidal endospore and with episore distended at both ends to form spouts closed by a small cap-valve. Monotypic.

TYPE SPECIES: *Faucispora phryganeae* (Berge - von - Emme, 1912) Baudoin, 1967 (= *Diplocystis phryganeae* Berg - von - Emme, 1912). TYPE HOST: *Phryganea striata*, *Agrypnia pagetana*, *Agrypnia obsoleta*; trophozoites on coelomic surface of larval intestine, gametocysts in coelom of adult. Ref. Levine (1988).

Genus **Spinispora**
Baudoin, 1967

Oocysts fusiform, covered with spines over their whole surface. Monotypic.

TYPE SPECIES: *Spinispora dytisci* Baudoin, 1967.
TYPE HOST: *Dytiscus marginalis* in coelom. Ref. Levine (1988).

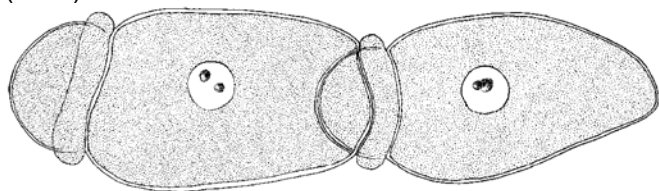


Fig. 28. *Todorogregarina stammeri*. Association. (Based on Geus, 1969.)

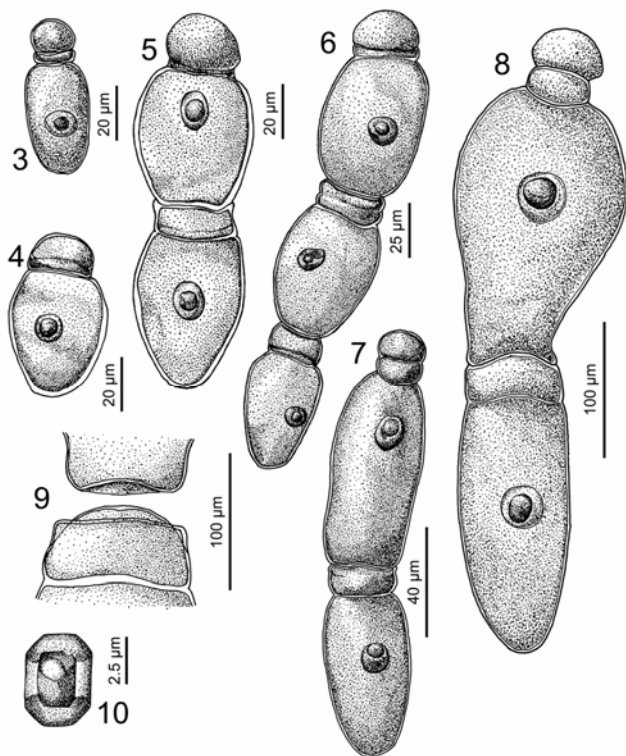


Fig. 29. *Todorogregarina sphinxi*. 3, 4. Trophozoites. 5, 6. Immature associations. 7, 8. Mature associations. 9. Detail of primite-satellite interface. 10. Oocyst.

Genus ***Bolivia***
Corbel, 1968

Trophozoites filiform; protomerite with an anterior depression and often with bulb at base; deutomerite cylindrical, with fine longitudinal striations; gametocysts spherical, with mucilaginous sheath, with a single, short broad sporoduct and a large residuum; oocysts dolioform, not emitted in chains but in an agglomerated mass. Monotypic.

Bolivia vellardi Corbel, 1968 (Fig. 30).

TYPE SPECIES. With the characters of the genus. Oocysts: Dolioform, length 4.0 μ m, width 2.0 μ m. TYPE HOST: *Gryllus* sp. Ref. Corbel (1967a), Levine (1988).



Fig. 30. *Bolivia vellardi*. Trophozoite. (Based on Corbel, 1967a [1968].)

Genus ***Cirrigregarina***
Levine, 1979

Similar to *Gregarina* (epimerite conical, button-shaped, globular or cylindrical; oocysts dolioform, navicular or spherical); found in barnacles. Two named species.

(See discussion of *Cirrigregarina* under "Genus *Gregarina* Dufour, 1828".)

Cirrigregarina spissa (Henry, 1938) Levine, 1979 (= *Gregarina spissa* Henry, 1938) (Figs. 31 & 32).

TYPE SPECIES. Trophozoite: Epimerite spherical or subspherical, length 16.0–31.0 μ m, width 31.0–35.0 μ m; simple, large, with a distinct covering of minute papillae; protomerite hemispherical, with slight anterior truncation, length 24.0–58.0 μ m, width 38.0–88.0 μ m; with deep constriction marking protomerite, deutomerite septum; deutomerite roundly conical, broadly tapering from the protomerite, deutomerite septum to a blunt point posteriad, length 35.0–88.0 μ m, width 40.0–88.0 μ m; nucleus spherical, with a single, large karyosome. Oocyst: Unknown. TYPE HOST: *Balanus cariosus*, *Balanus glandula*. Ref. Henry (1938), Levine (1979).

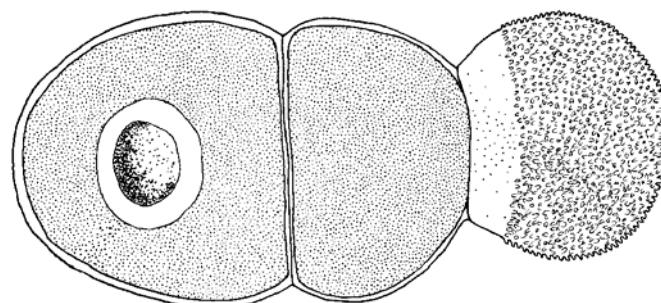


Fig. 31. *Cirrigregarina spissa*. Trophozoite. (Based on Henry, 1938.)

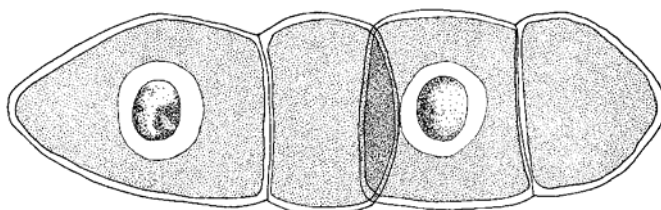


Fig. 32. *Cirrigregarina spissa*. Association. (Based on Henry, 1938.)

Genus ***Molluskocystis***
Levine, 1979

Similar to *Gregarina* (epimerite conical, button - shaped, globular or cylindrical; oocysts doliform, navicular or spherical); found in mollusks. Monotypic.

(See discussion of *Molluskocystis* under "Genus *Gregarina* Dufour, 1828".)

TYPE SPECIES: *Molluskocystis pterotracheae* (Stuart, 1871) Levine, 1979 (= *Zygocystis pterotracheae* Stuart, 1871; *Gregarina pterotracheae* [Stuart, 1871] Labbé, 1899).

TYPE HOST: *Pterotrachea* sp., coelom. **Notes:** Labbé (1899) and Kamm (1922) both provide short descriptions of this species, and Kamm (1922) includes both a sketch based on Stuart's original plates and a short discussion of Stuart's description. The genus *Molluskocystis* was erected to include this single species and distinguish it from *Gregarina* which do not infect mollusks. Ref. Kamm (1922), Levine (1979, 1988).

FAMILY METAMERIDAE
LEVINE, 1979

Epimerite simple; trophozoite with secondary segmentation of protomerite and deutomerite; in annelids.

This family contains 4 genera and 5 species, all parasites of annelids. Levine (1979) established this family to distinguish genera comprised of members with secondary segmentation from other members of Gregarinicae. Gametocysts and oocysts are known only for *Metamera* and *Gopaliella*. Thus the cohesion of this family remains subject to additional research.

Key to the genera of Metameridae

- 1. Secondary segmentation complete (secondary septa complete).....2
- 1'. Secondary segmentation incomplete (evidenced by partial septa).....3
- 2. (1') Protomerite with complete secondary segmentation..... *Cognettiella*
- 2'. (2) Protomerite with protomerite deutomerite septum only, without secondary segmentation..... *Gopaliella*
- 3. (1) Epimerite with branched digitiform processes *Metamera*
- 3'. (3) Epimerite with cupshaped apex, without digitiform processes *Deuteromera*

Genus *Metamera*
Duke, 1910

Epimerite subconical, apex eccentric, with many branched digitiform processes; gametocysts dehiscence by

simple rupture; oocysts biconical, navicular; in leeches. Two species.

Metamera schubergi Duke, 1910 (Fig. 33).

TYPE SPECIES. Isogamous. Trophozoite: Epimerite dome - shaped to subconical, apex eccentric, with a dense corona of branched digitiform processes at juncture with protomerite, with shorter, branched digitiform processes inside corona, without neck; protomerite hemispherical, flattened anteriorly at junction with epimerite, with slight constriction at protomerite deutomerite septum; deutomerite elongate cylindrical, bluntly rounded posteriorly, frequently with evidence of additional segmentation by incomplete septa in posterior third; nucleus spherical, irregular, diameter 18.0 µm; with one large vacuolated karyosome, diameter 8.0 µm; with several smaller karyosomes. Total length 150.0 µm, width 45.0 µm. Oocyst: Biconical to ellipsoid, navicular, length 9.0 µm, width 7.0 µm; with polar "pegs"; liberated from the gametocyst by simple rupture. TYPE HOST: *Glossosiphonia complanata* and *Hemiclepsis marginata*. Ref. Duke (1910).

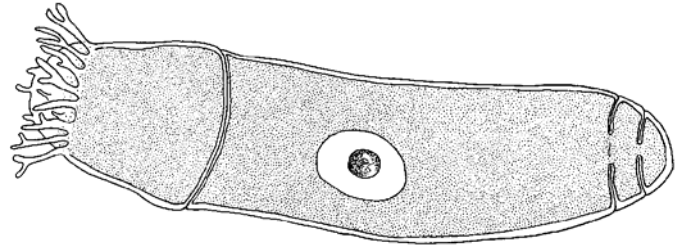


Fig. 33. *Metamera schubergi*. Trophozoite. (Based on Duke, 1910.)

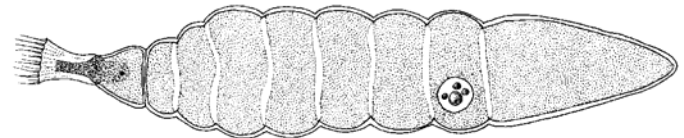


Fig. 34. *Gopaliella marphysae*. Trophozoite. (Based on Ganapati, Kalavati, and Sundaram, 1974.)

Genus *Gopaliella*

Ganapati, Kalavati & Sundaram, 1974

Epimerite umbrella - like, with a central, deeply staining rod; body with many segments (usually 8, occasionally 11); isogamous; oocysts spherical, with 8 sporozoites; gametocysts dehiscence by simple rupture. Monotypic.

Gopaliella marphysae Ganapati, Kalavati & Sundaram, 1974 (Fig. 34).

TYPE SPECIES. Trophozoite: Epimerite an inverted umbrella, opening anteriorly, anterior margin bordered by setaceous cytoplasmic processes; with a deeply staining axial rod; protomerite hemispherical to cardioid, tapering anteriorly to junction with epimerite; deutomerite roughly cylindrical, broadly tapering from the protomerite deutomerite septum to a blunt point

posteriad, with 8–11 segments separated by partial lateral septa, segmentation marked by marginal constrictions, last ultimate segment always the longest; nucleus spherical, placed centrally in penultimate segment, with large eccentric endosome. Total length 840.0 μm , width 120.0 μm . Oocyst: Spherical, diameter 8.0–10.0 μm , octozoic, with residual cytoplasm, liberated from the gametocyst by simple rupture. TYPE HOST: *Marphysa gravelyi*. **Notes:** Levine (1979) states that the oocysts of this genus are biconical. Although this is a direct reflection of the original diagnosis, the original figures and discussion clearly demonstrate that the oocysts are spherical (Ganapati, Kalavati & Sundaram, 1974). I believe that the original plates and discussion are clear, and have made the appropriate changes here. Ref. Ganapati, Kalavati & Sundaram (1974).

Genus *Deuteromera*
Bhatia & Setna, 1938

Epimerite subconical, with a cup - shaped apex; protomerite and deutomerite of trophozoite with incomplete secondary segmentation; syzygy, gametocysts, and oocysts unknown; in polychaetes. Monotypic.

Deuteromera cleava Bhatia & Setna, 1938 (Fig. 35).

TYPE SPECIES. Trophozoite: Epimerite subconical, length 105.0 μm , width 77.0 μm ; with distinct epicystal, longitudinal striations, apex mildly crateriform; protomerite broadly subconical, length 105.0 μm , width 147.0 μm ; protomerite deutomerite septum incomplete, oblique; deutomerite conical, length 192.5 μm , width 203.0 μm ; tapering from junction with protomerite to a blunt point posteriad, with two incomplete transverse septa rising from one lateral margin; nucleus ovoid, large, length 52.5 μm , width 45.5 μm ; posteriad in deutomerite, with a single eccentric karyosome, with peripheral condensed chromatin band. Oocyst: Unknown.

TYPE HOST: *Eunice siciliensis*. Ref. Bhatia and Setna (1938).

Genus *Cognettiella*
Pizl, Chalupský & Levine, 1983

Epimerite simple; protomerite and deutomerite of trophozoite with complete secondary segmentation; syzygy, gametocysts, and oocysts unknown; coelomic, in polychaetes. Monotypic.

Cognettiella legeri Pizl, Chalupský & Levine, 1983 (= *Taeniocystis legeri* Cognetti de Martiis, 1911; *Cognettia legeri* [Cognetti de Martiis, 1911] Levine, 1979) (Fig. 36). TYPE SPECIES. Trophozoite: Epimerite unknown; protomerite hemispherical, divided into 3 secondary segments by distinct septa, cytoplasm distinctly more dense than that of deutomerite; deutomerite elongate cylindrical, with 16–19 additional

secondary segments, secondary segmentation by septa complete; nucleus spherical, irregular, diameter 55.0–92.0 μm ; with large, eccentric karyosome, diameter 20.0–42.0 μm . Total length 700.0–1600.0 μm . Oocyst: Unknown. TYPE HOST: *Kynotus pitarelli*. Ref. Cognetti de Martiis (1911a, 1911b), Levine (1979), Pizl et al. (1983).

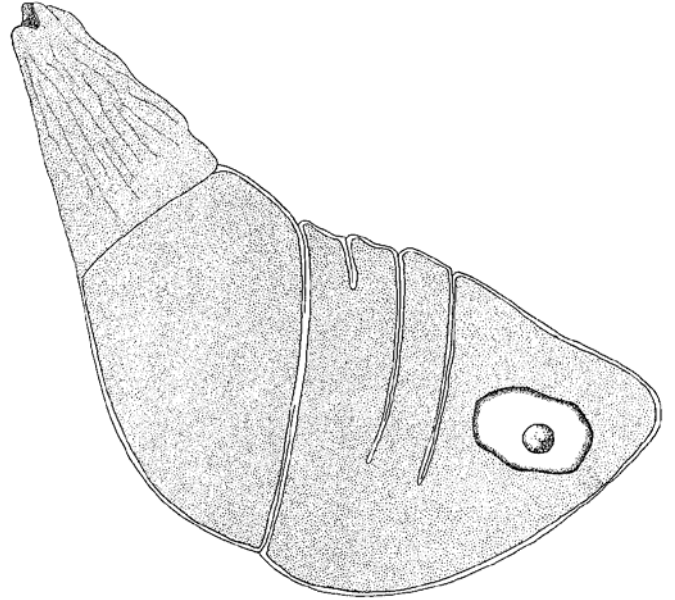


Fig. 35. *Deuteromera cleava*. Trophozoite. (Based on Bhatia and Setna, 1938.)

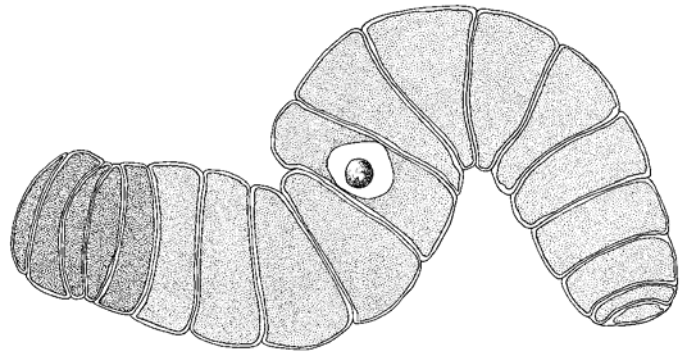


Fig. 36. *Cognettiella legeri*. Trophozoite. (Based on Cognetti de Martiis, 1911b.)

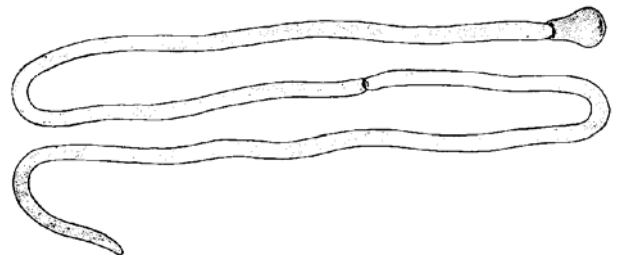


Fig. 37. *Didymophyes gigantea*. Syzygy. (Based on Léger, 1892.)

FAMILY DIDYMOPHYIDAE
LÉGER, 1892

Septum of satellite resorbed more or less slowly during syzygy; gametocysts spherical or somewhat elongate; oocysts with a loose episporangium and an ellipsoidal endospore; oocysts emitted in packets enveloped by a thin membrane (secondary cysts) by means of a single, very long sporoduct with a thin wall.

This family contains 1 genus and 41 species, all parasites of coleopterans. Members of this family possess gametocysts that dehisce through a single, large sporoduct. See Hirmocystidae (below) for a more complete discussion of the relationship between Didymophyidae and Hirmocystidae.

Genus *Didymophyes*
Von Stein, 1848

Epimerite cylindroconical, very degenerate, reduced to a small, pointed papilla; deutomerite with needle-like crystalloids of unknown chemical nature in endoplasm; gametocyst usually spherical; oocysts grouped in spherical packets in gametocysts. Forty-one named species.

All 41 named species of *Didymophyes* are intestinal parasites of beetles of the families Scarabaeidae or Hydrophilidae, and all reported hosts follow a coprophagous life style. Although these observations do not necessarily distinguish members of *Didymophyes*, they do suggest that a uniform set of environmental conditions may be required for development of member gametocysts.

Didymophyes gigantea von Stein, 1848 (= *Gregarina gigantea* Diesing, 1859; *Gregarina gigantea* Lankester, 1863) (Fig. 37).

TYPE SPECIES. Biassociative. Association: Epimerite a cylindroconical papilla; protomerite hemispherical to obovate, wider than deutomerite; protomerite absent in satellite, absorbed by deutomerite of primite; deutomerite cylindrical, very long; primite blunt posteriad at junction with satellite; satellite tapering to a sharp point posteriad; nucleus spherical to slightly ovoid, resting at the junction of the primite deutomerite and the satellite deutomerite, apparently coalescent on association. Total length 1000.0 µm, width 80.0–100.0 µm. Oocyst: Ovoidal, length 6.0 µm, width 6.5 µm; with episporangium. TYPE HOST: *Oryctes nasicornis* Ref. Geus (1969), Léger (1892), Watson (1916b).

FAMILY HIRMOCYSTIDAE
GRASSÉ, 1953

Epimerite ordinarily papilla-like or simple knob-like; gametocysts dehisce by simple rupture; oocysts ellipsoidal, prismatic, fusiform, ovoid, or even spherical.

This family contains 16 genera and 69 species. Members of this family possess gametocysts that dehisce by simple rupture. This character distinguishes Hirmocystidae from their most closely allied family, Didymophyidae.

Hirmocystidae was erected to comprise genera whose gametocysts dehisce by simple rupture rather than through sporoducts. The type genus was originally based on the multiple associations formed by trophozoites in the group (Lábbe, 1899). The state and position of the family has been the topic of some debate. Watson (1916b) placed *Hirmocystis* within the Gregarinidae. Grassé (1953) erected the family Hirmocystidae to comprise *Hirmocystis*, *Didymophyes*, and 5 related genera. This arrangement was accepted and clarified by Chakravarty (1960) who placed the members of Hirmocystidae Grassé with Didymophyidae Léger and declared Hirmocystidae a junior synonym. However, these arrangements failed to recognize differences in gametocyst dehiscence among member genera. Levine (1979) resurrected Hirmocystidae to comprise the nine genera of Didymophyidae *sensu* Chakravarty (1960) whose gametocysts dehisce by simple rupture. This arrangement left Didymophyidae with a single genus, *Didymophyes*. I think that *Didymophyes* forms a cohesive group distinct from members of Hirmocystidae. Levine (1985b) emended Hirmocystidae *sensu* Grassé to include general trends in epimerite structure. In my opinion, this emendation is valid, but should be viewed as a general trend, not a cardinal character. Although subject to change as additional data are gathered, I think that this arrangement is preferable to the more inclusive working concept of Didymophyidae *sensu* Chakravarty (1960). Note that Hirmocystidae *sensu* Grassé has been retained by some current authors (e.g. Vivier and Desportes [1990]).

Key to the genera of Hirmocystidae
(In part)

1. Multiple associations (>2 individuals) common.....2
- 1'. Associations usually binary (2 individuals).....4
2. (1') Associations forming linear chains (3 individuals common, forming chains of up to 10–12 individuals) *Hirmocystis*

- 2'. (2) Associations forming branching chains, or multiple satellites associated side - by - side3
3. (2') Association interface simple; not forming a "tongue and groove" interlocking system *Hyalospora*
- 3'. (3) Association interface with a "tongue and groove" interlocking system *Protomagalhaensia*
4. (1) Oocysts biconical, dolioform, spherical, or ovoidal5
- 4'. (4), Oocysts spindle shaped, with or without polar thickenings6
5. (4) Epimerite retractile *Retractocephalus*
- 5'. (5) Epimerite simple, spherical7
6. (4') Epimerite spherical, hyaline, with a corona of 14–16 ridges; oocysts spindle shaped without polar thickenings *Liposcelisus*
- 6'. (6) Epimerite spherical, with an anterior corona of four distinct sucker - like hyaline disks; oocysts spindle shaped with polar thickenings
..... *Quadruhyalodiscus*
7. (5') Oocysts biconical, dolioform, parasitizing arachnids *Arachnocystis*
- 7'. (7) Oocysts spherical, or ovoidal; with distinct pad forming junction between primites and satellites
..... *Dumbbellicephalus*

Genus ***Hirmocystis***
Labbé, 1899

Epimerite a conical button or papilla, labile; trophozoites often associated in chains; oocysts ovoid, ellipsoidal, or cylindroid, in insects. Thirty - seven named species.

Hirmocystis ventricosa (Léger, 1892) Labbé, 1899 (= *Eirmocystis ventricosa* Léger, 1892)

TYPE SPECIES. Association precocious. Trophozoite: Epimerite a papilla or button, length 20.0 µm, width 15.0 µm; without neck; protomerite narrowly pentagonal, with rounded angles, length 43.0–53.4–62.0 µm, width 33.0–39.9–46.0 µm, without constriction at protomerite deutomerite septum; deutomerite elongate ellipsoidal, length 112.0–124.4–139.0 µm, width 51.0–60.5–68.0 µm; tapering anteriorly to protomerite deutomerite septum, broadly tapering from the anterior third to a blunt point posteriorly; nucleus spherical, diameter 20.0–22.0–24.0 µm; with spherical karyosome, diameter 4.0–6.0 µm; eccentric. Association caudofrontal. Primate: Epimerite lost; protomerite length 51.0–56.0–60.0 µm, width 42.0–45.5–50.0 µm; deutomerite length 123.0–127.0–131.0 µm, width 65.0–65.5–67.0 µm. Satellite: Epimerite lost; protomerite trapezoidal, length 53.0–58.8–63.0 µm, width 45.0–47.8–

51.0 µm; with anterior indentation at junction with primate; deutomerite length 118.0–121.5–126.0 µm, width 67.0–68.0–69.0 µm. Oocyst: Ellipsoid, not fusiform, length 9.0 µm, width 6.0 µm; liberated from the gametocyst by simple rupture. **Notes:** Léger (1892) reports associations with 2 or 3 satellites are common in this species; however, Geus (1969) reported no multiple associations. TYPE HOST: *Tipula oleracea*. Ref. Geus (1969), Kamm (1922), Labbé (1899), Léger (1892).



Fig. 38. *Hirmocystis polymorpha*. Multiple linear syzygy. (Based on Léger, 1892.)

Hirmocystis polymorpha (Léger, 1892) Labbé, 1899 (= *Eirmocystis polymorpha* Léger, 1892) (Fig. 38). Trophozoite: Epimerite a simple cylindrical knob; protomerite hemispherical, length 19.0–20.33–22.0 µm, width 30.0–32.8–35.0 µm; with constriction at protomerite deutomerite septum; deutomerite ellipsoidal, length 119.0–124.2–128.0 µm, width 38.0–40.2–42.0 µm; rounded posteriorly; nucleus spherical, diameter 17.5 µm; with a single compact karyosome, diameter 4.0–7.0 µm. Association caudofrontal. **Notes:** Léger (1892) reports associations with up to 11 satellites of decreasing size arranged linearly or in multiple chains behind the primate. Geus (1969) reports linear associations of no more than 6 animals. Measurements reported above are taken from Geus (1969) and are consistent with the average reported dimensions of primites. Oocyst: Cylindrical, with rounded poles, length 11.4 µm, width 5.5 µm; liberated from the gametocyst by simple rupture. TYPE HOST: *Limnobia* sp., larvae Ref. Geus (1969), Kamm (1922), Labbé (1899), Léger (1892). **Notes:** Kundu et al. (1987) described two gregarine species and placed them within the genus *Didymophyes*. Neither of these species possesses a distinct sporoduct (a cardinal character of Didymophyidae). I have placed these species within *Hirmocystis*: *Hirmocystis indiae* (Kundu, Datta, and Haldar, 1987); Clopton, 1995 comb. nov. (= *Didymophyes indiae* Kundu, Datta, and Haldar, 1987); *Hirmocystis tridactylae* (Kundu, Datta, and Haldar, 1987) Clopton, 1995 comb. nov. (= *Didymophyes tridactylae* Kundu, Datta, and Haldar, 1987).

Genus ***Neohirmocystis***
Ghose, Ray, & Haldar, 1986

Epimerite apparently absent or vestigial; association caudofrontal, early (although some solitary individuals may remain); protomerite deutomerite septum present in satellite; gametocysts dehisce by simple rupture; oocysts spherical. Two named species. **Notes:** Ghose et al. (1986) erected *Neohirmocystis* as the type for a new family to distinguish gregarine forms that apparently

lack an epimerite from other members of the Gregarinicae. All other characters of the two described species of *Neohirmocystis* place them well within Hirmocystidae. The families within Gregarinicae are based largely on dehiscence of the gametocyst: genera within these families are often distinguished by the form of the epimerite (epimerite form is particularly labile within Hirmocystidae). I hesitate to confound the character structure of Gregarinicae at the family level. Thus, I have chosen to place *Neohirmocystis* within the Hirmocystidae. TYPE SPECIES: *Neohirmocystis grassei* Ghose, Ray, and Haldar, 1986. TYPE HOST: *Tribolium castaneum*. Ref. Ghose et al. (1986).

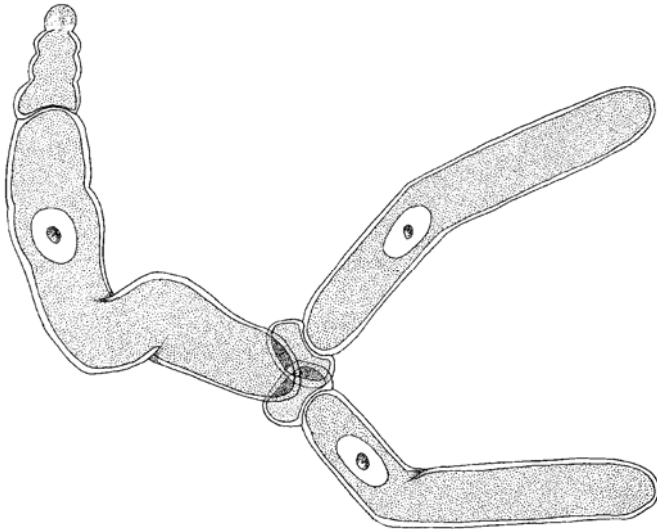


Fig. 39. *Hyalospora roscoviana*. Multiple lateral (branching) syzygy. (Based on Tuzet and Ormières, 1954.)

Genus *Hyalospora*
Schneider, 1875

Epimerite a globular button; young trophozoite endoplasm orange - yellow; oocysts ellipsoidal or fusiform. Nine named species.

Hyalospora roscoviana Schneider, 1875 (Fig. 39).

TYPE SPECIES. Trophozoite: Epimerite a globular papilla; protomerite hemispherical; deutomerite elongate cylindrical, rounded posteriad; nucleus spherical; with distinct spherical endosome. Association caudofrontal, multiple satellites not forming chains. Association total length 500.0 μm . Oocyst: Ovoid, length 14.5–15.5 μm , width 9.6 μm ; with contours angled, with episore rounding polar angles; liberated from the gametocyst by simple rupture. **Notes:** Tuzet and Ormières (1954) reported "formes géantès" as a part of the normal population range of *Hyalospora roscoviana*. These individuals form abortive associations. The association never enters syzygy, but the epimerite persists in the primite and all members of the association grow to abnormal size (associations up to 1000.0 μm in total length). Larsson et al. (1992) have distinguished

populations of these "formes géantès" from normal populations of *Hyalospora roscoviana*, and have placed them in a separate species *Hyalospora gigantea* Larsson, Bach de Roca, and Gaju - Ricart, 1992. TYPE HOST: *Holomachilis maritimus*. Ref. Larsson et al. (1992), Schneider (1875), Tuzet and Ormières (1954).

Genus *Tettigonospora*
L. M. Smith, 1930

Similar to *Hirmocystis*; epimerite spherical; primite resembling satellite; gametocysts dehiscence by simple rupture; oocysts hyaline and spherical. Monotypic.

This genus is poorly studied. In the original diagnosis, Smith (1929) distinguished *Tettigonospora* from *Hyalospora* on the basis oocyst shape and the color of the trophozoite endoplasm. In my experience the color of gregarine endoplasm, especially in parasites taken from orthopteran hosts, appears to be a function of pigments derived from vegetation in the host's diet. The plates in the original description demonstrate differences in oocyst structure, but I do not think the difference is sufficient to distinguish *Tettigonospora* from *Hyalospora*. Although I doubt the validity of this genus, a more appropriate placement would be difficult without incorporating additional observations of *Tettigonospora stenopelmati* within a larger revision of Hirmocystidae.

Tettigonospora stenopelmati (L. M. Smith, 1929) L. M. Smith, 1930 (= *Coccospora stenopelmati*, L. M. Smith, 1929; *Hirmocystis stenopelmati* [L. M. Smith, 1929] Corbel, 1968).

TYPE SPECIES. Trophozoite: Epimerite spherical, diameter 4.1–6.8–8.3 μm ; protomerite hemispherical, length 14.9–18.1–20.7 μm ; deutomerite broadly ellipsoidal, length 33.2–40.1–45.6 μm ; nucleus spherical, with two or more refractile inclusions. Oocyst: Hyaline, spherical, diameter 4.8–5.0 μm ; liberated from the gametocyst by simple rupture. TYPE HOST: *Stenopelmatus fuscus*, *Stenopelmatus pictus*. Ref. Smith (1929, 1930).

Genus *Dumbbellicephalus*
Bala & Kaur, 1988

Epimerite spherical with basal constriction, constriction in anterior portion of protomerite giving the appearance of a "dumbbell"; satellite with a distinct "pad", broad, anteriad, forming junction with primite; gametocysts dehiscence by simple rupture, oocysts spherical or ovoid. Monotypic.

Note: Bala and Kaur (1988) placed this genus within Didymophyidae; however, no sporoduct is reported. As described, this genus is clearly a member of Hirmocystidae. TYPE SPECIES: *Dumbbellicephalus haldari* Bala and Kaur, 1988.

TYPE HOST: *Aulacophora faoviecollis*. Ref. Bala and Kaur (1988).

Genus ***Euspora***
Schneider, 1875

Sporonts solitary; association caudofrontal; gametocysts dehiscence by simple rupture, without sporoducts; oocysts prismatic. Four named species.

TYPE SPECIES: *Euspora fallax* Schneider, 1875.
TYPE HOST: *Rhizotrogus aestivus*.

This genus is poorly defined. In my opinion, our knowledge of the member species, especially *Euspora fallax*, is insufficient to make responsible systematic decisions regarding this group. Ref. Allison (1969), Crawley (1903), Geus (1969), Schneider (1875).

Genus ***Tintinospora***
H. Hoshide, 1959

Trophozoites in associations of two or three; epimerite a simple globular papilla; gametocysts dehiscence by simple rupture; oocysts extruded in chains. Monotypic.

TYPE SPECIES: *Tintinospora soroniae* H. Hoshide, 1959. TYPE HOST: *Soronia japonica*.

Genus ***Arachnocystis***
Levine, 1979

Epimerite simple, spherical; gametocysts spherical, dehiscing by simple rupture, without residuum; oocysts biconical, with truncate ends; in arachnids. Three species.

The type of *Arachnocystis* was originally described in *Sycia*. However, Devdhar and Gourishankar (1971) were forced to redescribe *Sycia* in order to include this species. *Arachnocystis arachnoidea* are septate and described from *Opalina*, while all other members of *Sycia* are aseptate parasites of marine annelids. Levine (1979) erected *Arachnocystis* to alleviate this inconsistency and comprise other members of the superfamily that are parasitic in arachnids and whose gametocysts dehiscence by simple rupture.

Arachnocystis arachnoidea (Devdhar and Gourishankar, 1971) Levine 1979 (= *Sycia arachnoidea* Devdhar & Gourishankar, 1971). TYPE SPECIES. Trophozoite: Epimerite spherical, diameter 20.0 µm; protomerite hemispherical, elongate, length 84.0 µm, width 162.0 µm; tapering anteriorly to juncture with epimerite; deutomerite ellipsoid, slightly elongate, gradually tapering to a rounded point posteriorly; nucleus spherical to slightly ovoid, length 54.0 µm, width 41.0 µm; with 4–6 small karyosomes. Total length 734.0–918.0 µm, width 143.0–238.0 µm. Oocyst: Biconical, length 9.0 µm, width 4.2 µm; liberated from the gametocyst by

simple rupture. TYPE HOST: *Opalina* sp. Ref. Devdhar and Gourishankar (1971), Levine (1979).

Genus ***Acanthogregarina***
Kalavati, Narasimhamurti & Vniduyullatadevi, 1988

Epimerite a disc with approximately 14 peripheral indentations, arranged in two whorls of 7 indentation each; biassociative; gametocysts without sporoducts, oocysts cylindrical to dolioform with thickened poles, released in membrane-bound masses by rupture of the gametocyst. Monotypic.

TYPE SPECIES: *Acanthogregarina hoshidei* Kalavati, Narasimhamurti, and Vniduyullatadevi, 1988. TYPE HOST: *Liogryllus* sp. **Notes:** Kalavati et al. (1988) placed *Acanthogregarina* within the family Actinocephalidae. However, the presence of biassociative trophozoites precludes inclusion within the superfamily Stenophoricae and indicates affinities within Gregarinae. Lack of sporoduct development in the gametocyst is indicative of Hirmocystidae. I believe that *Acanthogregarina* represents a valid genus within Hirmocystidae. Ref. Kalavati et al. (1988).

Genus ***Protomagalhaensia***
Pinto, 1918

Development intracellular; young trophozoites always elongate; associations caudofrontal, with tongue-like interlock; oocysts dolioform, with corner spines, released from gametocyst by simple rupture. Three named species. TYPE SPECIES: *Protomagalhaensia serpentula* (de Magalhaes, 1900) Pinto, 1918 (= *Gregarina serpentula* de Magalhaes, 1900). TYPE HOST: *Periplaneta orientalis*.

Notes: Théodoridès (1952) suggested *Protomagalhaensia marottai* was synonymous with *Gregarina cavalierina*, and that perhaps *Protomagalhaensia* was synonymous with *Gregarina*. Filipponi (1952b, 1952c, 1953) disagreed and presented an experimental case for phenotype variation within *Protomagalhaensia marottai*. Unable to access type specimens or specimens from the type locality, I have examined live and preserved specimens of *Protomagalhaensia granulosa* from *Blaberus discoidalis* and completed the life cycle in the laboratory (Peregrine, 1970). Although Pinto (1922) erected *Protomagalhaensia* largely on the tongue and groove interlock mechanism of association, the method of cyst dehiscence clearly distinguishes members of *Protomagalhaensia* from *Gregarina* and provides the stabilizing intrinsic character of the genus. Ref: Filipponi (1952a, 1952b, 1952c, 1953), Peregrine (1970), Pinto (1922), Théodoridès (1952).

Protomagalhaensia granulosa Peregrine, 1970 (Fig. 40). Trophozoite: Epimerite an elongate papilla,

invasive; protomerite hemispherical; deutomerite rounded, becoming elongate ellipsoidal in mature individuals; nucleus spherical, diameter 15.0 μm ; with large central endosome. Total length 80.0–195.0–360.0 μm . Oocyst: Dolioform, length 7.0 μm , width 4.35 μm ; with one side depressed, with one blunt spine at each corner; liberated in chains from the gametocyst by simple rupture. **Notes:** Association caudofrontal, total length 1620.0 μm ; posterior end of primate fitting into a key - lock depression in anterior end of satellite; multiple associations have been reported. TYPE HOST: *Blaberus discoidalis*. Ref. Peregrine (1970).

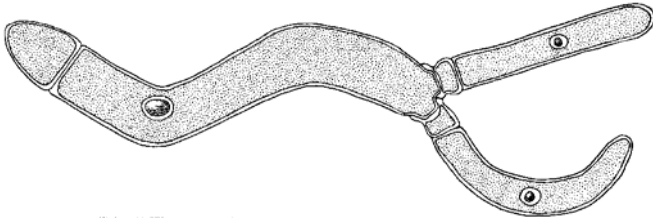


Fig. 40. *Protomagalhaensia granulosa*. Multiple syzygy with key - lock depression interface. (Based on Peregrine, 1970.)

Genus *Eliptocystis*

Sengupta, Ghosh & Haldar, 1991

Early development extracellular; young trophozoites elongate; associations caudofrontal, (with notched interlock); oocysts spherical, released from elliptical gametocyst by simple rupture. Monotypic. TYPE SPECIES: *Eliptocystis triboli* Sengupta, Ghosh and Haldar, 1991.

TYPE HOST: *Tribolium castaneum*.

Eliptocystis triboli Sengupta, Ghosh and Haldar, 1991. Trophozoite: Epimerite a simple hyaline papilla; protomerite hemispherical; deutomerite elongate ellipsoidal, becoming broadly ellipsoidal in mature individuals; nucleus subspherical, diameter 5.0–7.0 μm ; with distinct endosome. Mature total length 24.3–84.5–159.3 μm ; width 10.8–20.3–35.1 μm . Oocyst: Spherical, length 17.6 μm , width 15.1 μm ; liberated from the ellipsoidal gametocyst by simple rupture. **Notes:** Sengupta et al. (1991) placed *Eliptocystis* within the family Cephaloidophoridae, but found the morphology comparable with that of *Uradiophora* and *Pyxinioides* (both within Uradiophoridae). However, the presence of equatorial ridges or radial process on the oocyst is a cardinal character for inclusion in either family. No such elaborations of the oocyst are reported for *Eliptocystis*. I believe that *Eliptocystis* is a member of Hirmocystidae. The current placement within the family reflects the strong developmental similarities and association interlocks shared by *Eliptocystis* and *Protomagalhaensia*. TYPE HOST: *Tribolium castaneum*. Ref. Sengupta et al. (1991).

Genus *Pintospora*

Carini, 1944

Trophozoites at first intra - and then extracellular; gametocysts with smooth wall; oocysts unite in pairs, each one with thickened, rather pointed ends, with smooth walls, frequently free in coelomic cavity of host. Monotypic. TYPE SPECIES: *Pintospora bigemina* Carini, 1944. TYPE HOST: *Astylyus atromaculatus*.

Genus *Endomycola*

Théodoridès, Desportes, & Jolivet, 1972

Trophozoites solitary and globular, with button - like epimerite and spherical nucleus; entocyte and ectocyte very chromophilic; gametocysts and oocysts unknown. Two named species. TYPE SPECIES: *Endomycola baiyeri* Théodoridès, Desportes, and Jolivet, 1972. TYPE HOST: *Encyomon ruficollis*.

Théodoridès, Desportes, and Jolivet (1972), distinguished *Endomycola* from existing genera based on the form of the epimerite. They describe the following unique characters: paraglycogen storage vacuoles in the epimerite proper, and an enclosing epicytic mantle that effectively encloses both the protomerite and the epimerite, stretching from the apical margins of the epimerite to the edges of the protomerite. Théodoridès, Desportes, and Jolivet (1972) established *Endomycola* as a provisional genus, and lacking additional information, did not align *Endomycola* with any existing family. The current placement is after Levine (1988), and is subject to change as additional data are gathered. Ref. Théodoridès, Desportes, and Jolivet (1972).

Genus *Retractocephalus*

Haldar & Chakraborty, 1976

Epimerite globular, retractile into protomerite; initial development intracellular; association head to tail (caudofrontal); oocysts dolioform, liberated from the gametocyst in chains by simple rupture. Six named species.

Retractocephalus raphidopalpae (Haldar and Chakraborty, 1976) Haldar, Chakraborty & Kundu, 1982 (= *Retractocephalus raphidopalpii* Haldar and Chakraborty, 1976). TYPE SPECIES. Trophozoite: Initial development intracellular; epimerite globular, simple, hyaline, retractile (eversible ?); length 7.5–10.0–15.0 μm ; protomerite cylindrical, elongate, rounded anteriorly, length 15.0–26.5–32.5 μm , width 17.5–22.0–27.5 μm ; with anterior depression to receive retracted epimerite; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriorly, length 35.0–83.0–92.5 μm , width 20.0–28.5–37.5 μm ; nucleus spherical to slightly ovoid, with 1 or 2 karyosomes. Oocyst: Dolioform, length 7.0 μm , width 4.0 μm ; liberated in chains from the

gametocyst by simple rupture. TYPE HOST: *Rhaphidopalpa foveicollis*. Ref. Haldar and Chakraborty (1976), Haldar et al. (1982).

Genus *Liposcelis*
Sarkar & Haldar, 1980

Epimerite spherical, hyaline, with a corona of 14 to 16 ridges; gametocysts simple, dehiscing by simple rupture; oocysts spindle - shaped. Monotypic.

TYPE SPECIES: *Liposcelis coronata* Sarkar and Haldar, 1980. TYPE HOST: *Liposcelis* sp.

Sarkar and Haldar (1980) erected *Liposcelis* within Didymophyidae *sensu* Chakravarty (1960). Members of Didymophyidae possess gametocysts that dehiscence through a single, long, sporoduct; distinguishing them from Hirmocystidae, whose members possess gametocysts dehiscing by simple rupture. Members of *Liposcelis* possess gametocysts dehiscing by simple rupture, and clearly are not Didymophyidae. Although the epimerites of *Liposcelis* are not typical of those encountered among Hirmocystidae, I believe that the described epimerite structure of Hirmocystidae notes a general trend not a cardinal character. Thus I have placed this genus within Hirmocystidae. Ref. Sarkar and Haldar (1980).

Genus *Quadruhyalodiscus*
Kundu & Haldar, 1984

Epimerite spherical, with a corona of four anterior sucker - like hyaline disks, with short neck; trophozoites biassociative; gametocysts dehiscence by simple rupture; oocysts spindle - shaped (narrowly elliptic), with polar thickenings; development extracellular. Monotypic.

Kundu and Haldar (1984) placed *Quadruhyalodiscus* in Didymophyidae *sensu* Chakravarty (1960). Members of *Quadruhyalodiscus* possess gametocysts dehiscing by simple rupture. This indicates that they are more closely allied with Hirmocystidae than Didymophidae. Although the epimerites of *Quadruhyalodiscus* are not typical of those encountered among Hirmocystidae, I believe that the described epimerite structure of Hirmocystidae notes a general trend not a cardinal character. Thus I have placed this genus within Hirmocystidae. Additional discussion is contained under genus *Liposcelis* above.

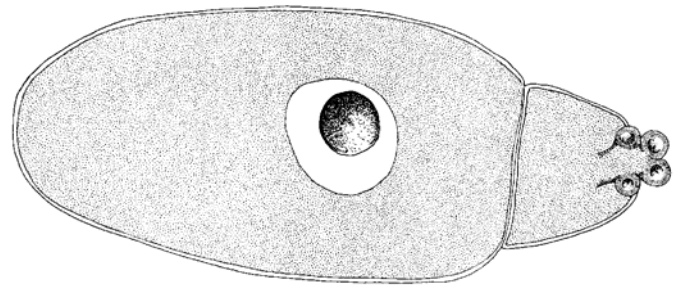


Fig. 41. *Quadruhyalodiscus gallerucidae*. Trophozoite. (Based on Kundu and Haldar, 1984.)

***Quadruhyalodiscus gallerucidae* Kundu & Haldar, 1984 (Fig. 41).**

TYPE SPECIES. Trophozoite: Epimerite a corona of four sucker - like hyaline disks, length 59.5–126.8–172.1 μm , width 8.5–11.8–17.0 μm ; borne on a short neck; protomerite hemispherical to conical, length 12.7–22.1–29.7 μm , width 19.1–11.8–17.0 μm ; deutomerite cylindrical, length 38.2–92.5–131.7 μm , width 23.2–36.7–68.0 μm ; broadly tapering from the protomerite deutomerite septum to a blunt point posteriad, without epicyteal striations; nucleus slightly ovoid, length 8.5–13.2–18.0 μm , width 7.4–12.4–18.0 μm ; with large central endosome. Mature trophozoites with total length 97.7–200.9–267.7 μm . Oocyst: Narrowly elliptic, length 11.6 μm , width 4.4 μm ; smooth, with thick spore wall and polar spore wall thickenings; liberated from the gametocyst by simple rupture.

TYPE HOST: *Gallerucida bicolor*. Ref. Kundu and Haldar (1984).

SUPERFAMILY STENOPHORICAE
LEVINE, 1984
(= SOLITARICAE CHAKRAVARTY, 1960)

Homoxenous, trophozoites solitary; development intracellular or extracellular; epimerite simple or complex; gametocysts with or without sporoducts.

This superfamily contains 14 families with ~103 genera and ~568 named species. Its members are differentiated from Porosporidae by a monogenic (one host) life cycle in which sporogony is completed in the gametocyst. Members of Stenophoricae characteristically remain solitary until the onset of syzygy, that is, they do not form associations prior to the onset of gametocyst formation. This distinguishes them from Gregarinicae members of which characteristically form early or precocious associations, that is, they form associations before maturity and long before the onset of syzygy.

Key to the families and subfamilies of Stenophoricae
(In part)

- 1. Gametocysts dehisce through sporoducts2
- 1'. Gametocysts dehisce by simple rupture, without sporoducts3
- 2. (1) Gametocysts with a single sporoduct; oocysts ellipsoidal or ovoida Monoductidae
- 2'. (2) Gametocysts with > 1 sporoduct, oocysts dolioform (keg - shaped) Leidyaniidae
- 3. (1') Protomerite deutomerite septem present; protomerite apparent in all growth stages4
- 3'. (2') Protomerite deutomerite septum present in young trophozoites only, atrophied in mature trophozoites and gamonts (i.e. mature trophozoites and gamonts apparently without protomerite) Sphaerocystidae
- 4. (3) Epimerite apparent in mature trophozoites, complex or at least strongly differentiated6
- 4'. (4) Epimerite in mature trophozoites absent, vestigial, invaginated, or reduced to a small cap or spherule5
- 5. (4') Epimerite in mature trophozoites absent or reduced and invaginated; oocysts ovoidal or ellipsoidal, with or without equatorial suture Stenophoridae
- 5'. (5) Epimerite in mature trophozoites reduced to a small cap or spherule; oocyst ellipsoidal Cnemidosporidae
- 6. (4) Epimerite varied; if a cupule, cone, or sucker, without digitations7
- 6'. (6) Epimerite a cupule, cone, or sucker; with digitations Dactylophoridae
- 7. (6) Epimerite with "bristles" or epicytic processes resembling a beard8
- 7'. (7) Epimerite varied, if present epicytic processes strong, digitate or hooked; not bristle - like9
- 8. (6) Epimerite with anterior bristles only, forming a fine anterior brush; oocysts spherical, with fine brush border Brustiphoridae
- 8'. (8) Epimerite with anterior and lateral bristles forming a dense beard; oocysts cylindrical, smooth Trichorhynchidae
- 9. (7') Oocysts biconical, cylindrobiconical, crescentic or irregular, liberated singly or in clumps, but not in chains; gametocyst with or without secondary cyst wall, when present usually loose and gelatinous Actinocephalidae 10
- 9'. (9) Oocysts purse - shaped or hat - shaped, dark brown or black, emitted in chains; gametocyst with loose, rugose, secondary cyst wall Stylocephalidae

- 10. (9) Oocysts smooth11
- 10'. (10) Oocysts with spines or thickenings at their poles, sometimes with spines along edges and equator Actinocephalidae; Acanthosporinae
- 11. (10) Oocysts biconical, cylindrobiconical or irregular; epimerite varied Actinocephalidae; Actinocephalinae
- 11'. (11) Oocysts crescentic Actinocephalidae; Menosporinae

**FAMILY STENOPHORIDAE,
LÉGER & DUBOSCQ, 1904**

Early development intracellular; epimerite absent or reduced to an invaginated form; syzygy head to tail, late (just before encystment); anisogamy accentuated, gametocysts open by simple rupture, eliminating oocysts singly; oocysts ovoid or ellipsoidal, with very ample epispore, with or without equatorial suture; in diplopods.

This family contains 3 genera and 93 species, all intestinal parasites of millipedes. *Stenophora* is by far the most taxonomically common genus, with 84 named species.

Genus *Stenophora*

Labbé, 1899

(= *Stenocephalus* Schneider, 1875)

(= *Spirosoma* Ishii, 1915)

Development intracellular; oocysts ovoid, with prominent equatorial suture. Eighty - eight species. *Stenophora larvata* is illustrated in Fig. 42.

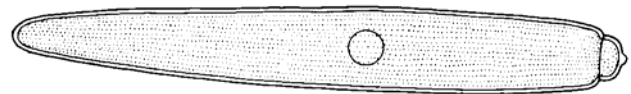


Fig. 42. *Stenophora larvata*. Trophozoite. (Based on Watson, 1916b.)

Stenophora juli (Frantzius, 1846), Labbé, 1899, the type species of this genus, has been debated for the better part of 100 years. Although there is no question that the species is valid, there does not appear to be a description sufficient to distinguish *Stenophora juli* from other members of the species complex. Additional information is required, preferably in the form of a stabilizing redescription. TYPE HOST: *Schizophyllum sabulosum* (= *Julus sabulosus*). Notes: In his original description of *Stenophora juli* (= *Gregarina juli*), von Frantzius (1848) reported the host simply as *Julus*. The

current description of the species is also based on the work of Schneider (1875), who worked with gregarines taken from *Schizophyllum sabulosum*. The reported distribution of *S. sabulosum* overlaps the collecting area of von Frantzius, thus *S. sabulosum* is accepted as the type host of *Stenophora juli*.”

Stenophora negotiosus Ramachandran, 1974 (Fig. 43). Trophozoite: Early development intracellular; epimerite a single anterior papilla, replaced by a closed apical pore in mature individuals; protomerite dome-shaped, length 30.0–62.5–105.0 µm, width 60.0–91.2–180.0 µm; tapering anteriorad to the apical pore; deutomerite elongate ellipsoidal, length 720.0–1282.2–2100.0 µm, width 120.0–218.8–345.0 µm; blunt posteriorad, length 46.7–125.3 µm, width 11.7–42.5 µm; nucleus fusiform, length 75.5–137.5 µm, width 18.55–37.5 µm; with large central endosome. Oocyst: Ovoid, length 4.05 µm, width 2.7 µm; without hyaline episporium; liberated from the gametocyst by simple rupture. TYPE HOST: *Phyllogonostreptus negotiosus*. Ref. Ramachandran (1972).

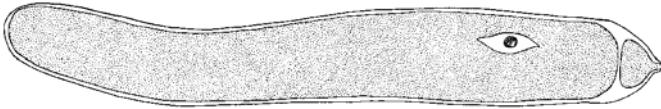


Fig. 43. *Stenophora negotiosus*. Trophozoite. (Based on Ramachandran, 1974.)

Stenophora akiyoshiensis H. Hoshide, Wakagi, & K. Hoshide, 1970. Trophozoite: Early development intracellular; epimerite a single anterior papilla, replaced by an apical pore in mature individuals; protomerite subglobular, rounded, tapering to a cone anteriorad, length 8.0–17.0–24.0 µm, width 11.0–18.5–32.0 µm; retractile in intracellular forms; deutomerite cylindrical to elongate ovoid, length 20.0–115.6–218.0 µm, width 12.0–31.2–55.0 µm; tapering from the equator to a blunt point posteriorad; nucleus ellipsoidal, length 35.0 µm, width 20.0 µm; with large ovoidal endosome. Oocyst: Unknown. TYPE HOST: *Skleroprotopus ikedai*. Ref. H. Hoshide et al. (1970).

Genus *Fonsecaia*
Pinto, 1918

Development intracellular; oocysts elongate ovoid, without equatorial ridge. Monotypic. TYPE SPECIES: *Fonsecaia polymorpha* Pinto, 1918. TYPE HOST: *Orthomorpha gracilis*.

Genus *Hyalosporina*
Chakravarty, 1935

Epimerite a diskoid collar (bordered with fine, invasive rootlets in mature trophozoites), with central tongue-like papillae; without neck; nucleus attached to posterior end of deutomerite by two lateral bundles of

myonemes; anisogamous; oocysts ovoid, with large polar episporium. Four species.

Hyalosporina cambolopsis Chakravarty, 1935 (= *Hyalosporina cambolopsisae* Chakravarty, 1935) (Figs. 44 & 45).

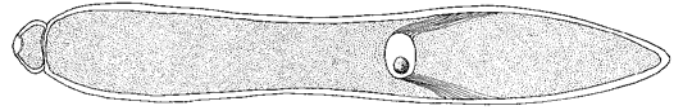


Fig. 44. *Hyalosporina cambolopsis*. Trophozoite with nucleus tethered by myoneme bundles. (Based on Chakravarty, 1935.)

TYPE SPECIES. Trophozoite: Epimerite a diskoid collar which adheres to the host epithelium, bordered with fine, invasive rootlets in mature trophozoites; with tongue-like papillae, central, invasive; without neck; protomerite conical, small, length 48.5 µm, width 61.0 µm; deutomerite elongate ellipsoid, length 799.0–913.2–1111.0 µm, width 80.0–111.0 µm; with slight equatorial constriction, sharply tapering in posterior 1/4 to a sharp point posteriorad; nucleus spherical to irregularly ovoid, length 35.0 µm, width 55.0 µm; with large central endosome, diameter 15.0 µm; attached to posterior end of deutomerite by two lateral bundles of myonemes. Oocyst: Ovoid, with conspicuous, assymetrical, hyaline episporium, length 8.0 µm, width 6.0 µm; liberated from the gametocyst by simple rupture.

TYPE HOST: *Cambolopsis* sp. Ref. Chakravarty (1935).

Genus *Leidyana*
Watson, 1915

Syzygy late; epimerite a simple globular knob; oocysts liberated from gametocyst through spore ducts (dehiscence by spore ducts); spores dolioform. Twenty - two species. Fig. 46 - 48. The life cycle is illustrated in Fig. 48.

Leidyana erratica (Crawley, 1907) Watson, 1916 (= *Gregarina achetaeabbreviatae* Leidy of Crawley[1903]; *Stenophora erratica* Crawley, 1907; *Leidyana solitaria* Watson, 1915) (Fig. 46). TYPE SPECIES. Trophozoite: Trophozoites solitary, never associative before syzygy; epimerite a simple knob, spherical, width 30.0 μ m; borne on a short neck; protomerite broadly conical, length 50.0-66.6-80.0 μ m, width 50.0-81.66-110.0 μ m; equatorially dilated, conspicuously constricted at protomerite deutomerite septum; deutomerite cylindrical to elongate ellipsoidal, length 240.0-356.6-420.0 μ m, width 60.0-131.6-160.0 μ m; sometimes tapering posteriad, always bluntly rounded posteriad; nucleus spherical; with 1 or 2 small karyosomes. Oocyst: Dolioform; length 6.0 μ m, width 3.0 μ m; liberated from the gametocyst in long chains through multiple spore ducts, usually 1 to 12. TYPE HOST: *Gryllus abbreviatus*. Ref. Corbel (1967b), Crawley (1907), Watson (1915, 1916b).

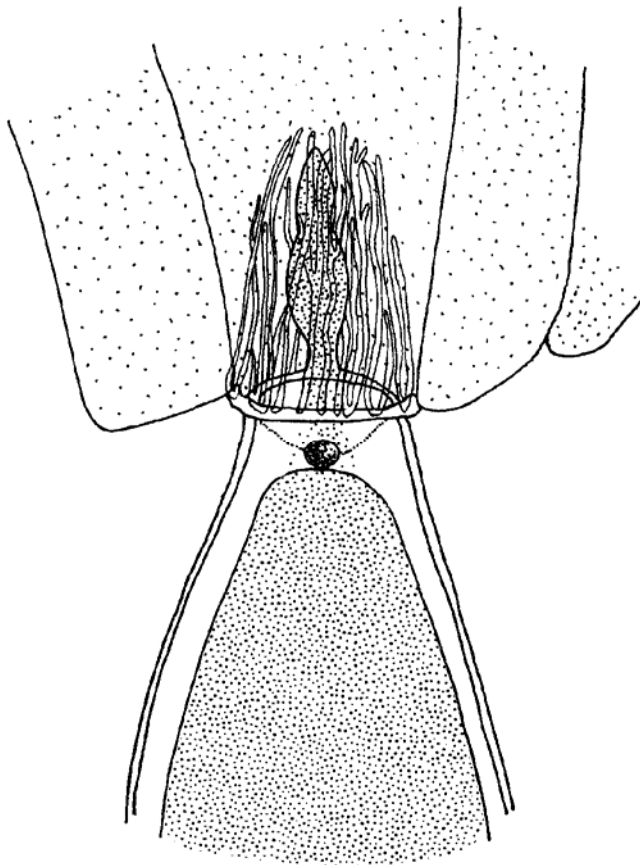


Fig. 45. *Hyalosporina cambolopsis*. Trophozoite with epimerite embedded in host epithelial cell. (Based on Chakravarty, 1935.)

FAMILY LEIDYANIDAE
KUDO, 1954

Similar to Gregarinidae, (epimerite simple; early development intracellular; syzygy caudofrontal, anisogamy moderately marked; gametocysts with sporoducts; oocysts clearly elongate or cylindrical, symmetrical), but solitary; epimerite simple, knob - like, gametocysts with several sporoducts; oocysts dolioform.

This family contains a single genus, *Leidyana*, with 29 named species. All are parasites of insects, primarily lepidopterans and orthopterans.

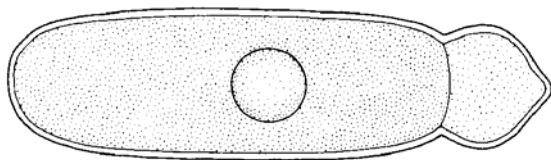


Fig. 46. *Leidyana erratica*. Trophozoite. (Based on Crawley, 1903.)

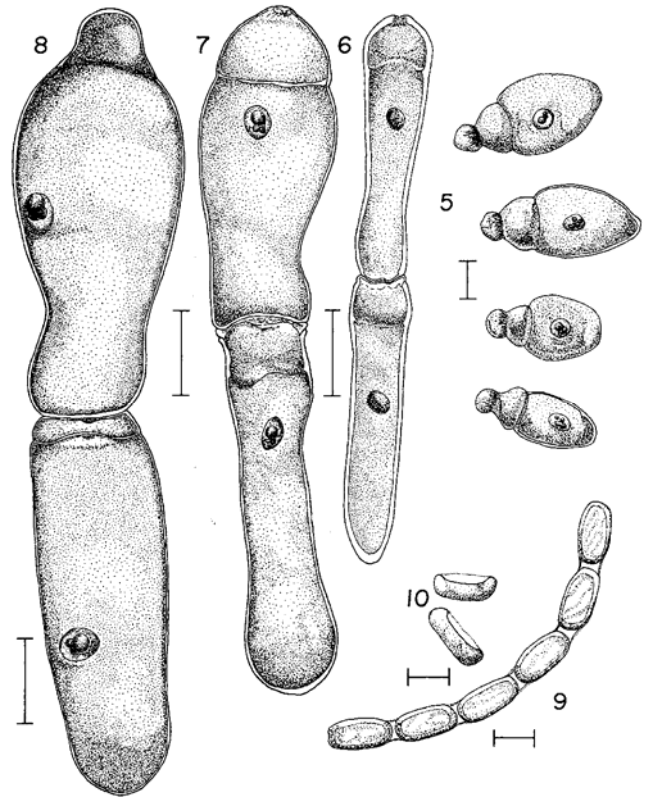
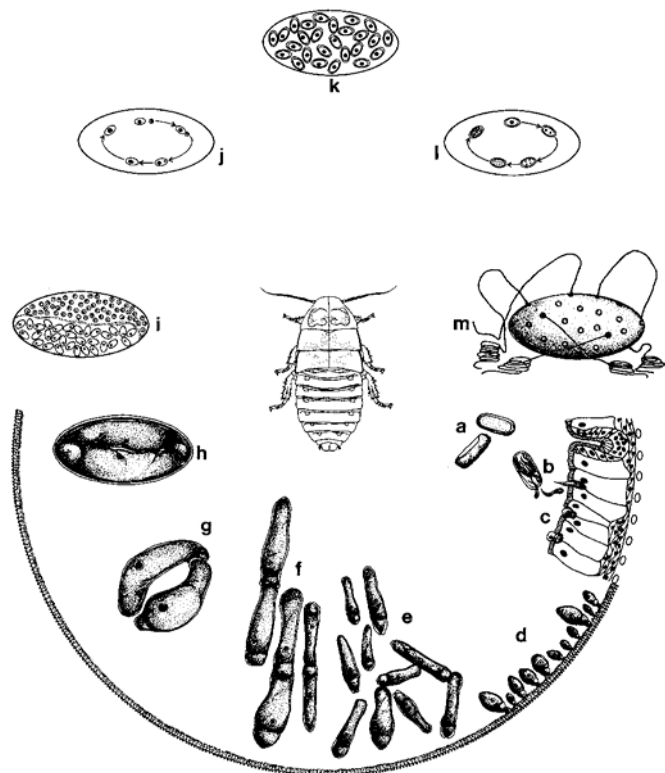


Fig. 47. *Leidyana migrator*. 5. Trophozoites reflecting normal population variation. Scale bar, 50 μ m. 6 - 8. Associations reflecting differences in maturation and normal population variation. Scale bar, 100 μ m. 9. Chain of oocysts, dorsal aspect. Scale bar, 5 μ m. 10. Chain of oocysts, lateral aspect. Scale bar, 5 μ m.



FAMILY CNEMIDOSPORIDAE
GRASSÉ, 1953

Young trophozoite at first fixed to intestinal cell by a voluminous epimerite which, in the course of development, regresses and becomes reduced to a small cap or spherule on the protomerite; sporoducts absent (?); oocysts ellipsoidal, in intestines of millipedes.

This family contains a single genus, *Cnemidospora*, with 4 named species. All are intestinal parasites of millipedes. Sporoducts have not been reported; however, gametocysts and spores have not been described for all species.

Genus *Cnemidospora*
Schneider, 1882

With the characters of the family. Four named species. TYPE SPECIES: *Cnemidospora lutea* Schneider, 1882 (Fig. 49). TYPE HOST: *Glomeris marginata*, *Glomeris conspersa*.

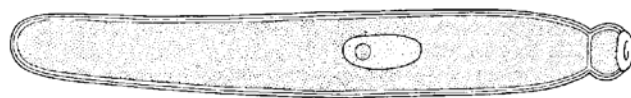


Fig. 49. *Cnemidospora lutea*. Trophozoite. (Based on Schneider, 1882.)

FAMILY MONODUCTIDAE
RAY & CHAKRAVARTY, 1933

Initial development intracellular; epimerite present or absent, if present, with prongs; gametocyst with a single sporoduct; oocyst ellipsoidal or ovoid, with hyaline episporic; octozoic (oocyst with eight sporozoites).

This family contains 3 genera and 19 species, primarily intestinal parasites of millipedes.

Fig. 48. Life cycle and development of *Leidyana migrator* in *Gromphadorina portentosa*. Oocysts in the environment (a) are consumed by a hissing cockroach. Enclosed sporozoites active in the host gut, escape the oocyst sheath, and migrate to the intestinal epithelium (b). Sporozoites establish infection between the cells of the intestinal epithelium and undergo an intercellular developmental phase (c). Gregarine trophozoites remain attached to the host epithelium by an epimerite during the luminal growth phase. Mature trophozoites (e) detach from the host epithelium, form reproductive associations (f), and undergo syzygy (g) to produce a reproductive gametocyst (h) that is shed in the host feces. Gametogony (l), fertilization, and zygote formation (j) occur in the exogenous gametocyst. Each zygote forms a protective oocyst envelope (k) and undergoes sporogony (l), producing 8 sporozoites. Gametocysts dehisce when mature (m), releasing infective oocysts into the environment to continue the cycle.

Genus *Monoductus*
Ray & Chakravarty, 1933

Epimerite a small elevation, with basally attached prongs, with a deep myocyte composed of two axial bundles, one retracting the epimerite; anisogamous; oocysts ellipsoidal to fusiform, with mediadorsal ridge; released from the gametocyst in a chain through a single sporoduct, in millipedes. Five named species.



Fig. 50. *Monoductus lunatus*. Trophozoite. (Based on Ray and Chakravarty, 1933.)

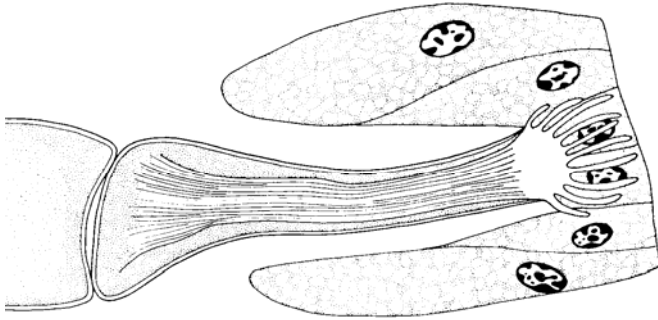


Fig. 51. *Monoductus lunatus*. Attachment of epimerite to host cell. (Based on Ray and Chakravarty, 1933.)

Monoductus lunatus Ray & Chakravarty, 1933 (Figs. 50 & 51). TYPE SPECIES. Trophozoite: Epimerite a small tumidus, with ~ 16 basal prongs, length 7.5–10.25 μm ; borne on a short neck, connected to protomerite deutomerite septum by axial myonemes; protomerite spherical to hemispherical, small, with constriction at protomerite deutomerite septum; deutomerite very elongate obvate, tapering to a blunt point posteriad, with conspicuous pellicular myonemes; nucleus hemispheric with posterior concave sinus, length 30.0 μm , width 12.0 μm ; shape maintained by myoneme anchors giving nucleus a parachute - like appearance; with large endosome, length 10.0 μm , width 6.0 μm . Total length 225.0–445.0 μm , width 33.0–47.0 μm . Oocyst: Ensiform, (obtuse anteriorly, acuminate posteriorly) in dorsal aspect length 10.25 μm , width 4.0 μm ; flattened ventrad, with longitudinal, mediodorsal ridge in pleural aspect; liberated from the gametocyst in a single long chain, obliquely joined, through a single sporoduct.

TYPE HOST: *Strongylosoma contortipes* Ref. Chakravarty (1935), Ray and Chakravarty (1933).

Genus ***Stenoductus***
Ramachandran, 1976

Epimerite absent in mature trophozoite; oocysts ellipsoidal, with hyaline episporangium, without mesodorsal ridge, extruded in chains; nucleus without myoneme tethers of *Monoductus*, in millipedes. Twelve named species.

Stenoductus penneri Ramachandran, 1976. TYPE SPECIES. Trophozoite: Epimerite reduced, papilliform, evident in intracellular individuals, absent in mature individuals; protomerite deeply dome - shaped, length 25.5–33.9–44.3 μm , width 44.1–59.8–86.3 μm ; deutomerite elongate ellipsoidal, widest in anterior third, broadly tapering in mature individuals from the protomerite deutomerite septum to a blunt point posteriad, length 576.3–750.9–1018.9 μm , width 116.0–230.6–411.4 μm ; nucleus spherical to slightly ovoid, large, with large central endosome; not tethered by myonemes. Oocyst: Ellipsoidal to fusiform, length 11.0

μm , width 7.4 μm , with rounded polar projections, with hyaline episporangium, liberated from the gametocyst in a single chain through a single sporoduct. TYPE HOST: *Floridobolus penneri*. Ref. Ramachandran (1976a, 1976b).

Genus ***Phleobum***
Haldar & Chakravarty, 1974

Epimerite absent; gametocyst with ectocyst, endocyst, and single sporoduct; oocysts oval, not extruded in chains; in insects. Two named species.

TYPE SPECIES: *Phleobum gigantinum* Haldar and Chakravarty, 1974 (= *Phleobum gigantinum* Haldar and Chakravarty, 1974 emend.) TYPE HOST: *Phleoba antennata*. Ref. Haldar and Chakravarty (1974).

FAMILY SPHAEROCYSTIDAE
CHAKRAVARTY, 1960

Epimerite sessile, a thick horizontal disk with milled border, or absent; protomerite in young trophozoites only, atrophied in mature trophozoite; gametocysts dehiscence by simple rupture; oocysts ovoid or biconical.

This family contains 4 genera and 12 species, primarily intestinal parasites of insects.

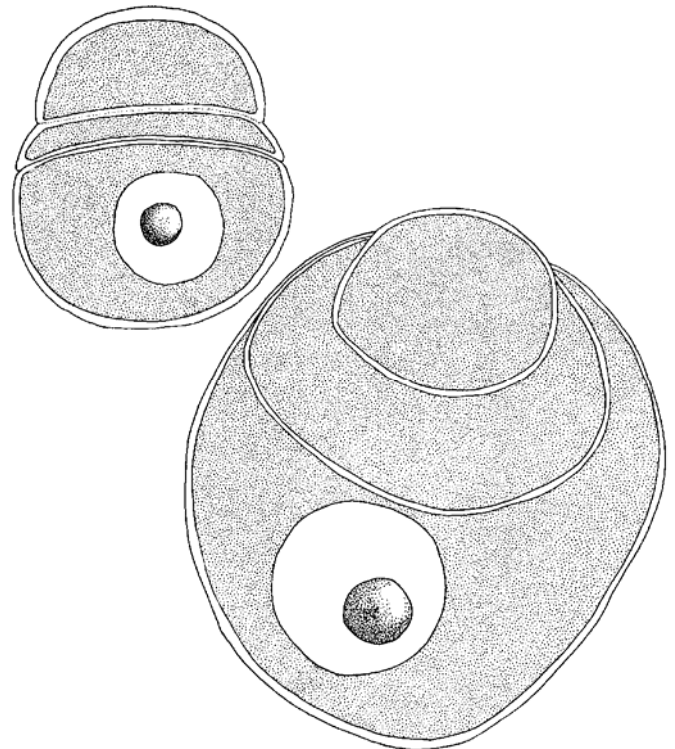


Fig. 52. *Sphaerocystis termitis*. Left, young Trophozoite;

Right, Mature Trophozoite. (Based on Desai and Uttangi, 1962.)

Genus **Sphaerocystis**
Léger, 1892

Epimerite labile; trophozoites apparently monocystic, solitary, parthenogenetic (?); oocysts ellipsoidal, with epispore; in insects. Four named species.

TYPE SPECIES: *Sphaerocystis simplex* Léger, 1892. TYPE HOST: *Cyphon pallidus*. Ref. Léger (1892)

Sphaerocystis termitis Desai & Uttangi, 1962 (Fig. 52). Trophozoite: Epimerite hemispherical, very large in young individuals, subsumed by protomerite with development; protomerite broadly hemispherical, flattened anteriorly at junction with epimerite, rounding and developing a small inverted epimerite dimple with development; protomerite deutomerite septum present in young trophozoites, absent in mature individuals; deutomerite round, flattened at protomerite deutomerite junction, becoming cordate with development; nucleus spherical with large endosome. Mature individuals, length 72.0–122.0 µm, width 60.0–122.0 µm. Oocyst: Ellipsoidal to ovoidal, length 7.5 µm, width 5.0 µm; liberated from the gametocyst by simple rupture. TYPE HOST: *Capritermes incola*. Ref. Desai and Uttangi (1962), Léger (1892).

Genus **Schneideria**
Léger, 1892

Epimerite a thick horizontal disk with milled border, with or without a central style; protomerite deutomerite septum lost (resorbed) early, oocysts biconical, smooth, swollen; in insects. Five named species.

TYPE SPECIES: *Schneideria mucronata* Léger, 1892. TYPE HOST: *Bibio marci*. Ref. Léger (1892)

Schneideria quadrinotatus Amoji & Rodgi, 1973 (= *Schneideria quadrinotata* Amoji and Rodgi, 1983) (Fig. 53). Trophozoite: Epimerite an umbraculate disk, with milled border, covering the protomerite and anterior region of the deutomerite; protomerite hemispherical, length 25.0–35.0 µm, width 30.0–45.0 µm; protomerite deutomerite septum absent in extracellular forms; deutomerite conoidal, elongate, length 275.0–565.0 µm, width 300.0–600.0 µm; sharply expanding from the protomerite deutomerite juncture and then broadly tapering to a sharp point posteriad; nucleus spherical, diameter 20.0–30.0 µm; with a single eccentric karyosome. Oocyst: Biconical, with sharp poles, length 6.0 µm, width 2.0 µm; liberated from the gametocyst by simple rupture. TYPE HOST: *Pirates quadrinotatus*.

Ref. Amoji and Rodgi (1973), Kamm (1922), Léger (1892).

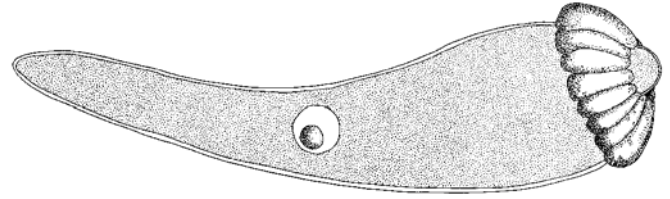


Fig. 53. *Schneideria quadrinotatus*. Trophozoite. (Based on Amoji and Rodgi, 1973.)

Genus **Paraschneideria**
Nieschulz, 1924

Epimerite simple, button-like; development intracellular; mature trophozoites without protomerite deutomerite septum; oocysts biconical; in insects. Monotypic.

Paraschneideria metamorphosa (Nowlin, 1922) Nieschulz, 1924 (= *Schneideria metamorphosa* Nowlin, 1922). TYPE SPECIES. Trophozoite: Epimerite a simple button-like bud, with plain border, without style; ephemeral, lost during intracellular phase leaving anterior epimerite scar; protomerite spherical with slight constriction posteriad; protomerite deutomerite septum present in intracellular forms, absent in extracellular forms; deutomerite elongate obvoidal, with slight tapering anterior to protomerite, tapering from the equator to a sharp point posteriad; nucleus spherical, with large endosome. Maximum total length 300.0 µm. Oocyst: Navicular, released into the alimentary canal of the host by simple rupture of the gametocyst, autoinfection not observed. TYPE HOST: *Sciara coprophila*. Ref. Nieschulz (1924), Nowlin (1922).

Genus **Neoschneideria**
Ormières, Manier, & Mathiez, 1965

Epimerite composed of a lobed pad in the center of which is a sharp papilla; epicyte longitudinally striated; trophozoite divided into segments, generally six; gametocyst with external wall forming two long prolongations opposite each other; oocysts biconical, with very loose epispore, emitted in chains; in insects. Two named species

TYPE SPECIES: *Neoschneideria douxi* (Hesse, 1926) Ormières, Manier, and Mathiez, 1965 (= *Asterophora douxi* Hesse, 1926). TYPE HOST: *Dixa autumnalis*.

FAMILY TRICHORHYNCHIDAE
ORMIÈRES, MARQUÈS, & PUISSÉGUR, 1977

Epimerite slightly lobed, carried on a long neck, limited by three unit membranes; epicyte ornamented by

numerous digitations forming a dense "beard"; epicytic folds absent but arches and longitudinal "apical" filaments regularly disposed in the membranes; bivalved gametocyst studded with teats or nipples [Fr. mamelons]; teats often missing along equatorial suture; dehiscence pressure provided by a lateral residuum ("pseudocyst") gametocysts dehisce by opening along equatorial suture; oocysts cylindrical, emitted in chains; in chilopods.

This family contains 1 genus with 2 species, both intestinal parasites of centipedes. The family was erected on the ultrastructural studies of Ormières, et al.(1977).

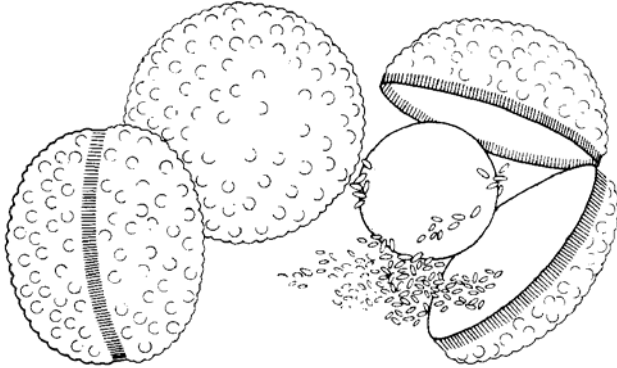


Fig. 54. *Trichorhynchus pulcher*. Dehiscence of gametocyst, showing gametocyst residuum ("pseudocyst") and oocysts. (Based on Schneider, 1882.)

Genus ***Trichorhynchus***
Schneider, 1882

With the characters of the family. Two named species.

TYPE SPECIES: *Trichorhynchus pulcher* Schneider, 1882 (= *Trichorhynchus insignis* Schneider, 1882; *Gregarina megacephala* Leidy, 1889) (Fig. 54). TYPE HOST: *Scutigera coleoptrata*. Ref. Ormières et al. (1977).

FAMILY DACTYLOPHORIDAE
LÉGER, 1892

Epimerite complex, digitate, without a long neck; nucleus in protomerite; syzygy (association) late, frontal (head to head); anisogamy very accentuated; gametocyst generally with a single residuum ("pseudocyst") coming from the male and serving for expulsion of the oocysts; oocysts cylindrical, with rounded ends; in intestine of chilopods and sometimes millipedes and insects.

Many genera and species of Dactylophoridae are poorly known. Many of the original descriptions are incomplete and/or plagued by poor or incomplete host identification. In some cases, the result has been confusion about the identity of species reported in later works. In other cases, these species have neither been reported nor redescribed since their original description, often more than 80 years ago. Our understanding of this group would benefit from a concerted survey of diplopod species with concomitant stabilization and distinction of named species.

This family contains 8 genera and 29 species, primarily intestinal parasites of centipedes.

Genus ***Dactylophorus***
Balbiani, 1899

Protomerite dilated, with a large number of strong papilliform rhizoids; gametocyst spherical; oocysts in more or less long chains. Two named species.

TYPE SPECIES: *Dactylophorus robustus* (Léger, 1892) Labbé, 1899 (= *Dactylophora robusta* Léger, 1892) (Fig. 55). TYPE HOST: *Cryptops hortensis*. Ref. Léger (1892).

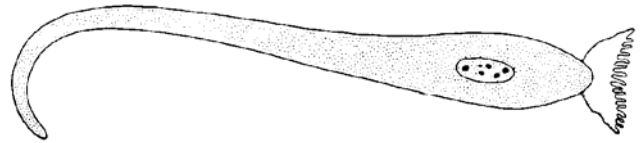


Fig. 55. *Dactylophorus robustus*. Trophozoite. (Based on Léger, 1892.)

Genus ***Echinomera***
Labbé, 1899

Epimerite an irregular cone ending in an eccentric point, bearing a number of short digitiform rhizoids; gametocysts without sporoducts, with residuum formed by male gamont; oocysts cylindrical, in chains. Eight named species.

Echinomera hispidi (Schneider, 1875) Labbé, 1899 (= *Echinocephalus hispidus* Schneider, 1875; *Echinomera hispida* [Schneider, 1875] Labbé, 1899) (Fig. 56).

TYPE SPECIES. Trophozoite: Epimerite an irregular, assymetrical cone, terminating in an eccentric point anteriad, bearing a corona of eight digitiform rhizoids; protomerite elliptical, broad, shallow, length 30.0–**32.6**–36.0 µm, width 40.0–**48.9**–64.0 µm; deutomerite regularly ellipsoidal, length 176.0–**215.0**–248.0 µm, width 66.0–**87.0**–108.0 µm; nucleus spherical to slightly ovoid, length 30.0–**32.6**–36.0 µm, width 32.0–**43.2**–36.0 µm; with large central endosome. Oocyst:

Cylindrical, length 22.0 μm , width 5.0 μm ; liberated in chains from the gametocyst by simple rupture. TYPE HOST: *Lithobius forficulatus*. Ref. Geus (1969), Labbé (1899), Lipa (1967), Schellack (1907), Watson (1916b).

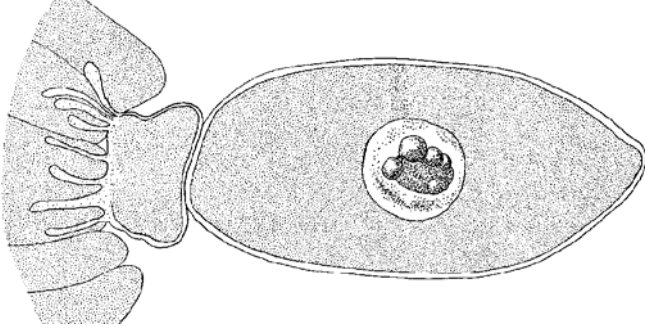


Fig. 56. *Echinomera hispidi*. Trophozoite attached to host epithelial cell. (Based on Schellack, 1907.)

Genus *Grebnickiella*
Bhatia, 1938

Protomerite spread out transversely, with numerous delicate rhizoids, made up of two long, narrow horizontal lobes fused and turned up spirally at one end, peripheral portion with many teeth from which long filaments project; oocysts long, ovoid, mostly in chains. Nine named species.

Goodrich (1938) and Misra (1942) provide excellent discussions and data on several species of *Grebnickiella*; however, the characters and state of species within the genus are not altogether clearly defined. Much of the taxonomic confusion within *Grebnickiella* arises from incomplete or incorrect identification of populations of *Scolopendra*. Additional data, including the ontogeny of the parasites, clear host identification, and stabilization of the type species is required to stabilize species of *Grebnickiella*.

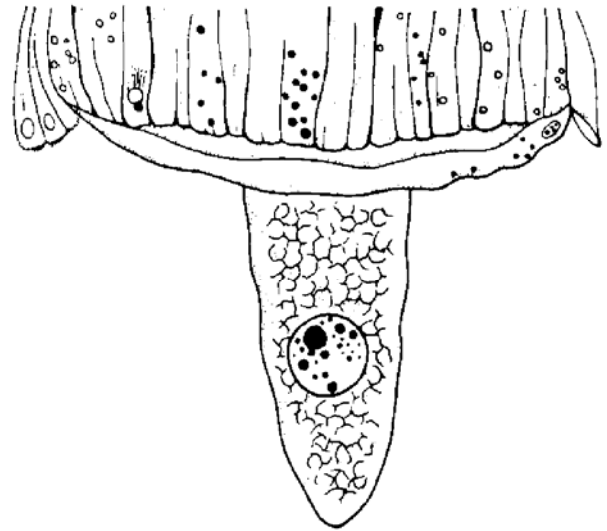


Fig. 57. *Grebnickiella gracilis*. Trophozoite attached to intestinal cells. (Based on Léger and Duboscq, 1909.)

TYPE SPECIES: *Grebnickiella gracilis* (Grebnitskii, 1873) Bhatia, 1938 (= *Nina gracilis* Grebnitskii, 1873; *Pterocephalus nobilis* Schneider, 1887) (Figs. 57 & 58). TYPE HOST: *Scolopendra cingulata* and *Scolopendra morsitans*. Ref. Goodrich (1938), Misra (1942).

Genus *Rhopalonia*
Léger, 1894

Epimerite a subspherical button, with ten or more digitiform processes; gametocyst with residuum ("pseudocyst"); oocysts cylindrical. Three named species.

Lipa (1967) and Geus (1969) each provided descriptions for new species of *Rhopalonia*; however, these descriptions are incomplete. In my opinion *Rhopalonia* remains valid but poorly known.

TYPE SPECIES: *Rhopalonia geophili* Léger, 1894 (= *Rhopalonia hispidio* [Schneider] of Kudo, [1960]*lapsus calami*). TYPE HOST: *Geophilus* sp. and *Geophilus gabrielis*. Ref. Geus (1969), Lipa (1967).

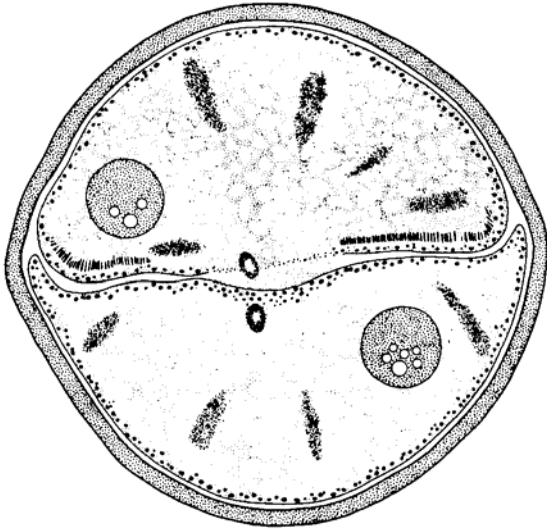


Fig. 58. *Grebnickiella gracilis*. Gametocyst, cross - section. (Based on Léger and Duboscq, 1909.)

Genus *Acutispora*
Crawley, 1903

Epimerite a button at the end of a long neck; gametocyst with or without residuum; oocyst biconical, with a thick, blunt endocystic rod at each end. Three named species.

TYPE SPECIES: *Acutispora macrocephala* Crawley, 1903. TYPE HOST: *Lithobius forficulatus*. Ref. Crawley (1903).

Genus *Seticephalus*
Kamm, 1922

Epimerite forming a thick tuft of short, anteriorly directed, brush - like bristles; protomerite broad and flat. Monotypic.

TYPE SPECIES: *Seticephalus elegans* (Pinto, 1918) Kamm, 1922 (= *Gregarina elegans* Pinto, 1918). TYPE HOST: *Scolopendra* sp.

Genus *Dendrorhynchus*
Keilin, 1920

Epimerite a disk or sucker with a border of ramified lobes (papillae); septate, but protomerite duetomerite septum often indistinct; transverse fibrils (epicytic, not forming septa) conspicuous, often giving the protodeutomerite a metameric appearance; gametocysts ellipsoidal, irregular; oocysts fusiform. Two named species.

TYPE SPECIES: *Dendrorhynchus systemi* Keilin, 1920. TYPE HOST: *Systemus* sp. Ref. Keilin (1920).

Genus *Mecistophora*
Ganapati & Narasimhamurti, 1960

Epimerite cup - shaped with numerous intracellular filaments; protomerite deutomerite septum present; gametes dissimilar; gametocyst with residuum; oocysts simple, octozoic. Monotypic.

Mecistophora legeri Ganapati & Narasimhamurti, 1960 (Fig. 59).

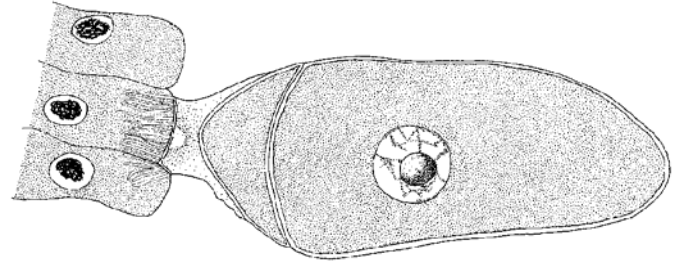


Fig. 59. *Mecistophora legeri*. Trophozoite attached to intestinal cells. (Based on Ganapati and Narasimhamurti, 1960.)

TYPE SPECIES. Trophozoite: Epimerite cup - shaped to crateriform, margins upturned, with margin frayed to form numerous filamentous processes; protomerite ovoidal, concave posteriad at the protomerite deutomerite septum; deutomerite broadly ovoidal, length 545.0 μm ; nucleus ovoidal, length 26.6 μm , width 22.6 μm ; with central endosome and a network of fine extra - karyosomic chromatin. Total length 595.0 μm , width 148.0 μm . Oocyst: Simple, rectangular, corners regularly rounded, length 6.5 μm , width 3.5 μm ; liberated from the gametocyst by simple rupture.

TYPE HOST: *Mecistocephalus punctifrons*. Ref. Ganapati and Narasimhamurti (1960), Goodrich, (1938).

FAMILY AMPHIPLATYSPORIDAE
KUNDU & HALDAR, 1984

Epimerite absent; solitary, association late, lateral; gametocysts ovoid with prominent ectocyst (pseudocyst), dehiscing by simple rupture; oocysts cylindrical, with polar plates, extruded in chains.

This family contains a single monotypic genus, *Amphiplatyspora*.

Genus *Amphiplatyspora*
Kundu & Haldar, 1984

With the characteristics of the family. Monotypic. TYPE SPECIES: *Amphiplatyspora striata* Kundu and Haldar, 1984 TYPE HOST: *Pteronemobius concolor*. Ref. Kundu and Haldar (1984).

FAMILY STYLOCEPHALIDAE
 ELLIS, 1912
 (= STYLORHYNCHIDAE SCHNEIDER, 1875)

Epimerite elongated, with or without appendages; development extracellular; syzygy (association) frontal, late; gametocyst residuum present; oocysts obtuse tetrahedroids, obtuse dorsad (purse - , stone - , or hat - shaped), emitted in chains, with a single brown or blackish wall, with a dehiscence line on the convex border; in arthropods.

This family contains 15 genera and 91 species, all parasites of insects.

Genus *Stylocephalus*
 Ellis, 1912
 (= *Stylorhynchus* Schneider, 1875)

Epimerite elongated into a neck, with subapical tumidus; gametocysts covered by papillae, with residuum ("pseudocyst"); oocysts purse - like, usually emerging in long chains in insects. Thirty - seven named species. Examples are illustrated in Figs. 60 & 61.

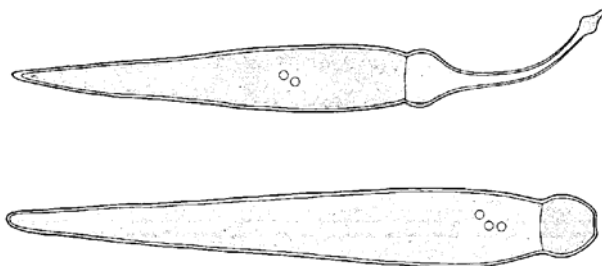


Fig. 60. *Stylocephalus longicollis*. Top, trophozoite with epimerite; Bottom, mature trophozoite. (Based on Schneider, 1884.)

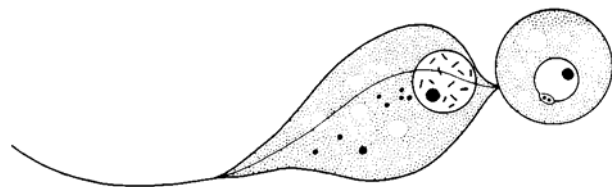


Fig. 61. *Stylocephalus longicollis*. Fertilization. (Based on Léger, 1904.)

Notes: Théodoridès (1963) defined 3 subgenera within *Stylocephalus*: *Stylocephalus Conicocephalus*, *Stylocephalus Stylocephalus*, and *Stylocephalus Xiphocephalus*, using the specific form of the epimerite proper to distinguish each of the 3 taxa. He also noted

strong correlation between the shape of the epimerite proper and the general form of the diamerite. *Stylocephalus Conicocephalus* is characterized by a broad, conical diamerite terminating in a distinctive nipple. *Stylocephalus Stylocephalus* is characterized by a cylindrical diamerite terminating in a simple sphere. *Stylocephalus Xiphocephalus* is characterized by a cylindrical, often filiform diamerite bearing a long, xiphoid or lanceolate epimerite with a blunt or sharp apex. Corbel (1971) elevated *S. Xiphocephalus* to the generic - level in his revision of the Stylocephalidae, but focused his diagnosis on the filiform nature of the diamerite. He did not alter the position of *S. Conicocephalus*. Subsequent authors have confirmed the *Xiphocephalus sensu strictu* hypothesis, describing 5 (Devdehar and Amoji, 1977; Patil and Amoji, 1985) of the genus' 6 species since Corbel (1971) elevated *Xiphocephalus*. In addition, gametocyst structure and developmental pattern and oocyst structures are consistent among known species of *Xiphocephalus*. Ref. Corbel (1971), Théodoridès (1963).

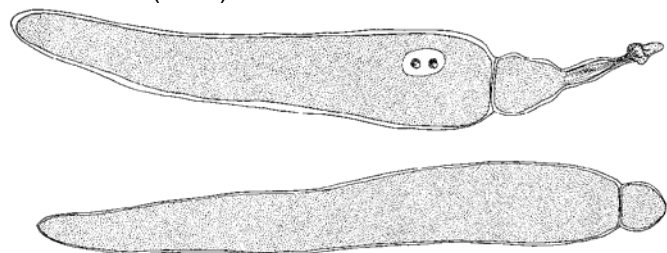


Fig. 62. *Stylocephalus oblongatus*. Top, trophozoite with epimerite; Bottom, mature trophozoite. (Based on Schneider, 1875.)

Stylocephalus oblongatus (Hammerschmidt, 1838) Watson, 1916 (= *Rhizinia oblongata* Hammerschmidt, 1838; *Sporadina oblongata* [Hammerschmidt, 1838] von Frantzius, 1848; *Gregarina oblongata* [Hammerschmidt, 1838] Diesing, 1851; *Stylorhynchus oblongatus* [Hammerschmidt, 1838] Schneider, 1875). (Figs. 62 & 63).

TYPE SPECIES. Trophozoite: Epimerite a flattened tumidus, with retractible, conical papilla; borne on a long neck, thick, cylindrical, retractile; protomerite globular, hemispherical to conical, constricted at protomerite deutomerite septum; deutomerite cylindrical, elongate, tapering from anterior half to a blunt end posteriad; nucleus ellipsoidal, with multiple karyosomes. Oocyst: Purse - shaped, brown, length 10.0 µm, width 7.0 µm; liberated in long chains from the gametocyst by simple rupture. **TYPE HOST:** *Asida grisea*. **Notes:** The following measurements have been reported for *Stylocephalus oblongatus*: young trophozoites - epimerite length 22.0–38.0 µm, total length 65.0–190.0–450.0 µm; mature trophozoites, protomerite length 66.0–75.6–88.0 µm, width 72.0–92.3–112.0 µm; deutomerite length 756.0–806.7–912.0 µm, width 126.0–178.8–232.0 µm; nucleus length 78.0–82.0–84.0 µm, width 58.0–

60.4–64.0 µm (Geus, 1969; Théodoridès, 1955c). Ref. Corbel (1971), Geus (1969), Schneider (1882), Théodoridès (1955c), Watson (1916b).

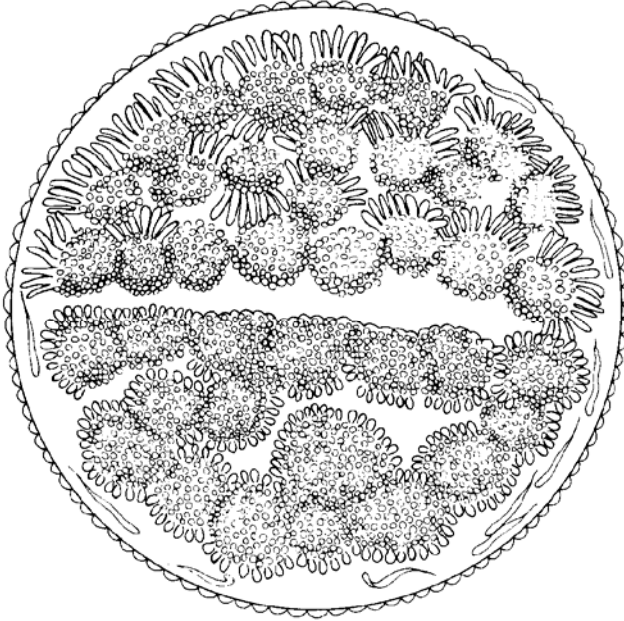


Fig. 63. *Stylocephalus oblongatus*. Gametocyst, cross-section. (Based on Léger, 1904.)

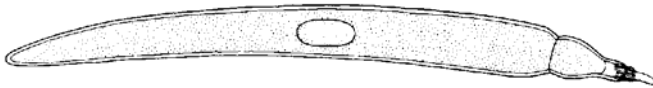


Fig. 64. *Stylocephalus giganteus*. Trophozoite. (Based on Ellis, 1912.)

Stylocephalus giganteus Ellis, 1912 (Fig. 64). Trophozoite: Epimerite a long pointed cone, broad with subapical tumidus, rugose; basal half cylindrical, non-rugose; protomerite hemispherical with anterior tapering; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriad; nucleus spherical, very large, often obscured by cytoplasm. Total length 214.0–1200.0–1800.0–2135.0 µm. Oocyst: Irregularly subspherical to purse-shaped, black, length 11.0 µm, width 7.0 µm; liberated in long chains from the gametocyst by simple rupture. TYPE HOST: *Eleodes* sp. Ref. Corbel (1971), Ellis (1912), Watson (1916b).

Stylocephalus depressicus Patil, 1982. Trophozoite: Epimerite conoid, flexible, length 23.0 µm, width 15.0 µm; borne on a short neck in young individuals, lengthening with maturity; protomerite sub-globular (sub-hemispherical), length 7.0 µm, width 14.0 µm in young individuals, becoming hemispherical with maturity; deutomerite elongate oval in young individuals, length 23.0 µm, width 19.0 µm; lengthening in mature individual and broadly tapering to a blunt point posteriad, length 108.0 µm; nucleus oval, length 10.0 µm, width

8.0 µm in young individuals, becoming elongate oval with maturity, length 70.0 µm, width 20.0 µm. Oocyst: Hat-shaped, length 7.0 µm, width 7.5 µm, liberated in long chains from the gametocyst by simple rupture. TYPE HOST: *Gonocephalum depressum*. Ref. Patil and Amoji (1984).

Genus ***Stylocephaloides***

Théodoridès, Desportes, & Jolivet, 1965

Epimerite a button; older trophozoites with epicytic ribs; protomerite often with thin axis; oocysts purse-like; in insects. Two named species.

TYPE SPECIES: *Stylocephaloides monodi* Théodoridès, Desportes, and Jolivet, 1965. TYPE HOST: *Ademsimia antiqua*, *Pimelia grandis*, and *Prionothecha coronata*.

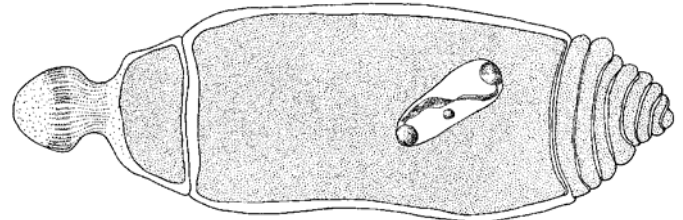


Fig. 65. *Cystocephalus algerianus*. Trophozoite. (Based on Théodoridès, 1954b.)

Genus ***Cystocephalus***

Schneider, 1886

Epimerite with short neck, broad at base, swollen into a bulb, and surmounted with a small, olive-shaped prolongation; oocysts hat-shaped; in insects. Ten named species.

Cystocephalus algerianus Schneider, 1886 (Fig. 65).

TYPE SPECIES. Trophozoite: Epimerite globose, with conical apex, diameter reaching 40.0 µm; punctate, sometimes with an equatorial band of fine, longitudinal striations; borne on a short neck, often with longitudinal striations; protomerite spherical, epicyte thickened anteriorly; deutomerite elongate ovoidal to ellipsoidal, posterior end rounded, posterior 1/2 often with transverse epicytic folds; nucleus elongate ellipsoidal, with several karyosomes and a chromatin band. Total length 350.0–4000.0 µm. Oocyst: Irregularly hat-shaped, brown, length 10.0 µm, width 10.5 µm. TYPE HOST: *Pimelia* sp. **Notes:** The literature contains descriptions of three varieties of this species based on geographical range. I have chosen to follow Corbel (1971) and have not reflected any varietal distinctions. Ref. Corbel (1971), Théodoridès (1954b, 1955b), Tuzet and Théodoridès (1951), Watson (1916b).

Genus **Bulbocephalus**

Watson, 1916

Epimerite consisting of stout, broad - based style borne on a long neck, with a central bulbous swelling; oocysts unknown; in insects. (**Note:** The oocysts of *Bulbocephalus indicus* Narain, 1961 are tear - drop shaped Narain [1961].). Three named species.

Bulbocephalus wardi Watson, 1916 (Fig. 66).

TYPE SPECIES. Trophozoite: Epimerite a stout broad - based apical style; borne on a long neck with a distinct tumidus, central, bulbous; length 40.0 µm, width 14.0 µm; protomerite broadly rounded anteriorly, slightly constricted at protomerite deutomerite septum, length 15.0–31.0–50.0 µm, width 18.0–30.4–42.0 µm; deutomerite elongate, rounded anteriorly, broadly tapering from a slight constriction at the protomerite deutomerite septum to a long, blunt point posteriorly, length 30.0–73.4–180.0 µm, width 28.0–36.2–45.0 µm; nucleus ellipsoidal, length 8.0–11.0 µm, width 15.0–27.0 µm; with a single karyosome. Oocyst: Unknown.

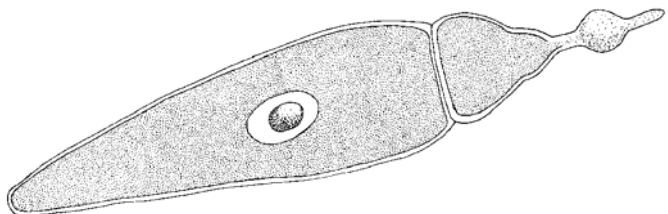


Fig. 66. *Bulbocephalus wardi*. Trophozoite. (Based on Watson, 1916a.)

TYPE HOST: Cleridae gen. sp. Ref. Narain (1961), Watson (1916a).

Genus **Xiphocephalus**

Théodoridès, 1964 Emend. Clopton, 1988

Epimerite complex elongated into a cylindrical, often filiform diamerite, expanding terminally to form the epimerite proper; epimerite elongated into a xiphoid process (including deltoid, ensiform, lanceolate and gladiate forms), terminating in a sharp or rounded point; gametocysts papillate, with internal pseudocyst residuum; oocysts purse - like, emerging in chains. Nine species.

(See systematic discussion under “Genus *Stylocephalus* Ellis, 1912”.)

Xiphocephalus gladiator (Blanchard, 1905) Corbel, 1971 (= *Stylorhynchus gladiator* Blanchard, 1905; *Stylocephalus gladiator* [Blanchard, 1905], Watson, 1916). (Fig. 67).

TYPE SPECIES. Trophozoite: Epimerite xiphoid (sword - shaped) to lanceolate, very long; borne on a distinct filiform neck; protomerite short, globular; deutomerite elongate cylindrical, slightly tapering posteriorly to a blunt end; posterior 1/3 with epicytic annulations in mature individuals; nucleus ovoid, length

10.0–35.0 µm, width 5.0–30.0 µm; with single large karyosome in young individuals, with two polar karyosomes in mature individuals. Total length: average 300.0–400.0 µm, maximum 720.0 µm. Width: average 30.0 µm, maximum 70.0 µm. Oocyst: Unknown. TYPE HOST: *Helenophorus collaris*. Ref. Corbel (1971), Théodoridès (1954a, 1963), Watson (1916b).

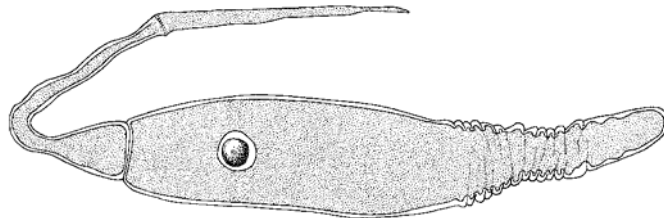


Fig. 67. *Xiphocephalus gladiator*. Trophozoite. (Based on Théodoridès, 1954a.)

Xiphocephalus ellisi Clopton, 1998. (Fig. 68).

Trophozoite: Developing trophozoites solitary, attached to host ventricular epithelium. Holdfast an epimerite complex of terminal epimerite and intercalating diamerite. Epimerite elongate, xiphoid, ensiform, terminally obtuse, with transverse basal tumidus, narrowing anteriorly, length 2 - 3 times width of basal tumidus, approximately equal that of diamerite; width approximately ½ that of basal tumidus, less than that of diamerite; enlarging posteriorly at fusion with diamerite to form a basal tumidus; tumidus toroidal, concavo - concave in anteroposterior axis, width approximately twice length; diamerite roughly cylindrical, tapering anteriorly with distinct constriction at junction with epimerite, little or no evidence of longitudinal folds, length approximately twice width; without visible septum at junction with protomerite but clearly differentiated by decreased density of cytoplasm. Protoneme broadly ovoid to very broadly ovoid. Protoneme - deutomerite septum clearly marked and constricted. Deutomerite obovoid to narrowly obovoid, Nucleus ellipsoid to broadly ellipsoid; with 2 - 3 distinct polysomal endosomes. Gamont: Protoneme depressed ovoid to very broadly ovoid, length 60.30 - 118.59 µm, width 85.28 - 168.70 µm. Protoneme - deutomerite septum clearly marked and constricted. Deutomerite obovoid to very narrowly obovoid, length 150.64 - 1,638.34 µm, width 101.25 - 303.84 µm. Total length 737.39 - 1,756 µm. Association: Frontal; isogamontic; late and ephemeral; leading directly to syzygy, associated pairs fusing laterally during syzygy; associations, syzygial pairs and gametocysts located between host ventricular peritrophic membrane and posterior ventricular epithelium. Gamonts in association morphometrically similar to solitary gamonts; epimerite absent. Gametocysts: White to opalescent in color, becoming tan to light brown with maturity; roughly spherical; length 285 - 480 µm, width 240 - 470 µm; no hyaline coat apparent, gametocyst wall desiccating to become paper - like, papillated. Gametocysts mature within 48–72 hr

and dehisce by simple rupture of the gametocyst walls. Oocysts are extruded in a coiled chain to form a single, tangled, sticky mass; epispore packet absent, gametocyst residuum present. Oocysts: Axially asymmetric, lithocystic (stone - shaped or seed - shaped) in lateral aspect, slightly keeled in dorsal aspect, very uniform in size and shape; length 9.73 μm ; height 8.45 μm ; with slight terminal protuberances or shoulders, height 1.98 μm ; with a single, central, spherical residuum, diameter 1.61 μm ; octozooic, sporozoites resting in tandem, folded around central residuum. Extruded in random chains. Oocysts dark brown under transmitted light, black under reflected light. TYPE HOST: *Eleodes opacus* (Say, 1824) (Insecta: Coleoptera: Tenebrionidae: Eleodiini).

or without a crown of small membraneous vesicles; nucleolus in the shape of a long, twisted sausage; oocysts hat - shaped, asymmetrical, in insects. Two named species.

I have accepted the emendation of Corbel (1971) for *Lophocephalus*.

Lophocephalus insignis (Schneider, 1882) Labbé, 1899 (= *Lophorhynchus insignis* Schneider, 1882) (Fig. 69).

TYPE SPECIES. Trophozoite: Epimerite a large cupule with crenulate margin anteriorly, longitudinally striated, surrounded basally by a crown of small upwardly directed digitiform vesicles; without neck; protomerite broad, depressed, giving rise to crown of digitiform vesicles anteriorly, length ~40.0–66.7 μm ; deutomerite massive, subspherical; longitudinally striated, length ~660.0–933.3 μm ; nucleus spherical, with a single large nucleolus in the shape of a long, twisted sausage. Oocyst: Hat - shaped, asymmetrical, length 10.0 μm ; released from the gametocyst in chains by rupture of the pseudocyst. TYPE HOST: *Helops striatus*. Ref. Corbel (1971), Geus (1969), Labbé (1899), Schneider (1882), Théodoridès (1958), Watson (1916b).

Genus *Lophocephaloides*

Théodoridès, Desportes, & Jolivet, 1965

Young trophozoites with a long, button - shaped epimerite on a short neck; epimerite of older trophozoites and gamonts a more or less flacid floral corolla somewhat resembling that of *Lophocephalus*; gametocysts of the usual cystocephalid type; oocysts in strings like beads; in insects. Two named species.

TYPE SPECIES: *Lophocephaloides thripteræ* Théodoridès, Desportes, and Jolivet, 1965. TYPE HOST: *Thriptera crinita*.

Genus *Sphaerorhynchus*

Labbé, 1899

(= *Sphaerocephalus* Schneider, 1886)

Epimerite a small sphere at the end of a long or sometimes short neck; in insects. Four named species.

TYPE SPECIES: *Sphaerorhynchus ophioides* (Schneider, 1886) Labbé, 1899 (= *Sphaerocephalus ophioides* Schneider, 1886; *Stylocephalus ophioides* [Schneider, 1886] Corbel, 1971). TYPE HOST: *Akis* sp.

Genus *Oocephalus*

Schneider, 1886

Epimerite a rounded button borne on a short conoidal neck hardly longer than wide; in insects. Two named species.

Oocephalus hispanus Schneider, 1886 (= *Stylocephalus hispanus* [Schneider, 1886] Corbel, 1971).

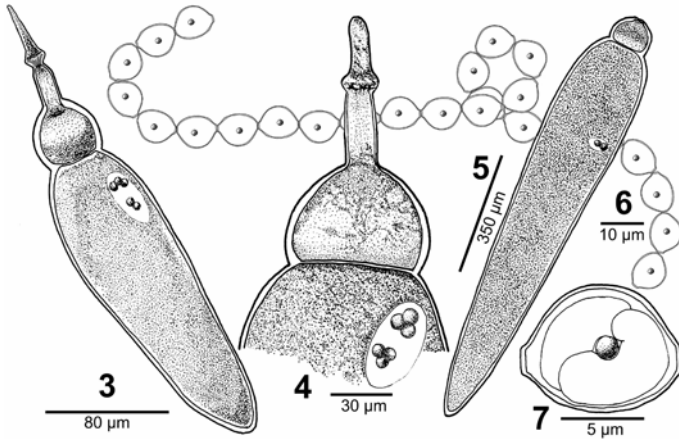


Fig. 68. *Xiphocephalus ellisi*. 3. Solitary trophozoite. 4. Protomerite and epimerite complex of trophozoite, detail. 5. Gamont. 6. Oocyst chain. 7. Oocyst with central residuum and enfolding sporozoites.

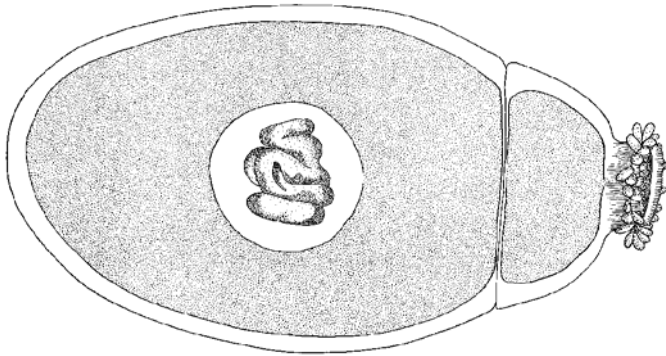


Fig. 69. *Lophocephalus insignis*. Trophozoite. (Based on Schneider, 1882.)

Genus *Lophocephalus*

Labbé, 1899

(= *Lophorhynchus* Schneider, 1882)

Epimerite a large cupule formed by a crenulate crown, with longitudinal striations and basal border, with

TYPE SPECIES. Trophozoite: Epimerite a round button, small; borne on a cylindrical neck, tapering to a conoid anteriorly; protomerite ellipsoidal, length 73.0–80.3–88.0 μm , width 132.0–139.3–152.0 μm ; deutomerite elongate, cylindrical, broadly tapering from the protomerite deutomerite septum to a point posteriorly, length 984.0–1158.0–1440.0 μm , width 175.0–191.3–221.0 μm ; nucleus ellipsoidal, length 75.0 μm , width 45.0 μm ; with many karyosomes, diameter < 25.0 μm . Oocyst: Unknown. TYPE HOST: *Morica* sp. Ref. Geus (1969), Levine (1988), Watson (1916b).

Genus ***Campanacephalus***
Théodoridès, 1955

Epimerite without neck, consisting of a quadrangular or truncated button; oocysts emitted in chains; in beetles. Two named species.

Campanacephalus villiersi Théodoridès, 1955 (Fig. 70).

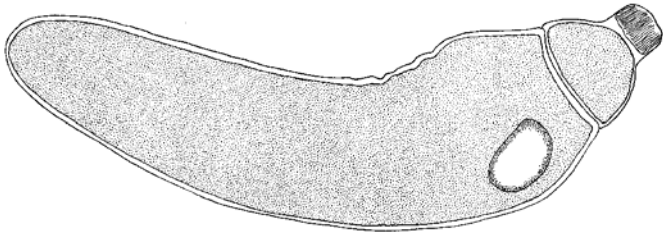


Fig. 70. *Campanacephalus villiersi*. Trophozoite. (Based on Théodoridès, 1955a.)

TYPE SPECIES. Trophozoite: Epimerite a large button, length 30.0 μm , width 30.0 μm ; quadrate or truncate, with fine longitudinal striations; fused to the protomerite (without neck); protomerite hemispherical, with well developed epicyte; deutomerite cylindrical, rounded posteriorly; nucleus roughly elliptical, margins indistinct but delineated by a distinct chromatin ring, maximum length 50.0 μm . Total length 300.0–410 μm . Oocyst: Hat-shaped (ellipsoidal, asymmetrical), length 14.0 μm , height 10.0 μm , depth 5.0 μm ; liberated from the gametocyst in chains by simple rupture. TYPE HOST: *Macropodia variolaris*. Ref. Corbel (1971), Nelson (1970), Théodoridès (1955a).

Genus ***Clavicephalus***
Théodoridès, 1959

Epimerite a quadrangular knob which prolongs the protomerite, finely punctate at apex, with a finely punctate "islet" differentiating the cytoplasm of the epimerite from that of the protomerite; syzygy head to tail; gametocyst and oocyst unknown; in insects. Three named species.

Clavicephalus madagascariensis Théodoridès, 1959 (= *Cystocephalus madagascariensis* [Théodoridès, 1959] Corbel, 1971) (Fig. 71).

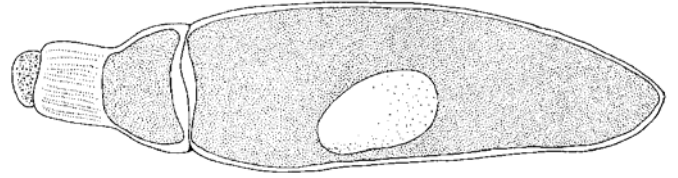


Fig. 71. *Clavicephalus madagascariensis*. Trophozoite. (Based on Théodoridès, 1959.)

TYPE SPECIES. Trophozoite: Epimerite a quadrangular knob which prolongs the protomerite, finely punctate at apex, with a finely punctate "islet" differentiating the cytoplasm of the epimerite from that of the protomerite; protomerite hemispherical; deutomerite elongate, cylindrical; nucleus oval. Total length, trophozoites, 120.0–200.0 μm ; gamonts, 1,300.0 μm . Oocyst: Unknown. TYPE HOST: *Melanocratus* sp. Ref. Corbel (1971), Théodoridès (1959).

Genus ***Cystocephaloides***
Théodoridès & Jolivet, 1963

Epimerite with a short neck, consisting of a button, surrounded by an epicytic collarette; with development the collarette disappears and the epimerite takes the form of a quadrangular button carried on a short neck; in insects. Monotypic.

Cystocephaloides prionothecae Théodoridès & Jolivet, 1963 (Figs. 72 & 73).

TYPE SPECIES. Trophozoite: Epimerite variable with age; initially conical to globular, borne on a short neck; surrounded by an epicytic collarette, finely striated, derived from the epicyte of the protomerite; the epimerite collarette structure resembles the manubrium and exumbrella of a hydrozoid medusae; with maturity the collarette constricts around the neck of the epimerite and forms a quadrate layer around the epimerite globulus; protomerite hemispherical, constricted at the protomerite deutomerite septum; deutomerite elongate, cylindrical; nucleus ovoid, length 30.0 μm , width 20.0 μm . Total length 100.0–400.0 μm . Oocyst: Unknown. TYPE HOST: *Prionotheca coronata*. Ref. Théodoridès and Jolivet (1963).

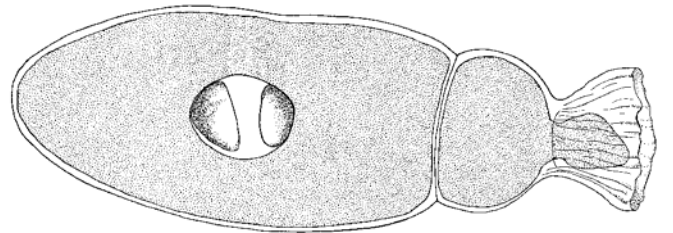


Fig. 72. *Cystocephaloides prionothecae*. Young trophozoite with veiled epimerite. (Based on Théodoridès and Jolivet, 1963.)

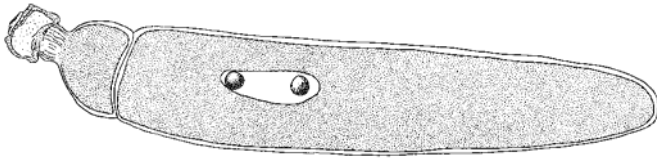


Fig. 73. *Cystocephaloides prionothecae*. Mature trophozoite with fully developed epimerite. (Based on Théodoridès and Jolivet, 1963.)

Genus ***Orbocephalus***
Nelson, 1970

Epimerite a dilated papilla surrounded by a flat disk; borne on a long neck (diamerite); gametocysts and oocysts unknown. Two named species.

Although Nelson (1970) attempts to clearly distinguish *Orbocephalus* from *Stylocephalus*, I believe that additional data are required to ensure that these differences are real and not artifacts of technique.

Orbocephalus bulbosus Nelson, 1970.

TYPE SPECIES. Trophozoite: Epimerite a round papilla, surrounded by a flat rough surfaced disk, neck bulbous; protomerite trapezoidal, with curved sides; deutomerite elongate, cylindrical; nucleus oval, with 1–3 karyosomes. Total length up to 3060.0 μm , width up to 120.0 μm . Oocysts: Unknown. TYPE HOST: *Eleodes* sp. Ref. Nelson (1970).

Genus ***Lepismatophila***
Adams & Travis, 1935

Epimerite at first elongated into a neck but then turning into a simple, symmetrical knob; mature trophozoites with a broad protomerite; gametocyst with a residuum; gametocyst walls ornamented with channels delimited by small granular areas; oocysts ovoid or ellipsoidal, assymetrical (hat - shaped), liberated from the gametocyst in uncoiling chains by simple rupture. Ten named species.

Tuzet et al. (1952) suggested substantial emendations to the original generic description. I have included those emendations here.

Lepismatophila thermobiae Adams and Travis, 1935.

TYPE SPECIES. Trophozoite: Epimerite smooth, globular, sessile, diameter 12.0–18.0–24.0 μm ; protomerite sub - hemispherical, length 15.0–35.2–55.0 μm , width 30.0–119.8–157.0 μm ; deutomerite conical, sometimes tapering abruptly to form a severe conoid process posteriad, length 52.0–222.0–348.0 μm , width 46.0–128.2–159.0 μm ; nucleus spherical, maximum diameter 31.0 μm . Oocyst: Ellipsoidal, brown, length 13.6 μm , width 6.8 μm ; released from the gametocyst in uncoiling spiral chains by simple rupture. TYPE HOST: *Thermobia domestica*. Ref. Adams and Travis (1935),

Crusz (1960), Haldar and Chakraborty (1977), Taschev and Golemansky (1973), Tuzet et al. (1952).

Genus ***Colepismatophila***
Adams & Travis, 1935

Epimerite a simple symmetrical knob, globular; oocysts hat - shaped, with polar filaments, curved; released from the gametocyst in wavy chains. Three species.

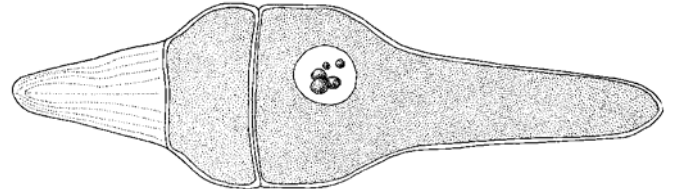


Fig. 74. *Colepismatophila burti*. Trophozoite. (Based on Crusz, 1960.)

Colepismatophila burti Crusz, 1960 (Fig. 74). Trophozoite: Epimerite elongate, thimble - shaped, length 26.5–36.9 μm , width 16.2–19.5 μm ; without neck; protomerite sub - hemispherical, constricted at protomerite deutomerite septum, length 12.9–35.6 μm , width 29.7–94.4 μm ; deutomerite conoid, broad anteriorly, narrowing abruptly posteriad, length 37.1–168.7 μm , width 37.1–97.5 μm ; nucleus ovoid to ellipsoid, diameter 18.1–24.4 μm . Oocyst: Sub - hemispherical [hat - shaped], length 12.4–15.6 μm , width 6.7–8.6 μm ; with a single filament at each pole, curved, length 8.0–15.3 μm , width 0.9–1.3 μm ; released in coiling chains by simple rupture of the gametocyst. TYPE HOST: *Peliolepisma calvum* Ref. Adams and Travis (1935), Crusz (1960).

FAMILY ACTINOCEPHALIDAE
LÉGER, 1892

Epimerite symmetrical, with or without appendage, syzygy (association) late, frontal; gametocysts without sporoducts, generally dehiscing by simple rupture; oocysts biconical, cylindrobiconical or irregular; simple or spiny; in intestine of arthropods or chordates.

This family contains 3 subfamilies, 61 genera and 283 species. Although these species are primarily intestinal parasites of insects and centipedes, some are reported from arrow worms and pelagic tunicates.

SUBFAMILY ACTINOCEPHALINAE
LÉGER, 1899

Oocysts without spines or thickenings at their poles; in insects, diplopods, chilopods, opilionids, and chordates.

This subfamily contains 38 genera and 187 species.

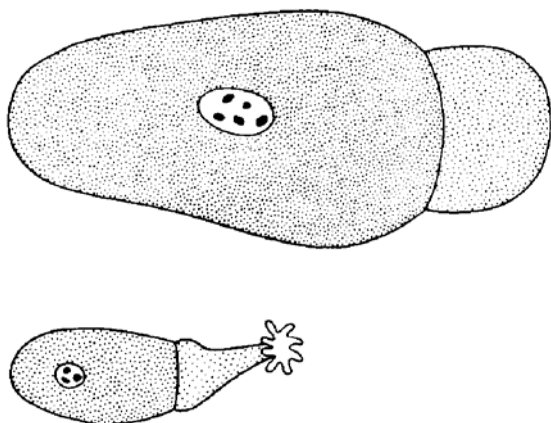


Fig. 75. *Actinocephalus parvus*. Top, mature trophozoites. Bottom, immature trophozoite. (Based on Wellmer, 1911.)

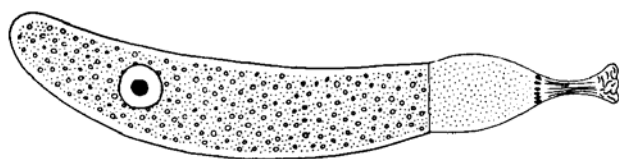


Fig. 76. *Actinocephalus licini*. Immature trophozoite. (Based on Tuzet and Théodoridès, 1951.)

Genus **Actinocephalus**

Von Stein, 1848

(= *Stephanophora* Léger, 1892)

Epimerite a hemispherical tumidus with eight to ten upwardly directed digitiform processes, borne on a short but prominent neck; neck persists more or less in trophozoite, but digitiform processes disappear; gametocysts dehisce through a hole in the gametocyst wall through which oocysts are extruded in a single thread; oocysts biconical or lemon-shaped; in insects. Forty named species. Several examples are illustrated in Figs. 75 & 76.

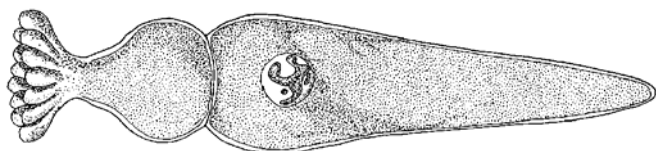


Fig. 77. *Actinocephalus conicus*. Immature trophozoite. (Based on Léger, 1892.)

Actinocephalus conicus (Dufour, 1837) von Frantzius, 1848 (= *Gregarina conica* Dufour, 1837; *Actinocephalus lucani* von Stein, 1848; *Actinocephalus lucanus* [von Stein, 1848] von Frantzius, 1848; *Gregarina lucani* [von Stein, 1848] Diesing, 1851; *Stephanophora radiosa* Léger, 1892; *Stephanophora lucani* [von Stein,

1848] Labbé, 1899; *Actinocephalus conicus* var. *magna* Théodoridès, 1955) (Fig. 77).

TYPE SPECIES. Trophozoite: Epimerite a hemispherical tumidus, with a peripheral corona of 12 or more digitiform processes, anteriorly - directed; borne on thick neck, persistent; protomerite spherical to pyriform, tapering anteriorly to epimerite neck, length ~100.0–133.3 μm ; deutomerite elongate ellipsoidal, broadly tapering from a deep constriction at the protomerite deutomerite septum to a blunt point posteriorly, length ~200.0–266.6 μm ; total length (without epimerite) 300.0–400.0 μm ; nucleus spherical, with a single, large, irregular endosome. Oocyst: Biconical, length 13.5 μm , width 4.5 μm . TYPE HOST: *Dorcas* (syn., *Lucanus*) *parallelopipedus*. Ref. Dufour (1826), Geus (1969), Watson (1916b).

Genus **Caulocephalus**

Bhatia & Setna, 1924

Epimerite dilated into a cauliflower shape anteriorly, narrower at base, persistent; protomerite with specialized cytoplasmic zone; oocysts ovoid or spherical in beetles. Three named species.

Caulocephalus bhatiasetnai Théodoridès, Desportes and Jolivet, 1964 (= *Caulocephalus crenatus* Bhatia and Setna, 1924, in part) (Fig. 78).

TYPE SPECIES. Trophozoite: Epimerite cauliflower-like, length 6.85 μm ; crenate, dilated anteriorly, narrowing basally at junction with protomerite; protomerite elongate, conical, length 25.14 μm , width 21.71 μm ; with specialized anterior cytoplasmic zone, distinctly constricted at protomerite deutomerite septum; deutomerite cylindrical, length 58.0 μm , width 24.85 μm ; gradually tapering to a rounded point posteriorly; nucleus spherical to slightly ovoid, diameter 12.71 μm ; with large vacuolated karyosome and small compact karyosome. Oocyst: ovoid to nearly spherical, diameter 12.0 μm ; liberated from the gametocyst by simple rupture. TYPE HOST: *Aulacophora foveicollis*. Ref. Bhatia and Setna (1924), Théodoridès, Desportes and Jolivet (1964, 1972).

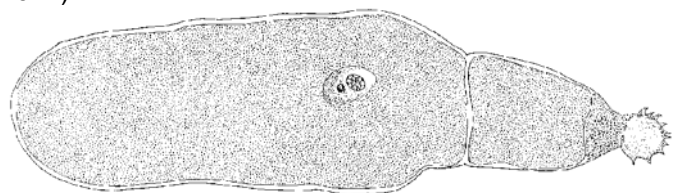


Fig. 78. *Caulocephalus bhatiasetnai*. Trophozoite. (Based on Théodoridès, Desportes, and Jolivet, 1964.)

Genus **Cornimeritus**

H. Hoshide, 1959

Trophozoites solitary; epimerite an acute claw with a long, large, flexible stalk; gametocysts spherical,

dehiscing by simple rupture; oocysts biconical, extruded in lateral chains. Monotypic.

TYPE SPECIES: *Cornimeritus ovalis* H. Hoshide, 1959. TYPE HOST: Nitidulidae gen. sp.

Genus ***Umbracephalus***

H. Hoshide, 1959

Trophozoites solitary, elongate cylindrical, with elongate ellipsoidal nucleus; epimerite with a very long neck bearing an anterior crown with about twenty recurved hooks; gametocysts spherical; oocysts unknown. Monotypic.

TYPE SPECIES: *Umbracephalus longicollis* H. Hoshide, 1959. TYPE HOST: *Lithobius* sp.

Genus ***Urnaepimeritus***

H. Hoshide, 1959

Trophozoites solitary, elongate, with spherical nucleus; epimerite with a short neck and a bowl - shaped crown with 30 or more recurved hooks; gametocysts spherical, dehiscing by simple rupture; oocysts spindle - shaped. Monotypic. TYPE SPECIES: *Urnaepimeritus spathiformis* H. Hoshide, 1959. TYPE HOST: *Prolamnonyx holstii*.

Genus ***Asterophora***

Léger, 1892

Epimerite a thick, horizontal disk with a milled border and a stout style projecting from the center; oocysts cylindrobiconical; in intestine or arthropods. Fourteen named species.

Asterophora mucronata Léger, 1892 (Fig. 79).

TYPE SPECIES. Trophozoite: Epimerite a flat disc with a milled border and a short central style, length 50.0 µm, width 70.0 µm; borne on a short, stout neck; protomerite elongate, length 90.3 µm, width 83.5 µm; tapering anteriorly to a blunt cone; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a point posteriorly, length 222.0 µm, width 105.3 µm; nucleus ovoidal, length 33.3 µm, width 25.3 µm; with several large karyosomes, diameter 10.0 µm. Oocyst: Cylindrobiconical, length 8.0, width 3.5; liberated from the gametocyst by simple rupture.

TYPE HOST: *Rhyacophila* sp., larvae. Ref. Geus (1969), Kamm (1922) Léger (1892).

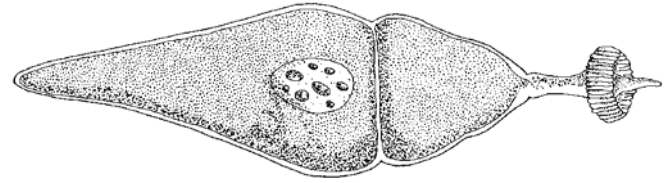


Fig. 79. *Asterophora mucronata*. Trophozoite. (Based on Léger, 1892.)

Genus ***Pileocephalus***

Schneider, 1875

Epimerite lance - shaped or a triangular button, with short neck; oocysts biconical; in insect larvae. Eighteen named species.

TYPE SPECIES: *Pileocephalus chinensis* Schneider, 1875(= *Cardiocephalus sororculae* Tsvetkov, 1929). TYPE HOST: *Anobolia sororcula*.

Pileocephalus heerii (Kölliker, 1845) Schneider, 1875 (= *Gregarina heeri* von Kölliker, 1845; *Stylorhynchus heeri* [von Kölliker, 1845] von Frantzius, 1848; *Gregarina frantziusiana* Diesing, 1851; *Asterophora heeri* [von Kölliker, 1845] Baudoin, 1967) (Fig. 80). Trophozoite: Epimerite in young specimens an elongate papilla, sharply acuminate, borne on a short neck; in older specimens distinctly lanceolate, length 60.0 µm; borne on a bulbous neck, length 30.0 µm; protomerite conical, length 98.0–111.2–122 µm, width 62.0–70.6–82.0 µm; truncate anteriorly, widest just above protomerite deutomerite septum; protomerite deutomerite septum deeply constricted; deutomerite elongate ellipsoidal, length 236.0–254.4–272.0 µm, width 56.0–63.6–76.0 µm; terminally acuminate broadly tapering from the protomerite deutomerite septum to a blunt point posteriorly; nucleus ellipsoidal, length 29.2 µm, width 22.0 µm; with many small karyosomes. Total length: 334–364–384 µm. Oocyst: Biconical, length 9.0 µm, width 4.0 µm; liberated from the gametocyst by simple rupture. TYPE HOST: *Phryganea varia*. Ref. Geus (1969), Kamm (1922), von Kölliker (1848).

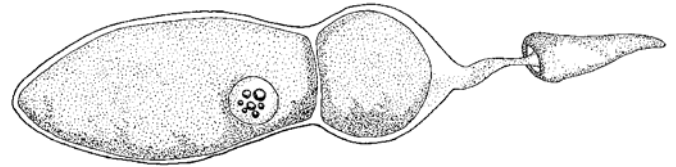


Fig. 80. *Pileocephalus heerii*. Immature trophozoite with lanceolate epimerite. (Based on Geus, 1969.)

Genus ***Gemmicephalus***

Baudoin, 1967

Epimerite in the form of an oval bud; oocysts slightly biconical. Two named species.

TYPE SPECIES: *Gemmicephalus mutabilis* Baudoin, 1967. TYPE HOST: *Athripsodes cinereus*.

Genus ***Pilidiophora***
Baudoin, 1967

Epimerite without a long differentiated neck and having the form of a small bonnet consisting of a dome prolonged toward the epimerite base by little tongues surrounding the epimerite base. Monotypic.

TYPE SPECIES: *Pilidiophora fragilis* Baudoin, 1967. TYPE HOST: *Agrypnia pagetana*.

Genus ***Geneiorhynchus***
Schneider, 1875

Epimerite a long neck with a tuft of short bristles at its end; oocysts cylindrical or cylindrobiconical; in odonate larvae. Two named species.

Geneiorhynchus monnieri Schneider, 1875 (= *Gregarina monieri* Schneider, 1875 of Geus [1969] *lapsus calami*) (Figs. 81 & 82).

TYPE SPECIES. Trophozoite: Epimerite a tuft of bristles, short, sharp; borne on a long, slender neck; protomerite broadly rounded to obvate, acuminate anteriorly, length 74.7 µm, width 49.8 µm; protomerite deutomerite septum sharply constricted; deutomerite elongate ellipsoidal to cardioid, broadly tapering from the protomerite deutomerite septum to a sharp point posteriorly, length 232.8 µm, width 71.5 µm; nucleus spherical, length 16.3 µm, width 19.3 µm; with several karyosomes. Oocyst: Sub - navicular; liberated from the gametocyst by simple rupture. TYPE HOST: *Libellula* sp. Ref. Crawley (1907), Ellis (1913b), Geus (1969), Kamm (1922), Schneider (1875).

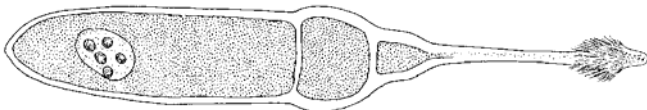


Fig. 81. *Geneiorhynchus monnieri*. Trophozoite. (Based on Schneider, 1875.)

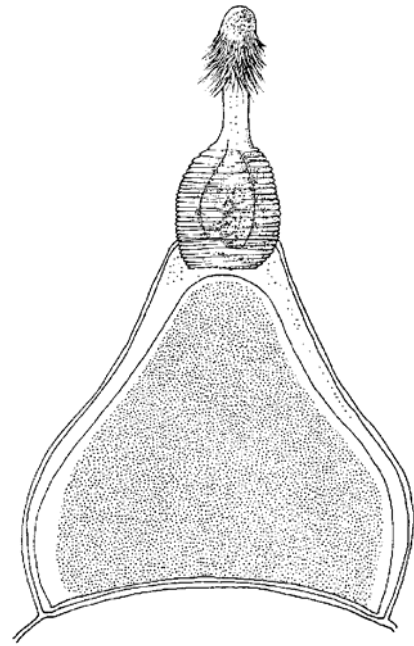


Fig. 82. *Geneiorhynchus monnieri*. Protomerite with retractile epimerite. (Based on Schneider, 1875.)

Genus ***Acanthoepimeritus***
H. Hoshide, 1959

Trophozoites solitary, with spherical nucleus; epimerite a swollen club, with nine or ten rows of hooks around it and with numerous recurved hooks covering its anterior surface. Monotypic.

TYPE SPECIES: *Acanthoepimeritus jimukade* H. Hoshide, 1959. TYPE HOST: *Mecistocephalus marmoratus*.

Genus ***Phialoides***
Labbé, 1899
(= *Phialis* Léger, 1892)

Epimerite with a long neck, consisting of a retractile papilla bordered by a cushion set peripherally with stout teeth, surrounded by a wider collarette; gametocysts spherical, without sporoducts; oocysts biconical, ventricose; in beetle larvae. Monotypic.

Phialoides ornata (Léger, 1892) Labbé 1899 (= *Phialis ornata* Léger, 1892) (Fig. 83).

TYPE SPECIES. Trophozoite: Epimerite a retractile papilla bordered by a cushion set peripherally with stout teeth, surrounded by a wider collarette, persistent, borne on a long neck, length up to 1200.0 µm; protomerite subglobular, as long as wide, with constriction at septum; deutomerite broadly ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriorly; total length 1200.0 µm; nucleus spherical, with several karyosomes. Oocyst: Biconical, ventricose, length 10.5 µm, width 6.75 µm; liberated from the

gametocyst by simple rupture. TYPE HOST: *Hydrous piceus*. Ref. Labbé (1899), Léger (1892), Watson (1916b).

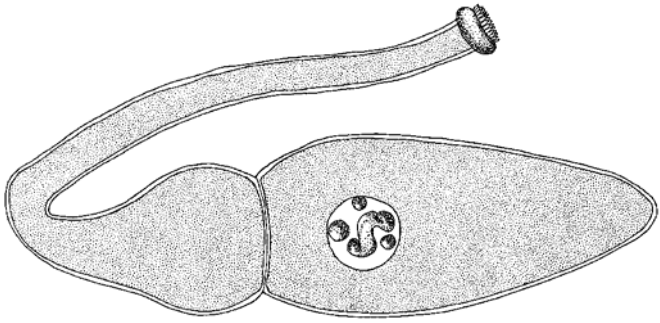


Fig. 83. *Phialoides ornata*. Trophozoite. (Based on Léger, 1892.)

Genus **Legeria**

Labbé, 1899

(= *Dufouria* Schneider, 1875)

Epimerite with a stalked, irregularly lobed, and folded plasma portion; protomerite surrounded by a collar; gametocysts without sporoducts; oocysts cylindrobiconical or subnavicular, with a thick wall; in beetle larvae. Monotypic.

Legeria agilis (Schneider, 1875) Labbé, 1899 (= *Sporadina dytiscorum* von Frantzius, 1848; *Dufouria agilis* Schneider, 1875) (Figs. 84 & 85).

TYPE SPECIES. Trophozoite: Epimerite a distal pediolate tumidus, irregularly pleated, borne on a pediolate neck; protomerite irregularly cylindrical, dilated in anterior third, terminated by an obtuse angled cone, as long as wide, length 188.4 μm , width 183.8 μm ; deutomerite irregularly cylindrical, tapering from middle to a sharp point posteriad, length 472.8 μm , width 211.1 μm ; nucleus ovoidal, length 67.5 μm , width 31.25 μm ; several karyosomes. Oocyst: Cylindrobiconical, liberated from the gametocyst by simple rupture.

TYPE HOST: *Colymbetes* sp. Ref. Geus (1969), Labbé (1899), Watson (1916b).

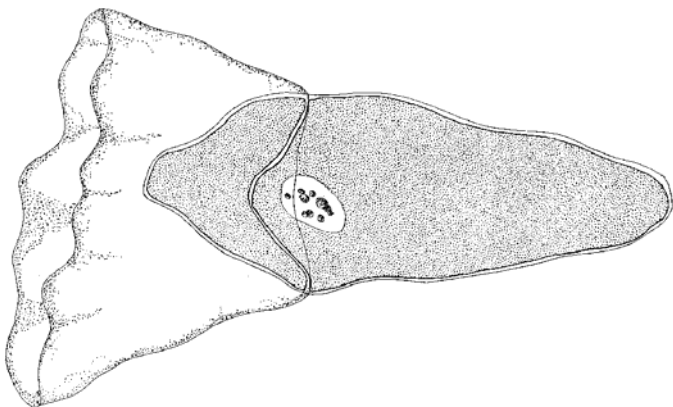


Fig. 84. *Legeria agilis*. Trophozoite. (Based on Geus, 1969.)

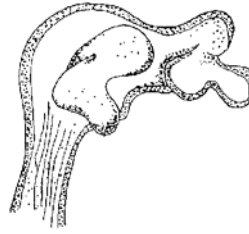


Fig. 85. *Legeria agilis*. Epimerite. (Based on Geus, 1969.)

Genus **Pyxinia**

Hammerschmidt, 1838

(= *Xiphorhynchus* Léger, 1892)

(= *Beloides* Labbé, 1899)

Epimerite a crenulate crateriform disk with or without hooks at its periphery, with a central conical style; gametocysts dehisce by formation of a hole in the wall through which oocysts are extruded in a single thread; oocysts biconical; in beetles. Thirteen named species. Examples are illustrated in Figs. 86–88.

Pyxinia rubecola Hammerschmidt 1838.

TYPE SPECIES. Trophozoite: Epimerite a flattened disk, crenulate, crateriform, with a short, conical, central style; borne on a short neck; protomerite spherical, length 60.0 μm , width 56.3 μm ; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum through a sharp constriction in the latter third of the deutomerite to a blunt point posteriad, length 173.9 μm , width 75.1 μm ; nucleus ovoid, length 20.0 μm , width 15.0 μm ; in the anterior half of the deutomerite, with large central endosome, diameter 6.0 μm . Oocyst: Biconical, length 14.0 μm , width 7.0 μm ; liberated from the gametocyst by simple rupture. TYPE HOST: *Dermestes lardarius* and *Dermestes vulpinus*. Ref. Geus (1969), Vincent (1922), Watson (1916b).

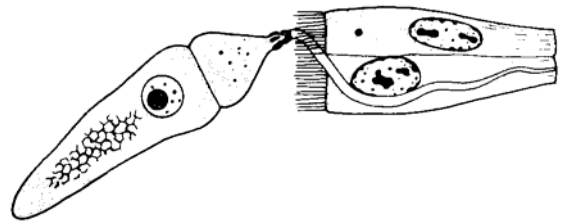


Fig. 86. *Pyxinia moebuszi*. Trophozoite attached to host intestinal cell. (Based on Léger and Duboscq, 1902.)

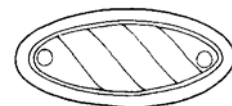


Fig. 87. *Pyxinia* sp. Oocyst. (Based on Léger, 1892.)



Fig. 88. *Pyxinia* sp. Exsporulation, oocyst releasing sporozoites. (Based on Léger, 1892.)

Genus ***Discorhyncus***

Labbé, 1899

(= *Discocephalus* Léger, 1892)

Epimerite a large spheroidal papilla with collar and short neck, non - persistent; oocysts biconical, slightly curved, slightly ventricose; in insect larvae. Monotypic.

Discorhyncus truncatus (Léger, 1892) Labbé, 1899
(= *Discocephalus truncatus* Léger, 1892).

TYPE SPECIES. Trophozoite: Epimerite a large spheroidal papilla with collar and short neck, lost early in development; protomerite spherical to cardioid, with slight anterior tapering; deutomerite regularly cylindrical to elongate ellipsoidal, with blunt point posteriad; total length to 300.0 µm; nucleus spherical, with 6 endosomes. Oocyst: Biconical, slightly swollen (ventricose), liberated from the gametocyst by simple rupture. TYPE HOST: *Sericostoma* sp. Ref. Labbé (1899), Léger (1892).

Genus ***Steinina***

Léger & Duboscq, 1904

Epimerite a short, motile, digitiform process which later changes into a flattened button; oocysts biconical, ventricose; in insects. Twenty - three named species.

Steinina ovalis (von Stein, 1848) Léger & Duboscq, 1904 (= *Clepsidrina polymorpha* Hammerschmidt, 1838 [in part]; *Stylorhynchus ovalis* von Stein, 1848; *Gregarina ovalis* [von Stein, 1848] Diesing, 1851; *Gregarina polymorpha* [Hammerschmidt, 1838] Lankester, 1863 [in part]) (Figs. 89 & 90).

TYPE SPECIES. Trophozoite: Epimerite a short, motile, digitiform process which later changes into a flattened button; protomerite cylindroconical, length ~ 40.0 µm, width ~ 40.0 µm; deutomerite short, ovoidal, swollen, terminating in an obtuse cone, length ~ 60.0 µm; total length 100.0 µm; nucleus spherical; with single large endosome. Oocyst: Biconical, equatorially swollen, slightly ventricose, length 9.0 µm, width 7.4 µm, liberated from the gametocyst by simple rupture. TYPE HOST: *Tenebrio molitor* larvae. Ref. Léger and Duboscq (1904), Watson (1916b).

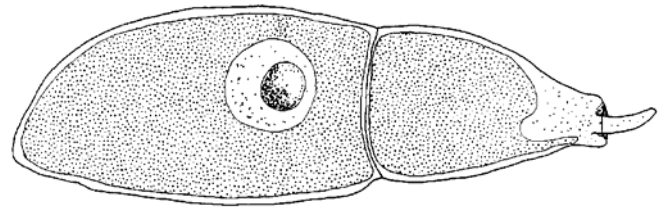


Fig. 89. *Steinina ovalis*. Trophozoite. (Based on Léger and Duboscq, 1904.)

Genus ***Bothriopsides***

Strand, 1928

(= *Bothriopsis* Schneider, 1875)

Epimerite without neck, lenticular, small, sessile, oval, with six or more long, slender, filaments projecting anteriorly; protomerite very large, mobile; protomerite deutomerite septum convex anteriorly; gametocysts spherical; oocysts biconical. Eight named species.

Bothriopsides histrio (Schneider, 1875) Strand, 1928 (= *Bothriopsis histrio* Schneider, 1875; *Iorella wegorecki* Lipa, 1967) (Fig. 91).

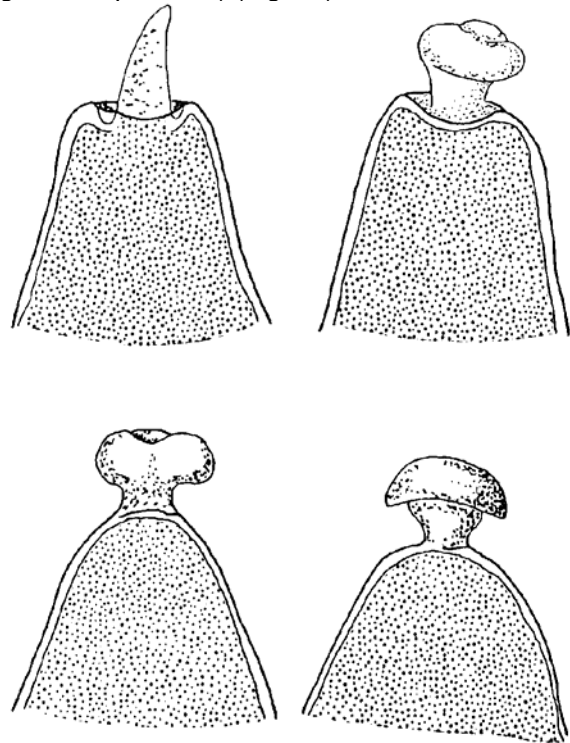


Fig. 90. *Steinina ovalis*. Various transitional stages in epimerite structure during development. (Based on Léger and Duboscq, 1904.)

TYPE SPECIES. Trophozoite: Epimerite lenticular, small, sessile, oval, with six or more long, slender, filaments, length ~ 80.0–90.0 µm; projecting anteriorly; without neck; protomerite elongate cylindrical with irregular anterior tumidus; length 50.0–95.0–137.0 µm, width 53.0–79.8–99.0 µm; protomerite deutomerite septum sharply convex anteriorly; deutomerite elongate

ellipsoidal, stout, tapering from the protomerite deutomerite septum to a sharp point posteriad, length 99.0–198.2–276.0 µm, width 33.0–49.7–62 µm; nucleus spherical to ellipsoidal, length 22.0–32.1–42 µm, width 14.0–20.5–32 µm; with several karyosomes. Total length 148.0–293.2–411.0 µm. Oocyst: Biconical, obese (swollen), length 7.2 µm, width 5.0 µm; liberated from the gametocyst by simple rupture. TYPE HOST: *Graphoderes* (syn., *Hydaticus*) *cinereus*, *Colymbetes fuscus*, *Acilius sulcatus*. Ref. Geus (1969), Schneider (1875), Strand (1928), Watson (1916b).

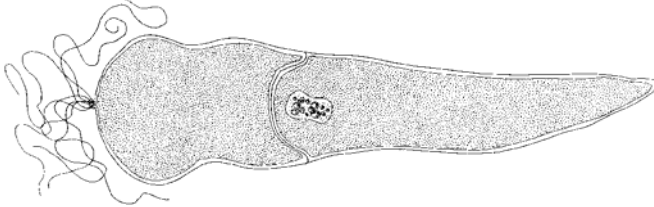


Fig. 91. *Bothriopsis histrio*. Trophozoite. (Based on Geus, 1969.)

Genus ***Pomania***
Baudoin, 1967

Epimerite composed of a point which may be transformed into a sucker and a cap covering the protomerite. Monotypic.

TYPE SPECIES: *Pomania hovassei* Baudoin, 1967.
TYPE HOST: *Potamophylax nigricornis*.

Genus ***Stictospora***
Léger, 1893

Epimerite with a short neck, a spherical crateriform ball with 9 to 12 posteriorly directed laminations set close to the neck, non - persistent; gametocysts with a gelatinous envelope and no sporoducts; oocysts biconical, slightly curved in insects. Six named species.

Stictospora provincialis Léger, 1893 (= *Stictospora provincialis* var. *anomala* Théodoridès, 1955) (Fig. 92).

TYPE SPECIES. Trophozoite: Epimerite a spherical papilla, anteriorly crateriform, with 12 posteriorly directed laminations, laminations sharply pointed posteriad, borne on a short neck; protomerite subglobular, becoming broadly conical anteriorly, length 204.3 µm, width 219.6 µm; deutomerite elongate cardioid, tapering from the protomerite deutomerite septum to a sharp point posteriad, length 1162.4 µm, width 259.9 µm; nucleus ellipsoidal, length 72.0 µm, width 45.3 µm; with several karyosomes. Oocyst: Biconical, slightly curved, liberated from the gametocyst by simple rupture. TYPE HOST: *Melolontha* sp. Ref. Geus (1969), Watson (1916b).

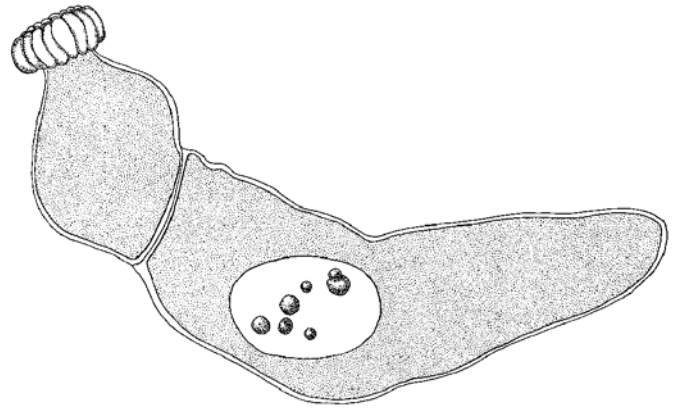


Fig. 92. *Stictospora provincialis*. Trophozoite. (Based on Geus, 1969.)

Genus ***Coleorhynchus***
Labbé, 1899
(= *Coleophora* Schneider, 1885)

Epimerite diskoid, poorly developed; protomerite large, forming a collarette or muscular sucker serving for attachment; trophozoites solitary; development parthenogenetic; oocysts biconical or navicular, octozoic; in intestine of insects. Monotypic.

Coleorhynchus heros (Schneider, 1885) Labbé, 1899 (= *Coleophora heros* Schneider, 1885) (Fig. 93).

TYPE SPECIES. Trophozoite: Epimerite diskoid, poorly developed; protomerite large, forming a collarette or sucker with a muscular band serving for attachment; protomerite deutomerite septum convex anteriorly; deutomerite ovoidal, blunt posteriad; Total length 200.0 µm, width 160.0 µm; nucleus spherical, diameter 40.0 µm; with a single large central karyosome, length 10.0 µm, width 6.0 µm; and 2 or 3 smaller karyosomes. Gamont total length 2,000.0–3,000.0 µm. Oocyst: Biconical to spindle - shaped, length 6.5–7.0 µm, width 4.0–5.0 µm, liberated from the gametocyst by simple rupture. TYPE HOST: *Nepa cinerea*. Ref. Geus (1969), Grell (1939), Kamm (1922).

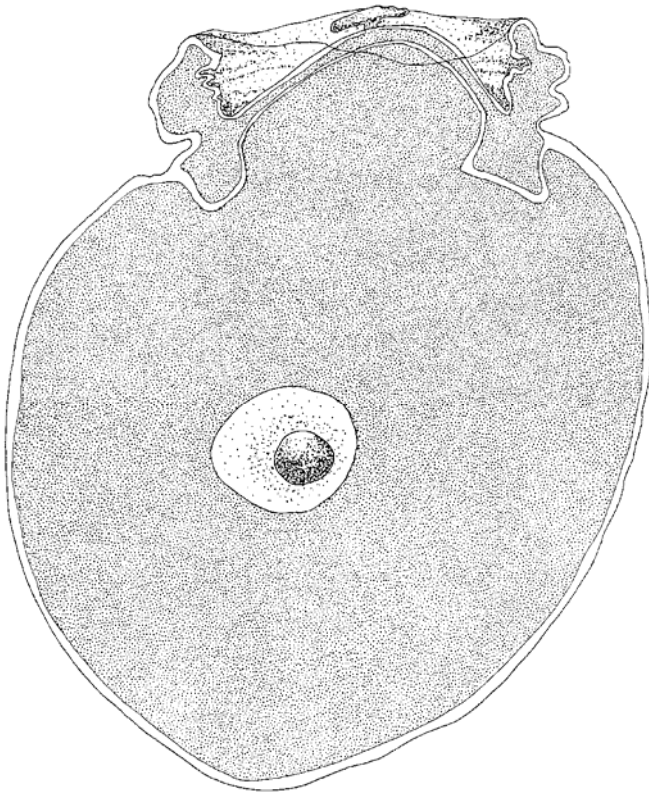


Fig. 93. *Coleorhynchus heros*. Trophozoite. (Based on Grell, 1939.)

Genus **Amphoroides**

Labbé, 1899

(= *Amphorella* Léger, 1892)

Epimerite a globular sessile papilla, lost early; protomerite globular, cup - shaped anteriorly; oocysts biconical or navicular, curved, without epispore; in millipedes. Four named species.

Amphoroides polydesmi (Léger, 1892) Labbé, 1899 (= *Amphorella polydesmi* Léger, 1892) (Fig. 94).

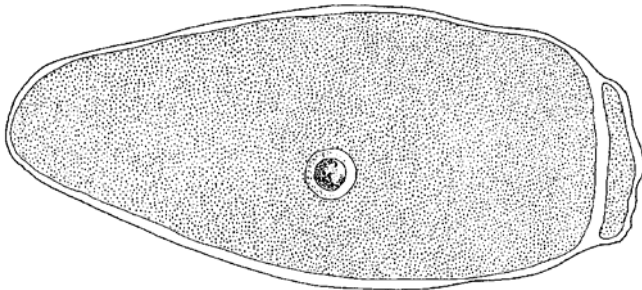


Fig. 94. *Amphoroides polydesmi*. Trophozoite. (Based on Geus, 1969.)

TYPE SPECIES. Trophozoite: Epimerite a cylindroconical papilla, without neck; protomerite cup - shaped or crateriform anteriorly, very short, depressed, length 5.0–6.75–8.0 μm , width 19.0–23.8–29.0 μm ; protomerite deutomerite septum sharply convex anteriorly,

sometimes forming a dome surrounded by the protomerite; deutomerite cylindrical to obvoid, broadly tapering from the anterior third to a rounded point posteriorly, length 105.0–142.8–164.0 μm , width 33.0–45.8–58.0 μm ; nucleus spherical, diameter 11.0 μm ; with large central endosome, ellipsoidal, length 5.0 μm , width 7.0 μm . Total length 11.0–148.8–172.0 μm . Oocyst: Biconical, length 7.8 μm , width 3.8 μm ; liberated from the gametocyst by simple rupture.

TYPE HOST: *Polydesmus complanatus*, *Polydesmus denticulatus*. Ref. Geus (1969), Léger (1892), Labbé (1899), Watson (1916b).

Genus **Stylocystis**

Léger, 1899

Epimerite simple, a sharply pointed process, normally recurved in a long hyaline point or spine, very sharp anteriorly; gametocysts mature entirely within host and do not contain residuum; oocysts biconical; in intestine of insects. Four named species.

TYPE SPECIES: *Stylocystis praecox* Léger, 1899. TYPE HOST: *Tanytus* sp.

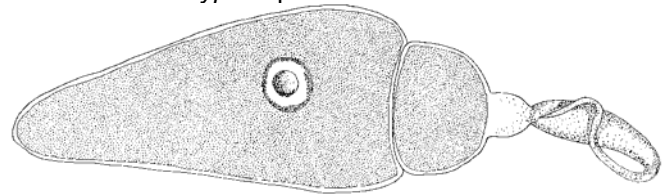


Fig. 95. *Stylocystis chowdhurya*. Trophozoite. (Based on Sarkar and Mazumder, 1983.)

Stylocystis chowdhurya Sarkar & Mazumder, 1983 (Fig. 95). Trophozoite: Epimerite a long, filamentous spine, sharply pointed, recurved, length 12.0–26.5–39.0 μm ; with basal tumidus or bulb, width 3.2–4.6–5.5 μm ; protomerite dome - shaped, length 8.1–13.4–29.7 μm , width 10.8–17.2–37.8 μm ; deutomerite elongate, tapering from the protomerite deutomerite septum to a blunt point posteriorly, length 35.1–64.4–135.0 μm , width 13.5–20.1–43.2 μm ; nucleus spherical, diameter 9.3–14.3–18.7 μm ; with large central endosome. Oocyst: Diamond - shaped, poles truncated, smooth, length 9.87 μm , width 4.0 μm ; liberated from the gametocyst by simple rupture. TYPE HOST: *Cryptophagus* sp. Ref. Léger (1899), Sarkar and Mazumder (1983).

Genus **Taeniocystis**

Léger, 1905

Epimerite sessile or with short neck, consisting of an apical tumidus with six to eight recurved hooks; deutomerite divided by septa into many serial segments; gametocysts spherical, opening by simple rupture; oocysts biconical; in insects. Three named species.

Taeniocystis mira Léger, 1904 (Fig. 96).

TYPE SPECIES. Trophozoite: Epimerite a small bulb with a corona of 6–8 recurved hooks, borne on a short neck; protomerite spherical with slight anterior tapering, mature width 30.0–35.0 μm ; deutomerite elongate, divided by septa into many serial segments, segment number increasing with length, superficially resembling a tapeworm, length 18.0–300.0–500.0 μm , width 30.0–35.0; nucleus spherical, appearing initially in the second deutomeric segment, deutomeric segment 6 or 7 in mature animals, diameter 12.0 μm in animals over 20.0 μm in length; with large central endosome. Oocyst: Biconical, strongly flattened, length 7.0 μm , width 3.0 μm ; poles thickened, refractive; liberated from the gametocyst by simple rupture.

TYPE HOST: *Ceratopogon solstitialis*. Ref. Geus (1969), Kamm (1922), Léger (1905, 1906).

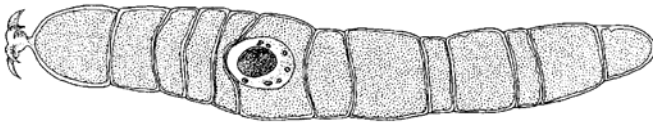


Fig. 96. *Taeniocystis mira*. Young trophozoite. (Based on Léger, 1906.)

Genus ***Sciadiophora***
Labbé, 1899
(= *Lycosella* Léger, 1896)

Epimerite a large sessile, disk with a crenulate border, lost early; protomerite with numerous vertical lamellae, broadening to an umbrella in the mature trophozoite, each rib of umbrella curved to form a spine pointing backward; oocysts biconical or ovoid, united into a string of beads; in opilionids. Six named species.

Sciadiophora phalangii (Léger, 1896) Labbé, 1899 (= *Lycosa phalangii* Léger, 1896 [in part]) (Fig. 97).

TYPE SPECIES. Trophozoite: Epimerite a large papilla, sessile, indented, with crenulate periphery; protomerite broadly conical at apex, with 15–16 vertical lamellar plates, recurved, terminally sharp; length 130.0–138.25–146.0 μm , width 148.0–153.0–160.0 μm ; very strong constriction at protomerite deutomerite septum; deutomerite elongate, broadly tapering from the protomerite deutomerite septum, long, slender, acuminate posteriad, length 1590.0–1621.25–1660.0 μm , width 306.0–315.25–325.0 μm ; nucleus ovoid to spherical, length 75.0 μm , width 90.0 μm ; with multiple karyosomes. Oocyst: Biconical, poles rounded, with intermediate shoulders, unique, length 9.0 μm , width 5.0 μm ; united into a string of beads, liberated from the gametocyst by simple rupture. **TYPE HOST:** *Phalangium opilio*. Ref. Geus (1969), Kamm (1922), Labbé (1899).

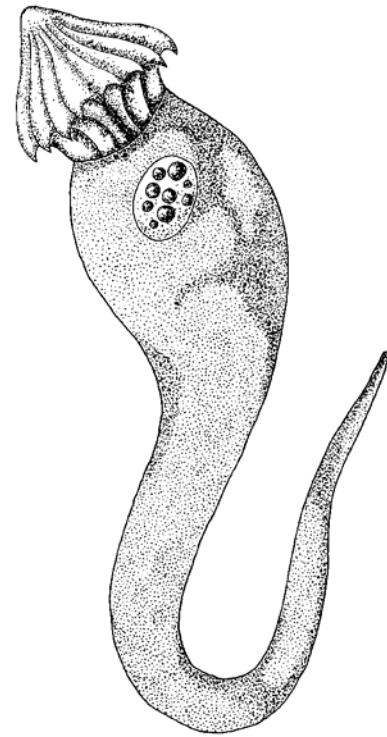


Fig. 97. *Sciadiophora phalangii*. Trophozoite. (Based on Geus, 1969.)

Genus ***Anthorhynchus***
Labbé, 1899
(= *Anthocephalus* Schneider, 1887)

Epimerite a large flattened, fluted disk; oocysts biconical or ovoid, in lateral chains. Three named species.

Anthorhynchus sophiae (Schneider, 1887) Labbé, 1899 (= *Anthocephalus sophiae* Schneider, 1887) (Fig. 98).

TYPE SPECIES. Trophozoite: Epimerite a broad, flattened corona, comprising digitiform processes, short, blunt, united laterally and curved inward, length 100.0 μm , width 150.0 μm ; without neck; protomerite spherical, flattened, length 120.0–144.0 μm , width 234.0–256.0 μm ; deutomerite conoidal, broadly tapering posteriad from a constriction at the protomerite deutomerite septum to a broad, blunt end, length 1226.0–1476.0 μm , width 420.0–494.0 μm ; nucleus round, diameter ~ 65.0 μm . Oocyst: Biconical, broad, length 6.0 μm , width 4.6 μm ; joined laterally into chains, liberated from the gametocyst by simple rupture. **TYPE HOST:** *Phalangium opilio*. Ref. Geus (1969), Kamm (1922), Labbé (1899).

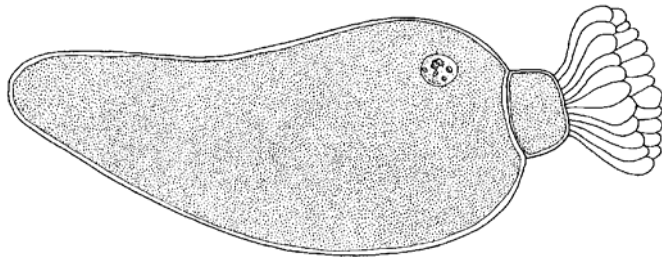


Fig. 98. *Anthorhynchus sophiae*. Trophozoite. (Based on Geus, 1969.)

Genus ***Agrippina***
Strickland, 1912

Epimerite a circular disk, with peripheral digitiform processes; oocysts symmetrical, ellipsoidal, unarmed; in flea larvae. Monotypic.

Agrippina bona Strickland, 1912 (Fig. 99).

TYPE SPECIES. Trophozoite: Epimerite a circular disk, cup - shaped, with peripheral digitiform processes; borne on a narrow neck; protomerite hemispherical to dome - shaped; deutomerite elongate ellipsoidal, broadly tapering posteriad from the protomerite deutomerite septum to a sharp point; total length 12.5–55.0 μm ; nucleus ovoid, with large band - like endosome and 2 smaller endosomes. Oocyst: Ellipsoidal, with polar thickening, symmetrical, unarmed (smooth), length 7.0 μm , width 3.0 μm ; liberated from the gametocyst by simple rupture in chains 2–3 oocysts abreast. TYPE HOST: *Ceratophyllus fasciatus*. Ref. Strickland (1912).

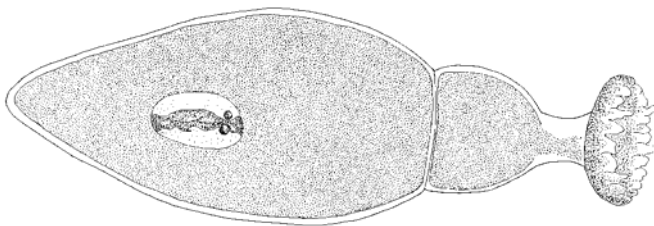


Fig. 99. *Agrippina bona*. Trophozoite. (Based on Strickland, 1912.)

Genus ***Globulocephalus***
Baudoin, 1965

Young trophozoite with globular epimerite with a permanent septum; syzygy late and ephemeral, intermediate between frontal and lateral; gametocysts dehisce by simple rupture; oocysts biconical; in intestine of trichopteran larvae. Monotypic.

TYPE SPECIES: *Globulocephalus hydropsyches* Baudoin, 1965. TYPE HOST: *Hydropsyche* sp.

Genus ***Alaspora***

Obata, 1953

Epimerite sessile in a jar - shaped sucker, with a deeply depressed anterior end; trophozoite solitary, elongate; gametocyst opens by simple rupture; oocysts cylindrobiconical, with three thin, triangular, longitudinal plates extending radially from the trunk; in intestine of beetles. Monotypic.

Alaspora depressa Obata, 1953 (Fig. 100).

TYPE SPECIES. Trophozoite: Epimerite a jar - shaped sucker, depressed to crateriform anterior, depression almost reaching the anterior end of the protomerite; without neck; protomerite conical, with slight constriction at septum, length 52.0–62.6–78.0 μm , width 60.0–68.9–120.0 μm ; deutomerite elongate conical, tapering from the protomerite deutomerite septum to a blunt point posteriad, length 160.0–211.4–338.0 μm , width 48.0–71.28–110.0 μm ; nucleus spherical to slightly ovoid, length 35.0–35.2–38.0, width 24.0–26.2–30.0 μm ; with many karyosomes. Total length 220.0–280.1–411.0 μm . Oocyst: Cylindrobiconical, with three longitudinal plates, triangular, thin, radiating at 120°; length 8.0 μm , width 3.0 μm , width with plates, 7.0 μm ; liberated from the gametocyst by simple rupture. TYPE HOST: *Anoplogenius cyanescens*. Ref. Obata (1953).

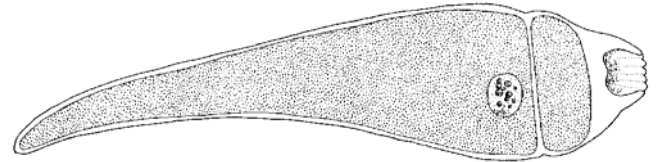


Fig. 100. *Alaspora depressa*. Trophozoite showing cross section through epimerite. (Based on Obata, 1953.)

Genus ***Ascocephalus***
Obata, 1955

Epimerite sessile, sucker - like, with a thick peripheral collar, depressed very deeply at anterior end, with cavity widened at bottom and a rugged ring of tooth - like projections around posterior periphery; trophozoites solitary, elongate ovoid; gametocyst spherical; gametocyst dehiscence and oocysts unknown; in intestine of beetles. Monotypic.

Ascocephalus armatus. Obata, 1955. (Fig. 101).

TYPE SPECIES. Trophozoite: Epimerite sessile, sucker - like, crateriform, margin thick, collar - like; crateriform depression deep, widening posteriad, posterior periphery a tooth - shaped ring, solid, rugged; protomerite semispherical, length 30.0–50.2–79.0 μm , width 62.0–107.1–210.0 μm ; deutomerite conical, tapering from the protomerite deutomerite septum to a rounded point posteriad, length 105.0–189.3–415.0 μm , width 69.0–115.6–227.0 μm ; nucleus spherical, diameter 26.0–33.3–43.0 μm . Oocyst:

Unknown. TYPE HOST: *Chlaenius nigricans*. Ref. Obata (1953).

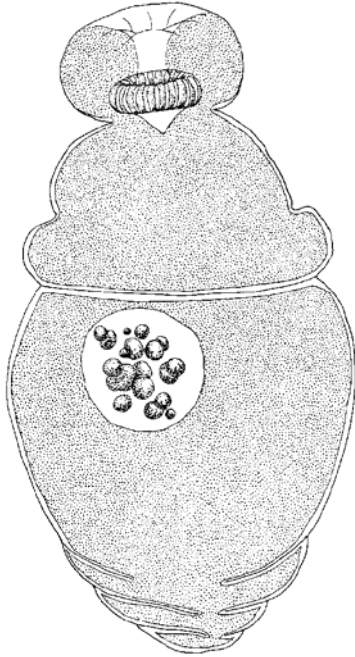


Fig. 101. *Ascocephalus armatus*. Trophozoite. (Based on Obata, 1953.)

Genus ***Amphorocephalus***
Ellis, 1913

Epimerite with a short dilated neck, consisting of a sessile button fluted on its sides; protomerite with a transverse superficial constriction; in chilopods. Seven named species.

Amphorocephalus amphorellus Ellis, 1913 (Fig. 102).

TYPE SPECIES. Trophozoite: Epimerite flask-shaped with fluted apical disk, apically constricted, sessile, persistent in specimens up to 600.0 µm, length ~ twice the length of the protomerite; protomerite cylindrical, with distinct equatorial constriction, tapering anteriorly from constriction, length 50.0 µm, width 60.0 µm; deutomerite elongate, pointed posteriorly, length 95.0 µm, width 60.0 µm. Total length 78.0–675.0–970.0 µm. Oocyst: unknown. TYPE HOST: *Scolopendra heros*. Ref. Ellis (1913a, 1913b).

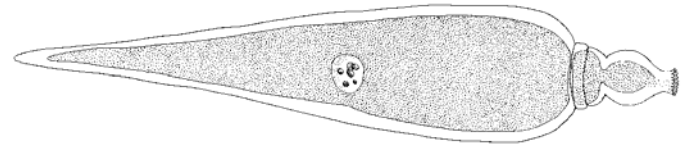


Fig. 102. *Amphorocephalus amphorellus*. Trophozoite. (Based on Ellis, 1913b.)

Genus ***Tricystis***
Hamon, 1951

Only gamont known; intracellular or between cells of digestive epithelium; epimerite, protomerite, and deutomerite present; in chaetognaths. Two named species.

TYPE SPECIES: *Tricystis planctonis* Hamon 1951. TYPE HOST: *Sagitta lyra* and *Sagitta bipunctulata*.

Genus ***Thalicola***
Ormières, 1965

Trophozoites with or without longitudinal striations; epimerite simple; syzygy head to tail; gametocysts spherical; oocysts and mode of dehiscence unknown; in salps. Four named species.

TYPE SPECIES: *Thalicola salpae* (Frenzel, 1885) Ormières, 1965 (= *Gregarina salpae* Frenzel, 1885). TYPE HOST: *Salpa maxima* and *Salpa fusiformis*.

Genus ***Epicavus***
Ormières & Daumal, 1970

Epimerite in the form of a deep cup with thick walls slightly striated longitudinally on their inner surface, carried on a neck; nucleus with a single large nucleolus; gametocysts spherical, dehiscing by simple rupture; oocysts subspherical, with rounded episporal polar plugs; in insects. Two named species.

TYPE SPECIES: *Epicavus araeoceri* Ormières and Daumal, 1970. TYPE HOST: *Araeocerus fasciculatus*.

Genus ***Gryllotalpia***
Hasselman, 1926

Epimerite a large knob set on a long stalk; gametocysts dehisce by simple rupture; oocysts biconical; in insects. Monotypic.

TYPE SPECIES: *Gryllotalpia magalhaesi* Hasselman, 1926. TYPE HOST: *Gryllotalpa* sp.

Genus ***Chilogregarina***
Levine, 1979

Epimerite simple or with nonpersistent digitiform processes at apex; gametocysts and oocysts unknown; in chilopods. Five named species.

TYPE SPECIES: *Chilogregarina striata* (Léger and Duboscq, 1903) Levine, 1979 (= *Actinocephalus striatus* Léger and Duboscq, 1903). TYPE HOST: *Scolopendra cingulata*.

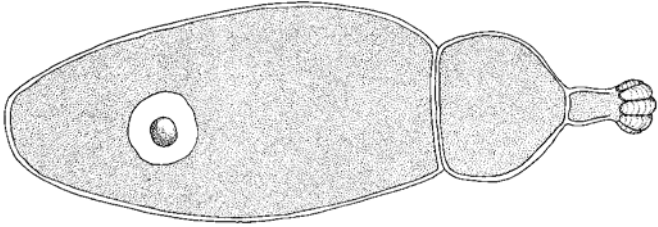


Fig. 103. *Crucocephalus dufouri*. Trophozoite. (Based on Sarkar, 1984.)

Genus ***Crucocephalus***
Sarkar, 1984

Young trophozoites ovoid, becoming cylindrical; epimerite with short, thick-walled neck, dilated at base, consisting of a globular tumidus with 6–8 broad, vertical, peripheral ridges; mature trophozoites fusiform to cylindroconical, solitary; gametocysts spherical, dehiscing by simple rupture; oocysts biconical, with sharply-pointed ends. Monotypic.

Crucocephalus dufouri Sarkar, 1984 (Fig. 103).

TYPE SPECIES. Trophozoite: Epimerite globular, length 5.2 μm , width 4.7 μm ; with 6–8 peripheral ridges, broad, vertical, giving the appearance of peripheral crenulation; borne on a short, thick-walled neck, length 7.0 μm ; posteriorly dilated; protomerite dome-shaped, length 12.5 μm , width 15.7 μm ; deutomerite elongate, tapering from the protomerite deutomerite septum to a blunt point posteriorly, length 41.9 μm , width 22.0 μm ; nucleus spherical, apparent, with a single round endosome. Oocyst: Biconical, smooth, poles sharply-pointed, length 8.5 μm , width 3.5 μm ; liberated from the gametocyst by simple rupture.

TYPE HOST: *Dermestes* sp., larvae. Ref. Sarkar (1984).

Genus ***Harendraia***
Sarkar, 1984

Trophozoites ovoid to fusiform; epimerite with narrow, elongated neck, consisting of a highly-complex, long, bowl-like structure with a bulb-like, round base, apex truncated, set with 4 short, slender symmetrical filaments or spines; mature trophozoites solitary, cylindrical; gametocysts spherical, dehiscing by simple rupture; oocysts ellipsoidal, released in lateral chains. Monotypic.

Harendraia intricata Sarkar, 1984 (Fig. 104).

TYPE SPECIES. Trophozoite: Epimerite a complex, long, bowl-like structure, length 45.8 μm , width 16.7 μm ; posteriorly rounded, bulb-like, terminally truncated, truncation set with 4 filaments or spines, long, slender,

length ~11.5 μm ; borne on a short, broad neck, length 2.4 μm ; protomerite dome-shaped, length 19.7 μm , width 14.7 μm ; deutomerite ovoid, length 74.8 μm , width 39.1 μm ; nucleus spherical, diameter 2.1 μm . Oocyst: Ellipsoidal, length 8.5 μm , width 5.0 μm ; terminally blunt; liberated from the gametocyst in a lateral chain by simple rupture. TYPE HOST: *Ptinus* sp. Ref. Sarkar (1984).

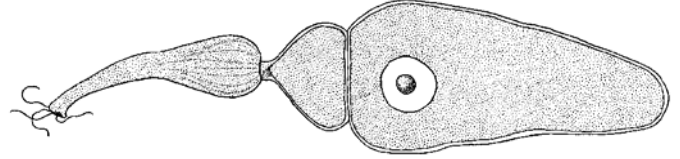


Fig. 104. *Harendraia intricata*. Trophozoite. (Based on Sarkar, 1984.)

Genus ***Levinea***
Kori, 1985

Early trophozoites solitary; epimerite cup-like at the apex of a short neck, with numerous peripheral digitiform processes; dehiscence of gametocysts by simple rupture; oocysts cylindrobiconical; in odonate insects. Monotypic.

TYPE SPECIES: *Levinea agriocnemidis* Kori, 1985. TYPE HOST: *Agriocnemis pygmaea*.

SUBFAMILY ACANTHOSPORINAE
LÉGER, 1892

Oocysts with spines or thickenings at their poles; sometimes at the equator and also along their edges; in carnivorous insects (especially aquatic insects), chilopods, and opilionids. This subfamily contains 20 genera and 75 species.

Genus ***Acanthospora***
Léger, 1892

Epimerite a conical papilla with an obtuse point; or simple, knob-shaped, papilla-like; or crateriform, with partial septa around it; oocysts biconical or ellipsoidal, with polar and equatorial spines, liberated from the gametocyst by simple rupture of the gametocyst wall; in insects. Six named species.

TYPE SPECIES: *Acanthospora pileata* Léger, 1892. TYPE HOST: *Cistelides* sp. and *Omoplus* sp.

Acanthospora bengalensis Sarkar & Haldar, 1981 (Fig. 105). Trophozoite: Epimerite bulb-like, globular, length 12.6–16.9–21.5 μm , width 16.8–21.2–25.8 μm ; borne on a short neck, length 12.6–24.3–37.8 μm ; protomerite conical, length 25.2–61.9–155.2 μm , width 33.6–42.2–68.9 μm ; deutomerite elongate cylindrical, length 126.0–298.5–551.7 μm , width 33.6–51.4–77.7 μm ; nucleus oval with reticulate or banded nucleoplasm. Oocyst: Spindle shaped, length 6.0 μm , width 4.5 μm ; hexagonal in cross section, poles truncated; with polar

spines and 6 meridional (equatorial) spines; liberated from the gametocyst by simple rupture. TYPE HOST: *Ceriagrion cerinorubellum*. Ref. Baudoin and Maillard (1972), Léger (1892), Sarkar and Haldar (1981c).



Fig. 105. *Acanthospora bengalensis*. Trophozoite. (Based on Sarkar and Haldar, 1981c.)

Genus **Grenoblia**
Hasselmann, 1927

Epimerite small, simple; protomerite conical; gametocysts and oocysts unknown. Monotypic.

TYPE SPECIES: *Grenoblia legeri* Hasselmann, 1927. TYPE HOST: *Hydrophilus* sp.

Genus **Corycella**
Léger, 1892

Epimerite with a central button bearing a crown of strong, recurved hooks that terminate in acute tips; oocysts biconical, with a tuft of fine hairs at the ends. Two named species.

Corycella armata Léger, 1892 (Fig. 106).

TYPE SPECIES. Trophozoite: Total length 280.0–300.0 μm ; epimerite a large globular papilla with a peripheral crown of 8 strong, stout, recurved, sharply pointed hooks; borne on a short, thick cylindrical collar or neck; protomerite spherical with slight anterior tapering, length $\sim 70.0\text{--}75.0$ μm ; wider than deutomerite; deutomerite elongate ellipsoidal, length $\sim 220.0\text{--}225.0$ μm ; broadly tapering from the protomerite deutomerite septum to a sharp point posteriad; nucleus spherical; with several distinct karyosomes. Oocyst: Biconical, truncate, length 13.0 μm , width 6.5 μm ; 4 small spines at each pole, no equatorial spines, liberated from the gametocyst by simple rupture. TYPE HOST: *Gyrinus natator*. Ref. Kamm (1922), Léger (1892).

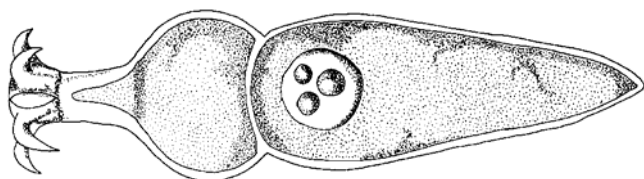


Fig. 106. *Corycella armata*. Trophozoite. (Based on Léger, 1892.)

Genus **Ancyrophora**
Léger, 1892

Epimerite consisting of a globular papilla with flexible or rigid appendages forming hooks which may be recurved; oocysts biconical, with polar tuft and 6

equatorial bristles or spines. Twenty - two named species.

Ancyrophora gracilis (Stein, 1848) Léger, 1892 (= *Gregarina acus* von Stein, 1848; *Actinocephalus acus* von Stein, 1848) (Fig. 107).

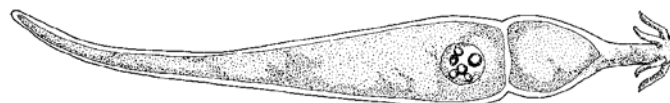


Fig. 107. *Ancyrophora gracilis*. Trophozoite. (Based on Léger, 1892.)

TYPE SPECIES. Trophozoite: Epimerite a globular papilla with 8 backwardly directed flexible tentacles, not forming hooks, borne on a short but distinct neck; protomerite conical with tumidus in basal third, tapering anteriorly to meet epimerite, length 57.1 μm , width 44.6 μm ; deutomerite elongate ellipsoidal to lanceolate, broadly tapering from the protomerite deutomerite septum to a sharp point posteriad, length 224.1 μm , width 64.2 μm ; nucleus spherical, diameter 24.3 μm ; with multiple karyosomes. Oocyst: Biconical, truncate, length 8.5 μm , width 5.1 μm ; with 4 spines at each pole and six equatorial spines, liberated from the gametocyst by simple rupture. **Notes:** Léger (1892) notes that this species attains a length of 2,000.0 μm ; however, no specimen of that size has since been recovered. The measurements provided here are taken from Geus (1969) and agree with the measurements of Baudoin (1971).

TYPE HOST: *Carabus* sp. (*C. auratus*, *C. violaceus*, *C. arcensis*, *C. auronitens*, *C. cancellatus*, *C. glabratus*, *C. hortensis*, *C. insulicola*, *C. intricatus*, *C. nemoralis*, *C. nitens*, *C. ullrichi*) Ref. Baudoin (1971), Geus (1969), Léger (1892), Tuzet, Ormières, and Théodoridès (1968), Watson (1916b).

Genus **Rhizionella**
Baudoin, 1971

Epimerite consisting of a central button bearing long, ascending, filamentous, root - like appendages; oocysts biconical, without polar truncation, with polar knobs and equatorial spines. Monotypic.

Rhizionella tenuis Baudoin, 1971 (Fig. 108).

TYPE SPECIES. Trophozoite: Epimerite a central button, length 12.0 μm , width 10.0 μm ; with a single peripheral crown of 8 long, gradually tapering, filamentous appendages, length reaching 40.0 μm ; protomerite small; deutomerite elongate, tapering to a sharp point posteriad; total length 500.0 μm . Oocyst: Biconical, length 7.0 μm , width 3.5 μm ; without truncated poles, with polar knobs and equatorial spines. TYPE HOST: *Procrustes purpurescens* and *Silpha atrata*. Ref. Baudoin (1971).

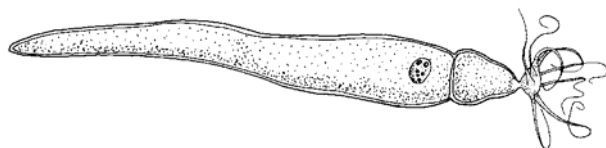


Fig. 108. *Rhizionella tenuis*. Trophozoite. (Based on Baudoin, 1971.)

Genus **Cometoides**
Labbé, 1899
(= *Pogonites* Léger, 1892)

Epimerite with neck or stalk, consisting of a spherical or flattened papilla surrounded by long, thin, flexible filaments; gametocysts dehisce by simple rupture; oocysts cylindroconical, with polar spines and two rows of equatorial spines in intestine of insects. Four named species.

TYPE SPECIES: *Cometoides crinitus* (Léger, 1892) Labbe, 1899 (= *Pogonites crinitus* Léger, 1892). TYPE HOST: *Hydrobius* sp.

Cometoides capitatus (Léger, 1892) Labbé, 1899 (= *Pogonites capitatus* Léger, 1892) (Fig. 109). Trophozoite: Total length 1500.0 μm . Epimerite spherical to globose, with a subequatorial band of 12–15 long slender flexible filaments, length 32.0–35.0 μm ; borne on a stalk; protomerite spherical to slightly subspherical, length ~115.0 μm , ~ width 115.0 μm ; with a distinct constriction at the protomerite deutomerite septum; deutomerite elongate ellipsoidal, tapering from the protomerite deutomerite septum to a blunt point posteriad, length ~1,385.0 μm , width ~172.0 μm ; nucleus spherical with several karyosomes. Oocyst: Cylindrobiconical, length 5.1 μm , width 2.5 μm ; apices truncate, each face octagonal, each pole with four spines, 2 rows of equatorial spines, liberated from the gametocyst by simple rupture. TYPE HOST: *Hydrochara caraboides*. Ref. Kamm (1922), Labbé (1899), Léger (1892), Tuzet, Ormières and Théodoridès (1968).

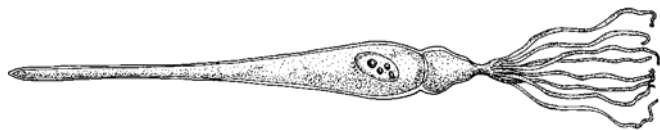


Fig. 109. *Cometoides capitatus*. Trophozoite. (Based on Léger, 1892.)

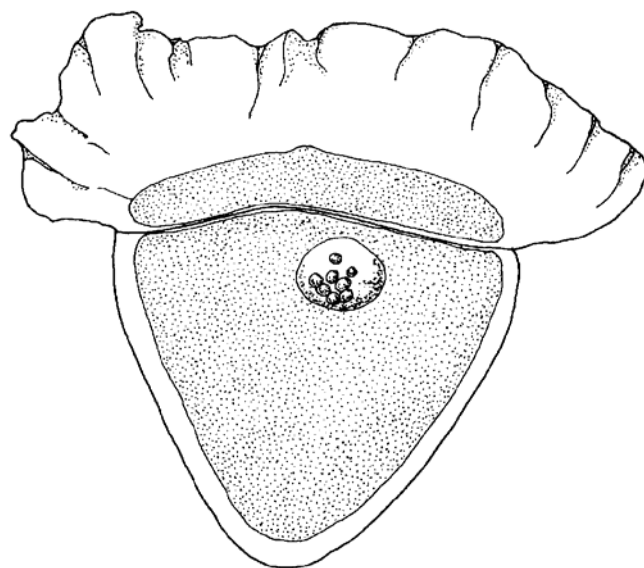


Fig. 110. *Pristaspora evansi*. Trophozoite. (Based on Ellis, 1914.)



Fig. 111. *Pristaspora evansi*. Epimerite. (Based on Ellis, 1914.)



Fig. 112. *Nubenocephalus nebraskensis*. Epimerite. (Clopton, Percival, and Janovy, 1993.)

Genus **Pristaspora**
Ellis, 1914

Epimerite subglobose with lateral, recurved hooks; oocysts prismatic, composed of a central, regular hexagonal prism capped at each end by a rectangular, truncated hexagonal pyramid; spines long, in two series of 6 each, inserted symmetrically in the tetrahedral angles at the junctions of the apical pyramids with the central prism; in dragonfly naiads. Monotypic.

Pristaspora evansi Ellis, 1914 (Figs. 110 & 111).

TYPE SPECIES. Trophozoite: Epimerite subglobose, length 15.0 μm , width 10.0 μm ; with eight recurved hooks, arranged in 4 pairs at right angles to each other, borne on a short neck, length 15.0 μm ; protomerite ovoid to subglobose, length ~ 33.3 μm ; deutomerite regularly conical, length ~ 66.6 μm ; broadly joined to the protomerite so that the greatest width of the

deutomerite is at or near its junction with the protomerite; nucleus obscured by endocyte in living specimens, diameter ~ 1/5 the greatest width of the deutomerite in cleared specimens, with numerous large endosomes. Oocyst: prismatic, composed of a central, regular hexagonal prism, length 7.0 µm, width 5.8 µm; capped at each end by a rectangular, truncated hexagonal pyramid; total length 11.0 µm; 2 rows of long spines, length ~ 7.0 µm long; 6 spines in each row, inserted symmetrically in the tetrahedral angles at the junctions of the apical pyramids with the central prism; liberated from the gametocyst by simple rupture. TYPE HOSTS: *Tramea lacerata* and *Sympetrum rubicundulum*. Ref. Ellis (1914).

Genus ***Nubenocephalus***

Clopton, Percival & Janovy, 1993

Epimerite broadly ovoid, truncated posteriad, with broad, flexible equatorial tumidi that do not form hooks, spines, or digitiform processes; borne on a long, slender stalk; oocysts dodecahedral, elongate, terminally truncate, hexagonal in equatorial cross section, without equatorial faces, with equatorial and terminal spines. Monotypic.

Nubenocephalus nebraskensis Clopton, Percival & Janovy, 1993 (Figs. 112, 113–115).

TYPE SPECIES. Trophozoite: Epimerite very broadly ovoid, length 22.0–46.0 µm, width 30.0–48.0 µm; truncate posteriad at union with epimerite stalk, with 6 equatorial lobiform tumidi; tumidi posteriorly bilobate and not forming hooks, spines, or digitiform processes; borne on a narrow basal stalk, length 20.0–54.0 µm, width 10.0–16.0 µm; obvious in young trophozoites, absent in sporonts; protomerite broadly obvoid to depressed obvoid, length 91.3–348.6 µm, width 124.5–489.7 µm; truncated without constriction at union with deutomerite; becoming crateriform in late trophozoites and sporonts, anterior margins unclift, expanded to form a broad crateriform, adhesive disk with apex distended to contact the host epithelium; anterior margins of protomerite in late sporonts cleft or folded, becoming corollate with 2 narrow ventral lobes and 1 broad dorsal lobe; deutomerite broadly obvoid in very young trophozoites, narrowly obvoid in late trophozoites, length 141.1–1,651.7 µm, width 116.2–481.4 µm; distended anteriorly at union with protomerite; nucleus narrowly elliptoid to elliptoid, length 50.0–88.0 µm, width 20.0–42.0 µm; placement consistent, abaxial and supraequatorial; nuclear endosomes variable in shape and number. Oocyst: Dodecahedral, axial length 7.84 µm, equatorial width 9.8 µm; elongate, terminally truncate, terminal width 1.47 µm; hexagonal in equatorial cross section, with 6 equatorial spines, 1 at each equatorial angle, spine length 3.92 µm; 12 terminal spines, 1 spine at each terminal angle; spine

length 2.94 µm; equatorially located spherical residuum, diameter 1.25 µm, liberated from the gametocyst by simple rupture. TYPE HOST: *Argia bipunctulata*. Ref. Clopton, Percival and Janovy (1993).



Fig. 113. *Nubenocephalus nebraskensis*. Young trophozoite. (Clopton, Percival, and Janovy, 1993.)



Fig. 114. *Nubenocephalus nebraskensis*. Mature trophozoite. (Clopton, Percival, and Janovy, 1993.)

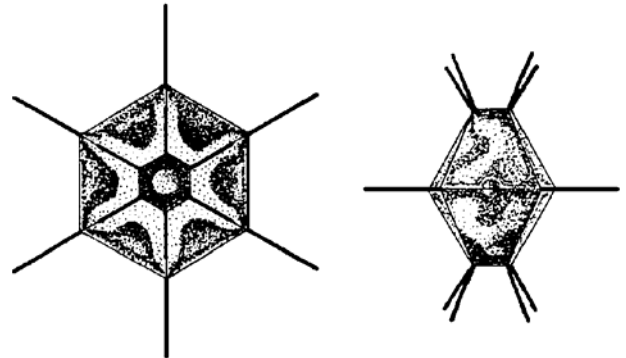


Fig. 115. *Nubenocephalus nebraskensis*. Oocyst: Left, dorsal aspect; Right, lateral aspect. (Clopton, Percival, and Janovy, 1993.)

Genus ***Tetraedrospora***

Tschudovskaia, 1928

Epimerite consisting of a flattened disk, bordered by 14 to 16 hooks; gametocysts develop and oocysts emerge in host gut; cysts elongate tetrahedral, with sides bearing a row of spines; in fungus gnats. Monotypic.

Tetraedrospora sciarae Tschudovskaia, 1928 (Fig. 116).

TYPE SPECIES. Trophozoite: Epimerite a sessile, flattened disk, centrally thickened; bordered by 14–16 marginal hooks, anteriorly thickened, tapering posteriorly; protomerite elongate spherical, length 58.0 µm, width 57.5 µm; deutomerite long and finger-like, tapering from the protomerite deutomerite septum to a rounded tip

posteriad, length 424.6 μm , width 59.3 μm ; nucleus spherical, diameter 27.8 μm ; with large eccentric karyosome. Oocyst: Elongate tetrahedrons, terminally truncate, length of lateral edges 14.0 μm , length of basal edges 12.0 μm ; oocyst surface bearing tiny, regularly dispersed, spines, edges bearing more pronounced spines; gametocysts developing completely within the host gut, oocysts liberated in host gut by simple rupture of the gametocyst. TYPE HOST: *Sciara militaris*, larvae. Ref. Geus (1969), Tschudovskaia (1928).

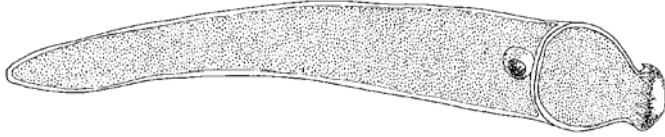


Fig. 116. *Tetraedrospora sciarae*. Trophozoite. (Based on Tschudovskaia, 1928.)

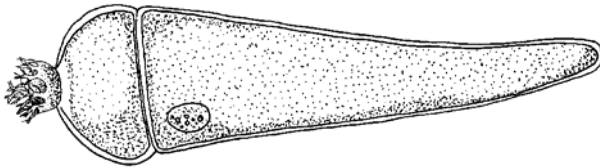


Fig. 117. *Ramicephalus ozakii*. Trophozoite. (Based on Obata, 1955.)

Genus ***Ramicephalus***
Obata, 1953

Epimerite dishlike, with many upward - projecting dendritic processes around the periphery; oocysts biconical, with one row of polar and one row of six equatorial spines. Thirteen named species.

The dendritic projections of *Ramicephalus* are thicker than those of *Cometoides* (Tuzet, Ormières and Théodoridès, 1968).

Ramicephalus ozakii Obata, 1953 (Fig. 117).

TYPE SPECIES. Trophozoite: Epimerite a sessile dish, many upward - projecting dendritic processes around the periphery; protomerite hemispherical, length 56.6 μm , width 115.0 μm ; with a slight constriction above the protomerite deutomerite septum; deutomerite elongate conical, length 209.7 μm , width 121 μm ; broadly tapering from the protomerite deutomerite septum to a blunt point posteriad; nucleus spherical to slightly ellipsoidal length 30.8 μm , width 27.8 μm ; with many karyosomes. Oocyst: biconical, length 6.0 μm ; with one row of polar and one row of six equatorial spines. TYPE HOST: *Chlaenius inops*. Refs. Obata (1953), Tuzet, Ormières and Théodoridès (1968).

Genus ***Coronoepimeritus***

H. Hoshide, 1959

(= *Quadruspinospora* Sarkar and Chakravarty, 1969)

Trophozoites solitary; Epimerite with a short neck, consisting of a crown - like, globular tumidus, covered with many small digitiform processes which may or may not be branched; oocysts ellipsoidal or ovoid, with long, filament - like polar spines, released from the gametocyst by simple rupture. Nine named species.

Coronoepimeritus japonicus H. Hoshide, 1959 (Fig. 118).

TYPE SPECIES. Trophozoite: Epimerite globular, crown - like, length 100.0 μm , width 70.0 μm ; numerous small digiform processes cover surface of crown; borne on short stalk; protomerite broadly spherical with slight anterior tapering; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriad. Total length 300.0–500.0 μm . Oocyst: Ellipsoidal, length 12.0 μm , width 6.0 μm ; with two long filament - like spines at each pole, length 30.0 μm ; liberated from the gametocyst by simple rupture. TYPE HOST: *Locusta migratoria*, *Oedaleus infernalis*, *Oxya japonicus*, *Oxya velox*. Ref. Haldar & Chakraborty (1975); H. Hoshide (1959), K. Hoshide (1978), Sarkar, 1987, Sarkar & Chakravarty (1969), .

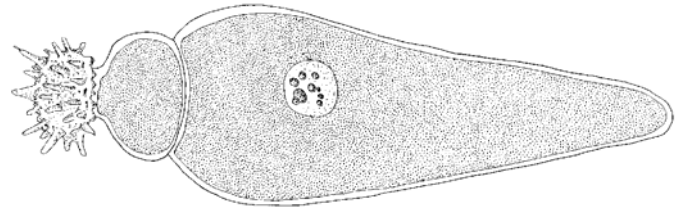


Fig. 118. *Coronoepimeritus japonicus*. Trophozoite. (Based on H. Hoshide, 1959.)

Genus ***Dinematospora***

Tuzet & Ormières, 1954

Development extracellular; epimerite hemispherical, flattened, becoming button - shaped with trophozoite maturity, attached by a short, broad, stalk to the protomerite at a chromophilic ring that persists until syzygy; deutomerite with a thick membrane; longitudinal myonemes well developed; paraglycogen granules and black granules present; nucleus spherical or slightly ovoid, with a single nucleolus; young trophozoites solitary; gametocysts dehisce by simple rupture; oocysts with 2 long polar filaments. Monotypic.

Dinematospora grassei Tuzet & Ormières, 1954 (Fig. 119).

TYPE SPECIES. With the features of the genus. Gamont length reaching 500.0 μm . Oocysts: ovoid, length 8.5 μm , width 7.0 μm ; with a single filament at

each pole, length 60.0–65.0 µm. Type Host: *Machilis tenuis*. Ref. Tuzet and Ormières(1954).

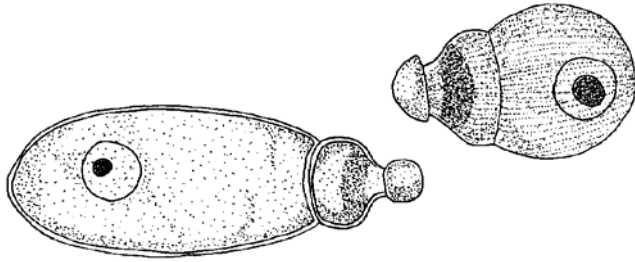


Fig. 119. *Dinematospora grassei*. Left, mature trophozoite; Right, young trophozoite. (Based on Tuzet and Ormières, 1954.)

Genus *Doliospora*
Ormières & Baudoin, 1969

Epimerite without ornamentation; oocysts asymmetrical, without terminal tufts, with two equatorial thickenings on the longitudinal cordons; in opilionids. Two named species.

TYPE SPECIES: *Doliospora repelini* (Léger, 1897) Ormières and Baudoin, 1969 (= *Acanthospora repelini* Léger, 1897). TYPE HOST: *Phalangium opilio*.

Genus *Acanthosporidium*
Georgévitch, 1951

Middle part of anterior end of epimerite in the form of a tapered snout; with a short neck separating the epimerite and protomerite; gametocysts and oocysts unknown. Two named species.

TYPE SPECIES: *Acanthosporidium gammari* Georgévitch, 1951. TYPE HOST: Trichoptera gen. sp.

Genus *Cosmetophilus*
Cockendolpher, 1991

Locomotion progressive by gliding and undulation. Gametocysts passed in the host's feces without sporoducts, dehiscing by simple rupture. Oocysts biconical with thickenings at poles and equator with row of spines on poles and along edges, released by the thousands but not in chains. Trophozoite divided into protomerite and deutomerite by septum. Epimerite symmetrical without hooks, filaments, striations, or ornamentation. Trophozoites, sporonts, and gametocysts develop in the intestine and intestinal caeca of cosmetid Opiliones. Monotypic.

TYPE SPECIES: *Cosmetophilus vonones* Cockendolpher, 1991. TYPE HOST: *Vonones sayi*. Ref. Cockendolpher (1991).

Genus *Contospora*
Devdhar & Amoji, 1978

Epimerite without neck, consisting of a conical tumidus with basal dentition and approximately 20 vertical lamellae; oocysts cylindrical, tapering to blunt polar points, with tufts of spines at each pole; in arthropods. Monotypic.

Contospora opalinae Devdhar & Amoji, 1978 (Fig. 120).

TYPE SPECIES. Trophozoite: total length 150.0–700.0 µm; Epimerite a conical tumidus, with approximately 20 vertical lamellae, each with a single basal dentition, without neck or stalk; protomerite broadly ovate; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriad; nucleus ovoid, with a large, irregularly shaped endosome, in anterior half of deutomerite. Oocyst: cylindrical, length (excluding spines) 8.0 µm, width 3.0 µm; tapering to blunt polar points, with tufts of spines at each pole, loosely connected by polar tufts into short chains or clusters and liberated from the gametocyst by simple rupture.

TYPE HOST: *Opalina* sp. Ref. Devdhar and Amoji (1978).

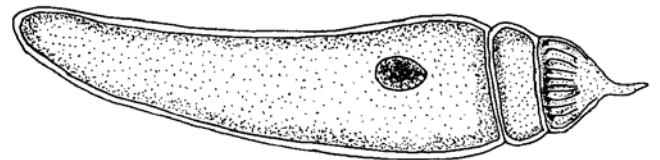


Fig. 120. *Contospora opalinae*. Trophozoite. (Based on Devdhar and Amoji, 1978.)

Genus *Tetractinospora*
Sarkar & Haldar, 1981

Epimerite a globular holdfast with more than 8 (~ 16) laminate, vertical (retroarcate) plates; borne on a short neck; trophozoites solitary; gametocysts dehisce by simple rupture; oocysts biconical, bent in the middle, with 2 sharp, stout spines at each pole. Monotypic.

Tetractinospora victoris Sarkar & Haldar, 1981 (Fig. 121).

TYPE SPECIES. Trophozoite: Epimerite globular, length 20.0 µm, width 23.2 µm; with about 16 laminate, retroarcate hyaline plates, borne on a short neck, length 6.3 µm; protomerite rectangular, length 35.4 µm, width 43.0 µm; deutomerite broadly fusiform, length 118.6 µm, width 49.8 µm; tapering posteriorly to a blunt tip; nucleus ovoid, length 36.0 µm, width 23.0 µm. Oocyst: Biconical, length 9.0 µm, width 4.5 µm; bent in the middle, each pole with 2 sharp, stout spines, length 4.5 µm; liberated

from the gametocyst by simple rupture. TYPE HOST: *Ceriagrion coromandelianum*. Ref. Sarkar and Haldar (1981a).

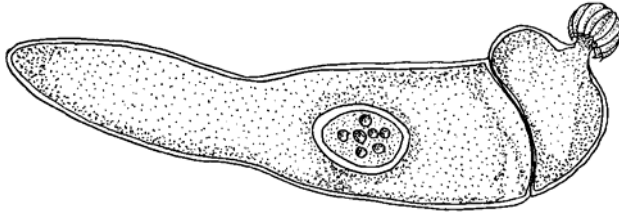


Fig. 121. *Tetractinospora victorisira*. Trophozoite. (Based on Sarkar and Haldar, 1981a.)

Genus ***Echinoocysta***
Levine, 1984

Epimerite a simple globular or spherical knob; protomerite dome - shaped or hemispherical, with striated rim around its base, set on a short cylindrical collar; oocysts biconical, with a row of 8–10 slender spines at each end; oocysts released from gametocyst in chains of 2 to 3 or more by simple rupture. Monotypic.

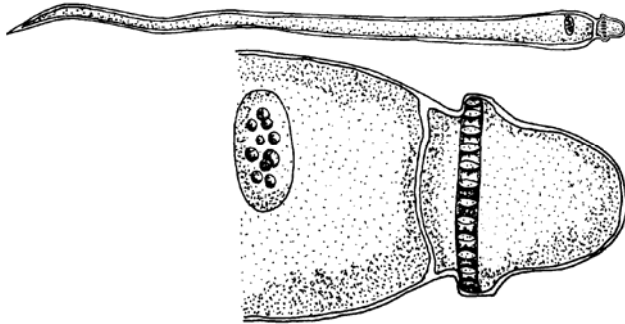


Fig. 122. *Echinoocysta phalangii*. Left, trophozoite; Right, anterior portion of trophozoite with elaborated protomeritic ridge. (Based on Amoji and Devdhar, 1979.)

Echinoocysta phalangii (Amoji and Devdhar, 1979) Levine, 1984 (= *Echinospira phalangii* Amoji and Devdehar, 1979) (Fig. 122).

TYPE SPECIES. Trophozoite: Epimerite a simple globular or spherical knob, length 18.0 μm , width 15.0 μm ; becoming rhomboidal as development progresses, length 20.0 μm , width 20.0 μm ; protomerite dome - shaped or hemispherical, length 15.0 μm , width 12.0 μm ; with development bearing a conspicuous serrated or frilled edge demarcated by a short, cylindrical stalk or constriction, length 5.0 μm , width 12.0 μm ; deutomerite elongate, length 55.0 μm , width 23.0 μm ; nucleus ovoidal. Mature trophozoite: Solitary; protomerite hemispherical, length 70.0 μm , width 120.0 μm ; set on a broad, stumpy stalk or constriction, length 15.0–20.0 μm , width 80.0–100.0 μm ; with a broad striated edge, length

7.0–8.0 μm ; deutomerite elongate, width 102.0–103.0 μm ; dilated posterior to protomerite deutomerite septum, gradually tapering to a narrow point; total length 1666.0–2040.0 μm ; nucleus oval, length 57.0 μm , width 24.0 μm ; with 6–8 small oval endosomes. Oocyst: Biconical, length 14.7 μm , width 7.0 μm ; with a row of 8–10 slender spines at each end; oocysts released from gametocyst in chains of 2 to 3 or more by simple rupture. TYPE HOST: *Opalina* sp. Ref. Amoji and Devdhar (1979), Levine (1984).

Genus ***Mukundaella***
Sarkar, 1981

Epimerite consisting of a very short neck ending in a cup with numerous striations or vertical folds; oocysts diamond - shaped, hexagonal in polar view, with polar and meridional spines; in insects. Three named species.

Mukundaella undulatus Sarkar, 1981 (Fig. 123).

TYPE SPECIES. Trophozoite: Epimerite a broad, wide cup, length 17.0 μm , width 28.4 μm ; with numerous striations or vertical folds, borne on a very short neck, length 5.2 μm ; protomerite conical to rectangular, length 24.8 μm , width 17.8 μm ; deutomerite broadly fusiform, length 139.4 μm , width 30.9 μm ; nucleus ovoid, length 17.8 μm , width 10.2 μm ; placed anteriorly in deutomerite. Oocyst: Diamond - shaped, length 8.5 μm , width 5.0 μm ; hexagonal in polar view, with four polar spines (two at each pole) and six equidistant meridional spines; liberated from the gametocyst by simple rupture. TYPE HOST: *Enallagma* sp. Ref. Sarkar (1981).

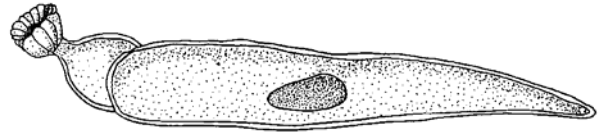


Fig. 123. *Mukundaella undulatus*. Trophozoite. (Based on Sarkar, 1981.)

Genus ***Tetrameridionospinospora***
Kori & Amoji, 1985

Epimerite consisting of a short but distinct neck ending in a globular or discoidal bulb with numerous peripheral tentacles or digitiform processes; oocysts biconical with four polar spines (two at each pole) and four meridional spines (two on each side). Two named species.

Tetrameridionospinospora karnatakii Kori & Amoji, 1985 (Fig. 124).

TYPE SPECIES. Trophozoite: Epimerite a globular or discoidal bulb, length 25.0 μm , width 25.0 μm ; with 34–39 sharp - tipped peripheral tentacles borne on a short but distinct neck, length 29.15 μm ; protomerite cordiform, length 51.8 μm , width 55.0 μm ; deutomerite

fusiform, broadly tapering from the protomerite deutomerite septum to a blunt point posteriad, length 313.5 µm, width 58.13 µm; nucleus ovoid, length 35.0 µm, width 19.5 µm. Oocyst: Refractile, biconical, length 7.0 µm, width 4.0 µm; with 4 polar spines (two at each pole) and four meridional (equatorial) spines (two on each side); liberated from the gametocyst by simple rupture. TYPE HOST: *Agriocnemis* sp. Ref. Kori and Amoji (1985).

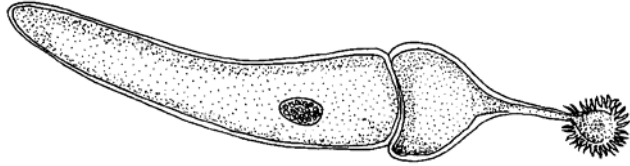


Fig. 124. *Tetrameridionospinispora karnatak*. Trophozoite. (Based on Kori and Amoji, 1985.)

SUBFAMILY MENOSPORINAE
LÉGER, 1892

Oocysts crescentic, smooth; in arthropods. This subfamily contains 5 genera and 24 species.

Genus *Menospora*
Léger, 1892

Epimerite very persistent, consisting of a long neck terminated by a cupule bordered by hooks; oocysts bent, banana - shaped (crescentic); in insects. Two named species.

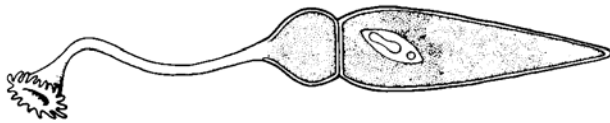


Fig. 125. *Menospora polyacantha*. Trophozoite. (Based on Léger, 1892.)

Menospora polyacantha Léger, 1892 (Fig. 125).

TYPE SPECIES. Trophozoite: Epimerite a cupule bordered by recurved hooks, length 77.0–90.0 µm, width 102.0–120.0 µm; borne on a long stalk, length 394.0–460.0 µm; protomerite spherical, tapering anteriorly, length 120.0–140.0 µm, width 132.0–155.0 µm; deutomerite elongate ellipsoidal, broadly tapering to a point posteriad, length 480.0–560.0 µm, width 150.0–175.0 µm; nucleus ovoid. Oocyst: Smooth, crescentic, length between distal tips 15.0 µm, width at center of arch 4.0 µm, liberated from the gametocyst by simple rupture. TYPE HOST: *Agriion puella*. Ref. Léger (1892).

Genus *Hoplorhynchus*
Carus, 1863

Epimerite consisting of a long neck terminated by a flattened disk bordered by hooks or spines; oocysts crescentic or ellipsoidal and curved. Twelve named species.

Hoplorhynchus oligacanthus [von Siebold, 1839] Carus, 1863 (= *Gregarina oligacantha* von Siebold, 1839; *Gregarina sieboldi* von Kölliker, 1848; *Stylorhynchus oligacanthus* [von Siebold, 1839] von Stein, 1848; *Acanthocephalus sieboldi* von Frantzius, 1848; *Actinocephalus sieboldi* [von Kölliker, 1848] von Frantzius, 1848; *Actinocephalus oligacantha* [von Siebold, 1839] Bütschli, 1882) (Fig. 126).

TYPE SPECIES. Trophozoite: Epimerite a flattened disk or corona of 6–8 recurved hooks, borne on a long stalk; protomerite distinctly cordiform, tapering anteriorly to junction with epimerite stalk; deutomerite elongate ellipsoidal, tapering posteriorly to a blunt point. Oocyst: Smooth, ellipsoidal and bent. TYPE HOST: *Agriion* sp. Refs. Geus (1969), Kamm (1922), Schneider (1875).

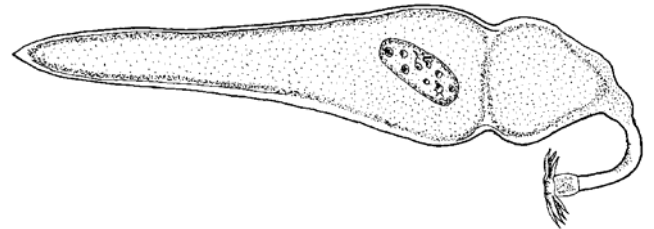


Fig. 126. *Hoplorhynchus oligacanthus*. Trophozoite. (Based on Schneider, 1875.)

Genus *Odonaticola*
Sakar & Haldar, 1981

Epimerite consisting of a long neck terminated by an umbrella shaped bulb with marginal petaloid spines; trophozoites solitary; gametocysts dehisce by simple rupture; development extracellular; oocysts smooth, navicular. Eight named species.

Odonaticola hexacantha Sarkar and Haldar, 1981 (Fig. 127).

TYPE SPECIES. Trophozoite: Epimerite umbrella shaped with six petaloid spines, length 9.0 µm, width 11.1 µm, borne on a long stalk, length 22.2 µm; protomerite cylindrical, length 20.3 µm, width 20.4 µm, with incipient convex septum marking epimerite stalk; deutomerite elongate ellipsoidal, length 34.9 µm, width 22.8 µm; nucleus ovoid. Oocyst: Smooth, navicular with terminal tumidi, length 7.5 µm, width 3.0 µm, liberated from the gametocyst by simple rupture, often in groups of three. TYPE HOST: *Brachythemis contaminata*. Ref. Sarkar and Haldar (1981b).

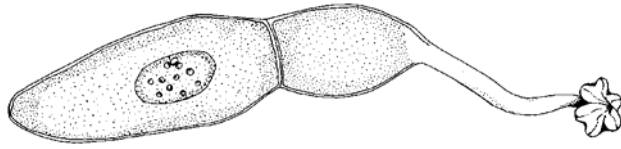


Fig. 127. *Odonaticola hexacantha*. Trophozoite. (Based on Sarkar and Haldar, 1981b.)

Genus ***Domadracunculus***
Clopton, 1995

Epimerite borne on a narrow basal stalk; a pleated cup or sucker, very broadly ovoid in lateral view, circular en face; with distinct pleats rising from the interior of the cup to form a rosette or crown. Gametocysts spherical; hyaline coat erratic (not present on all gametocysts); sporulation by simple dehiscence; no spore tubes or packet membranes were observed. Oocysts crescentic. Development solitary; association lateral, late. Monotypic.

Domadracunculus janovyi Clopton, 1995.

TYPE SPECIES. (Fig. 128). Trophozoite: Attached to host ventricular epithelium, solitary. Epimerite borne on a narrow basal stalk; length 12.0–200.0 μm , width 4.0–24.0 μm ; increasing proportionally with maturity. Epimerite a pleated cup or sucker, in lateral view very broadly ovoid, length 24.0–48.0 μm ; circular en face, diameter 24.0–48.0 μm ; with 16 distinct pleats, length 8.0 μm ; rising from the interior of the cup to form a rosette or crown. (A few specimens show only 14 or 15 pleats; however, it is likely that these pleat - counts represent artifacts of dissection technique or abnormal growth rather than variation in pleat number among members of the population.) Protomerite broadly ovoid to very broadly ovoid; length 44.0–144.0 μm , width 36.0–120.0 μm ; tapering anteriorly to junction with epimerite stalk, with strong posteriad constriction at protomerite - deutomerite septum. Deutomerite narrowly obvoid to obvoid, becoming distinctly obvoid in older trophozoites; length 120.0–384.0 μm , width 40.0–120.0 μm ; broadly rounded posteriad, especially in young trophozoites. Nucleus spheroid to ellipsoid; length 32.0–96.0 μm , width 24.0–64.0 μm ; placement roughly axial, equatorial; nuclear endosomes variable, usually a single, large, central endosome filling most of nucleus. Oocyst: Crescentic (“biconical, bent”), axially symmetric in lateral view; length (tip - to - tip) 13.5–16.7 μm , axial depth of bend 2.3–4.5 μm ; circular in axial cross - section, breadth 4.0–6.3 μm , liberated from the gametocyst by simple rupture. TYPE HOST: *Ischnura verticalis*. Ref. Clopton (1995).

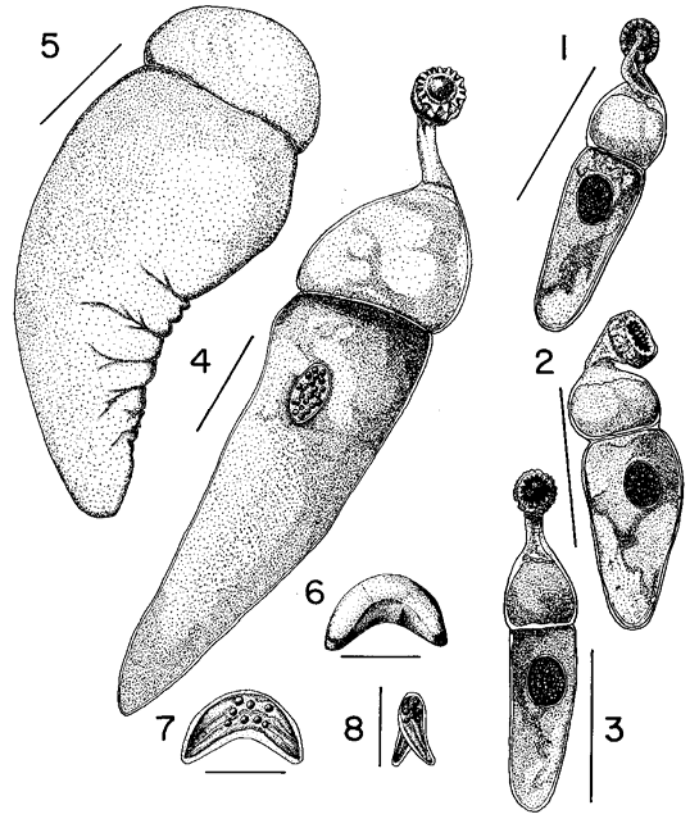


Fig. 128. *Domadracunculus janovyi*. 1. Young trophozoite, dorsal; bar = 100 μm . 2. Young trophozoite, lateral; bar = 100 μm . 3. Young trophozoite, ventral; bar = 100 μm . 4. Mature trophozoite; bar = 100 μm . 5. Gamont; bar = 100 μm . 6 - 8. Oocysts; bar = 10 μm .

Genus ***Steganorhynchus***
Percival, Clopton & Janovy, 1995

Epimerite set on a long vermicular stalk; an ovoid papilla enclosed in a retractile, globular sheath. Gametocysts spherical; hyaline coat present; sporulation by simple dehiscence; no spore tubes or packet membranes were observed. Oocysts crescentic. Development solitary; association lateral, late. Monotypic.

Steganorhynchus dunwoodyi Percival, Clopton & Janovy, 1995.

TYPE SPECIES. (Fig. 129) Trophozoite: Attached to host ventricular epithelium, solitary. Epimerite an ovoid papilla enclosed in a retractile, globular sheath; set on a long vermicular stalk. Protomerite very broadly ovoid; length 48.0–105.6 μm , width 57.6–153.6 μm ; tapering anteriorly to junction with epimerite stalk, with strong posteriad constriction at protomerite - deutomerite septum. Deutomerite obvoid; length 105.6–499.2 μm . Nucleus ellipsoid; ca. diameter 35.0 μm ; placement mesad in anterior half of deutomerite. Oocyst: Crescentic (“biconical, bent”), axially symmetric in lateral view; length (tip - to - tip) 11.0 μm , axial depth of bend

4.4 μm ; circular in axial cross - section, breadth 4.4 μm , liberated from the gametocyst by simple rupture. TYPE HOST: *Ischnura verticalis*. Ref. Percival et al. (1995).

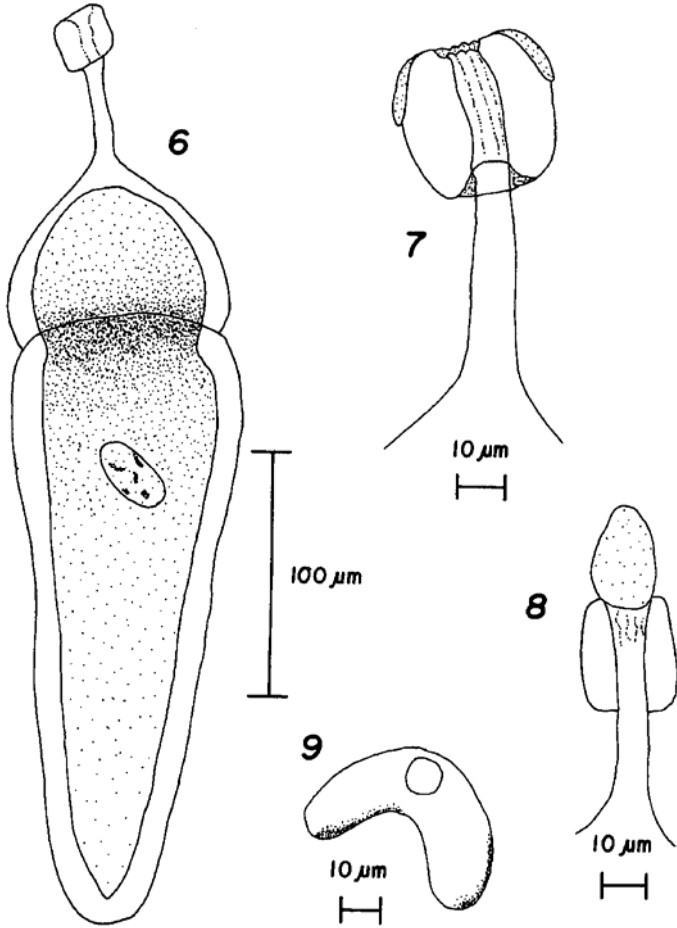


Fig. 129. *Steganorhynchus dunwoodyi*. Trophozoite, detail of epimerite with eversible sheath.

FAMILY BRUSTIOPHORIDAE
KUNDU & HALDAR, 1981

Trophozoites solitary; epimerite small, variously formed, with fine bristles, with short but distinct neck; gametocysts dehisce by simple rupture; oocysts spherical, set with brush borders and chained with fine filamentous processes.

This family contains 1 monotypic genus described from the intestine of a beetle.

Genus *Brustiospora*
Kundu & Haldar, 1981

Epimerite consisting of a short but distinct neck ending in a bundle of fine bristles; gametocysts dehisce by simple rupture; oocysts spherical, set with brush borders and connected by fine, filamentous processes into a chain. Monotypic.

Brustiospora indicola Kundu & Haldar, 1981 (Fig. 130).

TYPE SPECIES. Trophozoite: Epimerite a bundle of fine bristles, length 6.2–11.6 μm , width 3.1–11.6 μm ; borne on a short but distinct neck, length 4.8–29.7 μm ; protomerite spherical with slight anterior tapering, length 8.5–29.7 μm , width 9.0–29.7 μm ; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriad, length 46.7–125.3 μm , width 11.7–42.5 μm ; nucleus spherical to slightly ovoid, length 6.2–15.9 μm , width 6.2–15.9 μm ; with large central endosome. Oocyst: Brush bordered, spherical, diameter 3.8 μm ; connected by fine, filamentous processes into chains and liberated from the gametocyst by simple rupture. TYPE HOST: *Stethorus* sp. Ref. Kundu and Haldar (1981).

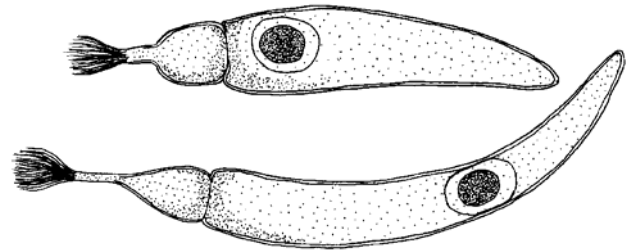


Fig. 130. *Brustiospora indicola*. Young trophozoites. (Based on Kundu and Haldar, 1981.)

FAMILY ACUTIDAE
STEJSKAL, 1965

Trophozoites solitary; epimerite simple, changing shape during development; gametocysts without sporoducts or residuum, dehiscing by opening in gametocyst wall; oocysts ellipsoidal, in insects.

This family contains 2 monotypic genera, both described from the intestines of domestic honey bees.

Genus *Acuta*
Stejskal, 1965

Epimerite simple, growing continually, at first spherical, then cylindrical and drop - shaped and breaking off, leaving a scar; gametocysts dehisce by rupture of a simple, irregular fissure in the gametocyst wall; in intestine of bees. Monotypic.

TYPE SPECIES: *Acuta rousseaui* Stejskal, 1965.
TYPE HOST: *Apis mellifera*.

Genus *Apigregarina*
Stejskal, 1965

Epimerite simple, at first large, becoming ovoid, then spherical, and finally conoidal in the course of

development; gametocysts dehisce by rupture of a round fissure in the gametocyst wall; in intestine of bees. Monotypic.

TYPE SPECIES: *Apigregarina stammeri* Stejskal, 1965. TYPE HOST: *Apis mellifera*.

FAMILY MONOICIDAE
GEUS, 1969

Autogamy present (i.e. each gamont forms gametes of both sexes).

This family contains 1 monotypic genus described from the intestines of domestic honey bees.

Genus *Monoica*
Stejskal, 1964

Epimerite simple; young trophozoites solitary; each gamont forms gametes of both sexes; gametes anisogamous; gametocysts dehisce by simple rupture; gametocyst residuum present; oocysts ellipsoidal; in bees. Monotypic.

TYPE SPECIES: *Monoica apis* Stejskal, 1964. TYPE HOST: *Apis mellifera*. Ref. Stejskal (1964, 1965)

SUPERFAMILY FUSIONICAE
STEJSKAL, 1965

Homoxenous; upon syzygy the nucleus and entocyte of the satellite go into the primite, where they fuse; anisogamous; gametocysts and oocysts unknown. This superfamily is monotypic.

FAMILY FUSIONIDAE
STEJSKAL, 1965

With the characters of the superfamily.

Genus *Fusiona*
Stejskal, 1965

With the characters of the family, in insects. Monotypic.

TYPE SPECIES: *Fusiona geusi* Stejskal, 1965. TYPE HOST: *Pycnoscelus surinamensis*.

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