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Latitudinal Diversity Gradients in Free-living Microorganisms – *Hoogenraadia* a Key Genus in Testate Amoebae Biogeography

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Abstract. The extent to which free-living microorganisms show cosmopolitan distributions has been a contentious aspect of microbial ecology over the last few decades. Testate amoebae are a group of free living protists that can provide important evidence for the nature of the biogeography of microorganisms because there are relatively good data on the distribution of their morpho-species (compared to many other microbial groups). Many testate amoebae appear to exhibit ubiquitous distributions, while some taxa have proven to be endemic to limited regions. The genus *Hoogenraadia* (Gauthier-Lièvre and Thomas 1958) is of particular interest in this context as it appears to be restricted to relatively low latitudes. There are six described species of the genus: *H. africana* Gauthier-Lièvre and Thomas 1958, *H. asiatica* Wang and Min 1987, *H. cryptostoma* Gauthier-Lièvre and Thomas 1958, *H. humicola* Bonnet 1976, *H. ovata* Bonnet 1976, and *H. sylvatica* Vucetich 1974. However, information on these taxa is scattered through a number of different papers – here we provide a summary of what is known about the taxonomy and ecology of this genus. We also reinterpret recent new records of putative *H. africana* from China (suggesting this identification is not reliable). As an example of a protist taxon largely restricted to the tropics this genus is of particular interest in microbial biogeography and this paper discusses its morphology, ecology and distribution in this context.

Key words: testate amoebae, *Hoogenraadia*, diversity, biogeography.

INTRODUCTION

Testate amoebae are a polyphyletic group of unicellular protists that build a test (shell), in which a single amoeboid cell is enclosed (Mitchell *et al.* 2008). They occur worldwide in a range of terrestrial, wetland, freshwater and even marine habitats. Their tests have proven to be useful paleoenvironmental proxies in peat

and lake sediment cores (Warner 1989, Patterson and Kumar 2002). Testate amoebae have been important in studies of protist diversity due to their particularly conspicuous shell morphology which has allowed the identification of a large number of morpho-species. They are also thought to have important roles in nutrient cycling in soils (Wilkinson and Mitchell 2010). More than 1900 species have been described in different publications (Meisterfeld 2002a, b). A large number of testate amoebae morpho-species exhibit cosmopolitan distributions, however some of the most convincing examples of restricted (non-cosmopolitan) distribu-

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tions in free living microorganisms also come from testate amoebae – such as *Apodera (Nebela) vas* (Foissner 2006, Smith and Wilkinson 2007) and *Nebela ansata* (Heger *et al.* 2011).

Genus *Hoogenraadia* is of particular interest as it appears to be restricted to relatively low latitudes. The genus was firstly observed in Africa by Gauthier-Lièvre and Thomas in 1958. The main characteristic of this genus is the smooth shell with an anterior cap or visor, which makes the aperture a slit opening. However, this genus has not been widely illustrated in the literature and does not feature in any of the more commonly used guides to testate amoebae identification – which tend to focus on higher latitude taxa (e.g. Ogden and Hedley 1980, Charman *et al.* 2000, Mazei and Tsyganov 2006). This makes an up-to-date account of its taxonomy important for ecologists and biogeographers working on testate amoebae.

This paper provides a summary of the six described species of genus *Hoogenraadia*: *H. africana* Gauthier-Lièvre and Thomas 1958, *H. asiatica* Wang and Min 1987, *H. cryptostoma* Gauthier-Lièvre and Thomas 1958, *H. humicola* Bonnet 1976, *H. ovata* Bonnet 1976, and *H. sylvatica* Vucetich 1974. As the original descriptions were published in four different European languages, with some of these journals being difficult to access, we consider it timely and useful to summarise the information on all known members of this genus in a single English language paper. We also reinterpret recent records of putative *H. africana* from China. As an example of a protist taxon largely restricted to the tropics this genus is of particular interest for microbial biogeography and we discuss its morphology, ecology and distribution in this context.

MATERIALS AND METHODS

We summarized the published literature on the genus *Hoogenraadia* along with some new records from China, including possible examples of *H. africana*, found in the rich organic soils of Shennongjia Mountains in central China. The regional climate of this part of China belongs to subtropic zones and there are extensive forest ecosystems. The samples were collected from the soils near the Dajiuhe peatland (31°15'–37°57'N, 109°59'–110°58'E) which located at the western of the Shennongjia Mountains. The upper 0–5 cm soils were collected into plastic bags. Samples were taken back to the laboratory, after sieving through 15–300 µm mesh, the testates were identified under light microscopy with magnification 400×. However, for some samples because the shells were adhered to clay and dirt, the samples were identified after drying under a stereomicroscope. The specimens

were identified following the descriptions in Gauthier-Lièvre and Thomas (1958), Bonnet (1976) and Meisterfeld (2002a, b).

In this paper morphological characters, such as shell length and width, of the various species are compared. The ecology of the different species in the genus are summarized and a map illustrating the global distribution of the genus *Hoogenraadia* was compiled based on these data.

RESULTS AND DISCUSSION

Records of *Hoogenraadia* in China

There were two extant *Hoogenraadia* taxa previously recorded in China, *H. cryptostoma* and *H. asiatica* to which can be added our new record of *an additional species of uncertain identity* (Shen 1983, Wang and Min 1987, Qin *et al.* 2011). In addition, the fossil *H. asiatica* was found in the sediments from late Pleistocene and Holocene (Wang and Min 1987). The limited nature of testate amoebae records from modern China make impossible to be sure if this species still exists or if it has become extinct.

The testate species illustrated in Fig. 1 is common in the soils of Shennongjia Mountains, and it is especially abundant in the soils near the Dajiuhe peatland. The occurrence of this species was briefly noted and illustrated in Qin *et al.* (2011) under the name *Planhoogenraadia africana* – here we provide full details of this finding. The size of the specimens are as follows (N = 17): shell length 115–155 µm, shell width 50–65 µm which is mid-range in size for this genus. This was identified as *Planhoogenraadia africana* by Qin *et al.* (2011) – who also implied that the genera *Planhoogenraadia* and *Hoogenraadia* may be synonymous. However, because of the shape of the ventral aperture (compare with Fig. 2c) we do not believe this taxon to be *Hoogenraadia africana* but tentatively assign it to c.f. *Hoogenraadia humicola*.

These new records clearly illustrate the current difficulties in assigning some specimens to an unambiguous morpho-species and suggest that there is more to learn about the occurrence of this genus in China and further work is obviously required. Molecular data would obviously be very useful in sorting out the current uncertainties about the status of these morphospecies.

Global records of *Hoogenraadia*

Genus *Hoogenraadia* was first described from Africa by Gauthier-Lièvre and Thomas in 1958. The main characteristic of this genus is the smooth shell with an

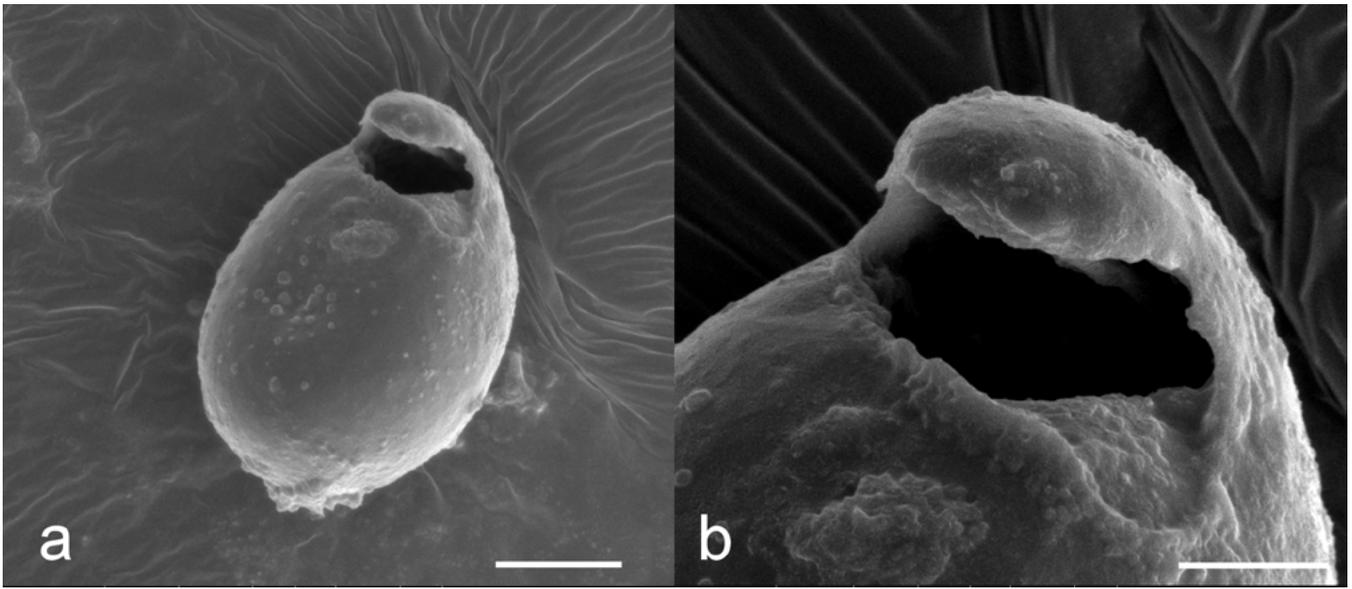


Fig. 1. SEM photos showing c.f. *Hoogenraadia humicola* found from soils in Shennongjia Mountains of central China (the left picture is from Qin *et al.* 2011). This was previously identified as *Planhoogenraadia africana* by Qin *et al.* (2011). Scale bars: 50 μm (a) and 20 μm (b).

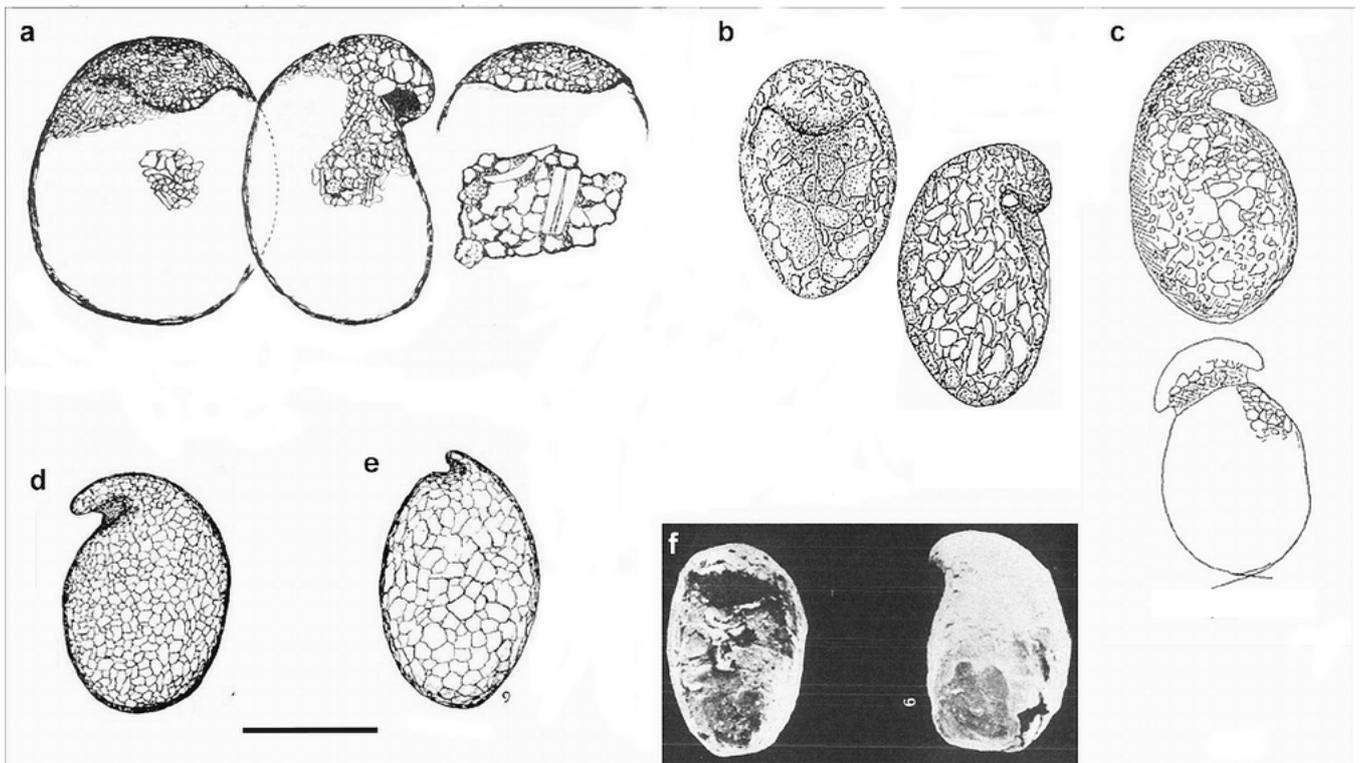


Fig. 2. Shell outline and SEM photos of six species of genus *Hoogenraadia* Gauthier-Lièvre and Thomas 1958, with scale bar 50 μm . **a** – *H. cryptostoma* Gauthier-Lièvre and Thomas 1958; **b** – *H. sylvatica* Vucetich 1974; **c** – *H. africana* Gauthier-Lièvre and Thomas 1958; **d** – *H. humicola* Bonnet 1976; **e** – *H. ovata* Bonnet 1976; **f** – *H. asiatica* Wang and Min 1987.

anterior cap or visor, which makes the aperture a slit opening. The shell is mainly built by organic materials with a few silica particles (idiosomes). Six taxa belonging to this genus have been described, based on their morphological characters (Fig. 2). We are not aware of any molecular work on *Hoogenraadia* taxonomy.

Different species in the genus *Hoogenraadia* show different habitat preferences. For example, *H. africana* has been mainly found in *Sphagnum* dominated peatlands and soils, but *H. humicola* is distributed in soils rich in organic debris in forest-gallery backwaters (Table 1). *H. cryptostoma* is more common in swampy sites beside streams. *H. asiatica* is only known as a fossil species which was found in late Pleistocene and Holocene deposit (Wang and Min 1987) – as noted above it is uncertain if this species is still living in modern habitats or extinct.

Previous studies of testate amoebae have implied that the variability of shell morphology, such as the surface and size of the shell, can be related to habitat (Charman 1999; Qin *et al.* 2010, 2011). For example, the variability of test aperture may indicate different moisture condition (Bobrov and Mazei 2004), although other factor can also effect the shape of the aperture (Wanner and Meisterfeld 1994).

However, for the taxonomy of *Hoogenraadia*, the difference of the shell aperture seems to be not significant. From the published illustrations summarized in figure 2, the differences of aperture between some species do not appear to be distinctive, which can make the taxonomy confusing if researchers take the aperture

as a key criterion for identification. Similar problems also exist in the use of aperture shape as a taxonomic character in other species of testate amoebae, for example the main difference between *Trigonopyxis arcula* Penard 1907 and *T. microstoma* Hoogenraad and Groot 1948 is the shape of their aperture. However, aperture of *T. arcula*, shows a high degree of variability, from regular triangular to quadrilateral or quinquangular (Bobrov *et al.* 1999, Charman *et al.* 2000, Qin *et al.* 2011). This illustrates some of the difficulties with the concept of testate amoebae morpho-species (Charman 1999, Qin *et al.* 2011) and the difficulties in using such data in studies of the biogeography of testate amoebae (Heger *et al.* 2009).

In order to investigate the variability of typical taxa, variation of shell size was analysed. The results however did not show any clusters of individuals with similar sizes, although the number of investigated individuals are low (Fig. 3). The c.f. *H. humicola* (Fig. 1) we found from the soils in Shennongjia Mountains is mid-range in size for this genus (N = 17).

Interestingly, a similar genus *Planhoogenraadia* has a very similar characters of shell morphology. The main differences are as follows: *Hoogenraadia* has a curved ventral surface and *Planhoogenraadia* has a curved dorsal surface but a flat ventral side, which could be explained as an adaptation to living in soils (Bonnet 1977; Meisterfeld 2002a, b). Some publications (e.g. Qin *et al.* 2011) have implied these genera may turn out to be synonymous. Molecular analysis is clearly required to help clarify the taxonomy of this genus. Until such data

Table 1. Characters and distribution of six species of the genus *Hoogenraadia* (L – length, W – width). Many of the earlier papers do not report a sample size for number of tests measured – so it is possible that some of these data may be based on a very low sample size.

Species	Size (µm)	Distribution regions and publication	Habitats
<i>H. africana</i>	L = 95–115, W = 47–60	Moyen-Congo (Gauthier-Lièvre and Thomas 1958), Guinea and Equatorial Guinea (Golemansky 1962), Brasil (Leiptniz <i>et al.</i> 2003), China (Qin <i>et al.</i> 2011)	<i>Sphagnum</i> , water, river, forest marsh
<i>H. asiatica</i>	L = 95, W = 70	China (Wang and Min 1987)	Quaternary deposit
<i>H. cryptostoma</i>	L = 130–140, W = 105–110	Moyen-Congo (Gauthier-Lièvre and Thomas 1958), States of Parana, Mato Grosso do Sul, Brasil (Velho <i>et al.</i> 1996, 2000)	Swamp quite shady in the bed of a stream
<i>H. humicola</i>	L = 143–146, W = 96–100	Nepal, Himalayas (Bonnet 1977, 1978), Philippines (Bonnet 1980), Cote d'Ivoire, Africa (Bonnet 1976, 1978), Tonga and Western Samoa Islands (Korganova 1994), China (this paper)	Soils rich in organic debris in forest-gallery backwaters. The ground litter and sublitter horizons of white subtropical soils
<i>H. ovata</i>	L = 60–67, W = 36–39	Cote d'Ivoire, Africa (Bonnet 1976)	Soils rich in organic debris in forest-gallery backwaters
<i>H. sylvatica</i>	L = 82–93, W = 60–70	Punta Lara Province of Buenos Aires, Argentina (Vucetich 1974)	Moss in marginal forest

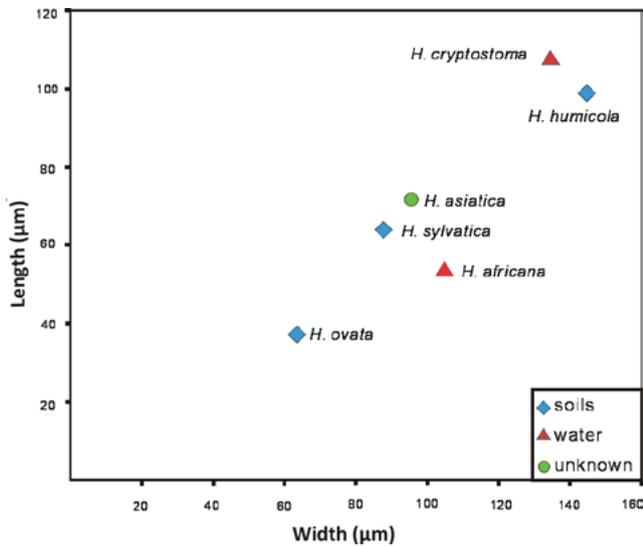


Fig. 3. Relationship between shell width and shell length of each species of the genus *Hoogenraadia*. The sample sizes on which these measurements are based is unclear as the older literature often doesn't specify the number of tests measured (see Table 1).

is available the summary of the suggested morphological differences between the species of *Hoogenraadia* – given in this paper – provide a provisional classification for this genus.

BIOGEOGRAPHY

One of the most well established patterns in the biogeography of macroscopic organisms is the tendency for most groups to have a high species richness in the tropics, which then declines as one moves into higher latitudes (for reviews see Cox and Moore 2010, Sherratt and Wilkinson 2009). However, it is much less clear if this pattern is also found in free living microorganisms. In a review of the evidence for this classic latitudinal diversity gradient in free-living microbes Sherratt and Wilkinson (2009) suggested that there was good evidence for its existence in foraminifera, but at best very limited evidence for it in other groups. In addition, a meta-analysis of a very large set of studies of diatom diversity showed that 'latitudinal gradients of species richness are largely absent for diatoms' (Hillebrand and Azovsky 2001). One group not considered by Sherratt and Wilkinson (2009) are the dictyostelid slime molds – here there is limited evidence for a peak in tropical

species richness (Swanson *et al.* 1999, Bonner 2009, Stephenson and Feest 2012). However, the majority of these data on which the slime mold analyses are based are rather old and it would be more convincing if new analyses could be performed incorporating molecular data. For example recent molecular work on dictyostelid slime molds has identified a latitudinal gradient within Europe (Perrigo *et al.* 2013), it would be very informative to see this type of analysis extended to a global scale. So for most groups of free living eukaryotic microbes it is currently unclear if they fail to show the patterns in latitudinal diversity common in larger organisms or if they show such a pattern but it is obscured by our limited knowledge of their global diversity.

The distribution pattern in testate amoebae is similarly unclear. One of the few attempts to establish the presence of a latitudinal gradient in testate amoebae was by Smith (1982). He plotted species richness for testate amoebae from a range of sites in the Antarctic and sub-Antarctic and pointed out that if one extended the regression line fitted through these data to the tropics it predicted the actual tropical species richness described in the limited number of available studies. Smith's (1982) regression line ranged from approximately 10 species in the Antarctic sites to just under 100 species in the tropics. However, more recent work (e.g. Vincke *et al.* 2006a, b) has greatly increased the number of species at several of Smith's sub-Antarctic sites potentially undermining his conclusions (Sherratt and Wilkinson 2009). In the absence of any convincing demonstration of the classic latitudinal diversity gradient in testate amoebae, a genus such as *Hoogenraadia* that appears to be restricted to relatively low latitudes, is of general interest for attempts to understand the diversity and biogeography of free living eukaryotic microorganisms. In addition in the context of ongoing skepticism by several authors on the applicability of the concept of ecological niches to free living microbes (Hutchinson 1961, Vickerman *et al.* 2000, Bonner 2013) a genus restricted to predominantly tropical conditions is clearly of some interest.

Species of the genus *Hoogenraadia* were previously thought to be endemic to the Gondwana tropic zone (Smith *et al.* 2008). The results of this study show that there are some species which ranges extend into Russia (Fig. 4). However, taxon richness in genus *Hoogenraadia* is the highest in tropical regions, a result consistent with previous studies. The new data of *Hoogenraadia* described in this paper are from the soils in Shennon-

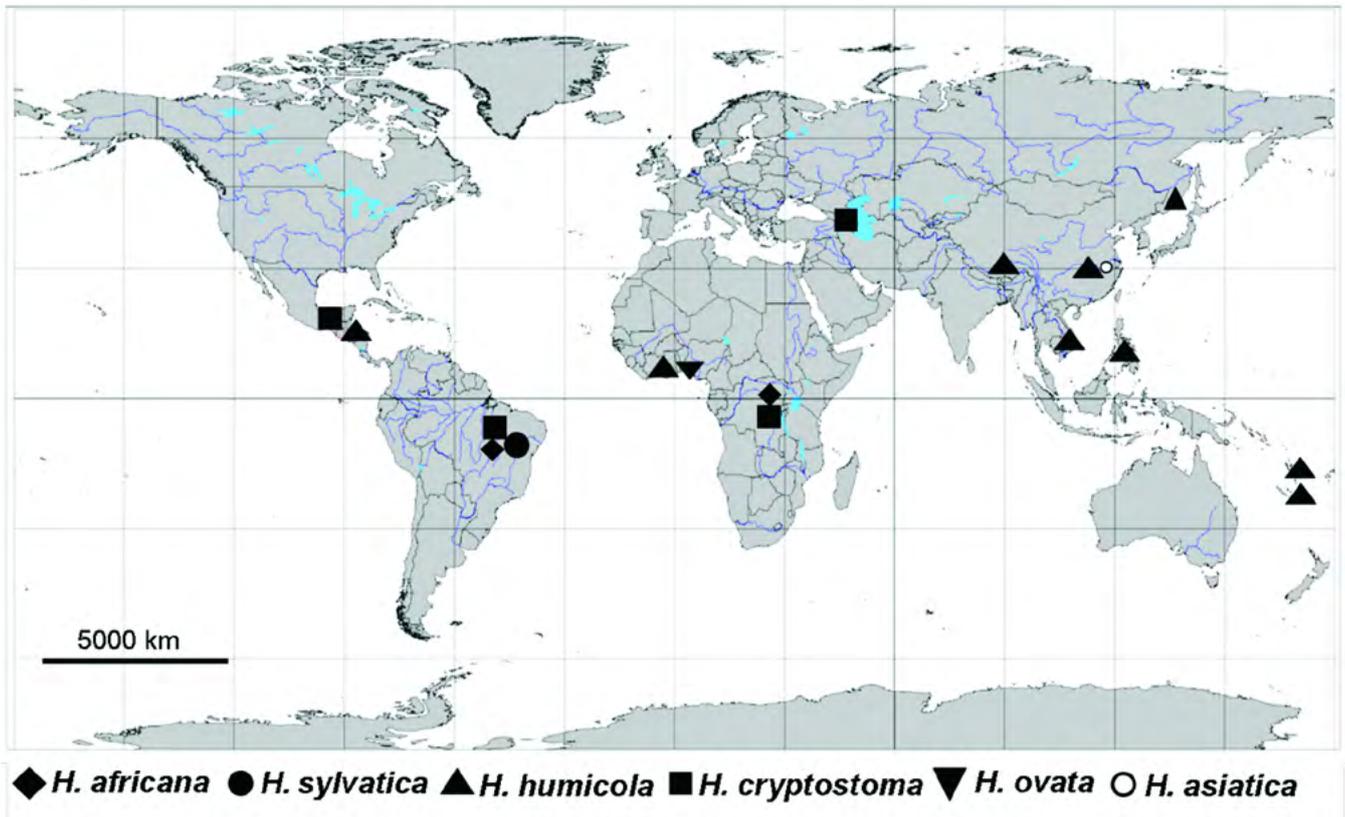


Fig. 4. Map showing biogeographically distribution of each species in genus *Hoogenraadia*.

gija Mountains of south-central China – also from subtropical regions (Fig. 4).

The potential explanations for the limited distribution are varied. Dispersal limitation could play a role, the size of most *Hoogenraadia* species are larger than 100 μm , with *H. ovata* as an exception, which may be one of the possible reasons for the restricted distribution. Some studies suggested that the dispersal ability of testate amoebae can be limited if the size is larger than 100–150 μm (Wilkinson 2001, Yang *et al.* 2010). The distribution map strongly suggests a link to tropical or subtropical climate – so this genus may also be limited by the distribution of climatically suitable niches. In this context the occurrence of *H. humicola* in Sikhote Alin in Russia is of particular interest as this is the furthest north of any occurrences we have been able to find. The habitat was oak woodland soils and the winter temperature can be -10°C or less (Bobrov 2001) however summer climates are more temperate. This suggests that for this species at least it may be the summer temperatures that are crucial (e.g. Seryodkin *et al.* 2013).

CONCLUSIONS

The nature of the distribution patterns of micro-organism is still a major area of uncertainty. A large number of testate amoebae morpho-species exhibit cosmopolitan distributions, however some of the most convincing examples of restricted (non-cosmopolitan) distributions are also found in the testate amoebae. The morphology, ecology and distributions of the six described species of genus *Hoogenraadia*: *H. africana* Gauthier-Lièvre and Thomas 1958, *H. asiatica* Wang and Min 1987, *H. cryptostoma* Gauthier-Lièvre and Thomas 1958, *H. humicola* Bonnet 1976, *H. ovata* Bonnet 1976, and *H. sylvatica* Vucetich 1974 are summarized above. Some uncertainty in the taxonomy, and possible reasons for the restricted distribution are also discussed. Future studies are clearly needed to investigate their distributions in larger scale. Taxonomic criteria also need to be improved both in morphology and molecular phylogeny.

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