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Taxonomy and Ecology of Sponge-Associate *Marionina* spp. (Clitellata: Enchytraeidae) from the Horomatangi Geothermal System of Lake Taupo, New Zealand

key words: Enchytraeidae, *Marionina*, new species, Spongillidae, *Heterorotula*, sponge association, New Zealand, sublacustrine thermal vents

Abstract

The dissection of *Heterorotula* sponges collected in an area of geothermal activity at 126–145 m depth on the floor of Lake Taupo (DE RONDE *et al.*, 2002) revealed a dense population of associated Enchytraeidae. They represent three species of *Marionina*, two of which known but exotic (the Palaeo-arctic *M. riparia* BRETSCHER, 1899 and the Chinese *M. seminuda* XIE and ROTA, 2001), and one new to science, *M. spongicola* sp. n. This is the first report of an ecological association between enchytraeids and poriferans in the lake profundal zone. The possible nature of such relationship (casual contact for feeding or dwelling for food and shelter) is discussed.

1. Introduction

A recent submersible investigation of geophysical and water chemistry anomalies in Lake Taupo, New Zealand, by the joint New Zealand/German *Taupo '98* dive project (http://www.minerals.co.nz/jago/jago_index.html, 3 July 2002; URL active as of October 2003), revealed deep hot spring vents and associated biological communities in the Horomatangi Reefs area (DE RONDE *et al.*, 2002). Vents occur at depths between 120 and 135 m at two distinct sites, named Te Hoata and Te Pupu. The lake floor at both sites is made mostly of undulating surfaces of unconsolidated pumice covered by a 5 cm thick layer of dark mud which in turn is overlain by 1–2 cm of brownish, flocculent, organic-rich detritus. Exposed rock outcrops, where present, consist of horizontally stratified ash beds interbedded with mudstones. Gas streaming and diffuse venting of hot water (ca. 45 °C) were seen emanating from cracks and fissures in the mudstones, with sediments near the vent fields showing temperatures 0.5–3.5 °C higher than that of the ambient lake water (ca. 11 °C). Several small fields of dead chimneys, 10–30 cm in height, were seen at the Te Pupu site; the walls of the chimneys contain silicified remnants of filamentous bacteria while diatom shells cover their surface and the surrounding substrate. Live bacterial mats mark all active outlets, and more peripherally, dense assemblages of the sponge *Heterorotula* sp. (Demospongiae: Haplosclerida: Spongillina: Spongillidae) (MANCONI, in prep.), are perched on top of dead chimneys and/or exposed outcrops. The crayfish *Paranephrops planifrons* WHITE, 1842 (Crustacea: Decapoda: Parastacidae) is the only epibenthic invertebrate observed in the

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area, but dissection of the sponge tissue revealed a diversified assemblage of associated fauna, mostly crustaceans and annelids (DE RONDE *et al.*, 2002; MANCONI *et al.*, 2002). The annelid collection, comprising some 40 specimens all belonging to the clitellate family Enchytraeidae, is described in this paper.

2. Material and Methods

Observations *in situ*, photo/video documentation, and sampling of the lakebed were made at the Te Hoata and Te Pupu sites during two dives of the manned research submersible *Jago* (hired from the Max Planck Institute for Behavioural Physiology, Seewiesen, Germany) on 18–19 October 1998. Difficult weather conditions prevented additional dives (DE RONDE *et al.*, 2002). Fragments of sponges were taken in the vicinity of venting by the hydraulic arm of the submersible and brought to the surface in insulated containers. Part of the samples, preserved in 70% ethanol, were sent to the second author in Italy for identification. Sponge fragments (0.5–1 cm in diameter) from 173 m, 127 m and 145 m (*Jago* samples NZ84, NZ85 and NZ86, respectively) were examined intact and subsequently dissected and prepared for study of spicules and gemmules. They appear to belong to an undescribed species of *Heterorotula* (MANCONI, in prep.). Samples NZ85 and NZ86 revealed a rich associated fauna including, in addition to the Enchytraeidae described herein, numerous amphipods, copepods, ostracods, along with nematodes and other as yet unidentified taxa.

Enchytraeid worms were stained in paracarmine, dehydrated, cleared in xylene and mounted whole in Canada balsam. All measurements refer to whole-mounted specimens. The patterns of anterior bifurcation of the dorsal blood vessel, i.e., marionine (= pharyngeal) and lumbriciline (= peristomial), are defined according to GIÈRE (1974). The holotype and two paratypes of the new species are deposited in the Museo Civico di Zoologia di Roma, Italy (MCZR); the other paratypes are deposited in the Swedish Museum of Natural History, Stockholm (SMNH).

3. Taxonomy

Genus *Marionina* MICHAELSEN, 1889 (*sensu lato*)

Marionina spongicola sp. n. (Fig. 1)

Holotype: MCZR Oligochaeta 0137, mature, whole mounted specimen.

Type locality: New Zealand, Lake Taupo, Horomatangi Reefs area, 145 m depth (sample NZ86), in *Heterorotula* sp. sponge, 19 October 1998, leg. KAREN HISSMAN.

Paratypes: MCZR Oligochaeta 0138–0139 and SMNH Type Coll. 5916–5917, four whole mounted specimens from same date and locality as holotype.

Other material examined: Nine specimens from type locality.

Etymology: Latin, for sponge inhabitant.

Description: Body length: 1.80–2.95 mm. Width: 85–100 μm at III, 82–90 μm at V, 100–137 μm at XII. Segments 24–26. Chaetal formula 0,2–0:2,1–1. Lateral chaetae 2 per bundle, only occurring in III, IV, V (i.e., missing in II and from VI onwards); ventral chaetae 2 per bundle in II–VIII or II–VII (left side of one specimen), 1 in all other segments; chaetae absent in XII in adult specimens (Fig. 1A). Lateral bundles located some 10 μm above the lateral lines. Chaetae (Fig. 1B) straight and pointed, entally hooked, equal-sized in a bundle; size increasing gradually towards posterior body end: shaft 17–26 μm long in preclitellar segments, 26–40 μm in postclitellar ones, from 1.3 to 2.2 μm thick at midpoint. Prostomium with evident epidermal sensory buds. Head pore at 0/1. Epidermal glands inconspicuous. Clitellum from 11/12 to chaetae of XIII. Clitellar gland cells squared to rectangular, large (6–12 μm wide), both hyaline and granular types transparent, arranged in 21–23 transverse rows ventrally interrupted. Paired male pores just posterior to middle of XII, ventrolateral, more than 40 μm apart from one another. Paired spermathecal pores in lateral lines in 4/5.

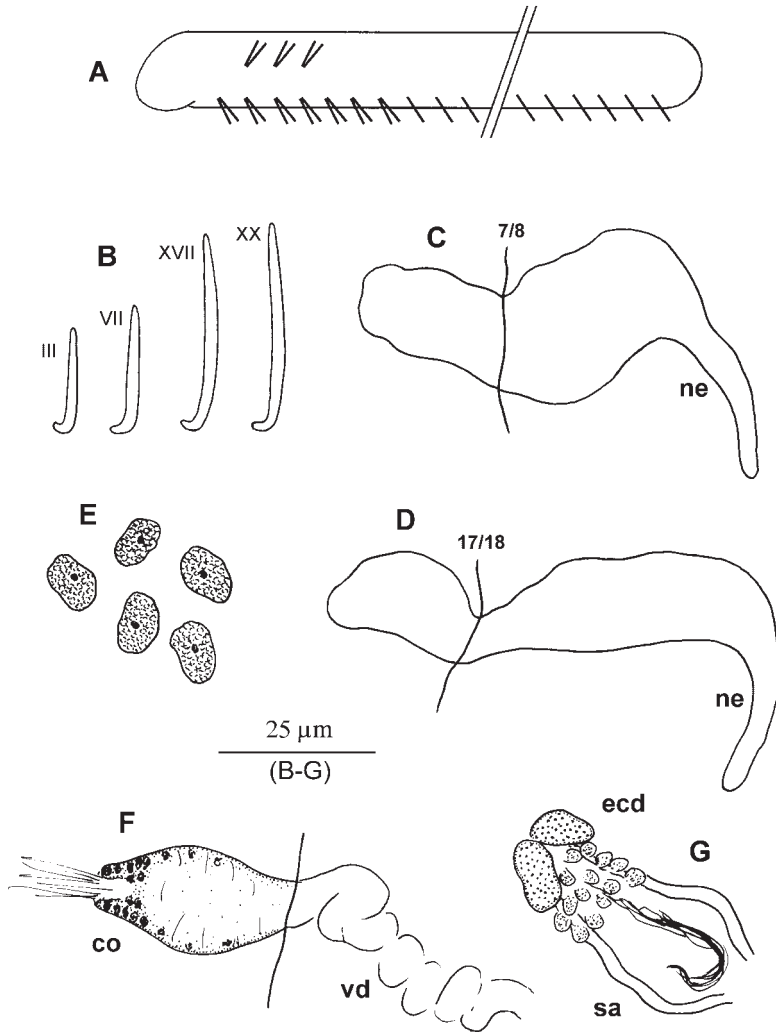


Figure 1. *Marionina spongicola* sp. n. A, scheme showing the distribution of chaetae along the body. B, ventral chaetae from different segments, indicated by Roman numerals. C–D, nephridia from pre- and post-clitellar regions (7/8 and 17/18 indicate the respective supporting septa). E, coelomocytes. F, male duct (only ental part of vas deferens shown). G, spermatheca. Abbreviations: co, collar of sperm funnel; ecd, ectal duct of spermatheca; ne, efferent duct of nephridium; sa, spermathecal ampulla; vd, vas deferens.

Brain in II–III, rounded or truncate posteriorly, 58–60 μm long. Pharyngeal glands 3 pairs, the anterior two pairs merging dorsally at 4/5 and 5/6, respectively, the third pair elongate, posteriorly converging but without dorsal connection at 6/7; separate ventral lobes in V. One pair of postpharyngeal bulbs in III. Peptonenphridia and other oesophageal appendages absent. Oesophagus passing gradually into intestine. Nephridia (Fig. 1C, D): two pairs pre-clitellar, in 7/8 and 8/9, and at least three pairs post-clitellar (seen in 15/16, 16/17 and 18/19; or in 16/17, 17/18, 19/20 and 21/22). Anteseptal part of nephridium large, oval, consisting of funnel and nephridial canal; postseptal elongate, ca. 2 times as long as ante-

septal, with short efferent duct arising ventro-terminally. Blood colourless. Dorsal vessel originating in XII–XIII, anteriorly bifurcating behind the pharynx. Coelomocytes (Fig. 1E) pale with granulated cytoplasm, oval or elliptical, only up to 12 µm long. No seminal vesicles. Sperm funnels (Fig. 1F) narrowing at both ends, small, 25–30 µm long, 14–20 µm wide, with collar 9 µm high and narrower than the body of funnel. Vasa deferentia unmodified, short, loose or coiled into a spiral in the anterior of XII, 4–5 µm thick. Penial bulbs small (25–28 µm long) and compact. One egg mature at a time. Spermathecae (Fig. 1G) communicating with oesophagus in middle of V through wide ental ducts. Ampullae globular, without diverticula, 16–21 µm across, with regular bundles of spermatozoa in lumen. Ectal ducts not distinctly set off from ampullae, ca. 13 µm wide at midcourse, slightly narrowing towards ectal pores. Many small gland cells around ectal duct and two or three larger accessory glands associated with ectal orifice (Fig. 1G).

Remarks: The combination of a small body size, the local reduction of chaetae, the large clitellar cells, the form of the brain, the marionine (= pharyngeal) bifurcation of the dorsal vessel and the shape and dimensions of the sperm funnels are reminiscent of the European *M. brendae* ROTA, 1995 and the Chinese *M. sinica* XIE and ROTA, 2001. The three species are distinguished from each other by: (1) details of the chaetal formula (in particular, the occurrence of chaetae at all lateral positions in *M. brendae* and *M. sinica*); (2) the different extension of the dorsal vessel (which in *M. brendae* originates in VIII–IX; see ROTA, 1995); (3) the size of the coelomocytes (in both *M. brendae* and *M. sinica* such cells appear, after fixation, spindle-shaped to elliptical and twice as large as in *M. spongicola*); (4) the morphology of the spermathecae (in *M. sinica* the ectal ducts are spindle-shaped and devoid of accessory glands also at the ectal orifices). Furthermore, both *M. brendae* and *M. sinica* are reported from terrestrial soils (woods, meadows).

Marionina seminuda XIE and ROTA, 2001

Marionina seminuda: XIE and ROTA, 2001: 1423–1425, Figure 3.

Material examined: New Zealand, Lake Taupo, Horomatangi Reefs area, two specimens from NZ85 and 22 specimens from NZ86, 127 m and 145 m depth respectively, in *Heterorotula* sp. sponge, 19 October 1998, leg. KAREN HISSMAN.

Description: Body length: 1.3–1.8 mm; width 75–90 µm at III, 75–80 µm at V, 100 µm at XII. Segments 22 (based upon the observation of 8 specimens). Chaetal formula 0–0:0,2–2. Lateral chaetae absent; ventral chaetae commencing from III, 2 per bundle, missing in XII at maturity. Chaetae straight, with distinct ental hook, equal-sized in a bundle, 22–31 µm long (maximum in XXI). Prostomium pointing downwards, 50 µm wide at base. Head pore at 0/1. Epidermal gland cells inconspicuous. Clitellum in XII-2/3XIII; gland cells up to 11–13 µm wide, arranged in 16–18 transverse rows. Paired male pores ventrolateral, 60 µm apart from one another. Spermathecal pores in lateral lines at 4/5.

Brain concave anteriorly, deeply incised posteriorly. Postpharyngeal bulbs prominent. Pharyngeal glands merging dorsally at 4/5 and 5/6, separate at 6/7. Preclitellar nephridia most often at 6/7, 7/8 and 9/10 (but may be missing from 6/7), frequently unpaired. Anteseptal part of nephridia containing loops of nephridial canal; efferent duct arising postero-ventrally from postseptal. Dorsal vessel from XIII, bifurcating behind pharynx, with the two anterior loops reaching forward to the front of brain. Coelomocytes not seen. Seminal vesicles absent. Minimal seminal material free in XI–XII. Sperm funnels oval, 27–32 µm long and 13–16 µm wide; collar not demarcated, narrower than funnel. Vasa deferentia regularly coiled in XII, ca. 3 µm wide. Penial bulbs small (length 19 µm) and compact. One mature egg present at a time. Spermathecae confined to V, connected with oesophagus by short ental ducts. Ampullae globular, 10–13 µm in diameter, with a bundle of spermatozoa in lumen. Ectal ducts ca. 8 µm thick, covered with small gland cells, accompanied by one or two larger cells at the ectal orifices.

Habitat and distribution: Previously collected in moist to wet soils from a variety of sub-aerial habitats (pine woodland, wetlands, mountain sites with moss, grassy slopes under *Cinamomum camphora* (L.)) along the Changjiang (Yangtze) river basin in the Sichuan, Hubei, Anhui, and Jiangxi Provinces of China.

Remarks: The Taupo specimens conform in all major respects with the original description (XIE and ROTA, 2001). Differences concern the size distribution of chaetae (maximal in IV in the Chinese specimens), the distribution of preclitellar nephridia (lacking at 6/7 but present at 8/9 in the Chinese specimens), the size/development of some reproductive organs (penial bulbs were 25–28 µm long, spermathecal ampullae reached 22 µm in diameter, and seminal vesicles were well developed in the Chinese specimens). The features of the coelomocytes (characteristically opaque in the Chinese specimens) could not be compared as the Taupo worms appear to have extruded all such cells upon fixation.

Marionina riparia BRETSCHER, 1899

For synonymy see ROTA (1994).

Material examined: New Zealand, Lake Taupo, Horomatangi Reefs area, three specimens from NZ86, 145 m depth, in *Heterorotula* sp. sponge, 19 October 1998, leg. KAREN HISSMAN.

Description: Body length: 2.7–3.2 mm; width 200 µm at III, V and XII. Segments 26 (n = 3). Chaetal formula 1,2,3,4–2,3:3,4–2,3. Chaetae sigmoid, bundles occupying four symmetrical corners around body circumference; missing in XII at maturity. Somatic epidermal glands inconspicuous. Clitellar gland cells arranged irregularly. Male pores opening in posterior half of XII, with lateral epidermal lips. Four pairs of preclitellar nephridia (6/7–9/10). Each ovary a conspicuous ‘bush’ of maturing oocytes.

Habitat and distribution: *Marionina riparia* is primarily an aquatic species, living principally in riparian and bed sediments of various running and limnic water bodies, as well as among algae, aquatic plant debris and other submerged substrates. Frequent in springs, subterranean waters and mountain streams (up to the alpine zone) (KASPRZAK, 1986; DUMNICKA, 2000), it can be encountered at some distance from the water’s edge or in neighbouring terrestrial soils, provided they are wet. KAHL and KONOPACKA (1981) recorded *M. riparia* in a mixed sample of *Spongilla lacustris* (L.) and *Ephydatia fluviatilis* (L.) from river Pilica, northeast Poland, while a review of the southern Polish records by DUMNICKA (2000) noted its presence in rivers with some level of pollution and the heated Konin lake system (cited sources: KAHL, 1983 and KASPRZAK, 1977, respectively). Distributed throughout Europe and North Africa, *M. riparia* is also known from Turkey, Lebanon, and China (WANG *et al.*, 1999).

4. Discussion

4.1. Ecology

The occurrence of enchytraeids in lakes has been recently reviewed by TIMM (1996). Their presence in the profundal zone is poorly known, but most available records suggest that the family typically colonizes the sediments of oligotrophic waterbodies, as these are less subject to hypoxic conditions. Freshwater sponges are also generally known as thriving in relatively clear, unproductive waters, where a continuous oxygen supply is ensured. However, eutrophic or organic-rich waters in general, with high densities of bacteria, represent the optimal habitat or favour a flourishing growth of many species in both tropical and temperate areas (MANCONI and PRONZATO, 1991, 2002; PRONZATO and MANCONI, 1991, 2002). Indeed, although both enchytraeids and sponges can live at depths of 1,000 m and more, as in Lake Baikal (MARTIN *et al.*, 1999; A. GEBRUCK, cited in DE RONDE *et al.*, 2002), neither group seems to normally represent a major component of the profundal benthos of lakes. An

ecological (trophic) association of the two taxa had not been seriously considered previously; available evidence suggested, at most, an opportunistic colonization of sponges (or sponge remains) by oligochaete populations, particularly in lotic habitats. For instance, OMODEO and COATES (2001) explained the abundance of sponge spicules and the unusually small proportion of sand grains in the gut contents of certain Alluroididae from Guyana streams, by suggesting that those relatively large worms ($30\text{--}32 \times 0.8\text{--}0.9$ mm) dwell among the debris of dead sponges. KONOPACKA and SICINSKI (1985) recorded a remarkable number of Oligochaeta and Chironomidae inhabiting *Spongilla lacustris* (L.) in River Gac, northeast Poland, with the greater densities and diversity of the two groups occurring among the dead sponge bodies of hibernating colonies from September to February. The analysis of the oligochaete gut contents (KAHL and KONOPACKA, 1981) revealed only a very few siliceous spicules, which were "probably ingested incidentally with other food", whereas "it may be assumed that the sponge body is a very favourable habitat for Oligochaeta, especially for tiny forms; sponge canals offer them, besides shelter, also the needed amount of nourishment". Indeed, the sponge-dwelling oligochaete assemblage in the River Gac was dominated by members of the small-sized Naididae; Enchytraeidae were also very frequent but, like Tubificidae, mostly were represented by immatures and thus were not identified (KAHL and KONOPACKA, 1981). Interestingly, however, in a reference sponge sample from the River Pilica (of which the River Gac is a tributary), the same authors identified *Marionina riparia*. To the best of our knowledge, the only previous record of oligochaetes associated with lake-dwelling sponges included members of Naididae, Propappidae, Lumbriculidae and Tubificidae found on the basal surface and in cavities between the substrate and the base of *Lubomirskia baicalensis* (PALLAS, 1773) (Demospongiae: Haplosclerida: Spongillina: Lubomirskiidae), a shallow-water (4–15 m) endemic of Lake Baikal (KAMALTYNOV *et al.*, 1993).

Enchytraeids living in profundal lake sediments are mostly small, which partly explains why, in past studies, they were commonly underreported or missing from samples, unless methods for meiobenthos had been used (TIMM, 1996). The three *Marionina* species herein reported are no exception: their body sizes (overall range: $1.3\text{--}3.2 \times 0.1\text{--}0.2$ mm) approach the minimum reported in the family (ROTA, 2001). Such miniature worms satisfy the structural constraints for being inhabitants of the smaller canals of sponges. The *Heterorotula* sponges found at the bottom of Taupo are 15 cm in average individual diameter and rise up to 25 cm above the substrate. Their bodies are massive, compressible but fragile, strongly lobated or flabellated, with the surface perforated by many small dermal pores. Water enters through such inhalant openings towards large subdermal cavities and passes out of the sponge through exhalant canals to large openings or oscula (up to 7–8 mm in diameter) located at the summit of some lobes. The branched tubular cavities forming the spongocoel are 0.3–1 mm in diameter.

"The filtration activity and excretion of biologically active metabolites make freshwater sponges powerful agents of environment formation. They provide specific conditions for life of many plants and animals" (TRYLIS, 1997; see also PRONZATO and MANCONI, 2002). It is thus unlikely that the Taupo sponges act as a neutral substrate for their associate invertebrate community and that the latter finds no benefit from living inside them. But how intimate can the sponge-enchytraeid association be? And how likely is it that none of the enchytraeid species is sponge-specific, but merely background lake fauna that, at least near the vent sites, find the internal sponge cavities to be a more favourable chemical/physical microhabitat or a concentration of food items?

All previous reports of enchytraeids living symbiotically with other animals have ultimately been considered cases of ectocommensalism, or opportunistic associations providing the worms with a safe milieu in critical habitats. For instance, DRAGO (1887) initially described his *Epithelphusa* (= *Lumbricillus*) *catanensis* as a frequent and abundant parasite of the gills of the river crab *Thelphusa fluviatilis* (= *Potamon fluviatile*) in Sicily. Later however, DRAGO (1899) noted that (1) no harm was evident in the host, (2) the worm's gut contents always

merely consisted of plant and inorganic debris, and (3) the degree of dependence upon the host not even had to be strong because, although all life history stages, including cocoons, were found in the crab's branchial chambers, the worms could survive free-living in a water dish for several days. HEALY (1996) recorded small enchytraeids and other oligochaetes, along with polychaetes, mites, chironomid larvae, and small amphipods, living cryptically among barnacles (in grooves between the skeletal plates and in empty shells) on wave exposed rocky shores, but she found the same enchytraeid species also occurring among the adjacent algal and lichen turfs and in mussel beds, as well as free-living in sediments in nearby rocks crevices. The few species found to live on the surface of earthworms (*Pelmatodrilus planariformis* MOORE, 1943, *Aspidodrilus kelsalli* BAYLIS, 1914 and *Fridericia parasitica* CERNOSVITOV, 1928) are the only epizotic Enchytraeidae showing structural modifications for taking a hold on the host, yet even for these species, there are no indications that the nutritional interaction extends beyond that of commensalism (GELDER, 1980).

Beside being preadapted as concerns size and form, the three *Marionina* species discussed herein show no morphological specialization for life inside sponges, nor appear to ingest their host's tissue or spicules. It can thus be assumed that their association with sponges be, once again for the family, just commensalistic, and indeed *M. riparia* and *M. seminuda* normally thrive free in riparial sediments or in wet soil. As mentioned above, *M. riparia* has previously been recorded in river sponges (KAHL and KONOPACKA, 1981), as well as in thermally disturbed waterbodies (KASPRZAK, 1977). However, a depth record of 145 m is unprecedented for the species; prior to the present study, its occurrence in lakes was thought to be restricted to the sandy sublittoral; CERNOSVITOV, 1942; TIMM, 1996. Future research should focus on determining whether nestling among sponges is essential for these worms to survive in the deepest zone of Taupo or simply enables them to colonize an otherwise physically unfavourable profundal area. For the time being, the question of sponge specificity/opportunism by *M. spongicola* remains open.

The Taupo deep vents produce relatively high levels of toxic elements and water temperature variations, but this does not prevent the sponges from forming dense assemblages and actively reproducing nearby, which indicates that they well tolerate these and other effects of venting. DE RONDE *et al.* (2002) suggested the possibility that the Taupo sponges may use detoxification mechanisms (cf. RICHELLE-MAURER *et al.*, 1994). Inhabiting such filter-feeding organisms offers the evident advantages of being in a milieu with never-ending water flowing, certainly ensuring more oxygen availability, as well as a concentration of microorganisms and organic detritus taken directly from the water column, and a lower exposure to potentially toxic compounds than in free sediments (see DE RONDE *et al.*, 2002, Table 1). Additional sampling in different sites of the lake and a survey of other freshwater habitats in the North and the South Island will tell how frequent the sponge-enchytraeid association is in this geographical area.

4.2. Zoogeography

Limited data are available to define the origin/distribution of the three *Marionina* species on a larger, zoogeographical scale. Prior to this study, the genus *Marionina*, a large, cosmopolitan, phylogenetically heterogeneous assemblage in need of reassessment (XIE and ROTA, 2001), had not been recorded from inland habitats in New Zealand or Australia. In fact, prior to the present study, the two taxa described by BENHAM in 1904, *Enchytraeus simulans* from Lake Taupo (depth unknown) and *Achaeta maorica* from Lake Manapouri (South Island; from 107 m depth), had been the only enchytraeids listed for New Zealand. Nor, on the other hand, have much larger collections and taxonomic efforts been made in non-marine habitats of Australia. This part of the world is thus virtually a blank spot regarding taxonomy and biodiversity studies of soil-dwelling and limnic Enchytraeidae.

In any case, the lineages represented by the three sponge-associates of Taupo seem to be anything but endemic: *Marionina riparia* occurs throughout Europe, northern Africa and the Middle East and has recently been recorded in China (WANG *et al.*, 1999); *M. seminuda* is widespread along the Yangtze River Basin (XIE and ROTA, 2001) and, like *M. spongicola*, shows its closest affinities with Palaearctic congeners.

BENHAM (1904) first commented on the lake-dwelling oligochaete fauna of New Zealand as being notable for its exotic nature. This can be particularly true for areas of tormented geological history such as the central North Island. The currently active part of this region, the Taupo Volcanic Zone (TVZ), contains all late Pliocene to Quaternary volcanic activity in the North Island resulting from subduction of the oceanic Pacific plate beneath the Australian plate. The TVZ has produced at least 10,000 km³ of magma or >90% of the eruptions known in New Zealand over the last 2 Ma (WILSON *et al.*, 1995). The volcano under Lake Taupo has erupted 28 times during the past 27,000 years, and the Horomatangi Reefs are in the exact area of the most recent, massive (about 100 km³) eruption of 186 AD. That eruption is acknowledged as the world's largest volcanic eruption in historical times, with its effects in the sky recorded in Roman and Chinese literature (WILSON *et al.*, 1980). Forests in the surroundings were buried in meters of volcanic fallout (e.g., CLARKSON *et al.*, 1988) and it is estimated that if the same eruption occurred today, ashfall and other debris would cause chaos from Hamilton to Palmerston North. Such a devastating event and the subsequent changes in soils and climates must have heavily re-shaped the landscape of the central North Island, and no doubt all inland waters in that area became azoic.

It is very likely, in fact, that none of the invertebrate populations presently inhabiting the sediments of Lake Taupo descended directly from those present before the eruption in 186 AD; rather, all of the animal communities now present have developed through gradual recolonization from other parts of the country. On the other hand, it should be emphasized that few lakes in New Zealand presently retain their natural or original indigenous biodiversity, in large part because of the impacts from land use changes and invasions of alien aquatic species. The large number of alien introductions since the beginning of European settlement, and the superior competitiveness and vigour of many alien aquatic plants, has resulted in the displacement of native vegetation in many lakes (J. CLAYTON, in "New Zealand native plants for use in aquariums and ponds", <http://www.thekrib.com/Plants/Plants/NZ/>, 29 October 1998; URL active as of October 2003). The import of exotic aquatic plants may have acted as vector for the accidental introduction of some invasive invertebrates, such as the cosmopolitan freshwater jellyfish *Craspedacusta sowerbyi* (LANKESTER, 1880) (Hydrozoa: Limnomedusae: Olindiidae), first recorded in Lake Taupo in the 1950s and now collected from all over mainland New Zealand (see BOOTHROYD *et al.*, 2002). Recent evidence points to the Yantze region of China as the native place of *C. sowerbyi* (see BOUILLON and BOERO, 2000), which would curiously parallel the apparent zoogeographic origin of *Marionina seminuda*.

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