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Soil Testate Amoebae (Amoebozoa, Rhizaria) of a Tropical Rainforest in Madagascar

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Abstract: The testate amoebae communities in soil of the tropical rainforest from the Maromizaha Protected Area in Madagascar were investigated. A total of 2848 individuals of 51 taxa (43 species and 8 intraspecific taxa) belonging to 19 genera of testate amoebae were found. *Phryganella acropodia* (224 ind., 7.9%), *Plagiopyxis minuta* (223, 7.8%), *Plagiopyxis declivis* (218, 7.7%), *Cyclopyxis eurystoma* (217, 7.6%), *Centropyxis stenodeflandriana* (211, 7.4%), *Plagiopyxis bathystoma* (184, 6.5%) and *Trinema lineare* (178, 6.2%) were the most frequently occurring species with the highest relative abundance. The genera *Centropyxis* (10 taxa), *Plagiopyxis* (6), *Trinema* (5), *Cyclopyxis* (5) and *Euglypha* (5) were most diverse. The majority of the recorded species belonged to the group of soil- or litter- inhabiting testate amoebae with cosmopolitan distribution. Some rare species with restricted geographical distribution of the Gondwanan Tropical group have also been found (*e.g*. *Apodera vas*, *Centropyxis stenodeflandriana*, *Lamtopyxis callistoma*, *Plagiopyxis bathystoma* and *Planhoogenraadia media*). The analysis of the distribution of the genus *Lamtopyxis* demonstrates that, similarly to *Apodera vas*, the species of this genus may also be used as an example that 'not everything is everywhere' in free-living microbial eukaryotes.

Keywords: Amoebozoa, Rhizaria, soil testate amoebae, biogeography, Madagascar

Introduction

Since the middle of the 20th century, many African countries have been subject to intensive research regarding their testate amoebae fauna. In this respect, among the better studied were some of the former French and Belgian colonies where high species richness was recorded: Ivory Coast (332 taxa), DR Congo (308 taxa), French Equatorial Africa (Congo-Brazzaville, Gabon, Chad, Ubangi-Shari and French Cameroon – more than 300 taxa), Guinea (161) and Maroco (130) (Van Oye 1926, 1948, 1958, 1959, Kufferath 1932, Decloître 1948, 1949, 1956a, 1958, 1961, 1962, 1965, Gauthier-Lièvre 1953, 1957, Gauthier-Lièvre, Thomas 1958, Thomas, Gauthier-Lièvre 1959a, 1959b, Golemansky 1962a, 1962b, 1963, Stepanek 1963, Chardez 1964). Almost all studies have been related mainly to the freshwater and bryophilic testate amoebae. A few articles on soil testate amoebae were also published: for Algeria (Bonnet 1960a), Angola (Bonnet 1960b, 1969a), Gabon (Bonnet 1966), Congo-Brazzaville (Bonnet 1967), Intertropical Africa (Bonnet 1969b), Ivory Coast (Bonnet 1974, 1975, 1976, 1978), but generally the soil testacean fauna of the continent has been considerably less studied.

Madagascar is one of the countries with poorly studied testacean fauna and scarce published data related to bryophilic and freshwater testate amoebae (Voeltzkow 1891, Decloître 1956b, 1959). The island is part of the African platform and was formed as a result of the prehistoric break-up of the supercontinent Gondwana, which separated the Madagascar-Antarctica-India landmass from the Africa-South America landmass around 135 million years ago. Later, about 88 million years ago, Madagascar split from the Indian subcontinent, which allowed existence of the plants and animals on the island in a

Table 1. List of testate amoebae found in the studied soils of tropical rainforests from Maromizaha Protected Area, Madagascar

Taxa	Number of individuals	Relative abundance (%)
Apodera vas Certes 1889	7	0.24
Arcella arenaria Greeff, 1866	3	0.10
Argynnia dentistoma Penard, 1890	5	0.18
Awerintzewia cyclostoma (Penard, 1902) Schouteden, 1906	24	0.84
Centropyxis aculeata (Ehrenberg, 1838) Stein, 1857	16	0.56
C. aerophila Deflandre, 1929	88	3.09
C. constricta (Ehrenberg, 1841) Deflandre, 1929	55	1.93
C. elongata (Penard, 1890) Thomas, 1959	95	3.34
C. plagiostoma Bonnet & Thomas, 1955	7	0.24
C. plagiostoma var. *terricola* Bonnet & Thomas, 1955	86	3.02
C. platystoma (Penard, 1890) Deflandre, 1929	14	0.49
C. stenodeflandriana Bonnet, 1979	211	7.41
C. sylvatica (Deflandre, 1929) Bonnet & Thomas, 1955	19	0.67
C. sylvatica var. *minor* Bonnet & Thomas, 1955	28	0.98
Corythion dubium Taranek, 1881	6	0.21
Cyclopyxis eurystoma Deflandre, 1929	217	7.62
C. eurystoma var. *gautheriana* Bonnet & Thomas, 1960	7	0.24
C. eurystoma var. *parvula* Bonnet & Thomas, 1960	96	3.37
C. kahli Deflandre, 1929	46	1.62
C. kahli var. *cyclostoma* Bonnet & Thomas, 1960	19	0.67
Difflugia bryophila (Penard, 1902) Jung, 1942	9	0.32
Euglypha ciliata (Ehrenberg, 1848) Leidy, 1878	2	0.07
E. compressa Carter, 1864	3	0.10
E. compressa f. *glabra* Wailes, 1915	2	0.07
E. laevis (Ehrenberg, 1845) Perty, 1852	13	0.46
E. rotunda Wailes & Penard, 1911	14	0.49
Heleopera petricola Leidy, 1879	31	1.09
H. petricola var. *amethystea* Penard, 1899	4	0.14
H. sylvatica Penard, 1890	14	0.49
Lamtopyxis callistoma Bonnet, 1974	81	2.85
Nebela collaris (Ehrenberg, 1848) Leidy, 1879	46	1.62
N. tincta (Leidy, 1879) Awerintzew, 1906	3	0.10
Padaungiella wailesi (Deflandre, 1936) Lara & Todorov, 2012	53	1.86
Phriganella acropodia (Hertwig & Lesser, 1874) Hopkinson, 1909	224	7.87
P. paradoxa Penard, 1902	6	0.21
Plagiopyxis bathystoma Bonnet, 1961	184	6.46
P. callida Penard, 1910	5	0.18
P. declivis Thomas, 1955	218	7.66
P. glyphostoma Bonnet, 1959	47	1.65
P. minuta Bonnet, 1959	223	7.83
P. penardi Bonnet & Thomas, 1955	19	0.67
Planhoogenraadia media Bonnet, 1979	1	0.03
Tracheleuglypha acolla Bonnet & Thomas, 1955	144	5.06
T. acolla var. *aspera* Bonnet & Thomas, 1955	7	0.24
T. dentata (Vejdovsky, 1882) Deflandre, 1953	7	0.24
Trigonopyxis arcula (Leidy, 1879) Penard, 1912	4	0.14
Trinema complanatum Penard, 1890	18	0.63
T. enchelys (Ehrenberg, 1838) Leidy, 1878	131	4.60
T. galeata (Penard, 1890) Jung, 1942	19	0.67
T. grandis (Chardez, 1960) Golemansky, 1963	89	3.13
T. lineare Penard, 1890	178	6.25
Total number of taxa: 51	**-**	**-**
Total number of individuals	**2848**	**100%**

relative isolation. As a consequence of that isolation, unique flora and fauna on the island remained and developed, with a resulting high percentage of endemic species, preserved in more than 50 National Parks and Protected Areas in the country. The aim of the present paper was to supplement the knowledge on the soil testacean fauna of Madagascar and to assess the biogeographical importance of some rare species of the Gondwanan Tropical Group, observed in the studied soil.

Material and Methods

Madagascar is the fourth largest island in the world and the biggest African island, with an area of 587 000 km^2. It is located in the western part of the Indian Ocean near the Southeast Africa, about 420 km from the coast of Mozambique. The island extends to more than 1570 km from north to south in its longest part.

The material for the present study was collected from the organic layer (litter, twigs and woody material) in rainforests from the Maromizaha Protected Area in October 2013. The protected area concerned is located in Central Madagascar, east of the capital Antananarivo and south of the village of Anevoka, on the eastern slopes of the Central Highlands (18º57′ S, 48º27′ E, 950 m a.s.l.). The climate in the studied region is tropical, with two seasons: a hot, rainy season from November to April and a cooler, dry season from May to October. The mean monthly temperatures range from 13 to 23°C; July is the coolest month,

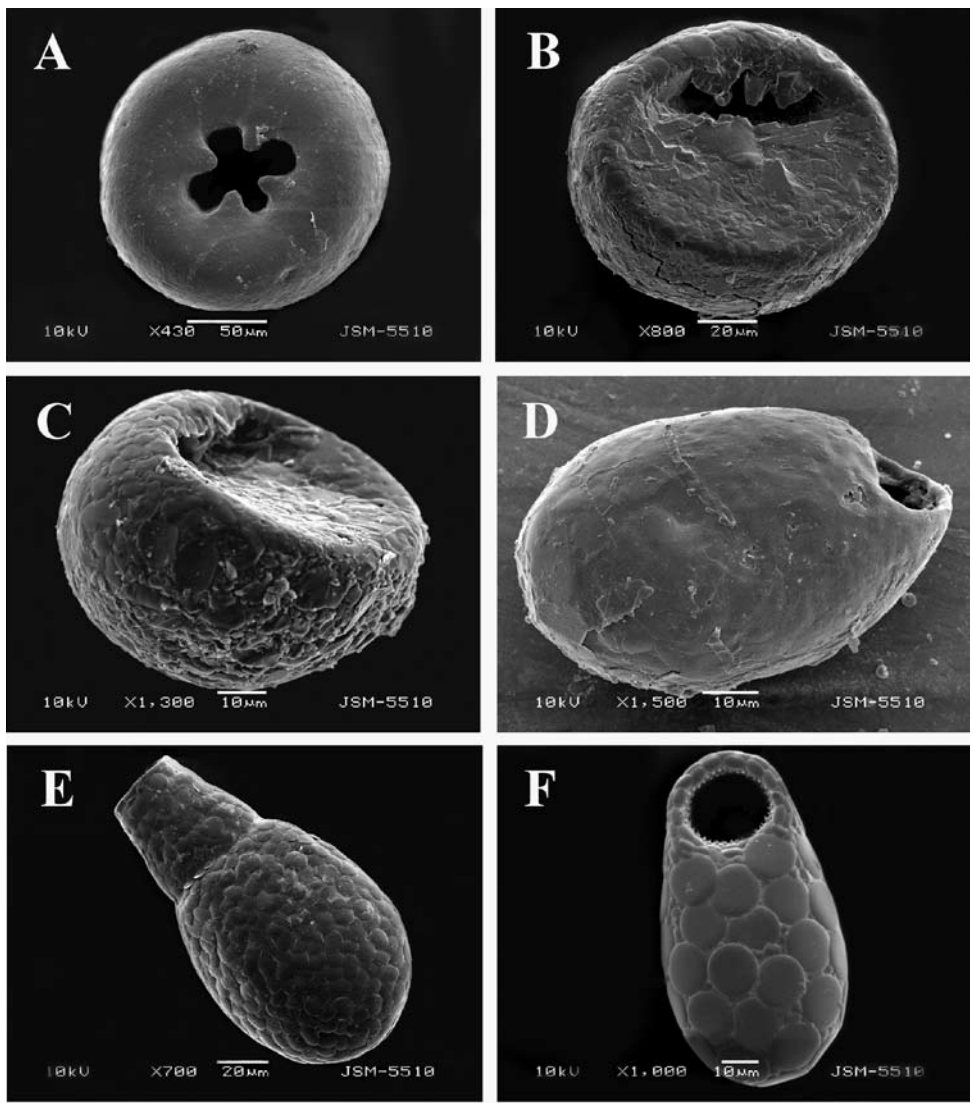

Fig. 1. Scanning electron micrographs of some soil inhabiting testate amoebae from Madagascar: A. *Lamtopyxis callistoma* – ventral view of specimen with four teeth; B. *Plagiopyxis glyphostoma* – ventral view, showing rough teeth on the aperture; C. *Plagiopyxis declivis* – latero-ventral view; D. *C. stenodeflandriana* – lateral view; E. *Apodera vas* – broad lateral view; F. *Trinema grandis* – ventral view

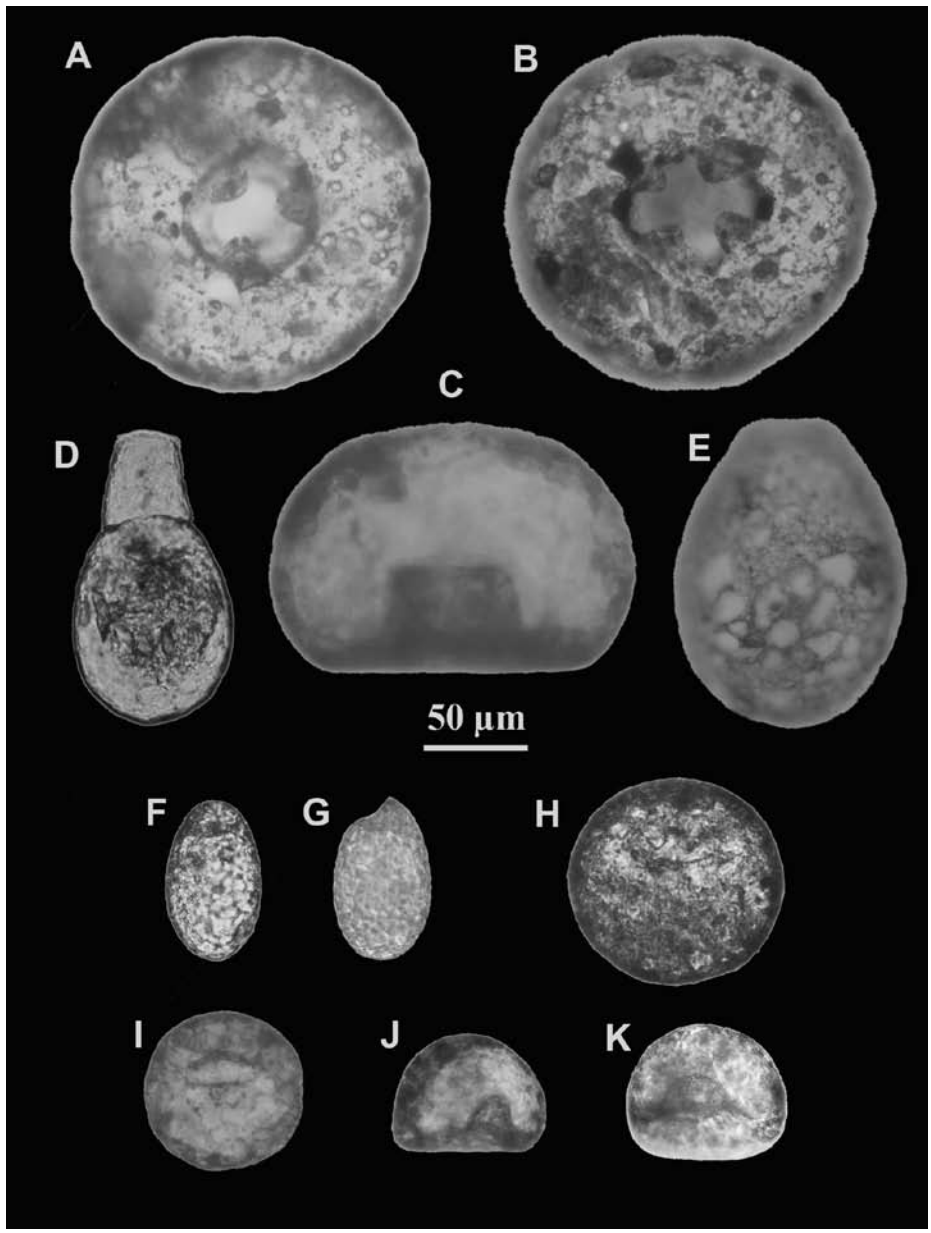

Fig. 2. Light micrographs of some soil inhabiting testate amoebae from Madagascar: A. *Lamtopyxis callistoma* – ventral view of specimen with three teeth, showing oval internal opening on the top of the apertural tube; B. *L. callistoma* – ventral view of specimen with four teeth; C. *L. callistoma* – lateral view, showing tubular invagination of the aperture; D. *Apodera vas* – broad lateral view; E. *Awerintzewia cyclostoma* – broad lateral view; F. *Centropyxis stenodeflandriana* – ventral view; G. *C. stenodeflandriana* – lateral view; H. *Plagiopyxis glyphostoma* – ventral view; I. *Plagiopyxis bathystoma* – ventral view; J. *P. bathystoma* – lateral view, showing deeply invaginated pseudostome; K. *P. bathystoma* – apical view

while December is the hottest month. Annual precipitations are moderate for the island – about 1000-1500 mm (less than those in the east coast where they reach 3000 mm and more than those (400-500 mm) in the western part of the island).

At the laboratory, the material was dried for one day in a thermostat at 60˚C. Then, for the microscopic analysis, the material was soaked and mixed in chlorinated tap water for about ten minutes, after which was filtered through a sieve with 500 µm mesh to remove large organic and mineral particles. The resulting filtrate was allowed to precipitate for two hours, the sediment was removed and the shells that floated on the surface were collected for examination. The study was carried out 12 hours after the flotation, when the gas bubbles inside the shells completely disappeared and the structure of the shells was well visible. The testate amoebae were determined and counted at 160x and 400x magnifications with an "Amplival" (Zeiss-Jena) optical microscope.

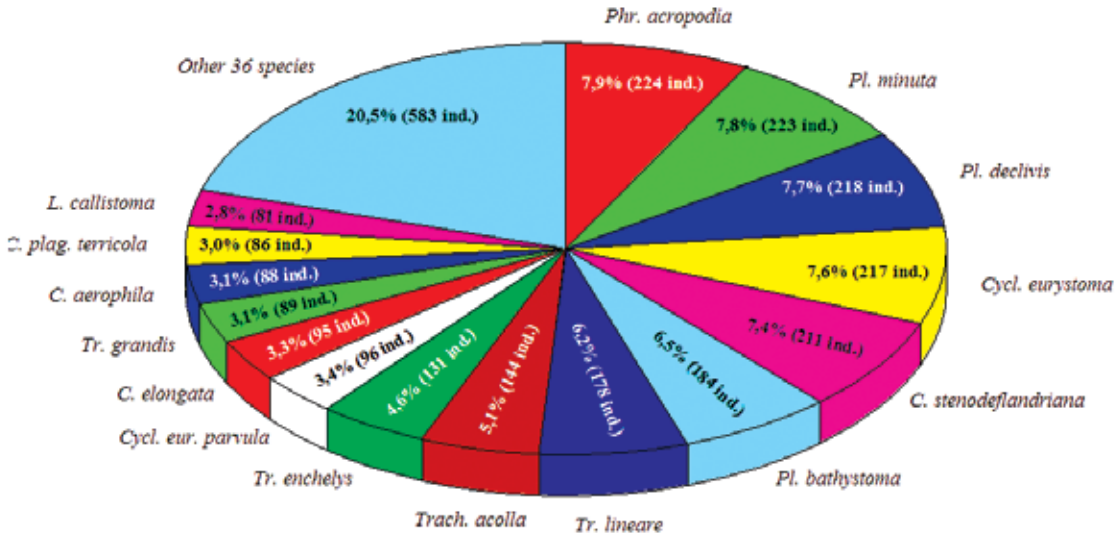

Fig. 3. Pie chart indicating the relative abundance of dominant species in the testacean community of studied soil from Madagascar

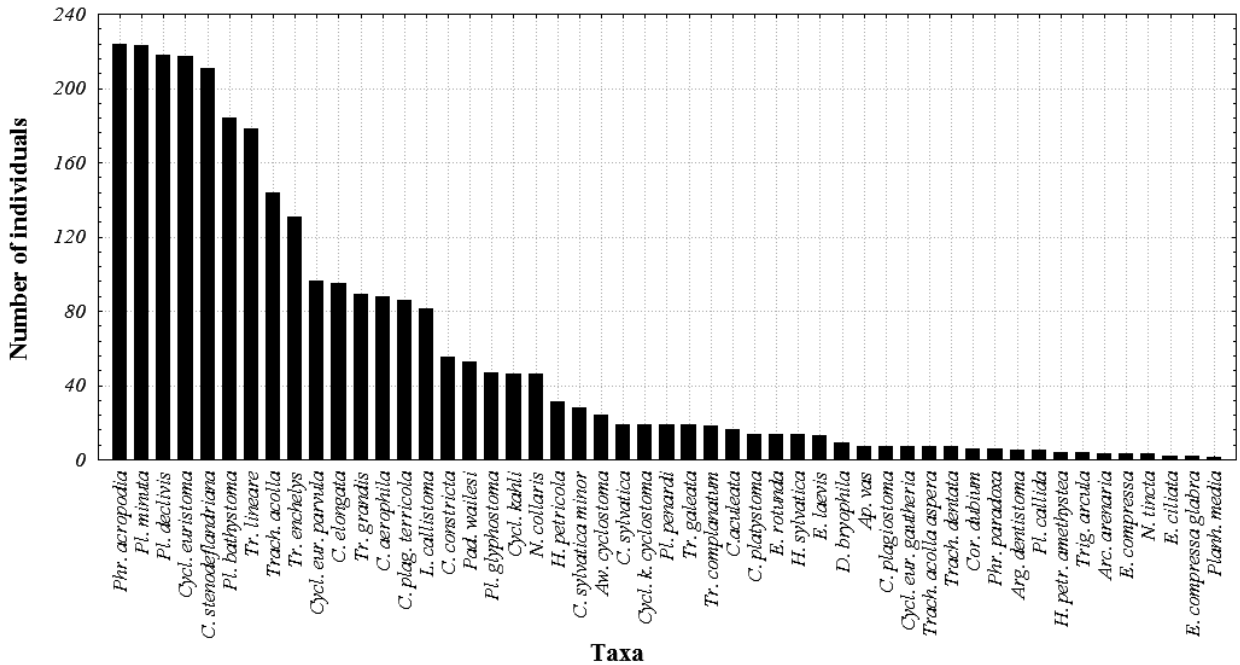

Fig. 4. Histogram of the dominant structure of the testacean community in the studied soils from Madagascar. Different species are given by their number of individuals in descending series

For scanning electron microscopy (SEM), the specimens were isolated by searching through small isolates of material in a Petri dish. The specimens were extracted using a glass micropipette, washed several times in distilled water, and then individual shells were positioned with a single-hair brush onto a small drop of Araldite on a previously cleaned standard aluminium stub and air-dried. The shells were coated evenly with gold in a vacuum coating unit. The photomicrographs were obtained using a JEOL JSM-5510, operating at 10 kV.

Results

A total of 2848 individuals of 51 taxa (43 species and 8 intraspecific taxa) belonging to 19 genera of testate amoebae were identified and counted (Table 1, Figs. 1, 2).

Phryganella acropodia (224 ind., 7.9%), *Plagiopyxis minuta* (223, 7.8%), *Pl. declivis* (218, 7.7%), *Cyclopyxis eurystoma* (217, 7.6%), *Centropyxis stenodeflandriana* (211, 7.4%), *Pl. bathystoma* (184, 6.5%) and *Trinema lineare* (178,

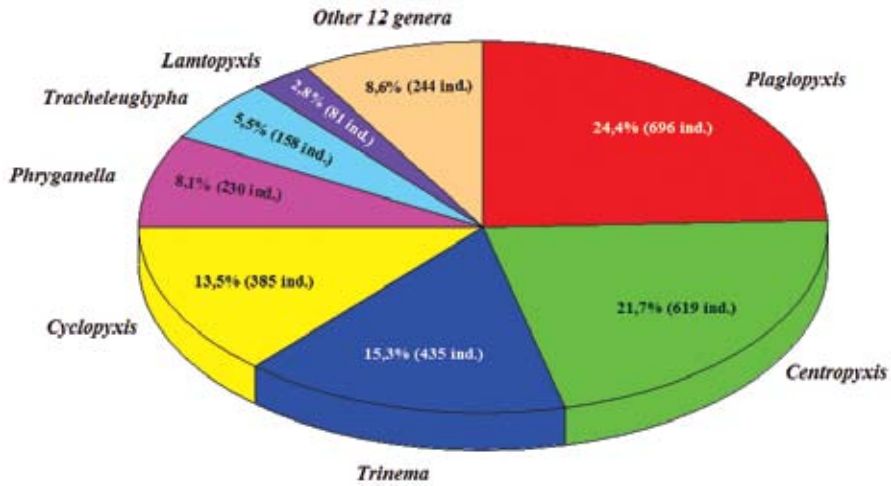

Fig. 5. Pie chart indicating the relative abundance of dominant genera within the testacean community in the studied soils from Madagascar

6.2%) were the most frequently occurring species with the highest relative abundance. These seven species constituted more than one half (51.2%) of the testacean community in the studied biotope. Most of the other species had significantly lower abundance and were represented by single specimens. About three-quarters of all taxa (36) had a total of only 20.5% relative abundance (Fig. 3). All five taxa of the genus *Euglypha* were registered with small number of individuals, each of them with relative abundance below 0.5%. *Planhoogenraadia media* was registered with one specimen only.

In accordance with the first biocenotic principle of Thienemann, the histogram of the dominant structure of testacean community in the studied soils (Fig. 4) shows that the conditions for the development of testate amoebae are favourable. There is no clearly dominant single species and more than two third of the found species have very low population density.

The genera *Centropyxis* (10 taxa), *Plagiopyxis* (6), *Trinema* (5), *Cyclopyxis* (5), and *Euglypha* (5) were the most diverse. All of them, except the genus *Euglypha*, were characterised by the highest number of individuals and relative abundance: *Plagiopyxis* (696 ind., 24.4%), *Centropyxis* (619, 21.7%), *Trinema* (435, 15.3%), and *Cyclopyxis* (385, 13.5%). These four genera constituted 75% of the testacean fauna and had predominance in the studied region. Relatively well represented were also the genera *Phryganella* (230 ind., 8.1%), *Tracheleuglypha* (158 ind., 5.5%), and *Lamtopyxis* (81 ind., 2.8%). Almost all of the remaining genera were represented by one or two species that had a low population density and relative abundance below 2% (Fig. 5).

Discussion

The species richness of testate amoebae in the studied soils of tropical rainforests was relatively low (only 51 taxa). The majority of the recorded species belongs to the group of soil- or litter- inhabiting testate amoebae with cosmopolitan distribution, and was characterised by a large species diversity of the families Centropyxidae, Plagiopyxidae and Trigonopyxidae (e.g. *Centropyxis aerophila, C. elongata, C. plagiostoma terricola, Plagiopyxis declivis, P. minuta, Cyclopyxis eurystoma, C. eurystoma parvula, C. kahli,* etc.). Some rare species of the Gondwanan Tropical group with restricted geographical distribution, which are of interest from the biogeographical point of view, were also observed (e.g. *Apodera vas*, *Centropyxis stenodeflandriana*, *Lamtopyxis callistoma*, *Plagiopyxis bathystoma* and *Planhoogenraadia media*). *Apodera vas*, a testate amoeba with limited geographical distribution (Figs. 1E, 2D), is particularly interesting. This species is largely recorded (more than 50 publications) south of the Tropic of Cancer, mainly in the Southern Hemisphere (i.e. in Gondwanaland continents); despite numerous studies on testate amoebae carried out in the Northern Hemisphere, this species has never been reported from Europe, North America, Asia north of the Himalayas and the Far East (Wilkinson 1994, Mitchel, Meisterfeld 2005, Smith, Wilkinson 2007). *A. vas,* with its characteristic morphology and restricted geographical distribution, is a key example in debates over the truth of the 'everything is everywhere but the environment selects' generalisation (Finlay, Clarke 1999, Foissner 1999, Esteban, Finlay 2002, Finlay *et al*. 2004, Mitchell, Meisterfeld 2005, de Wit, Bouvier 2006, Smith, Wilkinson 2007).

Lamtopyxis callistoma is another rare species from the Gondwanan Tropical group of the testate amoebae found in soils of the Madagascar's rainforests (Figs. 1A, 2A-C). It was first described by Bonnet (1974) from a gallery forest in Ivory Coast (the Savanna Lamto) and since then has been recorded from a few tropical countries: Ivory Coast (Bonnet 1976), Papua New Guinea (Bonnet 1980a), Philippines (Bonnet 1980b) and Indonesia (Bonnet 1992). This species, with its large size (170-180 µm in diameter) and specific apertural morphology, is easily recognisable and the probability of its being overlooked is too small.

Other four known species of the genus *Lamtopyxis* (*L. cassagnaui* Bonnet, 1977, *L. travei* Bonnet, 1977, *L. trifoliata* Bonnet, 1979 and *L. sarocchii* Coûteaux et Chardez, 1981), similarly to *L. callistoma*, have also been found only in soils of tropical forests from countries situated south of the Tropic of Cancer, namely: Nepal (Bonnet 1977b, 1981b), Mexico (Bonnet 1977a), Brazil and Paraguay (Bonnet 1979), Philippines (Bonnet 1980b), French Guiana (Coûteaux, Chardez 1981), Thailand (Bonnet 1981a, 1987, Golemansky, Todorov 2000), Indonesia (Bonnet 1985, 1992), Ecuador (Krashevska *et al*. 2007, 2010). The restricted geographical distribution of *Lamtopyxis* spp. shows that they may similarly be used as an example that in free-living microbial eukaryotes 'not everything is everywhere'.

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