The Gregarines:  
A generic level review

by

RICHARD E. CLOPTON, PhD
Associate Professor of Biology
Peru State College
Peru, Nebraska

This document is an electronic offprint and should be cited as follows:
# Contents

<table>
<thead>
<tr>
<th>Order</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eugregarinorida</td>
<td>1</td>
</tr>
<tr>
<td>Blastogregarinorida</td>
<td>1</td>
</tr>
<tr>
<td>Aseptatorina</td>
<td>1</td>
</tr>
<tr>
<td>Septatorina</td>
<td>1</td>
</tr>
<tr>
<td>Suborder Septatorina</td>
<td>1</td>
</tr>
<tr>
<td>Superfamily Poroporicae</td>
<td>2</td>
</tr>
<tr>
<td>Family Poroporidae</td>
<td>2</td>
</tr>
<tr>
<td>Genus Porospora</td>
<td>3</td>
</tr>
<tr>
<td>Genus Nematopsis</td>
<td>3</td>
</tr>
<tr>
<td>Genus Pachyospora</td>
<td>4</td>
</tr>
<tr>
<td>Superfamily Gregarinaceae</td>
<td>4</td>
</tr>
<tr>
<td>Family Cephaloidophoridae</td>
<td>5</td>
</tr>
<tr>
<td>Genus Cephaloidophora</td>
<td>5</td>
</tr>
<tr>
<td>Genus Caridohabitans</td>
<td>6</td>
</tr>
<tr>
<td>Genus Rotundula</td>
<td>6</td>
</tr>
<tr>
<td>Family Cephalolobidae</td>
<td>6</td>
</tr>
<tr>
<td>Genus Cephalolobus</td>
<td>6</td>
</tr>
<tr>
<td>Genus Callynthrochlamys</td>
<td>7</td>
</tr>
<tr>
<td>Family Uradiophoridae</td>
<td>7</td>
</tr>
<tr>
<td>Genus Uradiophora</td>
<td>7</td>
</tr>
<tr>
<td>Genus Heliospora</td>
<td>8</td>
</tr>
<tr>
<td>Genus Pyxinioidea</td>
<td>8</td>
</tr>
<tr>
<td>Genus Nematoides</td>
<td>9</td>
</tr>
<tr>
<td>Genus Bilida</td>
<td>9</td>
</tr>
<tr>
<td>Family Gregarinidae</td>
<td>9</td>
</tr>
<tr>
<td>Genus Gregarina</td>
<td>10</td>
</tr>
<tr>
<td>Genus Gymnospora</td>
<td>13</td>
</tr>
<tr>
<td>Genus Triseptata</td>
<td>13</td>
</tr>
<tr>
<td>Genus Gamocystis</td>
<td>13</td>
</tr>
<tr>
<td>Genus Anisolobus</td>
<td>13</td>
</tr>
<tr>
<td>Genus Anisoloboides</td>
<td>14</td>
</tr>
<tr>
<td>Genus Garnhamia</td>
<td>14</td>
</tr>
<tr>
<td>Genus Amoebogregarina</td>
<td>14</td>
</tr>
<tr>
<td>Genus Torogregarina</td>
<td>15</td>
</tr>
<tr>
<td>Genus Faucispora</td>
<td>15</td>
</tr>
<tr>
<td>Genus Spinispora</td>
<td>15</td>
</tr>
<tr>
<td>Genus Bolivia</td>
<td>15</td>
</tr>
<tr>
<td>Genus Cirrigregarina</td>
<td>16</td>
</tr>
<tr>
<td>Genus Molluskocystis</td>
<td>16</td>
</tr>
<tr>
<td>Family Metameridae</td>
<td>16</td>
</tr>
<tr>
<td>Genus Metamera</td>
<td>16</td>
</tr>
<tr>
<td>Genus Gopaliella</td>
<td>17</td>
</tr>
<tr>
<td>Genus Deuteromera</td>
<td>17</td>
</tr>
<tr>
<td>Genus Cognettiella</td>
<td>17</td>
</tr>
<tr>
<td>Family Didymophyidae</td>
<td>18</td>
</tr>
<tr>
<td>Genus Didymophyes</td>
<td>18</td>
</tr>
<tr>
<td>Family Hirmocystidae</td>
<td>19</td>
</tr>
<tr>
<td>Genus Hirmocystis</td>
<td>19</td>
</tr>
<tr>
<td>Genus Neohirmocystis</td>
<td>20</td>
</tr>
<tr>
<td>Genus Hyalospora</td>
<td>20</td>
</tr>
<tr>
<td>Genus Tetragonospora</td>
<td>21</td>
</tr>
<tr>
<td>Genus Dumbbellicephalus</td>
<td>21</td>
</tr>
<tr>
<td>Genus Eupsora</td>
<td>21</td>
</tr>
<tr>
<td>Genus Tintinospora</td>
<td>21</td>
</tr>
<tr>
<td>Genus Arachnocyrtis</td>
<td>21</td>
</tr>
<tr>
<td>Genus Acanthogregarina</td>
<td>22</td>
</tr>
<tr>
<td>Genus Protomagalhaensis</td>
<td>22</td>
</tr>
<tr>
<td>Genus Eliptocystis</td>
<td>22</td>
</tr>
<tr>
<td>Genus Pintospora</td>
<td>22</td>
</tr>
<tr>
<td>Genus Endomycola</td>
<td>23</td>
</tr>
<tr>
<td>Genus Retractocephales</td>
<td>23</td>
</tr>
<tr>
<td>Genus Liposcelis</td>
<td>23</td>
</tr>
<tr>
<td>Genus Quadruhyalodiscus</td>
<td>23</td>
</tr>
<tr>
<td>Superfamily Stenophoricae</td>
<td>24</td>
</tr>
<tr>
<td>Family Stenophoridae</td>
<td>25</td>
</tr>
<tr>
<td>Genus Stenophora</td>
<td>25</td>
</tr>
<tr>
<td>Genus Fonseccia</td>
<td>25</td>
</tr>
<tr>
<td>Genus Hyalosporina</td>
<td>25</td>
</tr>
<tr>
<td>Family Leidyaniidae</td>
<td>26</td>
</tr>
<tr>
<td>Genus Leidyana</td>
<td>26</td>
</tr>
<tr>
<td>Family Cnemidosporidae</td>
<td>27</td>
</tr>
<tr>
<td>Genus Cnemidospora</td>
<td>27</td>
</tr>
<tr>
<td>Family Monoductidae</td>
<td>27</td>
</tr>
<tr>
<td>Genus Monoductor</td>
<td>28</td>
</tr>
<tr>
<td>Genus Stenoductus</td>
<td>28</td>
</tr>
<tr>
<td>Genus Phloebum</td>
<td>28</td>
</tr>
<tr>
<td>Family Sphaerocystidae</td>
<td>28</td>
</tr>
<tr>
<td>Genus Sphaerocystis</td>
<td>29</td>
</tr>
<tr>
<td>Genus Schneideria</td>
<td>29</td>
</tr>
<tr>
<td>Genus Paraschneideria</td>
<td>29</td>
</tr>
<tr>
<td>Genus Neoschneideria</td>
<td>30</td>
</tr>
<tr>
<td>Family Trichorhynchidae</td>
<td>30</td>
</tr>
<tr>
<td>Genus Trichorhynchus</td>
<td>30</td>
</tr>
<tr>
<td>Family Dactylophoridae</td>
<td>30</td>
</tr>
<tr>
<td>Genus Dactylophorus</td>
<td>30</td>
</tr>
<tr>
<td>Genus Echinomera</td>
<td>31</td>
</tr>
<tr>
<td>Genus Grebnickiella</td>
<td>31</td>
</tr>
<tr>
<td>Genus Rhoanolia</td>
<td>31</td>
</tr>
<tr>
<td>Genus Acutispora</td>
<td>32</td>
</tr>
<tr>
<td>Genus Seticephalus</td>
<td>32</td>
</tr>
<tr>
<td>Genus Dendrorhynchus</td>
<td>32</td>
</tr>
<tr>
<td>Genus Mecistophora</td>
<td>32</td>
</tr>
<tr>
<td>Family Amphiplatysporidae</td>
<td>32</td>
</tr>
<tr>
<td>Genus Amphiplatyspora</td>
<td>32</td>
</tr>
<tr>
<td>Family Stylocephalidae</td>
<td>33</td>
</tr>
<tr>
<td>Genus Stylocephalus</td>
<td>33</td>
</tr>
<tr>
<td>Genus Stylocephaloides</td>
<td>34</td>
</tr>
<tr>
<td>Genus Cystocephalus</td>
<td>34</td>
</tr>
<tr>
<td>Genus Bulbocephalus</td>
<td>35</td>
</tr>
<tr>
<td>Genus Xiphonecephalus</td>
<td>35</td>
</tr>
<tr>
<td>Genus Lophocephalus</td>
<td>36</td>
</tr>
<tr>
<td>Genus Lophocephaloides</td>
<td>36</td>
</tr>
<tr>
<td>Genus Sphaerorhynchus</td>
<td>36</td>
</tr>
<tr>
<td>Genus Oocephalus</td>
<td>36</td>
</tr>
<tr>
<td>Genus Campanacephalus</td>
<td>37</td>
</tr>
<tr>
<td>Genus Claviccephalus</td>
<td>37</td>
</tr>
<tr>
<td>Genus Cystocephaloides</td>
<td>37</td>
</tr>
<tr>
<td>Genus Orocephalus</td>
<td>38</td>
</tr>
<tr>
<td>Genus Lepismatophila</td>
<td>38</td>
</tr>
<tr>
<td>Genus Colepismatophila</td>
<td>38</td>
</tr>
<tr>
<td>Family Actinocephalidae</td>
<td>38</td>
</tr>
<tr>
<td>Subfamily Actinocephalinae</td>
<td>38</td>
</tr>
<tr>
<td>Genus Actinocephalus</td>
<td>39</td>
</tr>
</tbody>
</table>
Order Eugregarinorida

Table of Contents

Genus **Caulocephalus** ........................................ 39
Genus **Cormimeritus** ........................................ 39
Genus **Umbracephalus** ....................................... 40
Genus **Ureaepimeritus** ....................................... 40
Genus **Asterophora** ........................................ 40
Genus **Pileoccephalus** ....................................... 40
Genus **Gemmicephalus** ....................................... 40
Genus **Pilidiophora** .......................................... 40
Genus **Geneiorhynchus** ....................................... 41
Genus **Acanthoeperimitus** ................................... 41
Genus **Phialoides** ........................................... 41
Genus **Legeria** ................................................ 41
Genus **Pyxinia** ................................................ 42
Genus **Discorhynchus** ....................................... 42
Genus **Steinina** .............................................. 43
Genus **Bothriopsides** ........................................ 43
Genus **Pomania** ............................................... 44
Genus **Stictospora** .......................................... 44
Genus **Coleorhynchus** ....................................... 44
Genus **Amphoroides** ......................................... 44
Genus **Stylcystis** ............................................ 45
Genus **Taeniocystis** ......................................... 45
Genus **Sciadiophora** ......................................... 45
Genus **Anthorhynchus** ....................................... 46
Genus **Agrippina** ............................................. 46
Genus **Globulocephalus** ..................................... 46
Genus **Alaspora** ............................................. 47
Genus **Ascocephalus** ......................................... 47
Genus **Amporphoscepalus** .................................... 47
Genus **Tricystis** ............................................. 48
Genus **Thaliccola** ............................................ 48
Genus **Epicaevus** ............................................ 48
Genus **Gryllotalpia** .......................................... 48
Genus **Chilogregarina** ....................................... 48
Genus **Cruccephalus** ......................................... 48
Genus **Harendraia** ............................................ 48
Genus **Levinea** ................................................. 49

Subfamily Acanthosporinae ...................................... 49
Genus **Acanthospora** ......................................... 49
Genus **Grenoblia** ............................................ 49
Genus **Corycella** ............................................. 49
Genus **Ancyrophora** .......................................... 49
Genus **Rhizonella** ............................................ 50
Genus **Cometoides** ........................................... 50
Genus **Prismatospora** ........................................ 51
Genus **Nubenocepalus** ....................................... 51
Genus **Tetraedrospora** ....................................... 52
Genus **Ramicephalus** ........................................ 52
Genus **Coroneopiperitus** .................................... 53
Genus **Dinematospora** ........................................ 53
Genus **Doliospora** ............................................ 53
Genus **Acanthosporidium** .................................... 53
Genus **Cosmetophilus** ........................................ 53
Genus **Contospora** ............................................ 54
Genus **Tetractinospora** ....................................... 54
Genus **Echinocephrya** ....................................... 54

Genus **Mukundaella** .......................................... 55
Genus **Tetrameridionosphinospora** ......................... 55
Subfamily Menosporinae ......................................... 55
Genus **Menospora** ............................................ 55
Genus **Hoplorhynchus** ....................................... 55
Genus **Odonaticola** .......................................... 56
Genus **Domadracunculus** .................................... 56
Genus **Steganorhynchus** ..................................... 57
Family Brustiophoridae ........................................... 57
Genus **Brustiospora** .......................................... 57
Family Acutidae .................................................. 58
Genus **Acuta** .................................................. 58
Genus **Apigregarina** .......................................... 58
Family Monoicidae ............................................... 58
Genus **Monoica** .............................................. 58
Superfamily Fusionicae .......................................... 58
Family Fusionidae ............................................... 58
Genus **Fusiona** ............................................... 58
The Gregarines:
A generic level review

by
RICHARD E. CLOPTON, PhD
Associate Professor of Biology
Peru State College
Peru, Nebraska

from
Illustrated Guide to the Protozoa
2nd edition

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 specious 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.

Grassè (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 ontogenetic 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 Gregarinaceae and syzygy is delayed until growth and development are complete. In contrast, members of Stenophoricae remain isolated until gametocyst formation. Individuals in association are often called gamonts without reference to the onset of gametophyte 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 primite during syzygy............................... Fusionicae
   2. (2) Nucleus and endocyte of primite and satellite remain isolated until gametocyst formation ............ 3

3. (2') Association precocious (associations formed before trophozoites mature and enter syzygy ) ............
   3'. (3) Trophozoites solitary (associations are not formed until the onset of syzygy)............................... Gregarinaceae
   3'. (3') Association precocious but gamonts still unite (associations are formed only after trophozoites mature) 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. Prütherch (1940) ostensibly completed the life cycle of *Nematospsis 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. Théodorides (1961, 1962) has suggested that *Nematospsis* 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.

Key to the genera of Porosporicai

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; gymnospores 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, Trochocochlea 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; gymnospores 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, 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.

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 gymnospore; m. Engulfment of gymnospore 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 gymnospores that are infective to the molluscan host. Gymnospores are transmitted to the molluscan host, and engulfed by host leukocytes where they form resistant oocysts. However, Hatt (1931) suggested that individuals of Nematopsis
Nematopsis ostrearum Pyrtherch, 1938 (Fig. 1). Crustacean hosts are infected by ingesting infective, monozoic 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 primates 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 a clump of 8–16 sporozoites called a gymnospore. Oocyst and gametocyst walls rupture to release these gymnospores through the crab's anus into the surrounding sea. Molluscan hosts are infected when gymnospores are carried into the shell with the feeding current. Gymnospores attach to the gill or mantle and penetrate the epithelium with a pseudopod projected from the central sporozoite. Gymnospores 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. Pyrtherch (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 Ormières, 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. Ormières (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 Gregarinaceae 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 Gregarinaceae

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 sporoducts...........................................................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

**FAMILY CEPHALOIDOPHORIDAE**
**KAMM, 1922**

Epimerite present; early development intracellular; association head to tail (caudofrontal), early, with primitite different from satellite; marked anisogamy; gametocysts open by simple rupture; oocysts ovoid or spherical, with protruding equatorial ridge; no distinct epispore; 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.
posterior end of the deutomerite of primite. 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.

**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.


**Genus Rotundula**
Goodrich, 1949

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

**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 - Siebold, 1848] Théodoridès, 1967) (Fig. 7). Epimerite a round button, persistent in primite; 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 posterior, 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:** Gamarus 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 microvillousities of the stomach epithelium; association precocious, composed of a primite 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**
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).

**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 spherical .........................................................2
2. 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 epispore, 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*
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 epispore; in amphipods. Three named species.


**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 epispore; liberated from the gametocyst by simple rupture. **TYPE HOST:** *Gammarus pulex*. Ref. Geus (1967, 1969), Goodrich (1949), Kamm (1922), von Kölliker (1848), Lipa (1968).

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 posteriadi, 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.** 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.** 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).
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 - ..............

2’. (2) Epimerite present; papillate or acicular; oocysts ovoid............................................................... Gamhamia

3. (1) Epimerite apparent ..................... Gregarina (in part)

3’. (3) Epimerite apparently absent ......................... 4

4. (3’) Protomerite rounded anteriad, not forming an adhesive disk ..................................................... 5

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 Mediterranea 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 nudem 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 synonomy 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 synonyms 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 anteriad 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 posteriad; 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).

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 anteriad, 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 posteriad, 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 sporoducts. TYPE HOST: Timarcha tenebricosa. Ref. Geus (1969), Labbé (1899), Théodoridès (1988), Watson (1916b).
trimosa Schneider, 1875; Clepsidrina cuneata [von Stein, 1848] Pfeffer, 1910; Gregaria xylopini 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 19.2–40.9–6.4 µm, width 28.8–46.7–67.2 µm; deutomerite elongate cylindrical, primit 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.


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

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

**Fig. 21.** Life cycle of Gregaria 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 dehisce, releasing infective oocysts into the environment to continue the infection cycle.
**Gregarina cuneata** Berndt, 1902 (Fig. 22). Excystation of oocysts: (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 anteriad 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 posteriad, primite 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.

**Gymnospora** Moniez, 1886

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


**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.

**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 posteriad; 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.


---

**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 posterior; 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 reduced to a thin transverse band; deutomerite becoming hemispherical. Oocyst: Unknown. TYPE HOST: *Dacne rufifrons*. Ref. Levine (1988), Vincent (1924).

---

**Genus Anisolobooides**
Théodoridès, 1992

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

**Anisolobooides joliveti** Théodoridès, 1992.

(TYPE HOST: *Brachyomus histro*. Ref. Théodoridès (1992).)

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

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

**Fig. 26.** *Gamhamia 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 sporocysts; oocysts ovoid, extruded in chains; in silverfish. Monotypic.

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


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 sporocysts; oocysts dolioform, dehiscing in chains. Monotypic.

Amoebagregarina 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 - 468.0 µm; width 216.0 - 348.0 µm; dehiscing through sporocysts 48 - 72 hr after removal from host alimentary canal. Yellow under dissecting microscope. Oocysts: Dolioform. TYPE HOST: Melanoplus differentialis (Acrididae:Melanoplinae).

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 ellipsoid, length 93.0 – 101.5 – 112.0 µm, width 60.0 – 74.9 – 86.0 µm; blunt posterior; 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 epispore distended at both ends to form spouts closed by a small cap - valve. Monotypic.


Genus Spinispora
Baudoin, 1967

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

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

**Fig. 29. Torogregarina sphinxi.** 3, 4. Trophozoites. 5, 6. Immature associations. 7, 8. Mature associations. 9. Detail of primate-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 doliform, not emitted in chains but in an agglomerated mass. Monotypic.

**Bolivia vellardi** Corbel, 1968 (Fig. 30).

**Genus Cirrigrregarina**
Levine, 1979

Similar to *Gregarina* (epimerite conical, button-shaped, globular or cylindrical; oocysts doliform, navicular or spherical); found in barnacles. Two named species.
(See discussion of *Cirrigrregarina* under “Genus *Gregarina* Dufour, 1828”.)

**Cirrigrregarina spissa** (Henry, 1938) Levine, 1979 (= *Gregarina spissa* Henry, 1938) (Figs. 31 & 32).
TYPE SPECIES. Trophozoite: Epimerite spherical or subspherical, length 16.0–31.0 µm, width 31.0–35.0 µm; simple, large, with a distinct covering of minute papillae; protomerite hemispherical, with slight anterior truncation, length 24.0–58.0 µm, width 38.0–88.0 µm; 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 µm, width 40.0–88.0 µm; nucleus spherical, with a single, large karyosome. Oocyst: Unknown. TYPE HOST: *Balanus cariosus, Balanus glandula*. Ref. Henry (1938), Levine (1979).

**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 Sturart 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 dehisce 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 anteriad at junction with epimerite, with slight constriction at protomerite deutomerite septum; deutomerite elongate cylindrical, bluntly rounded posteriad, 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: Biconcial to elliptoid, 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.)

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 dehisce by simple rupture. Monotypic.

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

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

Fig. 34. Gopaliella marphysae. Trophozoite. (Based on Ganapati, Kalavati, and Sundaram, 1974.)
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 epicytal, longitudinal striations, apex mildly crateriform; protomerite broadly subconical, length 105.0 µm, width 147.0 µm; protomerite deutomerite septum incomplete, oblique; deutomerite concial, 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).
FAMILY DIDYMOPHYIDAE

LÉGER, 1892

Septum of satellite resorbed more or less slowly during syzygy; gametocysts spherical or somewhat elongate; oocysts with a loose epispore 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 colepterans. 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 crystraloids 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 obvate, wider than deutomerite; protomerite absent in satellite, absorbed by deutomerite of primate; deutomerite cylindrical, very long; primate blunt posteriad at junction with satellite; satellite tapering to a sharp point posteriad; nucleus spherical to slightly ovoid, resting at the junction of the primate 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 epispore. 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, Didymophidae.

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, 1889). 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

19
2'. (2') Associations forming branching chains, or multiple satellites associated side-by-side.

3. (2') Association interface simple; not forming a "tongue and groove" interlocking system. 

3'. (3) Association interface with a "tongue and groove" interlocking system.

4. (1) Oocysts biconical, dolioform, spherical, or ovoidal. 

4'. (4) Oocysts spindle shaped, with or without polar thickenings.

5. (4) Epimerite retractile. 

5'. (5) Epimerite simple, spherical.

6. (4') Epimerite spherical, hyaline, with a corona of 14–16 ridges; oocysts spindle shaped without polar thickenings. 

6'. (6) Epimerite spherical, with an anterior corona of four distinct sucker-like hyaline disks; oocysts spindle shaped with polar thickenings.

7. (5') Oocysts biconical, dolioform, parasitizing arachnids. 

7'. (7) Oocysts spherical, or ovoidal; with distinct pad forming junction between primites and satellites.

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 anteriad to protomerite deutomerite septum, broadly tapering from the anterior third to a blunt point posteriad; nucleus spherical, diameter 20.0–22.0–24.0 μm; with spherical karyosome, diameter 4.0–6.0 μm; eccentric. Association caudofrontal. Primitive: 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 primitive; deutomerite length 118.0–121.5–126.0 μm, width 67.0–68.0–69.0 μm. Oocyst: Elliptoid, 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 posteriad; 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.*. Ref. Geus (1969), Kamm (1922), Labbé (1899), Léger (1892). **Notes:** Kundu et al. (1987) described two gregarine species and placed them within the genus *Didymophyids*. 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 tridactyiae* (Kundu, Datta, and Haldar, 1987) Clorton, 1995 comb. nov. (= *Didymophyes tridactyiae* 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 Gregariniaceae. All other characters of the two described species of *Neohirmocystis* place them well within Hirmocystidae. The families within Gregariniaceae 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 Gregariniaceae 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 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 *Tettigonospora*
L. M. Smith, 1930

Similar to *Hirmocystis*; epimerite spherical; primate resembling satellite; gametocysts dehisce 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 orthopterans, 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 primate; gametocysts dehisce 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.

Genus *Euspora* Schneider, 1875

Sporonts solitary; association caudofrontal; gametocysts dehisce 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 dehisce 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 aspetate 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 dehisce 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 anteriad 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: Biconal, 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, Narasimahamurti & Vnidyullatadevi, 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, Narasimahamurti, and Vnidyullatadevi, 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 superfamly 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 granulosae* 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 granulosae* 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: Tribolium castaneum. Ref. Peregrine (1970).

Fig. 40. Protomaghaliaenia 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 elliptoidal 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 Protomaghaliaenia. Type Host: Tribolium castaneum. Ref. Sengupta et al. (1991).

Genus Pintospora

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: Astylus 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 baieri Théodoridès, Desportes, and Jolivet, 1972. Type Host: Encymon 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 anteriad, 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 posteriad, 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

Genus \textit{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.


Sarkar and Haldar (1980) erected \textit{Liposcelis} within Didymophyidae \textit{sensu} Chakravarty (1960). Members of Didymophyidae possess gametocysts that dehisce through a single, long, sporoduct; distinguishing them from Hirmocystidae. Although the epimerites of \textit{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 \textit{Quadruhyalodiscus}  
Kundu & Haldar, 1984

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

Kundu and Haldar (1984) placed \textit{Quadruhyalodiscus} in Didymophyidae \textit{sensu} Chakravarty (1960). Members of \textit{Quadruhyalodiscus} possess gametocysts dehiscing by simple rupture. This indicates that they are more closely allied with Hirmocystidae than Didymophidae. Although the epimerites of \textit{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 \textit{Liposcelis} above.

\begin{figure}[h]  
\centering  
\includegraphics[width=0.5\textwidth]{Fig_41.png}  
\caption{\textit{Quadruhyalodiscus gallerucidae}. Trophozoite. (Based on Kundu and Haldar, 1984.)}  
\end{figure}
1. Gametocysts dehisce through sporoducts ..........................2
1'. Gametocysts dehisce by simple rupture, without sporoducts .................................................................3

2. (1) Gametocysts with a single sporoduct; oocysts ellipsoidal or ovoida ..........................Monoductidae
2'. (2) Gametocysts with > 1 sporoduct, oocysts dolioform (keg - shaped) ......................Leidyanidae

3. (1') Protomerite deutomerite septum present; protomerite apparent in all growth stages ..........4
3'. (2') Protomerite deutomerite septum present in young trophozoites only, atrophied in mature trophozoites and gamonts (i.e. mature tophozoites and gamonts apparently without protomerite)........... Sphaerocystidae

4. (3) Epimerite apparent in mature trophozoites, complex or at least strongly differentiated ..........6
4'. (4) Epimerite in mature trophozoites absent, vestigial, invaginated, or reduced to a small cap or spherule................................................................. Stenophoridae

5. (4') Epimerite in mature trophozoites absent or reduced and invaginated; oocysts ovoidal or ellipsoidal, with or without equatorial suture .................. ......................................................... Actinocephalidae
5'. (5) Epimerite in mature trophozoites reduced to a small cap or spherule; oocyst ellipsoidal................................................................. Cnemidosporidae

6. (5) Epimerite varied; if a cupule, cone, or sucker, without digitations.........................................................7
6'. (6) Epimerite a cupule, cone, or sucker; with digitations ................................................................. Dactylophoridae

7. (6) Epimerite with “bristles“ or epicytic processes resembling a beard.........................................................8
7'. (7) Epimerite varied, if present epicytic processes strong, digitate or hooked; not bristle - like .................9

8. (6) Epimerite with anterior bristles only, forming a fine anterior brush; oocysts spherical, with fine brush border......................... Brustiophoridae
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
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 smooth ....................................................11
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 STENOPOHORIDAE,
LÉGER & DUBOSCOQ, 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 episepore, with or without equatorial suture; in diploids.

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 julii* (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 julii* 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 julii* (=Gregarina julii), 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 anteriad to the apical pore; deutomerite elongate ellipsoidal, length 720.0–1282.2–2100.0 µm, width 120.0–218.8–345.0 µm; blunt posteriad, 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 epispore; liberated from the gametocyst by simple rupture. TYPE HOST: Phyllogonostreptus negotiosus. Ref. Ramachandran (1972).

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 anteriad, 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 posteriad; 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 epispore. 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 ellipsoidal, 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 posteriad; 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 epispore, length 8.0 µm, width 6.0 µm; liberated from the gametocyst by simple rupture.

**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 µm; borne on a short neck; protomerite broadly conical, length 50.0–66.6–80.0 µm, width 50.0–81.66–110.0 µm; equatorially dilated, conspicuously constricted at protomerite deutomerite septum; deutomerite cylindrical to elongate ellipsoidal, length 240.0–356.6–420.0 µm, width 60.0–131.6–160.0 µm; sometimes tapering posteriad, always bluntly rounded posteriad; nucleus spherical; with 1 or 2 small karyosomes. Oocyst: Dolioform; length 6.0 µm, width 3.0 µm; 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. 47. *Leidyana migrator*. 5. Trophozoites reflecting normal population variation. Scale bar, 50 µm. 6 - 8. Associations reflecting differences in maturation and normal population variation. Scale bar, 100 µm. 9. Chain of oocysts, dorsal aspect. Scale bar, 5 µm. 10. Chain of oocysts, lateral aspect. Scale bar, 5 µm.

**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, gametocytes 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 epispore; 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 lumenal 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 mediodorsal 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 ateriad, acuminate posteriad) 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.


Genus Stenoductus Ramachandran, 1976

Epimerite absent in mature trophozoite; oocysts ellipsoidal, with hyaline epispore, without mesodorsal ridge, extruded in chains; nucleus without myonene 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 epispore, liberated from the gametocyst in a single chain through a single sporoduct. TYPE HOST: Floridobolus penneri. Ref. Ramachandran (1976a, 1976b).

Genus Phleobum

Haldar & Chakraborty, 1974

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


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 dehisce by simple rupture; oocysts ovoid or biconical. This family contains 4 genera and 12 species, primarily intestinal parasites of insects.

Genus 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 anteriad 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 quadrinotota 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 posteriori; nucleus spherical, diameter 20.0–30.0 µm; with a single eccentric karyosome.  
Oocyst:  Biconial, 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).

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 posteriori; 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 posteriori; 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  
(Ormières, 1926)  
Hesse, 1926 (= 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
Order Eugregarinorida

Clopton - - -

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).

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 concommitant 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:

Fig. 56. *Echinomera hispidi*. Trophozoite. (Based on Schneider, 1875.)

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).

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

**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.
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.

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 systeni* Keilin, 1920. **TYPE HOST:** *Systenus* 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 posteriorly 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 extrakaryosomic 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.


---

**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.

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.

Notes: Théodoridès (1963) defined 3 subgenera within Stylocephalus: Stylecephalus Conicocephalus, Stylecephalus Stylecephalus, and Stylecephalus 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. Stylecephalus Conicocephalus is characterized by a broad, conical diamerite terminating in a distinctive nipple. Stylecephalus Stylecephalus is characterized by a cylindrical diamerite terminating in a simple sphere. Stylecephalus 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–
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:** *Ademsmia antiqua*, *Pimelia grandis*, and *Prionotheca coronata*.

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.

**TYPE SPECIES.** *Cystocephalus algerianus*  
Schneider, 1886  
**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.  
Illustrated Guide to the Protozoa

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 anteriad, 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 anteriad, broadly tapering from a slight constriction at the protomerite deutomerite septum to a long, blunt point posteriad, 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.)


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 (= *Styrlorhynchus gladiator* Blanchard, 1905; *Styrochecephalus 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 posteriad 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 anteriad, 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 posteriad at fusion with diamerite to form a basal tumidus; tumidus toroidal, concavo-concave in anterioposterior axis, width approximately twice length; diamerite roughly cylindrical, tapering anteriad 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. Protomerite broadly ovoid to very broadly ovoid. Protomerite - deutomerite septum clearly marked and constricted. Deutomerite obovoid to narrowly obovoid. Nucleus ellipsoidal to broadly ellipsoidal; with 2–3 distinct polysomal endosomes. Gamont: Protomerite depressed ovoid to very broadly ovoid, length 60.30–118.59 µm, width 85.28–168.70 µm. Protomerite - 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).

**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.

**Genus Lophocephalus**

Labbé, 1899

(=* Lophorhynchus* Schneider, 1882)

Epimerite a large cupule formed by a crenulate crown, with longitudinal striations and basal border, with or without a crown of small membranous 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 anteriad, 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 anteriad, 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.*


**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 thripterae* Théodoridès, Desportes, and Jolivet, 1965. TYPE HOST: *Thriptera crinita.*

**Genus Sphaerocephalus**

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:** *Sphaerocephalus 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).
Illustrated Guide to the Protozoa

**TYPE SPECIES.** Trophozoite: Epimerite a round button, small; borne on a cylindrical neck, tapering to a conoid anterior; 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 posterior, 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: *Moricca* 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.)](image)

**TYPE SPECIES.** Trophozoite: Epimerite a large button, length 30.0 µm, width 30.0 µm; quadrat or truncate, with fine longitudinal striations; fused to the protomerite (without neck); protomerite hemispherical, with well developed epicyte; deutomerite cylindrical, rounded posterior; 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; 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 quadrat 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.)](image)

---

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

![Fig. 71. Clavicephalus madagascariensis. Trophozoite. (Based on Théodoridès, 1959.)](image)
Genus *Orbocephalus* Nelson, 1970

Epimerite a dilated papilla surrounded by a flat disk; borne on a long neck (diemerite); 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.


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

*Lepismatophila thermobiae* Adams and Travis, 1935 (Fig. 74). 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 posteriorly, 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.)

**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.
Illustrated Guide to the Protozoa

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 radios* 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 anteriad 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 posteriad, 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*) *parallelopedus*. 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 posteriad; 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.


**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.


**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.


**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 anteriad to a blunt cone; deutomerite elongate ellipsoidal, broadly tapering from the protomerite deutomerite septum to a blunt point posteriad; nucleus ovoidal, length 33.3 µm, width 25.3 µm; with several large karyosomes, diameter 10.0 µm. Oocyst: Cylindrobiconical, length 8.0, width 4.0 µm; liberated from the gametocyst by simple rupture.


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: *Anabolia sororcula*.

**Pileocephalus heerii** (Kölliker, 1845) Schneider, 1875 (= *Gregarina heerii* 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 distinct 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 anteriad, 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 posteriad; 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.


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.

Genus *Philidiophora*
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.


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 anteriad, 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 posteriad, 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. 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.


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 posteriad; total length 1200.0 µm; nucleus spherical, with several karyosomes. Oocyst: Biconical, ventricose, length 10.5 µm, width 6.75 µm; liberated from the

**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 posterior, 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.


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

**Genus Pyxinia**

Hammerschmidt, 1838

(= *Xiphorynchus* 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 posterior, 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.)
**Illustrated Guide to the Protozoa**

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

![Illustration of Pyxinia sp. Oocyst]

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; oocysts biconical, ventricose; in insect larvae. 85 named species.

*Bothriopsides histrio* (Schneider, 1875) Strand, 1928  
(= *Bothriopsis histrio* Schneider, 1875; *Iorella we Gorecki* Lipa, 1967) (Fig. 91).
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. Bothriopsides 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 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. anomalae Théodoridès, 1955) (Fig. 92).

TYPE SPECIES. Trophozoite: Epimerite a spherical papilla, anteriorly crateriform, with 12 posteriorly directed laminations, laminations sharply pointed posteriord, borne on a short neck; protomerite subglobular, becoming broadly conical anteriad, 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 anteriad; 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).
Illustrated Guide to the Protozoa

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 anterior; 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 anterior, very short, depressed, length 5.0–6.75–8.0 µm, width 19.0–23.8–29.0 µm; protomerite deutomerite septum sharply convex anterior, sometimes forming a dome surrounded by the protomerite; deutomerite cylindrical to obvoid, broadly tapering from the anterior third to a rounded point posterior, 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.


Genus Stylocystis Léger, 1899

Epimerite simple, a sharply pointed process, normally recurved in a long hyaline point or spine, very sharp anterior; 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: Tanypus sp.

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 posterior, 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.


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.


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 posteriorly, 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, broad, length 6.0 µm, width 4.6 µm; united laterally into chains, liberated from the gametocyst by simple rupture. TYPE HOST: *Phalangium opilio*. Ref. Geus (1969), Kamm (1922), Labbé (1899).

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 posteriorly 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; united laterally into chains, liberated from the gametocyst by simple rupture. TYPE HOST: *Phalangium opilio*. Ref. Geus (1969), Kamm (1922), Labbé (1899).
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 posteriorly 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.

**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 anteriad, 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 posteriorly, 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 120º; length 8.0 µm, width 3.0 µm, width with plates, 7.0 µm; liberated from the gametocyst by simple rupture. TYPE HOST: *Anoplogenus 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 posteriorly, 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 posteriorly, 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:

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, persistant in specimens up to 600.0 µm, length ~ twice the length of the protomerite; protomerite cylindrical, with distinct equatorial constriction, tapering anteriad from constriction, length 50.0 µm, width 60.0 µm; deutomerite elongate, pointed posteriad, length 950.0 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. 101. Ascocephalus armatus. Trophozoite. (Based on Obata, 1953.]

**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.


Genus **Gryllotalpia**
Hasselmann, 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 nonpersistant digitiform processes at apex; gametocysts and oocysts unknown; in chilopods. Five named species.

49

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

Genus Crucecephalus
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.

Crucecephalus 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 posteriad, 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.


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 Grenobia**  
Hasselmann, 1927

Epimerite small, simple; protomerite conical; gametocysts and oocysts unknown. Monotypic.  
**TYPE SPECIES:** *Grenobia 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 ~70.0–75.0 µm; wider than deutomerite; deutomerite elongate ellipsoidal, length ~220.0–225.0 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 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).  

**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:** *Gyrinus* natator. Ref. Kamm (1922), Léger (1892), Tuzet, Ormieres, 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 purpurascens* and *Silpha atrata*. Ref. 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)
Labbé, 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. 108.** *Rhizonella tenuis*. Trophozoite. (Based on Baudoin,
1971.)

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

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

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

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

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

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

**Fig. 115.** *Nubenocephalus nebraskensis*. Epimerite. (Clopton,
Percival, and Janovy, 1993.)

**Fig. 116.** *Nubenocephalus nebraskensis*. Epimerite. (Clopton,
Percival, and Janovy, 1993.)

Genus **Prismatospora**
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.

**Prismatospora 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, apparent in most trophozoite stages, 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 uncleft, 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 anteriad 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 sciareae* 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.)

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).

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

TYPE SPECIES. Trophozoite: Epimerite a sessile dish, 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.

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

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

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

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).

**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).

**Fig. 119. Dinematospora grassei.** Trophozoite. (Based on Tuzet & Ormières, 1954.)

**54**
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.


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 ceca of cosmètid Opiliones. Monotypic.


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 opalniae Devdar & 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 posteriorly; 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.


Fig. 120. Contospora opalniae. 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

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 phalangi. Left, trophozoite; Right, anterior portion of trophozoite with elaborated protomeritic ridge. (Based on Amoji and Devdhar, 1979.)

Echinoocysta phalangi (Amoji and Devdhar, 1979) Levine, 1984 (= Echinospora phalangi Amoji and Devdhar, 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 smal 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).

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

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).

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 karnataki 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 kamataki. 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: Agrion 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: Agrion 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).
Illustrated Guide to the Protozoa

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.

*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 anteriad 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 elliptoid; 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) 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).

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.


**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 anteriad 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).

**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).

**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 rousseau* 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.

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.


**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.


**Acknowledgements**

I thank John Janovy, Jr., the School of Biological Sciences, University of Nebraska--Lincoln, and the Department of Entomology, Texas A&M University for the space, facilities and support required to complete this work. Dr. J. Théodoridès provided insightful discussion and made available his valuable literature and specimen collections. I am grateful for his contributions.

This work is continually updated with partial support from the National Science Foundation under NSF9705179. This edition updated and corrected May 19, 1998

This work is by no means exhaustive. I would be grateful for notification of omissions and errors.

**LITERATURE CITED**


Ganapati, P. N. & Narasimhamurti, C. C. 1960. On a new cephaline gregarine Mecistophora legeri n. gen. n. sp. from a


Keilin, D. 1920. On two new gregarines, Altantocystis dasyheleni n. g., n. sp., and Dendrorhynchus systeni n. g., n. sp., parasitic in the alimentary canal of the dipterous larvae, Dasyhelea obscura Winn. and Systenus sp. Parasitology, 12:154–158.


Tuzet, O. & Omières, R. 1954. Contribution à l'étude des grégarines des thysanores: *Hyalospora rosovianna* Schneider


Vincent, M. 1924. On a new gregarine, *Anisolobus dacnecola* n. g.n.sp., a parasite of *Dacne rufitrons* Fabr. (Coleoptera). *Parasitology*, 16:44–47.


---

**Illustrated Guide to the Protozoa**

**Systematic Index**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthopimeritus</td>
<td>41</td>
</tr>
<tr>
<td>Acanthogregarina</td>
<td>22</td>
</tr>
<tr>
<td>Acanthospora</td>
<td>49</td>
</tr>
<tr>
<td>Acanthosporidum</td>
<td>53</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Subtaxon</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthosporinae</td>
<td>49</td>
</tr>
<tr>
<td>Actinocephalidae</td>
<td>38</td>
</tr>
<tr>
<td>Actinocephalinaceae</td>
<td>38</td>
</tr>
<tr>
<td>Actinocephalus</td>
<td>39</td>
</tr>
<tr>
<td>Acuta</td>
<td>58</td>
</tr>
<tr>
<td>Acutida</td>
<td>58</td>
</tr>
<tr>
<td>Acutispora</td>
<td>32</td>
</tr>
<tr>
<td>Agrippina</td>
<td>46</td>
</tr>
<tr>
<td>Alaspora</td>
<td>47</td>
</tr>
<tr>
<td>Amoebogregarina</td>
<td>14</td>
</tr>
<tr>
<td>Amphiplatyspora</td>
<td>32</td>
</tr>
<tr>
<td>Amphiplatysporida</td>
<td>32</td>
</tr>
<tr>
<td>Amphorella</td>
<td>44</td>
</tr>
<tr>
<td>Amphoroccephalus</td>
<td>47</td>
</tr>
<tr>
<td>Amphoroides</td>
<td>44</td>
</tr>
<tr>
<td>Ancyrophora</td>
<td>49</td>
</tr>
<tr>
<td>Anisoloboides</td>
<td>14</td>
</tr>
<tr>
<td>Anisolobus</td>
<td>13</td>
</tr>
<tr>
<td>Anthecephalus</td>
<td>46</td>
</tr>
<tr>
<td>Anthorhynchus</td>
<td>46</td>
</tr>
<tr>
<td>Apiogregarina</td>
<td>58</td>
</tr>
<tr>
<td>Arachnocystis</td>
<td>21</td>
</tr>
<tr>
<td>Ascocephalus</td>
<td>47</td>
</tr>
<tr>
<td>Aseptatorina</td>
<td>1</td>
</tr>
<tr>
<td>Asterophora</td>
<td>40</td>
</tr>
<tr>
<td>Beloides</td>
<td>42</td>
</tr>
<tr>
<td>Bifilida</td>
<td>9</td>
</tr>
<tr>
<td>Blastogregarinorina</td>
<td>1</td>
</tr>
<tr>
<td>Bolivia</td>
<td>15</td>
</tr>
<tr>
<td>Bothriopsides</td>
<td>43</td>
</tr>
<tr>
<td>Bothriopsis</td>
<td>43</td>
</tr>
<tr>
<td>Brustiophoridae</td>
<td>57</td>
</tr>
<tr>
<td>Brustiospora</td>
<td>57</td>
</tr>
<tr>
<td>Bulbocephalus</td>
<td>35</td>
</tr>
<tr>
<td>Callynthroclamys</td>
<td>7</td>
</tr>
<tr>
<td>Campanacephalus</td>
<td>37</td>
</tr>
<tr>
<td>Caridohabitans</td>
<td>6</td>
</tr>
<tr>
<td>Caulocephalus</td>
<td>39</td>
</tr>
<tr>
<td>Cephaloidophora</td>
<td>5</td>
</tr>
<tr>
<td>Cephaloidophoridae</td>
<td>5</td>
</tr>
<tr>
<td>Cephalolobidae</td>
<td>6</td>
</tr>
<tr>
<td>Cephalolobulus</td>
<td>6</td>
</tr>
<tr>
<td>Chilogregarina</td>
<td>48</td>
</tr>
<tr>
<td>Cirrigregarina</td>
<td>16</td>
</tr>
<tr>
<td>Clavicephalus</td>
<td>37</td>
</tr>
<tr>
<td>Cnemidospora</td>
<td>27</td>
</tr>
<tr>
<td>Cnemidosporidae</td>
<td>27</td>
</tr>
<tr>
<td>Cognettiella</td>
<td>17</td>
</tr>
<tr>
<td>Coleophora</td>
<td>44</td>
</tr>
<tr>
<td>Coleorhynchus</td>
<td>44</td>
</tr>
<tr>
<td>Colepismatophila</td>
<td>38</td>
</tr>
<tr>
<td>Cometoides</td>
<td>50</td>
</tr>
<tr>
<td>Contospora</td>
<td>54</td>
</tr>
<tr>
<td>Cornimeritus</td>
<td>39</td>
</tr>
</tbody>
</table>

---

66
<table>
<thead>
<tr>
<th>Family</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eugregarinorida</td>
<td>1</td>
</tr>
<tr>
<td>Dactylophoridae</td>
<td>30</td>
</tr>
<tr>
<td>Dactylophorus</td>
<td>30</td>
</tr>
<tr>
<td>Dendrohynchus</td>
<td>32</td>
</tr>
<tr>
<td>Deuteromera</td>
<td>17</td>
</tr>
<tr>
<td>Didymophyes</td>
<td>18</td>
</tr>
<tr>
<td>Didymophyidae</td>
<td>18</td>
</tr>
<tr>
<td>Dinematospora</td>
<td>53</td>
</tr>
<tr>
<td>Discoccephalus</td>
<td>42</td>
</tr>
<tr>
<td>Discorhynchus</td>
<td>42</td>
</tr>
<tr>
<td>Doliospora</td>
<td>53</td>
</tr>
<tr>
<td>Domadracunculus</td>
<td>56</td>
</tr>
<tr>
<td>Dufouria</td>
<td>41</td>
</tr>
<tr>
<td>Dumbbellicephalus</td>
<td>21</td>
</tr>
<tr>
<td>Echinomera</td>
<td>31</td>
</tr>
<tr>
<td>Echinocysta</td>
<td>54</td>
</tr>
<tr>
<td>Eliptocystis</td>
<td>22</td>
</tr>
<tr>
<td>Endomycolae</td>
<td>23</td>
</tr>
<tr>
<td>Epicavus</td>
<td>48</td>
</tr>
<tr>
<td>Eugregarinorida</td>
<td>1</td>
</tr>
<tr>
<td>Euspora</td>
<td>21</td>
</tr>
<tr>
<td>Faucispora</td>
<td>15</td>
</tr>
<tr>
<td>Fonsecaia</td>
<td>25</td>
</tr>
<tr>
<td>Fusiona</td>
<td>58</td>
</tr>
<tr>
<td>Fusionia</td>
<td>58</td>
</tr>
<tr>
<td>Fusionidae</td>
<td>58</td>
</tr>
<tr>
<td>Gamocystis</td>
<td>13</td>
</tr>
<tr>
<td>Garnhamia</td>
<td>14</td>
</tr>
<tr>
<td>Gemnicephalus</td>
<td>40</td>
</tr>
<tr>
<td>Geneiorhynchus</td>
<td>41</td>
</tr>
<tr>
<td>Globulocephalus</td>
<td>46</td>
</tr>
<tr>
<td>Gopaliella</td>
<td>17</td>
</tr>
<tr>
<td>Grebnickiella</td>
<td>31</td>
</tr>
<tr>
<td>Gregarina</td>
<td>10</td>
</tr>
<tr>
<td>Gregarinidae</td>
<td>4</td>
</tr>
<tr>
<td>Grenobilia</td>
<td>49</td>
</tr>
<tr>
<td>Gryllotalpia</td>
<td>48</td>
</tr>
<tr>
<td>Gymnospora</td>
<td>13</td>
</tr>
<tr>
<td>Harendraia</td>
<td>48</td>
</tr>
<tr>
<td>Heliospora</td>
<td>8</td>
</tr>
<tr>
<td>Hirmocystidae</td>
<td>19</td>
</tr>
<tr>
<td>Hirmocystis</td>
<td>19</td>
</tr>
<tr>
<td>Hoplorhynchus</td>
<td>55</td>
</tr>
<tr>
<td>Hyalospora</td>
<td>20</td>
</tr>
<tr>
<td>Hyalosporina</td>
<td>25</td>
</tr>
<tr>
<td>Legeria</td>
<td>41</td>
</tr>
<tr>
<td>Leidyana</td>
<td>26</td>
</tr>
<tr>
<td>Leidyaniidae</td>
<td>26</td>
</tr>
<tr>
<td>Lepismatophila</td>
<td>38</td>
</tr>
<tr>
<td>Levinea</td>
<td>49</td>
</tr>
<tr>
<td>Liposcelisus</td>
<td>23</td>
</tr>
<tr>
<td>Lophocephaloides</td>
<td>36</td>
</tr>
<tr>
<td>Lophocephalus</td>
<td>36</td>
</tr>
<tr>
<td>Lophorhynchus</td>
<td>36</td>
</tr>
<tr>
<td>Lycosella</td>
<td>45</td>
</tr>
<tr>
<td>Mecistophora</td>
<td>32</td>
</tr>
<tr>
<td>Menospora</td>
<td>55</td>
</tr>
<tr>
<td>Menosporinae</td>
<td>55</td>
</tr>
<tr>
<td>Metamera</td>
<td>16</td>
</tr>
<tr>
<td>Metameridae</td>
<td>16</td>
</tr>
<tr>
<td>Molluskocystis</td>
<td>16</td>
</tr>
<tr>
<td>Monoductidae</td>
<td>27</td>
</tr>
<tr>
<td>Monoductus</td>
<td>28</td>
</tr>
<tr>
<td>Monoica</td>
<td>58</td>
</tr>
<tr>
<td>Monoicidae</td>
<td>58</td>
</tr>
<tr>
<td>Mukundaella</td>
<td>55</td>
</tr>
<tr>
<td>Nematooides</td>
<td>9</td>
</tr>
<tr>
<td>Nematopsis</td>
<td>3</td>
</tr>
<tr>
<td>Neohirmocystis</td>
<td>20</td>
</tr>
<tr>
<td>Neoschneideria</td>
<td>30</td>
</tr>
<tr>
<td>Nubencephalus</td>
<td>51</td>
</tr>
<tr>
<td>Odonaticola</td>
<td>56</td>
</tr>
<tr>
<td>Oocephalus</td>
<td>36</td>
</tr>
<tr>
<td>Orbocephalus</td>
<td>38</td>
</tr>
<tr>
<td>Pachyporospora</td>
<td>4</td>
</tr>
<tr>
<td>Paraschneideria</td>
<td>29</td>
</tr>
<tr>
<td>Phialis</td>
<td>41</td>
</tr>
<tr>
<td>Phialoides</td>
<td>41</td>
</tr>
<tr>
<td>Phleobum</td>
<td>28</td>
</tr>
<tr>
<td>Pileocephalus</td>
<td>40</td>
</tr>
<tr>
<td>Pilidiophora</td>
<td>40</td>
</tr>
<tr>
<td>Pintospora</td>
<td>22</td>
</tr>
<tr>
<td>Pogonites</td>
<td>50</td>
</tr>
<tr>
<td>Pomania</td>
<td>44</td>
</tr>
<tr>
<td>Porospora</td>
<td>3</td>
</tr>
<tr>
<td>Porosporicae</td>
<td>2</td>
</tr>
<tr>
<td>Porosporidae</td>
<td>2</td>
</tr>
<tr>
<td>Pristatospora</td>
<td>51</td>
</tr>
<tr>
<td>Protomagalhaensia</td>
<td>22</td>
</tr>
<tr>
<td>Pyxina</td>
<td>42</td>
</tr>
<tr>
<td>Pyxinooides</td>
<td>8</td>
</tr>
<tr>
<td>Quadruhyalodiscus</td>
<td>23</td>
</tr>
<tr>
<td>Quadruspinospora</td>
<td>53</td>
</tr>
<tr>
<td>Ramicephalus</td>
<td>52</td>
</tr>
<tr>
<td>Retractocephalus</td>
<td>23</td>
</tr>
<tr>
<td>Rhizionella</td>
<td>50</td>
</tr>
<tr>
<td>Rhopalonia</td>
<td>31</td>
</tr>
<tr>
<td>Rotundula</td>
<td>6</td>
</tr>
<tr>
<td>Schneideria</td>
<td>29</td>
</tr>
<tr>
<td>Sciaidiophora</td>
<td>45</td>
</tr>
<tr>
<td>Seiptatorina</td>
<td>1</td>
</tr>
<tr>
<td>Seticephalus</td>
<td>32</td>
</tr>
<tr>
<td>Sphaerocephalus</td>
<td>36</td>
</tr>
<tr>
<td>Sphaerocystidae</td>
<td>28</td>
</tr>
<tr>
<td>Sphaerocystis</td>
<td>29</td>
</tr>
<tr>
<td>Sphaerorhynchus</td>
<td>36</td>
</tr>
<tr>
<td>Spinispora</td>
<td>15</td>
</tr>
<tr>
<td>Spirosoma</td>
<td>25</td>
</tr>
</tbody>
</table>
Steganorhynchus ................................................. 57
Steinina .............................................................. 43
Stenocephalus .................................................... 25
Stenoductus ......................................................... 28
Stenophora .......................................................... 25
Stenophoricae ...................................................... 24
Stenophoridae ....................................................... 25
Stephanophora ..................................................... 39
Stictospora .......................................................... 44
Stylocephalidae ..................................................... 33
Stylocephaloides ................................................... 34
Stylocephalus ....................................................... 33
Stylocystis ............................................................ 45
Stylorhynchidae .................................................... 33
Stylorhynchus ....................................................... 33
Taeniocystis .......................................................... 45
Tetractinospora ...................................................... 54
Tetraedrospora ...................................................... 52
Tetrameridionospinospora ....................................... 55
Tettigonospora ....................................................... 21
Thalicola .............................................................. 48
Tintinospora ........................................................ 21
Torogregarina ....................................................... 15
Trichorhynchidae ................................................... 30
Trichorhynchus ...................................................... 30
Tricystis ............................................................... 48
Trisepatata ........................................................... 13
Umbracephalus ..................................................... 40
Uradiophora .......................................................... 7
Uradiophoridae ...................................................... 7
Urnaepimeritus ...................................................... 40
Xiphocephalus ...................................................... 35
Xiphorhynchus ..................................................... 42