

Protozoa in biogeocenoses of some Seychelles Islands: soil shell amoebae (Testaceae)

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Abstract: Testacea were found to be an essential component of nanofauna in biogeocenoses of Seychelles. 94 species and subspecific taxa (10 families, 18 genera) were isolated from 40 samples (mainly soils and plant litter). Cosmopolitan eurybionts and stenobionts prevailed, 8 species were regarded as representatives of the tropical group. Testacean communities in atolls and high granite islands were found to be different.

Key words: Protozoa, fauna, population, abundance, distribution, ecological preferences, tropical species.

Introduction

There is an extensive literature dedicated to different animal groups in insular ecosystems, but unicellular soil inhabitants are given little, if any, attention. This is probably due to the fact that in the beginning of the XX century Protozoa were often considered as occasional and inactive in soil habitats. Furthermore, microscopic organisms are far more difficult to handle than larger metazoans, in their identification and isolation from such a dense and opaque medium as soil. Their great importance in soil biological economy is now in no doubt and is stressed by many authors (e. g., Bamforth, 1980; Foissner, 1987; Geltzer, 1993). Being an essential component of soil biota, Protozoa represent the base of heterotrophic eucaryotic food webs, consuming a significant portion (> 50%) of bacterial productivity, enhancing nutrient cycles and energy flows in soil ecosystems to the benefit of microorganisms, plants and animals (Foissner, 1999). Their high reproductive rate, short life and generation time ensure a notable biomass, comparable with that of earth-worms, and about 10% of total carbon input produced in respiration process (Sleigh, 1989).

In this paper I present the results of protozoological investigations, carried out in 1984 in the course of a multi-disciplinary expedition of the research vessel "Akademik Alexander Vinogradov" to the Seychelles Archipelago. The expedition was undertaken by the USSR Academy of Sciences as a contribution to the UNESCO "Man and Biosphere" Programme, project 7 - "Insular ecosystems and their rational use". According to the available literature, the object of our study - shell amoebae (Protozoa: Rhizopoda: Testacea) - had not been given special attention in Seychelles, except for occasional collections on Mahé island (Wailles, 1912). Other regional data include those obtained by Hennuy & Chardez (1988) for Mauritius, and by Decloitre (1956, 1959) for Madagascar.

Investigation of this rhizopod group, of interest in itself, provides more information on many protozoological and ecological problems than do other protozoans. Testacea build taxonomically useful hard shells, which remain intact in soil for a long time. So fauna, population and community structure can be appraised even when the cell itself is dead. The proportion of particular life forms (types of shell morphologies) in different habitats make it possible to observe visually the influence of different ecological situations on testacean complexes. Faunal and ecological investigation in Seychelles presents additional data on the geo-

graphical distribution of Testacea. Although mostly cosmopolitan, some testacean taxa are restricted to equatorial regions. The irregularity of, and the reason for this distribution of allochorous unicellular animals has attracted much attention and has been widely discussed over the last decades.

Testacean populations are considered in the present paper with special reference to faunal composition, species distribution in specific insular ecosystems, colonization of small islands and are discussed in terms of common patterns of protozoans and metazoans distribution.

Localities, materials and methods

Protozoological investigations were performed on 7 islands. According to their geomorphology and landscape, they belong to 3 groups - high mountainous granite and syenite islands (Silhouette, Félicité, Mahé, La Digue; the altitude up to 760 m asl, area up to 190 km²), low atolls of reef origin (Poivre, Farquhar; up to 5 m asl, 5-15 km²) and elevated atolls (Assumption, up to 32 m asl, 15 km²). Climatically the islands are subdivided into northern (Silhouette, Mahé, Félicité, La Digue, Poivre) and southern (Assumption, Farquhar) groups. The former characterized by equatorial marine climate with precipitation almost the year round, with a poorly defined short dry period; the latter situated in the tropical marine climatic zone with a 7-8 month dry period and strong aridization. Natural complexes of low atolls are simple and homogenous: strand forests of pantropical and ruderal plants (*Casuarina*, *Scaevola*, *Pemphis*) are usual on the beaches, with coconut palm plantations in the centre of the islands. The islands are flat, the relief is not differentiated and humus carbonate soils have short (some cm) accumulative profiles. Trade winds and intensive wave action form a specific substratum: banks of algae (Southern Poivre).

The relief of Assumption is a strongly karsted limestone surface. The soil formation in the coastal zone is at its initial stages (crusts of algae, "desert varnish"). In the marine terrace, soil is sandy humus carbonate with high pH, similar to that of low atolls. The xerophytization of plant communities (scrub) is related to the aridity of the island.

The mountainous relief of Silhouette results in local differentiation of the amount of precipitation. The level of moisture condensation is observed at about 600m altitude, being more than 1000 mm annually. Four vertical vegetation zones can be discerned. Moist tropical forests (*Dillenia*, *Ficus*) with abundant epiphytes and mosses, covering trunks still remain on almost inaccessible elevations (760m). The other high granite islands are covered with secondary tropical forests mainly with *Calophyllum* and *Cinnamomum*. Red-yellow soils of mountain tropical forests with varying humidity prevail, as well as soils of brown series.

The material was collected in the main habitats. The biotopes, recurrent in all the islands (such as litter under *Casuarina*, soil under palm plantations, etc.), as well as specific (algal crusts, "suspended soils") and optimal (moss epiphytic epibioses) for testaceans development were involved (Table 1). Samples were taken at 5 points of homogenous plots, averaged and treated according to the adopted technique (Korganova & Geltzer 1977). Triplicate stained smears were prepared and examined microscopically, the water suspension of the substrata were examined additionally to reveal rare and scanty forms. The depth of sampling in horizons A0 (plant litter), A1 (humus layer) or not differentiated A0A1 was up to 3-4cm. The number of testaceans (both living amoebae and empty shells) was recorded as individuals

Table 1. Sampling sites.

Island, number of samples	Sample number & substrate characteristic
Mahé, 4	1 - AOA1 under <i>Casuarina</i> , the Agricultural station, slope ca. 100 m altitude; 2 - cortical moss on <i>Terminalia</i> , same site; 3 - brown tropical soil, vicinity of the town of Victoria, secondary forest, <i>Cinnamomum</i> , slope, ca. 300-350 m; 4 - humus in dead trunks of trees, same site.
Poivre (north & south), 8	5 - cortical moss on a palm, plantation; 6 - substrate from leaf axils of palm, same site; 7 - AOA1 under <i>Casuarina</i> , beach; 8 - "algal" bank (pieces of <i>Thalassia</i>), same site; 9 - humus in the base of a dead palm, plantation; 10 - A1, humus carbonate soil, same site; 11 - fertilized soil, same site; 12 - phosphorized soil variant, same site.
Assumption, 7	13 - humus in water tank, coast; 14 - humus accumulation under rhizomes of <i>Caparis</i> , scrub; 15 - filamentous algae on walls of a karst sink; 16 - "crusts" (blue-greens, soft lichens) on limestone plates; 17 - algal bank, beach, AOA1 under <i>Casuarina</i> , coast; 18 - AOA1 under <i>Casuarina</i> , coast; 19 - A1, humus carbonate soil, plantation.
Farquhar (north & south), 6	20 - epigeal moss, coast; 21 - AOA1 under <i>Hernandia</i> , <i>Ficus</i> , the center of the island; 22 - A1, humus carbonate soil, plantation; 23 - fertilized soil, same site; 24 - A0 under <i>Casuarina</i> , coast; 25 - substrate from leaf axils of a palm, plantation; 26 - algal bank, beach.
Silhouette, 9	27 - humus strips at a temporary water course, the 1st plant belt; 28 - same site, on syenite blocs along rhizomes, the 2nd belt; 29 - decomposed wood, trunks of dead palms, same site; 30 - epilithic moss, same site; 31 - red-yellow soil under <i>Tabebuia</i> , <i>Leucaena</i> , same site; 32 - AOA1 under <i>Adenanthera</i> , the 3rd belt; 33 - substrate in leaf axils of <i>Lodoicea</i> , same site; 34 - AOA1 under <i>Dillertia</i> , <i>Calophyllum</i> , thick cortical moss with epiphytic ferns, orchids on <i>Ficus</i> (the combined sample of substrata in the 4th belt); 35 - humus stripes on syenite, coast exposed to storms.
Félicité, 1	36 - AOA1 under <i>Calophyllum</i> .
La Digue, 4	37 - AOA1, secondary forest, <i>Cinnamomum</i> , slope, ca. 100 m; 38 - humus under green moss, same site; 39 - cultivated soil, cabbage field, the Agricultural station; 40 - early-ripening compost, same site.

g^{-1} oven dried weight of the substratum, its field humidity being determined. The total mass of living cells was calculated by the formula: $P = k \times n \times d \times M$, where "k" - the mass of the cell, "n" - the number of protozoans g^{-1} oven dried weight of the substratum; "d" - the volume weight (the specific weight) and "M" - the volume of the substratum. The average mass of the one cell (23.3 \cdot 6 mg) was estimated as the mean between small (about 25-45 microns) and large (50-100) organisms (for details see Geltzer *et al.* 1980).

Results

A wide range of habitats (40 samples altogether) collected on islands of different size, origin and ecological status provided reliable data on testacean species diversity in soil and other natural habitats.

Fauna and population

94 species and subspecific testacean taxa (10 families, 18 genera) were found (Table 2). The most abundant was the Centropyxidae family (34 species, over 34% of the fauna), the Hyalospheniidae and Euglyphidae were also rather diverse - 17 and 12 species (18 and 12.5 %, respectively). Other families were monogeneric or included two genera, with few species. Rare Arcellidae (*Arcella*) shells lost their shape and clear species characters. Diffugiidae

(*Diffugia*) were represented by a sole specimen of *D. oblonga* and some small *Diffugia* sp. Identification of variable Centropyxidae (*Centropyxis aerophila*, *C. castis*) in some cases was not quite certain because of "leathery" appearances of shells in crusts of algae on the soil surface of Assumption, which lacked sand grains, usually used for shell building. The identification of *Cyclopyxis ambigua*, *C. trilobata*, *Trigonopyxis arcula*, *T. minuta* was also difficult due to great variation of test size and form of pseudostome.

The distribution of Testacea in island biotopes is fairly non-homogenous (Fig. 1): representatives of *Cyclopyxis* live almost everywhere (over 80% of samples), *Centropyxis* is very frequent, *Phryganella* and *Euglypha* occur in about 50% of samples; *Paraquadrula*, *Trigonopyxis* and *Tracheleuglypha* only in 15%. Most species were rare (found in 1-10% of samples) (Fig. 2, A). High frequency (30-80%) was observed only for 6 species, the most common being *Cyclopyxis eurytoma* and *Centropyxis aerophila*.

The distribution of samples according to the shell numbers is shown in Fig. 2, B. The majority of samples (80%) were found to have no more than hundreds or one-two thousand shells, and the high proportion (63%) of the species belongs to the group with rare occurrence.

The species diversity in samples varied from 1 to 48 forms; mostly moderate (20) or low (10), the maximum (35-48) occurring on Mahé and Silhouette (Table 3). Similarly, maximum abundance (about $25 \times 10^3 \text{ g}^{-1}$) was recorded on these same islands. In samples with low or moderate abundance (Assumption, Farquhar) the species were represented by eurybionts of standard aerophilous complex (*Centropyxis aerophila*, *Cyclopyxis eurytoma*, etc.) and some stenoionic forms; in samples with higher abundance (Silhouette) representatives of Hyalospheniidae reached up to 50% of the population. There was only one case of superdomination (*Phryganella paradoxa* in humus accumulation in the trunk of a dead tree on Mahé). The local development of this species was the reason for the extremely high number of shells in the sample (about $73 \times 10^3 \text{ g}^{-1}$), also dominating the living cells (over 80%) and making up a relatively high biomass (0.65 gm^{-2}), the highest value in all the biotopes studied. In other habitats the biomass was low, making up several dozen mg m^{-2} of substrate. The proportion of trophically active cells varied by 2-28% in the sample.

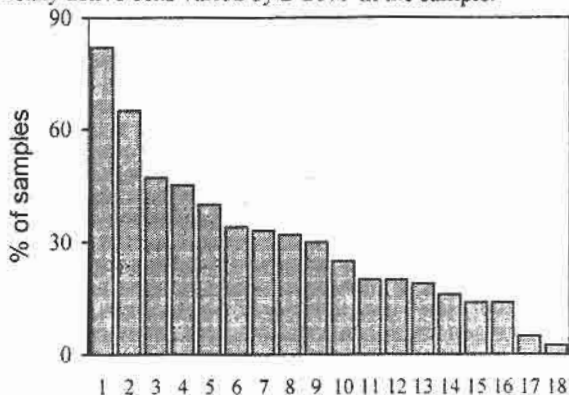


Fig. 1. Frequency of Testacea in surveyed habitats: 1 *Cyclopyxis*, 2 *Centropyxis*, 3 *Phryganella*, 4 *Euglypha*, 5 *Plagiopyxis*, 6 *Heleopera*, 7 *Trinema*, 8 *Pseudawerintzewia*, 9 *Bullinularia*, 10 *Arcella*, 11 *Nebela*, 12 *Hyalosphenia*, 13 *Quadrulella*, 14 *Trigonopyxis*, 15 *Tracheleuglypha*, 16 *Paraquadrula*, 17 *Diffugia*, 18 *Euglyphella*.

Shell amoebae, found on the islands, are mostly (more than 85% of the species) widely distributed, common forms. They are supplemented by some species with a limited range in Southern hemisphere ("Gondwana", "southern" or "tropical" forms - according to Bonnet, 1977). There are 8 such forms in our material:

1. *Centropyxis latideflandriana* - Silhouette: substrate in leaf axils of *Lodoicea*, primary tropical forest, 400-500 m asl; AOA1 under *Dilleneia*, *Calophyllum*, thick cortical moss layer with epiphytes on *Ficus*, primary tropical forest, more than 700 m asl; frequency 5% of the total number of the samples.
2. *C. stenodeflandriana* - Silhouette: as (1); Mahé: vicinity of the town of Victoria, brown tropical soil under secondary forest with *Cinnamomum*, 300-350 m asl; Félicité: AOA1, secondary forest, under *Calophyllum*; 10%.
3. *Cyclopyxis dulcis* - Silhouette: as (1, 2); Mahé: as (2); Félicité: as (2); La Digue: humus under green moss, secondary forest with *Cinnamomum*, about 100 m asl; 12,5%.
4. *C. intermedia* - Silhouette: AOA1 under *Adenanthera*, primary tropical forest, 400-500 m asl; substrate in leaf axils of *Lodoicea*, the same site; Mahé: as (2, 3); La Digue: AOA1, secondary forest with *Cinnamomum*, about 100 m asl; 10%.
5. *C. lithostoma* - Silhouette: substrate in leaf axils of *Lodoicea*, the same site as (1, 4); Mahé: local humus accumulation in dead trunks of trees, the same site as (2); 5%.
6. *C. stephanostoma* - Silhouette: as (4); Mahé: as (2, 3, 4); 5%.
7. *Quadrulella tropica* - Silhouette: as (1, 2, 3); Mahé: as (2, 3, 4, 6); La Digue: as (4); 10%.
8. *Pseudawerintzewia deharvengi* - Mahé: as (2, 3, 4, 6, 7); Félicité: as (2, 3); Poivre: palm plantation, humus carbonate soil; the same - fertilized variant; Assumption: local humus accumulation under rhizomes of *Caparis*, scrub; palm plantation, humus carbonate soil; Farquhar: AOA1 under *Hernandia*, *Ficus*, the centre of the island; 20%.

The species, as is shown by their frequency (mostly 5-10% of the total number of the samples), occur irregularly and sparsely, excluding *P. deharvengi* more common on atolls.

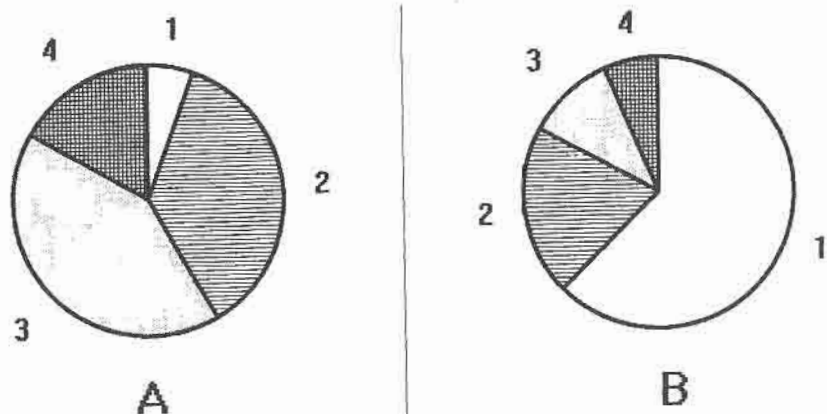


Fig. 2. Occurrence (A) and number (B) of Testacea in samples: 1 - proportion of species found in 1-10% of the samples (for A); proportion, %, of samples with tens shells g⁻¹ (for B); 2 - in 11-20% and with 100s of shells, accordingly; 3 - in 21-30% and with 1000s of shells; 4 - < 30% of the samples and with 10,000s of shells.

Table 2. Distribution of Testacea in biotopes of investigated islands.

Family, species	Sample number	Frequency *
Arcellinidae		
<i>Arcella arenaria</i> Greeff	16	2.5
<i>A. catinus</i> Pen.	10,14,19,21,36,37,39	17.5
<i>A. rotundata</i> var. <i>aplanata</i> Defl.	14	2.5
<i>Arcella</i> sp.	1,14,21,27,37	12.5
Centropxyidae		
<i>Centropyxis aculeata</i> (Ehrbg.) Stein	1,10,27,32,33	12.5
<i>C. aculeata</i> var. <i>minuta</i> Van Oye	35	2.5
<i>C. aerophila</i> Defl.	1-5,10,14,16,18,19,21,23,27,28,30-34,36-38	55.0
<i>C. aerophila</i> var. <i>grandis</i> Step.	3	2.5
<i>C. aerophila</i> var. <i>minuta</i> Chardez	21	2.5
<i>C. aerophila</i> var. <i>sphagnicola</i>	27	2.5
<i>C. cassis</i> (Wallich) Defl.	1-3,14,27,28,30,36,37,39	32.5
<i>C. constricta</i> (Ehrbg.) Pen.	3,4,27,34	10.0
<i>C. discoides</i> (Pen.) Defl.	27,31	5.0
<i>C. ecomis</i> Leidy	14,21,31,33	10.0
<i>C. ecomis</i> var. <i>minuta</i> Golem.	11	2.5
<i>C. elongata</i> (Pen.) Thomas	3,5,10,14,27,30,35,37,38,39	25.0
<i>C. laevigata</i> Pen.	19,21,34	7.5
<i>C. llatideflandriana</i> Bonnet	33,34	5.0
<i>C. minuta</i> Defl.	4,32-34,37-39	17.5
<i>C. orbicularis</i> Defl.	37	2.5
<i>C. plagiostoma</i> Bonnet & Thomas	3,4,14,21,37	12.5
<i>C. plagiostoma</i> var. <i>terricola</i> Bonnet & Thomas	18,19,24,31,33,37,38	20.0
<i>C. platistoma</i> (Pen.) Defl.	2	2.5
<i>C. spinosa</i> Cash	31	2.5
<i>C. stenodeflandriana</i> Bonnet	3,33,34,36	10.0
<i>C. sylvatica</i> (Defl.) Thomas	21	2.5
<i>Cyclopyxis ambigua</i> Bonnet & Thomas	3,4,29,32-34,37-39	22.5
<i>C. arboricola</i> Chardez	4,33	5.0
<i>C. dulcis</i> Couteaux-Munsch	3,33,34,36,38	12.5
<i>C. eurtstoma</i> Defl.	1-7,9-12,14-16,19-23,27,29-39	80.0
<i>C. eurtstoma</i> var. <i>gauthieriana</i> Bonnet & Thomas	3,29,33,37,38	12.5
<i>C. eurtstoma</i> var. <i>parvula</i> Bonnet & Thomas	16	2.5
<i>C. intermedia</i> Kufferath	3,32,33,37	10.0
<i>C. kahli</i> Defl.	3,20,32,35,39	12.5
<i>C. kahli</i> var. <i>cyclostoma</i> Bonnet & Thomas	3,10-12,14,19,20,28,31,37,39,40	30.0
<i>C. lithostoma</i> Bonnet	4,33	5.0
<i>C. stephanostoma</i> Bonnet	3,32	5.0
<i>C. trilobata</i> Bartos	29,37,38	7.5
Trigonopyxidae		
<i>Trigonopyxis arcula</i> (Leidy) Pen.	4,33	5.0
<i>T. minuta</i> Schonb.	4,33	5.0
Plagiopyxidae		
<i>Plagiopyxis callida</i> var. <i>grandis</i> Thomas	3	2.5
<i>P. declivis</i> Thomas	3,36,37,39	10
<i>P. declivis</i> var. <i>oblonga</i> Bonnet & Thomas	36	2.5
<i>P. intermedia</i> Bonnet	2,3,10,11,22,27,28,30,36-39	40.0
<i>P. minuta</i> Bonnet	3,21,36	7.5
<i>P. penardi</i> Thomas	2,3,30,36	10.0
<i>P. penardi</i> var. <i>oblonga</i> Bonnet	27	2.5
<i>Bullinularia gracilis</i> Thomas	5,9,10,14,16,21,24,28,35	30.0

Family, species	Sample number	Frequency *
<i>B. indica</i> Pen.	16	2.5
Diffugiidae-		
<i>Diffugia oblonga</i> Ehrbg.	27	2.5
<i>Diffugia</i> sp	14	2.5
Hyalospheniidae		
<i>Nebela collaris</i> (Ehrbg.) Leidy	27,30,37,39	12.5
<i>N. lageniformis</i> Pen.	3,30,33,34	10.0
<i>N. militaris</i> Pen.	38	2.5
<i>N. minor</i> Pen.	3,34,37	7.5
<i>N. penardiana</i> Deffl.	3	2.5
<i>N. penardiana</i> var. <i>minor</i> Deffl.	3,34,38	7.5
<i>Quadrullella elegans</i> Gauth.-Liev.	34	2.5
<i>Q. symmetrica</i> Wallich	27,28,33,34,37,39	15.0
<i>Q. symmetrica</i> var. <i>longicollis</i> Taranek	3,14,34,37	10.0
<i>Q. tropica</i> Wailes	3,33,34,37	10.0
<i>Hyalosphenia insecta</i> Harnisch	14,35	5.0
<i>H. minuta</i> Cash	3,29,34,38	10.0
<i>H. subflava</i> Cash	3,29,31,32,38	12.5
<i>H. undans</i> Couteaux	33,34,37	7.5
<i>Heleopera petricola</i> var. <i>amethistea</i> Pen.	36	2.5
<i>H. petricola</i> var. <i>humicola</i> Bonnet & Thomas	14	2.5
<i>H. sylvatica</i> Pen.	1,20,21,26,27,31,33,36,39	22.5
Paraquadrulidae		
<i>Paraquadrula globulosa</i> Pen.	26,33	5.0
<i>P. irregularis</i> (Arch.) Deffl.	14,15,21,26,31	15.0
Phryganellidae		
<i>Phryganella acropodia</i> (Hertw. & Less.) Hopk.	3,5,7,10,14,16,19-21,23,31-34,36-38	42.5
<i>Ph. paradoxa</i> Pen.	3,4,16,29	10.0
Euglyphidae		
<i>Euglypha ciliata</i> (Ehrbg.) Leidy	27,30,31,33,36,37	15.0
<i>E. ciliata</i> fma. <i>glabra</i> Wailes	3,31-34,39	15.0
<i>E. cristata</i> Leidy	3,30,34,37	10.0
<i>E. cristata</i> fma. <i>decora</i> Jung	3,27,33,34	10.0
<i>E. laevis</i> Perty	1,3,19,30,31,33,34,36,38	22.5
<i>E. rotunda</i> Wailes	36,37	5.0
<i>E. strigosa</i> (Ehrbg.) Leidy	4,5,33	7.5
<i>E. simplex</i> Decl.	1,3,14,31,37	12.5
<i>Euglypha</i> spp.	3,9,27,30,31,33,34,36-40	30.0
<i>Euglyphella delicatula</i> Schonb.	3	2.5
<i>Tracheleuglypha acolla</i> Bonnet & Thomas	1,2,21,27,33,34,37	17.5
<i>T. acolla</i> var. <i>aspera</i> Bonnet & Thomas	33	2.5
Trinematiidae		
<i>Trinema complanatum</i> Pen.	3,31,33,34,37,38	15.0
<i>T. complanatum</i> var. <i>aerophila</i> Bonnet & Thomas	27,34	5.0
<i>T. complanatum</i> fma. <i>elongata</i> Chardez	3	2.0
<i>T. complanatum</i> var. <i>globulosa</i> Chardez	30,32	5.0
<i>T. enchelys</i> (Ehrbg.) Leidy	1,2,3,27,30,31-34,36-38	30.0
<i>T. lineare</i> Pen.	3,20,21,29-31,33,34,36,37	25.0
<i>T. lineare</i> var. <i>minuscule</i> Chardez	3,34	5.0
<i>T. penardi</i> Thomas & Chardez	3,34	5.0
<i>Pseudawerintzemia calcicola</i> Bonnet **	7,11,12,14,19,21,22,34-36	27.0
<i>P. deharvengi</i> Bonnet **	3,7,11,12,14,19,21,36	20.0

* % of the number of samples; ** species of uncertain taxonomic position.

Table 3. Main characteristics of communities of the Testacea.

Island	Sample number	Shell abundance *	Number of species	% trophically-active celles	Biomass (gm ⁻²)
Mahé (56 species)	1	2.54	10	-	-
	2	7.22	6	11.6	0.005
	3	5.07	48	4.9	0.030
	4	72.90	10	7.6	0.65
Poivre (15)	5	18.60	5	2.2	0.025
	6	0.17	1	-	-
	7**	0.17	3	-	-
	9	1.10	3	-	-
	10	0.61	10	-	-
	11	1.90	7	-	-
	12	0.32	5	-	-
Assumption (28)	14	0.73	20	-	-
	15	0.05	2	-	-
	16	2.20	9	12.6	0.015
	18	0.20	3	-	-
	19	0.60	11	-	-
Farquhar (23)	20	2.20	4	28.5	0.035
	21	0.94	18	7.5	0.005
	22	0.29	3	-	-
	23	1.20	4	-	-
	24	0.07	2	-	-
	26	0.20	3	-	-
Silhouette (68)	27	24.40	21	1.2	0.035
	28	0.41	6	-	-
	29	1.80	9	8.0	0.010
	30	15.15	16	7.2	0.065
	31	2.04	18	9.7	0.015
	32	3.22	18	20.0	0.050
	33	13.00	30	9.1	0.070
	34	7.28	35	4.7	0.030
	35	0.36	7	-	-
	36	2.26	22	9.8	0.020
Félicité (22)	37	8.37	30	3.3	0.020
	38	1.0	16	25.0	0.060
	39	17.9	21	2.7	0.005
	40	0.81	3	-	-

* x 10³ g⁻¹ over dried substrate; ** .n samples 8, 13, 17, 25 no testaceans were found.

Spatial distribution

Different patterns of testacean chorology were observed in low biogenic and high granite islands.

Islands of reef origin. More than 50 species were found altogether in all atoll biogeocenoses. Table 4 lists the species recorded in the most common and characteristic habitats in the atolls - palm plantation soils and beaches. The testacean population was characterized by calciphilous species *Bullinularia gracilis*, *Pseudawerintzewingia calcicola*, *Paraquadrula irregularis*, some *Heleopera*, *Hyalosphenia*, being supplemented with few eurybionts of aerophilous complex, such as *Centropyxis aerophila*. Even algal banks, moved by wave action and mixed with coral sand (Farquhar, sample 26) contained 2-3 species

(*Heleopera sylvatica*, *Paraquadrula irregularis*, *P. globulosa*).

Despite the extreme aridity, the species assembly on Assumption was much the same due to substrate similarity; sometimes one more calciphilous species - *Hyalosphenia insecta* - was recorded. Filosea, even such common forms as *Euglypha laevis* and *Trinema lineare*, were rather rare.

The species diversity in biogeocenoses of biogenous islands was limited to 10 forms, rarely up to 20, their abundance was usually low (a few hundred — 1-2 ths of shells g⁻¹). The trophically active organisms were found in a few soil samples (Table 3).¹ At the same time they accounted for over 12% in crusts of algae (sample 16) on the soil surface of Assumption (surprising for this very dry and extremely lifeless substratum), and about 28% in Farquhar (sample 20). In atolls living cells were recorded in populations of *Arcella arenaria*, *Centropyxis aerophila*, *Cyclopyxis eurytoma*, *C. kahli*, *Heleopera sylvatica*, *Quadrullella symmetrica*, *Paraquadrula irregularis* and *Euglypha laevis*.

In young palm plantations, along with natural humus carbonate soil, its cultivated (fertilized) variant was examined (e.g., sample 11 in Poivre). The layers of palm leaves and

Table 4. Some characteristic testacean groups in the substrata of tropical islands.

Species	Pacific Ocean	Indian Ocean
Islands of reef origin, calciphilous group		
<i>Bullinularia gracilis</i>	+	+
<i>Centropyxis laevigata</i>	+	+
<i>C. plagiostoma</i> *	+	+
<i>Plagiopyxis intermedia</i>	+	+
<i>Pseudawerintzewia calcicola</i>	+	+
<i>P. deharvengi</i>	+	+
<i>Heleopera petricola</i> *	+	+
<i>H. sylvatica</i>	+	+
<i>Hyalosphenia insecta</i>	-	+
<i>Paraquadrula globulosa</i>	+	+
<i>P. irregularis</i>	+	+
<i>Lamtopyxis trifoliata</i> **	+	-
Granite and volcanic islands, tropical forms		
<i>Centropyxis latideflandriana</i>	+	+
<i>C. stenodeflandriana</i>	+	+
<i>Cyclopyxis intermedia</i>	+	+
<i>C. dulcis</i>	-	+
<i>C. lithostoma</i>	-	+
<i>C. stephanostoma</i>	-	+
<i>Hoogenradia humicola</i>	+	-
<i>Apolimia rotundistoma</i>	+	+
<i>Quadrullella tropica</i>	-	+
Forms characteristic for mor and moder humus types		
<i>Cyclopyxis ambigua</i>	+	+
<i>Trigonopyxis arcuata</i>	+	+

* Species include, respectively, *C. plagiostoma* var. *terricola* and *Heleopera petricola* var. *amethystea*, *H. petricola* var. *humicola*. ** Species belongs to the tropical forms.

1. Actually some trophically active cells occurred in water suspension and in other samples from atoll (14, 15, 19, 20).

but due to their low number their proportion was not estimated. Coconut waste in different stages of decomposition, arranged around the perimeter of the crown, served as fertilizer. The testacean communities did not differ significantly from natural variant and contained up to 10 species, whereas their abundance was three times as high as that of unfertilized soil (about $2 \times 10^3 \text{ g}^{-1}$).

Granite islands. In primary and secondary forests of larger mountainous granite and syenite islands the species diversity and abundance of protozoans were higher (Tables 2, 3). Mahé was noted for humified brown tropical soil in fissures of granite blocks (secondary forest with *Cinnamomum*), where testacean communities were most diverse, containing almost 50 species. Along with eurybionts, there were ecological groups of bryophils (*Nebela*), pedobionts (*Plagiopyxis*), etc., as well as all the tropical species recorded in the present study. In the same site (sample 4) the maximum numbers of $73 \times 10^3 \text{ g}^{-1}$ was recorded, due to the intensive development of *Phryganella paradoxa*.

On Silhouette and La Digue the communities were diverse (30-35 species) and abundant (about $25 \times 10^3 \text{ g}^{-1}$) in litter, substrate in leaf axils of *Lodoicea*, humid moss epiphytic growths on trees in primary and secondary wet tropical forests. The communities consisted of eurybionts, representatives of the tropical group, as well as small filose *Euglypha* and *Trinema* species (e.g., in sample 31 over 50% of the total number), which were rather scarce or entirely absent in atoll biotopes.

The species composition of living shells in forest soils, litter and other substrata of granite islands was much richer: in addition to those, listed for atolls, they were found in populations of *Centropyxis aerophila* var. *sphagnicola*, *C. cassis*, *C. constricta*, *C. plagiostoma* var. *terricola*, *Cyclopyxis ambigua*, *C. duclis*, *C. eurystoma* var. *gauthieriana*, *C. stephanostoma*, *Plagiopyxis declivis*, *P. declivis* var. *oblonga*, *P. intermedia*, *Phryganella paradoxa*, *Nebela collaris*, *N. lageniformis*, *Hyalosphenia minuta*, *H. subflava*, some *Euglypha* and *Trinema* species. The fact shows more active life status of these populations in high islands habitats.

On La Digue island, apart from the forest soil, some samples were taken in an Agricultural station. In compost heaps only a few eurybionts occurred (*Cyclopyxis eurystoma*, *Euglypha* spp.), while in soils of a cabbage field there were 16 species. This was a set of widely distributed forms without clear dominants, including *Trigonopyxis arcua*, *Cyclopyxis ambigua*, typical of coarsely humified substrates (mor - moder type humus).

Discussion

Data on protozoans in Seychelles and other islands, adjacent to the continent of Africa, are very scarce. Decloitre (1956, 1959) was the first to publish a list of 50 testacean species inhabiting water bodies, mosses and lichens of Madagascar (up to 2400m altitude), comparing it with equatorial Africa and Seychelles. In particular, the absence in Seychelles of some common species was noted, the fact resulting, in my opinion, from inadequate and irregular studies, rather than from actual faunistic differences: some such species (widely distributed *Centropyxis aerophila*, *Cyclopyxis eurystoma*, *Heleopera petricola*, etc.) were found in the present samples.

In compost (Mauritius) 12 species and varieties of Testacea were found by Hennuy & Chardez (1988). Such media were considered by the authors as favourable habitats for Testacea, the fact was stressed as especially important for tropical and subtropical regions, where com-

post often develops naturally. Rapidly ripening compost, investigated in the present study in La Digue (coconut waste, manure), contained only 3 species. This can probably be related to differences in composition and ripeness.

Having analyzed samples of moss and bottom sediment of ponds in Mahé (Seychelles), Wailes (1912) recorded over 40 testacean species. Most belonged to *Nebela* and *Euglypha*, thereby pointing to the prevalence of bryobionts and hydrobionts. Some new forms were described, of them *Quadrutella tropica* was revealed in our material.

I have found 23 of the species recorded by Wailes (1912). As there were no permanent water courses in the areas studied, our collections contained practically no hydrobionts (*Diffugia* and *Arcella* were very rare). On the other hand, no Testacea, inhabiting low coral islands, were found in the list composed by Wailes. The main feature of atoll ecosystems is coral sand and hence the abundance of substrata with excess free calcium. The group of species I recorded in atolls, according to Bonnet's (1959) classification (who used phytosociological principles), were typical of the association *Bullinularion gracilis*, *Pseudawerintzetum calcicolae*, *Paraquadruletum-Hyalosphenietum insectae*, developing in biotopes with pH above 7, and having a great indicative value. Their pantropical distribution in the substrata of the same type was confirmed by our investigations of Pacific Ocean atolls (Korganova 1985b) (Table 4). Representatives of the tropical group were not found in atolls (excluding calcephilous species *Pseudawerintzetia deharvengi*), presumably due to the fact that in secondary forests on atolls plant litter is dry, not developed and often practically absent.

The list by Wailes (1912) indicated the species with limited range only among *Nebela*. In our collection some of *Nebela* were absent (e.g., *Nebela scutellata* Wailes), but generally the "southern" forms in our material were more diverse, both in species and genera. The number of such forms was always low, but due to their large size (*Cyclopyxis dulcis* about 200 microns) their share in biomass is rather high.

The question of the specificity in testacean geographical distribution, firstly noted by Penard (1910; cited after Hoogenraad & De Groot 1979), has been widely discussed. As a result of intensification of protozoological investigations in the Southern hemisphere the group of some dozens species with a limited tropical range was distinguished in the last decades. The fact, that there are some protozoans, confined to particular large regions, is also proved for some infusorian species, occurring only in Australia (Houseman 1988) (cf. testaceans-"australobionts", according to Jung, 1942). Some "Gondwanan" testacean families are considered as a separate line of evolution, developed as a result of continental drift (e.g., Jung 1942; Decloitre 1973; Hoogenraad & De Groot 1979; Bonnet 1979).

The other, ecological explanation of limited "southern" species range is the assumption that their expansion into northern regions is prevented by natural geographical barriers (the direction of water streams and winds, deficit of optimal media) (Chardez, 1967). It is possible moreover, that such forms are difficult to find due to their rarity in northern biotopes and their position in communities as *L*-selected ("drowsy") species, presented in minimal number (Whittaker 1980; Korganova 1985a). I agree with the ecological explanation and consider, that the extension of zoogeographical investigations, primarily with respect to territory, can give new information concerning testacean distribution. Indeed, there have been some interesting and surprising finds of southern taxa in the Northern hemisphere made re-

cently (Bonnet & Gomez-Sanchez 1984; Wanner 1991; Zakhidov 1991; Bobrov 2000). Bonnet & Gomez-Sanchez explained the facts by ancient contacts of the Iberian peninsula with south end of North America and with Central America, as well as the existence of common floristic elements and some forest refugia in Europe. It is clear, that the question of testacean world distribution is far from its final solution.

A considerable number of our samples (22 of 40) were collected on coral islands. If we follow Jung (1942) in considering the samples as optimal (1-4, 27-34, 36-40) and unfavourable, extreme and even aggressive media for protozoans (5-26, 35) (even though the separation is not strict) it is the samples from atolls which belong to the latter. The soils in such small flat pieces of land are unstable habitats readily affected by climatic fluctuations, in particular by intensive drying. For instance, the annual dryness index (the ratio of evaporation to precipitation) on Assumption is as high as 2.0, as against 0.95 in coastal parts of Silhouette and even 0.77 on its summit. Nevertheless, in atolls we found a moderate species diversity in a distinct calciphilous complex (Bonnet 1973; Korganova 1985b) which characterised the atoll's testacean population. It is composed chiefly of stenobionts-calciphiles, with the addition of some species tolerant of high salinity and some eurybionts. According to our observations, the latter were *Quadrullella symmetrica*, *Heleopera sylvatica* and *Paraquadrula irregularis* and *P. globulosa* (the only species, found in soil from a cliff, with 100% of cells being trophically active; see Korganova 1985b). Being found in algal banks in Farquhar, they demonstrated the highest resistance to wave action and, in Assumption substrata, to high dryness: the living cells were recorded even in such dry samples as crusts of algae. Other species were found as single specimens.

Extreme habitats like carbonaceous soils can be compared with arid soils in steppe plots of Mongolia (Korganova 1990) where conditions of over-dryness (field humidity as low as 3%) and mobility of upper horizons (eolian mounds) approach the survival limit for trophically active protozoans. Only 1-2 *Euglypha* and *Trinema* species in extremely low number (tens individuals g⁻¹) were found; unlike to atolls, there were no calciphilous species in Mongolian steppe soils.

The species recorded on atolls were mostly rather small, common forms with simple test morphology, lacking any special adaptations to soil conditions. However, in contrast to Jung (1942), who defines testacean communities in extreme habitats as being not ecologically specific, in our material they are highly specific, having at least seven stenoionic characteristic species (even more than in optimal habitats; Table 5) restricted to biotopes with high pH. This calciphilous association, typical of atolls, belong to Lobosea, Filosea being at a minimum, therefore the ratio of Filosea/Lobosea is lower than in optimal habitats and the average value for the entire material (21.2%).

Analyzing ecological features of representatives of the genus *Plagiopyxis*, Bonnet (1988) outlines stable habitats populated by *K*-selected species and non-stable ("aggressive") habitats rich in *r*-selected forms. To the latter this author attributes *P. intermedia* - a common soil species, preferring the xerophilous media with higher CaCO₃ content; the fauna accompanying it is poor in Filosa. The characteristic is true of the situation in low atolls of Seychelles, where *P. intermedia* is not abundant, but permanent in associations of humic carbonate soils (Table 4), *Euglypha* and *Trinema* being rare and low in numbers. Luftenegger et al. (1985) defined some infusorian species (Colpodea) as *r*-selected, the fact might explain their

wide distribution in unfavourable terrestrial habitats.

There were no *Nebela* species, a typical element of the bryophilous complex, in aeral mosses from atolls. *Nebela* species avoid media with pH higher than 7, their absence is related to the fact that all the habitats in atolls (even mosses) are influenced by coral sand, and the soil pH is about 8 (Trudgill, 1979). At the same time, in epilithic mosses on the granite island of Silhouette *Nebela* species, including living cells, make up a considerable portion of the numbers - over 30% in sample 30.

Species diversity, the main faunistic quantitative and structural parameters of communities, in optimal habitats of granite islands (especially in mountainous forests) are considerably higher than those of extreme habitats (e.g., the average number of shells is higher by an order of magnitude; Table 5). The much wider range of habitats in moist tropical forests gives the opportunity for colonization by many different testacean ecological groups, as well as by tropical species, for which such forests represent typical habitats (Bonnet, 1977a).

Protozoan colonization of small islands, remote from large land masses, faunal composition and chorology on islands of different size and origin have been discussed in detail for Pacific islands (Korganova, 1985a, b, c). It is interesting to compare these investigations with the results of the present study. The main ecological features of tropical islands of reef origin (excess free calcium) and granite or volcanic ones (large areas of primary or secondary forests with humified light soils and specific "tropical" substrata) are to a great extent similar in both regions. Accordingly, there is a certain similarity of faunal structure of Pacific and Indian Ocean islands: most of the fauna consists of representatives of Centropyxidae, Hyalospheniidae and Euglyphidae families (about 90%). They comprise a complex of widely distributed forms, supplemented in the islands of both oceans by some tropical forms. 11 tropical species were found altogether. Practically all were in mountainous forests (soil, litter and mosses) in granite (Seychelles, Indian Ocean) and volcanic (Tonga and Western Samoa, in the Pacific Ocean), but their combinations were different. Representatives of calciphilous complex, being stenobionts, showed pantropical distribution. One more complex, which can be distinguished in the material, collected on all the islands, included *Cyclopyxis ambigua* and *Trigonoipyxis arcuata*, inhabiting "suspended soils" and substratum under epiphytes (i.e. mor - moder type humus). Thus, the characteristic testacean complexes (disregarding eurybionts) were quite different in three habitats types, but had great similarity in pantropical biotopes (Table 4).

Table 5. Parameters of Testacea community structure in extreme and optimal habitats.

Parameters	Extremal habitats	Optimal habitats
Total number of species in group	37	84
Range in number of species in communities	1-20	6-48
Average abundance in group, $\times 10^3$ g ⁻¹ oven dried substratum	1.7	11.0
Number of genera	13	15
Generic number *	2.8	5.6
Percentage of large species, % **	2.7	6.0
Number of communities with more than one "southern" form	0	5
Number of communities with more than one stenoionic form	7	5
Filosea species, %	10.7	23.8

* The number of species divided by the number of genera. ** Small - about 50, large - about 100 microns.

We characterized protozoan fauna on Pacific islands as, to a certain extent, impoverished in comparison with the continental one - the source of species distribution. Not only some species, but also families (such as Arcellidae and Diffugiidae, widely distributed in Europe) were shown to be virtually absent. The absence of these families is noted in the present study as well. Furthermore, Euglyphidae are poor in genera (there are no *Assulina* and *Corythion*, which are especially abundant in coniferous forests of Eurasia; pers. obs.). Such "defectiveness" is a peculiar characteristic of the macrofauna of remote islands and in biogeographical studies is traditionally explained by difficulties of colonization due to isolation and lack of space. For microscopic and easily dispersed Testacea we consider as highly important not such "external" factors, but the "internal" factors - the scarcity or lack of optimal biotopes², in particular of permanent water bodies (main habitats of *Arcella* and *Diffugia*). Tropical moist primary forests with their great habitat variety present stable media with high and stable humidity (up to 500% in high moss hummocks on volcano craters; Korganova 1985b), favourable for development of all testacean ecological groups (bryobionts, geobionts, litter inhabiting forms, hydrophiles, etc.) and are densely populated by protozoans.

Conclusion

Testacean (Protozoa) populations have been studied in different substrata (soil, plant litter, mosses, suspended soils, local humus accumulations and algal banks) in low (Farquhar, Poivre) and elevated (Assumption) atolls and granite islands (Silhouette, Félicité, Mahé and La Digue) of the Seychelles Archipelago. 94 species and intraspecific taxa were recorded, biomass reaching 0.65 gm⁻². The presented list more than doubles the number of testacean species, known for Seychelles. The main part of the fauna consists of ubiquitous species of various ecological groups, supplemented by tropical forms. The diverse species composition and high numbers were observed in the substrata of primary and secondary tropical mountain forests in granite islands, having stable humidity and high humus content. The species composition in islands of reef origin is not rich, and is uniform, irrespective of the location of the island, being determined by the prevailing habitats with excess free calcium. A certain "defectiveness" of the fauna (poor representation of Arcellidae and Diffugiidae) as compared with the mainland are explained by the absence of favourable habitats. Spatial distribution of allochorous unicellular shell amoebae in insular biogeocenoses demonstrated an uneven dessemination, dependant upon the substrata, optimal for the definable protozoan ecological groups (Korganova 1999) and is similar to testacean communities in the Pacific Ocean.

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² Occasional distribution patterns can also be observed, e.g. colonization of a limited substrate by a species (here a dense population of *Phryganella paradoxa* in a dead trunk, in nearby forest soil only single specimens found).

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