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Translation of Bogolepova, I. I. 1953. Gregariny iz zaliva Petra Velikogo [= Gregarines from the Gulf of Peter the Great]. *Trudy Zool. Inst. Akademii Nauk SSSR* 13: 38-56

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Bogolepova, I. I. and Plous, Frederick K. Jr., "Translation of Bogolepova, I. I. 1953. Gregariny iz zaliva Petra Velikogo [= Gregarines from the Gulf of Peter the Great]. *Trudy Zool. Inst. Akademii Nauk SSSR* 13: 38-56" (1953). *H. W. Manter Laboratory Library Materials*. 71.
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COLLEGE OF VETERINARY MEDICINE
UNIVERSITY OF ILLINOIS
URBANA, ILLINOIS

TRANSLATION NO. 25

Translated from Russian by Frederick K. Plous, Jr.
Edited by Norman D. Levine

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1953. Gregariny iz zaliva Petra Velikogo. [Gregarines from the Gulf of Peter the Great] Trudy Zool. Inst. Akad. Nauk SSSR, 13:38-56.

The data in the literature on parasitic protozoa from invertebrates inhabiting the seas of the USSR cannot be considered properly complete. However, the gregarines parasitizing the invertebrates of the Far Eastern seas have not yet been investigated at all. Nevertheless, the gregarines, which parasitize the most varied types of marine invertebrates, are interesting not only from a systematic, but also a zoogeographic standpoint.

The present work on parasitic protozoa of the order Gregarinida constitutes an attempt at filling some of that gap. The material we processed was collected in the period of July-September 1937 in the Gulf of Peter the Great by the Far-Eastern Expedition of the Leningrad State University under the leadership of Prof. V. A. Dogel'. This expedition investigated a significant number of polychaetes, gephyrae, echinoderms, crabs and ascidia. It might be said that the coastal invertebrates in the Sea of Japan were rather widely dealt with during the parasitologic research.

Processing of the material was conducted in the Protistological Laboratory of the Zoological Institute, Academy of Sciences, USSR. The material was studied primarily in the form of smears fixed in Schaudinn's fluid and stained with iron hematoxylin, as well as in 3-5 μ sections.

I regard it as my pleasant duty to express profound acknowledgement to my mentor, Prof. Valentin Aleksandrovich Dogel'.

Order Gregarinida

The gregarines under consideration here belong to both suborders of this order--Eugregarinida and Schizogregarinida.

Suborder Eugregarinida

1. Lankesteria tethyi Bogolepova, nov. sp. (Fig. 1).

This species was observed in the intestinal cavity of Tethyum aurantium, an ascidian which is widely distributed in the Gulf of Peter the Great. This is a new species of the genus Lankesteria. The gregarines had longish bodies, somewhat flattened on one surface and tapering gradually toward the posterior end. The anterior part of the body was stretched out into the contractile mucron characteristic of the genus Lankesteria. In several specimens slight longitudinal and transverse striations of the body surface

were visible. The nucleus is rounded, generally ellipsoidal, and lies nearer the anterior end of the body. Within the nucleus is a karyosome which rarely occurs singly. Examination of 50 individual gregarines showed that 6 had a single karyosome, 35 had 2 karyosomes of the same or different sizes, while the remaining 9 individuals had 3-4 karyosomes apiece, one of which was significantly larger than the others. When 2 or 4 karyosomes were present, they were situated along the longitudinal axis of the body, with one closer to the anterior and the lower closer to the posterior poles. The dimensions of the gregarines were not great: they were 50-140 μ long, and their greatest width (at the end of the anterior third of the body) was 15-40 μ .

Gregarines of similar structure have already been described from several ascidia. The species we examined is closest to L. ascidae (Lankester, 1872), but at the same time it differs noticeably from it. Where L. ascidae is pear- or teardrop-shaped and is broadly rounded at the anterior end, L. tethyi is more solid and elongate.

The mucron of L. ascidae is 13-15 times narrower than the width of the body and is approximately equal in size to the karyosome of the nucleus. L. tethyi, on the other hand, has a considerably larger mucron whose width is only 2.5-3 times less than the greatest body width. The nucleus of L. ascidae is situated in the last third of the body, but in our species it is almost in the middle.

The form of the proboscis differs sharply from that of L. siedleckii Duboscq and Harant.

2. Urospora pulmonalis Bogolepova, nov. sp. (Fig. 2).

In dissection of the hothurian Cucumaria japonica, spherical gregarines and their cysts were observed twice in their gills. U. pulmonalis forms spherical or sickle-shaped bodies scattered irregularly along the length of the gills. Some of the parasites are situated along the fine branches, others in the ends of the gills. As a rule, the gregarines are embedded between the epithelium covering the gill cavity and the coelomic covering of the gill, thrusting the latter somewhat into the body cavity. In this case some of the individuals were almost forced into the coelom. In such gregarines it was possible to distinguish the delicate layer of coelomic epithelium covering them only with great difficulty.

The diameter of the gregarines was 200-250 μ . Their microscopic structure showed that we were dealing with the neogamic form. The parasite's body is integral but contains 2 bubble-like nuclei, i. e., it is the product of an early and complete union of two gregarines. Both nuclei almost touch each other; they are sometimes separate from each other by as much as 30-50 μ . The nucleus contains a large intranuclear body (the karyosome), lying somewhat eccentrically. The spores are oval, with a comparatively low crater on one of the poles. The spores are 14-17 μ long and 8 μ wide. The posterior end of the spore is only slightly pointed and is free of appendages, which distinguishes U. pulmonalis from all other species of gregarines of the genera Urospora and Lithocystis which live in holothuria. In the form of the posterior end our species recalls to some extent L. brachycercus described by Pixell-Goodrich (1925) from Chiridota laevis. However, L. brachycercus is clearly distinguished by the absence of neogamy, and has spores with a short tail appendage. It also has a different location (on the walls of the intestine).

3. Urospora intestinalis Bogolepova, nov. sp. (Fig. 3).

Like the preceding species, these gregarines occur in Cucumaria japonica. They are rare, but they cause heavy infections. Of 100 holothuria examined, only 2 were infected. Approximately the middle third of the intestine was infected thruout its walls by numerous tiny milk-white spheres, situated in some areas in large clusters. The spheres very rarely protruded above the surface of the coelomic wall of the intestine. Each sphere was a double, i. e., neogamic, gregarine. Most of the gregarines were in the latter stages of spore-formation. The cyst diameter of U. intestinalis is 250-300 μ . The true position of the cysts is easily visible in serial sections thru the intestine: the gregarines are located in the deep layers of the epithelium, their depth varying amongst the individual parasites. Some of them touch the subepithelial connective tissue and musculature of the intestine; others lie within the epithelium itself. In cysts with nuclei which divide in the protoplasm the entire interior of the cyst is taken up by the cytoplasmic contents. In cysts with completely formed spores the latter occupy approximately only 1/2 of the cyst cavity, while the other half is filled with a clot of coagulated fluid. Cysts with ripened spores are for the most part situated close to the surface of the intestinal epithelium, so that evacuation of the spores obviously occurs thru the posterior end of the intestine and the cloaca. The spores have the shape typical of this genus: they are longish, with the outer wall of the spore stretched on one end into a short but sharp tail, the other end forming a small, low-sided funnel. The spores are 11-12 μ long and about 3 μ wide.

In addition to position in the host, this species differs from U. pulmonalis in its somewhat greater cyst diameter, the shape of the posterior end of the spore and its considerably smaller spore size. In the form of the posterior end of the spore U. intestinalis is more like L. brachycercus Pixell-Goodrich and L. minchini (Woodcock, 1904). L. minchini lives under the coelomic epithelium of the body wall in Cucumaria saxicola, and the spores of L. minchini have on their surface a large number of cuticular mounds, which clearly differentiates this species from ours.

L. brachycercus, tho similar in location to U. intestinalis, differs substantially from this species in several features mentioned in the comparison of it and U. pulmonalis.

4. Urospora lagidis de St. Joseph, 1898

In the body cavity of the only polychaete in our collection, Lagis koreni, we found about a dozen rounded cysts with the characteristic spores of Urospora lagidis. One end of the spore had a crater, the other a broad, flat tail appendage.

The holothuria are rather rich in coelom and tissue gregarines while gregarines are almost never encountered in the intestinal lumen itself. At the same time, all the forms found in the holothuria are distinguished by one general property of spore structure. The external wall of the spore forms an obvious crater or funnel at one end, while at the other it stretches into a short or long, simple or leaf-like, flattened tail appendage.

Another feature, tho one that is far from common to all the gregarines of holothuria, is a tendency toward early reproduction, followed by complete union of the 2 individuals, so that almost thruout their whole lives the gregarines have the appearance of a rounded cytoplasmic body with 2 large nuclei inside. As a result of this, Woodcock (1906) called such forms early-mating, or neogamic.

Up to the present time the following species of gregarines have been described from various holothuria:

1) Urospora synaptae (Cuénot, 1891) from the body cavity of Synapta inhaerens; spores with a long, filament-like appendage, a spore crater with 4 small teeth;

2) Urospora mülleri (Cuénot, 1892) from the body cavity of Synapta digitata; spore appendage thin and filament-like;

3) Urospora chiridotae (Dogiel, 1906) from the spinal blood vessel and body cavity of Chiridota laevis; the tail appendage of the spore is filament-like;

4) Urospora holothuriae (A. Schneider, 1858), in stalked vesicles on the blood vessels of Holothuria tubulosa, adult forms in the body cavity; posterior appendage has the shape of a flat, end-tapering plate; neogamic species;

5) Lithocystis brachycercus Pixell-Goodrich, 1925, from Chiridota laevis; the gregarines are on the walls of the intestine, protruding into the coelom, but are covered by the coelomic epithelium; tail appendage of spore is short, conical;

6) Lithocystis minchini (Woodcock, 1904) on the walls of the gills of Cucumaria saxicola; posterior end of spore is stretched into a short, sharpened appendage; external wall of cell forms short mounds; infection probably occurs thru the cloacal aperture; neogamic species; according to Pixell-Goodrich's later data (1920), this species does not parasitize the gills but lies under the coelomic epithelium of the body wall; but the following species lives in the gills themselves;

7) Gonospora irregularis (Minchin, 1893) from the blood vessels of Holothuria forskalii; spores have a crater, but with a rounded opposite end; neogamic species;

8) Diplodina gonadipertha (Djakonov, 1923) from the sex glands of Cucumaria frondosa in the Murman area; spores with a crater but without a tail appendage; altho this species is assigned by Djakonov to a separate genus, the structure of the spores and the neogamic character of D. gonadipertha tail to distinguish it from other representatives of the forms we have studied.

In examining the generic autonomy of the "genera" of gregarines found in the holothuria, we should first of all ask ourselves the question: should we regard a single, and moreover, a qualitatively limited feature--the shape of the posterior pole of the spore--as a sufficient criterion for division

of a known group of species into separate genera? For such, precisely, is the difficulty in the case of the genera Urospora, Gonospora, Lithocystis and Diplodina. Pixell-Goodrich's assertion (1929) that in Urospora the male gametes have the form of a spermatozoon, while in Lithocystis they do not, is based only on examination of a very limited number of species, and can therefore be regarded as unproved, as Reichenow (1932) quite properly observes. There is a basis for assuming that a single feature of length and shape of the spore's tail appendage is insufficient ground for division of the gregarines of holothuria and some other marine invertebrates into separate genera. For such, precisely, is the difficulty in the case of the genera Urospora, Gonospora, Lithocystis and Diplodina. Pixell-Goodrich's assertion (1929) that in Urospora the male gametes have the form of a spermatozoon, while in Lithocystis they do not, is based only on examination of a very limited number of species, and can therefore be regarded as unproved, as Reichenow (1932) quite properly observes. There is a basis for assuming that a single feature of length and shape of the spore's tail appendage is insufficient grounds for division of the gregarines of holothuria and some other marine invertebrates into separate genera.

In comparing species of gregarines of the genera Urospora, Gonospora and Lithocystis (some species occur in polychaetes, gephyrea and marine gastropods in addition to the holothuria) it is easy to see that one or another structure of the spore's tail appendage can combine with the most varied other features, such as: an ability to act neogamically, mobility, location in the host, and the species of host. Thus, if we take the distribution of gregarines from various groups of holothuria (Apoda, Aspidochirota, Dendrochirota) we can find gregarines of various genera in the representatives of each group, such as Dendrochirota, which is a host of Lithocystis and Gonospora. Moreover, in addition to the holothuria, some species of Gonospora are found in polychaetes and gastropoda, some species of Lithocystis in the Spatangoidea and various species of Urospora are known from the Spatangoidea, polychaetes, nemertines and gephyrea. Location of the gregarines (coelom, body wall, intestinal wall, blood vessels, gills, gonads of the holothuria) may also vary in each of the 3 genera.

Neogamic species occur both in the genera Lithocystis and Urospora and in the genus Gonospora. Each genus contains both highly motile and nonmotile species. The only regular relationships which we noticed in the gregarines of holothuria consist in the fact that their neogamic forms have been found so far only in the Pedata (Lithocystis minchini, L. cucumariae, Gonospora irregularis, Urospora holothuriae), not in the Apoda. There are likewise no neogamic forms in the other animals (Spatangoidea, worms).

Departing now from the consideration that neogamy is a substantive feature of the life cycle, it would be more natural to combine the neogamic species into one genus, as Calkins (1926) does, recognizing thus a special neogamic genus Cystobia.

It might also be noted that all gregarines of holothuria, both neogamic and non-neogamic, belong to the nonmotile forms, while Urospora, Gonospora and Lithocystis of other animals are for the most part definitely motile.

This criss-crossing of various features we have just enumerated in the genera Urospora, Gonospora and Lithocystis attest to the fact that all forms now distributed among these 3 "genera" actually make up one large polymorphic genus with several poorly defined spore types, neogamic properties and other features of a species group.

The gregarines of holothuria represent a series of gradations located in various spots within the host's body. Actually, in this group of gregarines we find almost all possible combinations of features in the location of the gregarines and methods of eliminating them into the external environment.

The coelomic gregarinae probably arose from the intestinal ones, so that the above described Urospora intestinalis has here been stipulated as the 1st level in a series of forms penetrating more and more deeply thru the wall of the intestine and into the body of the host. This gregarine spends its whole life in the wall of the intestine beneath the intestinal epithelium; the spores are apparently eliminated here thru the intestine and cloaca.

The next stage is represented by Urospora chiridotae and Lithocystis brachycercus. U. chiridotae pierces the submucosa and the muscular fascia of the intestine and ends in the spinal blood vessel. Part of the parasites sporulate in the vessel, but the greater part, once sporulated, pass over into the body cavity. Thus, the cysts, with their spores, turn up in the coelom; their elimination to the outside is probably accomplished by autotomy of the host animal. The same picture occurs in L. brachycercus, with the distinction that these gregarines 1st occur in the walls of the intestine, then bulge out the walls of the intestine (without preliminary passage thru the spinal blood vessel) into the body cavity, where they are separated from the latter only by a delicate layer of coelomic epithelium. Elimination of spores to the outside occurs in the same manner as in the preceding species.

Finally, Lithocystis minchini from Cucumaria saxicola goes even farther into the interior, abandoning all connection with the intestine: these gregarines live in the coelomic epithelium, beneath the external body wall of Cucumaria.

Urospora pulmonalis and Lithocystis cucumariae from various species of Cucumaria follow another line of development. They live in the connective tissue layer of the gills of the holothuria. Spore infection obviously occurs not thru the mouth and stomach, but thru the cloaca during inspiration. Evacuation of the cysts with their spores could most likely occur thru the gill and cloacal openings. However, the strong protuberance of the cysts of U. pulmonalis from the walls of the gills into the body cavity speaks more loudly in favor of the movement of adult cysts into the coelom, as in the 2 previous species.

The final type of localization is seen in Gonospora (Diplodina) gonadipertha, described by Djakonov (1923) from the sex glands of Cucumaria frondosa. The method by which these gregarines infect the host is not known, but elimination of the spores to the outside occurs thru the sexual passages of the host.

Such are the probable paths of the evolution of parasitism among gregarines living in holothuria.

5. Lecudina pyriformis Bogolepova, nov. sp. (Fig. 4).

This species was observed in the intestine of Nereis cyclurus. Some of the gregarines were found in the intestinal lumen; other parasites were found attached to the intestinal wall. The anterior end of the body does not have any noticeable epimerite. In some of the individuals removed from the epithelium the anterior end has the form of a somewhat more darkly colored truncated cone. The body of L. pyriformis is massive, sometimes almost regularly oval, resembling a lemon, more often pear-shaped, with a narrower posterior end. The gregarines when fixed are 86-125 μ long and 63-90 μ wide. According to V. A. Dogel', the width of live gregarines is somewhat less, while they are somewhat flattened in smears.

The protoplasm is divided into a grainy endoplasm and a more brightly colored homogeneous ectoplasm which forms a delicate peripheral layer. This layer is thickest at the anterior end of the body, part of which it occupies entirely, and is slightly thicker at the posterior end. The nucleus is spherical, primarily central, 15-20 μ in diameter. There is one karyosome (in 50% of individuals), 2 (in 30%) or as many as 3 or 4 (in 20%). When more than one karyosome is present one is always larger than the others.

The same gregarines, but somewhat smaller in size, was also observed in Nereis agassizi. In view of the lack of other differences and the close relationship of the 2 hosts we regard these 2 gregarines as the same species.

A comparison of the species described and the earlier known species of the genus Lecudina confirms their distinction with sufficient clarity. L. pellucida (Kölliker, 1848) is the closest to L. pyriformis.

However, our species differs from L. pellucida in Reichenow's (1932) description by virtue of its size (125 μ for L. pyriformis as against 60 μ for L. pellucida), a rounder body shape, the length-width ratio, the ratio of nuclear size to greatest body width (in L. pellucida the diameter of the nucleus is less than the greatest width of body by 2-2.5 times, while in L. pyriformis the nucleus is 1/4 or 1/5 of the body width).

The information which Ganapati (1946a) gave on the dimensions and structure of L. pellucida can hardly be applied to this species.

6. Lecudina arrhyncha Bogolepova, nov. sp. (Fig. 5).

This species was found in the intestine of Nereis sp. It is very similar to the previous one, but is considerably smaller. The body is oval or egg-shaped; the posterior end is sometimes sharpened. The body is 42-76 μ long and 29-50 μ in greatest width. The nucleus lies approximately at the middle of the body. The karyosome is single (in 55%), less often there are 2, 3 or 4. A characteristic property of this species is the fact that in 95% of individuals the karyosome extends to the internal wall of the nuclear membrane. As a result of this the karyosome is hemispherical or even forms a flat disc (or discs) adjacent to the nuclear wall. The nuclear diameter is 10-15 μ . The anterior end of the body is the same as that of L. pyriformis. In many individuals there are slight longitudinal striations.

7. Lecudina euphrosynes Bogolepova, nov. sp. (Fig. 6).

A very small number of Lecudina belonging to this new species were observed in the intestine of one of 4 individuals of Euphrosyne sp. The body of L. euphrosynes is swollen at the anterior end and lack an epimerite. Toward the rear it grows gradually thinner and sharper, so that in general the animal resembles a carrot. In the swollen anterior third of the body there is an oval, longitudinally stretched nucleus. In a few of the individuals we studied the karyosome had a rather unique structure. It consisted of several spherical bodies, partially connected with one another by delicate cross-members. It might be that such a formation indicates a definite degree of viscosity in the karyosome matter, so that the latter may as a result remain joined, without spreading out over greater distances. The gregarine is 394-458 μ long and 100-126 μ wide at its widest place; the nucleus is 55-65 μ long and 33-40 μ wide.

Our species is closest in general body form to Ganapati's (1946b) L. lisidicae Bratia 1938 from Lisidice collaris from the Andaman Islands region. This species is distinguished from L. euphrosynes by its narrower body: the ratio of length to width in L. euphrosynes is about 4; in L. lisidicae it fluctuates between 2.3 and 3.

The basic difference (according to Ganapati's description) is that L. lisidicae has a long conical epimerite which is entirely absent from our species.

8. Polyrhabdina cirratuli Bogolepova, nov. sp. (Fig. 7).

This species was found in the intestine of one Cirratulus cirratus among several adults which had separated from the epithelium.

The boundaries of the genus Polyrhabdina are not yet clearly demarcated. It includes those gregarines with a corolla of branching appendages on the epimerite (P. spionis [Kölliker, 1845]), and gregarines with a simple, cupoloid epimerite [P. polydorae (Léger, 1893)].

The form we are to describe apparently belongs to the 2nd category. The anterior end of the gregarine's body is rather clearly (though not to the degree seen in Polycystidae) differentiated into a cupola or a hemisphere. The actual body of the parasite is more or less swollen, but it gradually narrows toward the posterior end; it is circular in transverse section. In the enlarged part of the body the protoplasm is large-grained, with flaky elements which stain rather strongly in green hematoxylin. The hemispherical anterior outgrowth is more homogeneous and fine-grained. An oval or round nucleus is situated in the broadened part of the body. The nucleus contains one small karyosome. The gregarine is 134-165 μ long and 50-70 μ in greatest width; the epimerite is 15-20 μ long. The nucleus is about 20 μ in diameter.

In its structure our species is most similar to P. polydorae (Léger, 1893), but it differs from the latter by its greater size (165 vs. 35 μ), its more constricted and extended posterior end and the absence of the small conical elevation on the top of the epimerite. Only 2 species of gregarines of the genus Selenidium--S. virgula Caullery and Mesnil, 1919 and S. plicatum Ray, 1930--are known from the intestine of C. cirratus in the seas of Europe.

9. Polyrhabdina nereicota Bogolepova, nov. sp. (Fig. 8).

This intestinal form occurs in polychaetes of the genus Nereis which have not been determined down to species.

At first glance the gregarines recall many Polycystidea which have thrown off their epimerites. This impression is created because the hemispherical, rounded-in-front epimerite of P. nereicola is set off from the rest of the body by an obvious gap and resembles the protomerite of the Polycystidea. However, the partitions which transect the body transversally are absent from their accustomed place. During active movement of the gregarine the epimerite may tuck itself away at the point of partition. The body form is longish, the cuticle is thick and bi-contoured. The posterior of the body is either rounded or slightly sharpened. The nucleus lies approximately in the middle of the body and is either spherical or oval, stretched along the longitudinal axis of the body. There can be either one or 2 karyosomes; in the latter case the karyosomes are at the anterior and posterior ends of the nucleus. The diameter of the spherical nucleus varied in individuals of different size from 10-30 μ . In individuals with an elongate nucleus the longitudinal axis was 12-30 μ long and the transverse one 7-23 μ long. The smallest gregarines were only 98 μ long and 22 μ wide; the largest ones were 275 μ long and 88 μ wide. So large a range of fluctuation in the free stage shows, perhaps, that a considerable span of time passes between the freeing of the gregarines from the intestinal wall and the onset of sexual reproduction.

This species belongs to a group of species of the genus Polyrhabdina having a simple, cupoloid epimerite. It most resembles P. polydora (Léger, 1893), but in P. polydora the epimerite is approximately 6 times shorter than the body length (the same as in P. cirratuli), while in P. nereicola the epimerite is relatively small and has no conical elevation on top; the body length is approximately 13 times greater. In addition, this species differs from P. polydora and other species of the same genus by its very large size (275 μ for P. nereicola vs. 35 μ for P. polydora).

10. Cygnicollum attenuatum Bogolepova, nov. gen., nov. sp. (Fig. 9).

In a single sample of Lumbriconereis japonica we found a small number of gregarines which by their features did not resemble any of the genera known to occur in the intestines of the Polychaeta.

The gregarines had very long and relatively narrow bodies, whose length (exclusive of the epimerites) exceeded the width by 13 times; if the epimerite be taken into consideration, the above ratio was expanded to 18:1. The absolute dimensions of Cygnicollum are as follows: length of whole body, including epimerite, 688-707 μ ; length of epimerite, 163-165 μ ; width of body, 30-38 μ , length of nucleus, 30-34 μ ; width of nucleus, 21-22 μ . As the figures show, the epimerite is distinguished by its very great length. In this connection our form resembles Lecythion thalassemae described from the intestine of Thalassema neptuni (Echiuridea) (Mackinnon and Ray, 1933). However, in Lecythion, during the formation of the proboscid epimerite one finds something akin to a "protomeritic nucleus," a cluster of siderophilic granules surrounded by a bright field. This formation is absent in Cygnicollum. In addition, in Lecythion the end of the epimerite is webbed with insections, and small, pointed mounds are scattered over the whole cuticle of the body,

which does not occur in our form. The anterior part of the body of Cygnicollum, right behind the epimerite, is noticeably puffed out and gives the impression of a protomerite. The place of transition into actual body is clearly noticeable, and here, apparently, the epimerite becomes detached from the body. At any rate, we found gregarines in which the epimerite was absent. On the other hand, in Lecythion the epimerite is not detached, but merges right into the body of the gregarine. The epimerite of Cygnicollum is long, delicate and proboscid. Its distal end, with which it attaches itself to the intestinal epithelium, has a slight swelling; in one individual we saw a round, siderophilic grain inside the swelling.

We have assigned the genus described to the family Lecudinidae, since, as was already pointed out above, it is most similar to the genus Lecythion, which is a part of this family.

11. Cephaloidophora chthamalicola Bogolepova, nov. sp. (Fig. 10).

This species was found only once--2 individuals in the intestine of a Chthamalus challengeri. Their body length is 102-106 μ and greatest body width 58-59 μ . The deutomerite was 65-71 μ and the protomerite 31-41 μ long. It follows from these measurements that the gregarines are relatively short and broad and have a very large protomerite. No traces of either an epimerite, or the so called "protomeritic nucleus," seen in some representatives of the genus Cephaloidophora were noticed. The large oval nucleus (22 x 19 μ) contained one karyosome.

So far 2 genera of gregarines--Cephaloidophora, so named by Mavrodiadi in 1914, and Pyxinioides, placed into a special genus by Tregubov in 1912--have been recognized. Cephaloidophora has a flat, weakly developed epimerite, while Pyxinioides has a pin-shaped, swollen epimerite with a delicate proboscis on the end. Tregubov did well to say that these forms belonged to different genera, since the entire initial part of the development of Cephaloidophora takes place intracellularly in the intestinal epithelium, while in Pyxinioides the entire life cycle occurs in the lumen of the intestine, starting with the sporozoite.

Representatives of Cephaloidophora have been known hitherto only among the Cirripedia (various species of Balanus), while both known species of Pyxinioides are found (one in Balanus, the other in Chthamalus stellatus) in the Mediterranean.

It seems to us more correct to assign our gregarine to the genus Cephaloidophora both on the basis of the absence of an epimerite and on the basis of general body proportions; in Pyxinioides chthamali Tregouboff the body is much more swollen. Our form differs clearly from Cephaloidophora communis from Balanus in its considerably greater size (106 μ vs. 70 μ in C. communis), and the presence of a single karyosome (in C. communis the karyosome occurs in multiples); our species parasitizes a different genus of host.

12. Nematopsis dorippe Bogolepova nov. sp. (Fig. 11).

In the intestine of the crab Dorippe granulata we saw gregarines in syzygy, either double, or consisting of 3 individuals situated one behind the other. The primate had a definite hemispherical protomerite with no

trace of an epimerite. In preparations stained with iron hematoxylin it was sometimes possible to see, at the division between proto- and deutomerite, a dark stripe or plate recalling the similar formation in Pyxinioides (after Tregubov, 1912). The protomerite is always atrophied in the satellites, so that its body is single. The body of the gregarines is covered with a solid cuticle which forms coarse folds during the animals' contractions. It is interesting that in some especially successful preparations it is possible to see rather numerous, rather tightly spaced transverse striations with 2 longitudinal rows of small thickenings on them in the endoplasm. These transverse streaks recall in an embryonic form the transverse septa described by Léger (1906) in Taeniocystis mira.

The syzygies are 250-508 μ long and 38-60 μ wide. The nucleus of N. dorippe is large, in young syzygies rounded, in older ones more oval, stretched longitudinally. The nuclei in the large syzygies reach 21 μ in length and 17 μ in width. One large spherical karyosome is visible in the nuclei of young syzygies; in the more mature syzygies the karyosome stretches somewhat transversely, forming a broad belt which intersects the nucleus. The position of the nuclei observes certain regularities. In the primate the nucleus is always closer to the posterior end of the gregarine. In the satellite it is less removed toward the posterior pole and sometimes lies almost in the middle of the satellite.

The above described parasites recall many gregarines from European crabs. More than anything else they resemble certain representatives of the family Porosporidae from the genus Nematopsis--namely N. legeri (Beauchamp, 1910), which parasitizes Eriphia spinifrons from the Mediterranean Sea. Our species differs from that just named in several features and in particular by virtue of its smaller size (syzygies of N. dorippe are up to 508 μ long, and of N. legeri up to 750 μ), and by the fact that N. dorippe very often (in 50 per cent of cases) forms triple syzygies, while only double ones are characteristic of N. legeri.

13. Nematopsis lamellaris Bogolepova, nov. sp. (Fig. 12).

In the intestine of one of the shoreline species of crabs, the species of which we could not accurately determine, one syzygy turned up from this highly interesting species of gregarine. The syzygy consisted of 3 lineally situated and closely united individuals. The primate had a protomerite strongly flattened, like a cap, but these features were absent in the satellites. The deutomerite of the primate, starting from the front and running right up to the nucleus, was divided into numerous transverse plates separated from each other by narrow, chink-like spaces. Such construction, in the observations of V.A. Dogel', was very distinctly noticeable on the live specimen. The rest of the primate was occupied by the usual (for gregarines) granular protoplasm. Anterior to the central nucleus is a transverse partition, the posterior portion being interrupted in the middle. Apparently these partitions are the anterior and posterior borders of the middle satellite. In such a case the middle satellite flattens anterior-posteriorly; it is 60 μ long. The posterior satellite has the usual structure, is free of septa and contains a nucleus situated somewhat closer to the anterior end. The syzygy was 655.5 μ long and 130.6 μ wide. Thus, the length-width ratio was somewhat less than 4:1. The irregularly rounded nucleus was 37.8 x 29,4 μ .

It is interesting to note that a whole series of gregarines belonging to various families show a tendency toward working out the transverse septa within the body, an example being Taeniocystis and the 2 species of Nematopsis we described. This property is properly regarded as an adaptation which hinders the separation of the body and occurs during life in the lumen of the intestine.

A feature as original as the presence of numerous transverse plates of protoplasm is sufficient for assigning the parasite to a separate species.

Suborder Schizogregarinida

14. Selenidium orientale Bogolepova, nov. sp. (Fig. 13)

This species was observed in the intestine of Phascolosoma japonicum. The gregarines found are shaped like most members of the genus Selenidium. The body is stretched longitudinally and tapers sharply at both ends; turned to one side, the animal appears to be flat. On each of the flat sides of the body pass 8 longitudinal stripes. The nucleus is irregularly round, with a single central karyosome; it lies approximately in the middle of the body. Spore formation and asexual reproduction could not be observed.

The number of species of intestinal gregarines described for the Gephyrea is not large. Dogel' (1907) described the gregarine Schizocystis sipunculi from Sipunculus nudus in Naples. On more detailed investigation it proved to be a member of the genus Selenidium.

In the same year Brasil (1907) found 2 species of Selenidium, which he unfortunately neglected to name, in Phascolosoma vulgare and Ph. elongatum. Finally, in 1939 Hukui (1939) described gregarines from Siphonosoma cumanense (Keferstein). One of the intestinal gregarines described by this author represents a completely original form and is assigned to its own genus Filipodium. Hukui, however, was wrong in assigning this genus to the family Dactylophoridae on account of a few superficial features, namely the shape of the epimerite and other properties. Filipodium belongs to quite another group of gregarines, since it has no transverse septum as all Dactylophoridae do. Thus, Filipodium has an epimerite and an aseptate body, while the Dactylophoridae have an epimerite, a protomerite and a deutomerite. The error in assigning Filipodium to the Dactylophoridae is already evident in the fact that Filipodium is encountered in the Gephyrea, while all the Dactylophoridae are parasites of Myriapoda. The second of the gregarines described by Hukui, Selenidium folium, is an undoubted Selenidium, easily distinguishable from the species we found because of its relatively short but flat body with its large number of longitudinal striations running down each side (22 of them in the drawing). Finally, he called the third gregarina Exoschizon siphonosomae, but it is highly probably that this is actually another species of Selenidium. In this case it ought to be named S. siphonosomae. Under his new generic name Hukui described the stages of asexual reproduction of Selenidium as they occur freely in the lumen of the host's intestine. According to V. A. Dogel' (1907) the schizogony of S. sipunculi occurs in exactly the same way as in S. siphonosomae, except that it takes place in special pocketlike protuberances on the wall of the

intestine. In any case, Selenidium (=Exoschizon) siphonosomae differs from the species we describe from Phascolosoma japonicum, since it has a different number of longitudinal striations on the body. Hukui noted that the number of these stripes is completely determined and drew 13 of them on each of the flattened sides of the body. In contrast, our S. orientale has a total of only 8 striations on each side.

From the survey it follows that among the intestinal gregarines of the Gephyrea representatives of the genus Selenidium (6 species) predominate, including "Exoschizon" and S. orientale, and one species of the special genus Filipodium.

15. Selenidium curvicollum Bogolepova, nov. sp. (Fig. 14).

This species was found only once in the intestine of the polychaete Stylarioides plumosus. The anterior end of all the individuals found was extended into a rather long nose, bent halfway down its length into a blunt angle. The cytoplasm of the anterior outgrowth is apparently denser and contains none of the tiny granules which fill the remaining body of the gregarines. The anterior end of the nose has uneven contours at the place where it probably became detached from that part of the epimerite which had penetrated into the intestinal wall. Thus, the anterior end of the individuals found was somewhat damaged. The body of the gregarine is relatively short and broad, and along its surface run 13-15 longitudinal striations on each side. In body length this species best recalls S. sabellae (Lank.) in Ray's (1930) classification. The endoplasm is fine-grained. The nucleus is comparatively small, irregular and is situated approximately in the middle of the body. The diameter of the nucleus in the largest individuals reached only one third the width of the body. The gregarines are 38-70 μ long and 10-20 μ wide; the diameter of the nucleus in the larger individuals is 6 μ .

Compared with the other species we examined, this is a tiny one. It may be that the small dimensions stem from the fact that we failed to collect completely matured individuals. In any case, S. curvicollum deserves to be named as a separate species on the basis of the structure of the anterior end of the body.

16. Selenidium flabelligerae Bogolepova, nov. sp. (Fig. 15).

This species is a very frequent parasite of Flabelligera sp.

During preparation of the gregarines most of them fell in a free state onto the slide, but a few isolated individuals had intact epimerites which were still attached to pieces of the intestinal wall. The free individuals took the form of a typical ribbon-shaped Selenidium with a more blunt anterior and a somewhat tapered and pointed anterior end. Among them also were a few more contracted but broadened individuals which may have been preparing for syzygy. In these examples the body is slightly pinched at the line where the nucleus occurs. The anterior end of the body has the greater variety of structure, which depends on the degree of preservation of the epimerite in various individuals and on the age of the gregarines. The younger ones are shaped like short worms. The anterior end of the body has a bundle of 6-8 short, somewhat forward-merging siderophilic ribbons or "lignes siderophiles" mentioned by Brasil (1907). At approximately the middle of the body there is a narrow, longitudinally stretched nucleus with a small karyosome.

Individuals of this configuration were 15-17 μ long. In the larger specimens (around 30 μ long) the anterior end of the body, containing the siderophilic lines, distinguishes itself from the rest of the body thru a slight partition and forms a short "nose", obviously serving for attachment to the intestinal epithelium. In the more mature stages (70 μ or more long) one observes a sort of continuation of these lines right behind the nose; they look like more or less regular rows of siderophilic granules. A few of these individuals had 6 longitudinal striations like the characteristic myonemes of the genus Selenidium on both of the flat sides. Ultimately the nose changes stretching out into a long, straight, or slightly curved proboscis or twig which penetrates the epithelium. The base of the twig is slightly thickened in the shape of a cone, on which one may see 6-8 longitudinal thickenings which stain with iron hematoxylin. In all the gregarines which had separated from the intestinal wall the twig was ripped, which could be seen from its uneven and irregular edges; obviously this tip had remained stuck in the epithelium of the intestine. The largest individuals which had a twig reached a length of 120-140 μ , of which 10 μ alone were twig. Individuals with a twig often had 6 or 7 longitudinal myonemes.

In youth the posterior end of the body is always strongly stretched and tapered, but, starting with individuals 100-130 μ long, it often has the same width as the rest of the body and is smoothly rounded. The proper principles of the relationship in time between contraction and broadening of the posterior portion could not be noted.

During further growth the gregarines contract even more and broaden, then mate, conjugating with their posterior ends. The conjugated pairs in our material were 185-200 μ long and 50-57 μ wide.

The nucleus of S. flabelligerae is narrow and longitudinally stretched. The comparatively small karyosome is mostly situated toward the anterior end of the nucleus. The nucleus in the adult gregarines (over 100 μ long) fluctuates between 10-15 μ long and 5-7 μ wide. The longest gregarine in this species is 200-210 μ long.

In viewing the structure of the anterior end of S. flabelligerae, one might say that the species of Selenidium which most resembles it is S. foliatum Ray. The distinct "nose" of our form corresponds to the anterior "knob-like portion" which Ray (1930) mentioned. According to Ray, the knob ends simply in a short point, but in his drawing he shows a continuation of the knob in the form of a comparatively long, thin stiletto. However, in addition to the considerably greater stretching of the "nose," our species differs from S. foliatum in its different body form and the number of longitudinal striations (in S. foliatum 16-24; in our species 6-8).

Siedleckia nematoides Caullery and Mesnil (Fig. 16).

We found this form of schizogregarine in the intestine of Aricia norvegica M. Sars. The forms we found did not differ in any way from the typical S. nematoides described in detail by the French authors.

GENERAL REMARKS ON GREGARINES IN THE SEA OF JAPAN

As a result of our dissection of a whole series of invertebrates from the Gulf of Peter the Great we found 17 species of gregarines. In many of the host-animals subjected to study (worms, echinoderms and crabs) parasitic protozoa of the order Gregarinida were not observed. Thus, the polychaetes dissected included many Spirorbis, Potamilla reniformis, Polynoidae and others; the arthropods without gregarines included Balanus, the hermit-crabs Crangon, Sclerocrangon, Pougetia, several species of Isopoda and Amphipoda; the echinoderms included several species of starfish, Strongylocentrotus nudus, S. pulchellus, Echinocardium cordatum and Echinarachnius parma.

In the study we observed an unusually strong predominance of intestinal gregarines (14 species) over coelomic types (3 species). We did not find such common coelomic gregarines as Pterospora maldaneorum or the various species of Lithocystis and Urospora in Echinocardium, or Gonospora.

Among the intestinal gregarines the greatest variety is found in schizogregarinae of the genus Selenidium (3 species) and gregarines of the genus Lecudina (3 species).

Most of the species we described (15) proved to be new ones. The structure of one species was so unique that we had to put it in a new genus Cygnicollum. Two species--Urospora lagidis and Siedleckia nematoides--are identical to those described earlier from the seas of Europe.

Also interesting is the fact that in some hosts which are also found along the European coast we found different parasites in the Sea of Japan. Thus, the Japanese Cucumaria japonica, which is close to the species C. frondosa, has, as we have seen, 2 gregarines of the genus Urospora: U. pulmonalis from the walls of the gills and U. intestinalis from the walls of the intestine. Along the shores of the Murman Sea, Cucumaria does not have these gregarines, but is still often infected with another species, Diplodina gonadipertha, which infects the gonads of the holothuria.

It is highly probable that, upon further investigation of the invertebrates of the Sea of Japan, more gregarines will be observed which have already been described from the seas of Europe. The presence of a considerable number of representatives of the European invertebrate fauna in the Sea of Japan allows this prediction to be made.

There is special interest in our previously remarked finding in the Sea of Japan of parasites not encountered in the circumboreal animals in the Atlantic, even when these same Atlantic animals harbor no parasites of Atlantic origin. This circumstance indicates the possibility of using parasites, including protozoa (gregarines) for zoogeographic characterizations of the different seas.

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Figure captions

- Fig. 1. Lankesteria tethyi Bogolepova, nov. sp. 1-5--five stages of growth.
- Fig. 2. Urospora pulmonalis Bogolepova, nov. sp. A.-five cysts of gregarines in the connective-tissue layer of holothuria gills; B.-adult neogamic gregarina; C.-two spores.
- Fig. 3. Urospora intestinalis Bogolepova, nov. sp., four cysts of gregarines in intestinal wall of a holothurian. Cysts contents have contracted because of effects of reagents.
- Fig. 4. Lecudina pyriformis Bogolepova, nov. sp., adult gregarine.
- Fig. 5. Lecudina arrhuncha Bogolepova, nov. sp. A.-adult gregarine; B.-schematic layout of position of intranuclear bodies.
- Fig. 6. Lecudina euprosynes Bogolepova, nov. sp. Adult gregarine and nucleus of another individual to show position of intranuclear bodies.
- Fig. 7. Polyrhabdina cirratuli Bogolepova, nov. sp., adult gregarine.
- Fig. 8. Polyrhabdina nereicola Bogolepova, nov. sp., adult gregarine.
- Fig. 9. Cygnicollum attenuatum Bogolepova, nov. gen., nov. sp. A.-whole gregarine; B.-anterior part of gregarine with ripped-off portion of intestinal epithelium attached to its epimerite.
- Fig. 10. Cephaloidophora chthamalicola Bogolepova, nov. sp., adult gregarine.
- Fig. 11. Nematopsis dorippe Bogolepova, nov. sp. A, C. syzygies from 2 individuals. Fig. C shows thick folds of cuticle; B. syzygies from 3 individuals.

- Fig. 12. Nematopsis lamellaris Bogolepova, nov. sp., syzygies of 3 individuals.
- Fig. 13. Selenidium orientale Bogolepova, nov. sp., adult gregarine.
- Fig. 14. Selenidium curvicollum Bogolepova, nov. sp., A-young gregarine;
B-adult gregarine.
- Fig. 15. Selenidium flabelligerae Bogolepova, nov. sp. 1-7. stages of growth
of gregarines.
- Fig. 16. Siedleckia nematoides Caull. and Mesnil, young individual.