DISCOVERY

58(317), May 2022

Zoogeography and Diversity of Endemic Pill-Millipedes in the Southern Hemisphere (Sphaerotheriida: Diplopoda)

Cheviri N. Ambarish[1], Kandikere R. Sridhar[2*]

To Cite:
Ambarish CN, Sridhar KR. Zoogeography and Diversity of Endemic Pill-Millipedes in the Southern Hemisphere (Sphaerotheriida: Diplopoda). *Discovery*, 2022, 58(317), 385-398

Author Affiliation:
[1]Department of Biochemistry, St. Aloysius College, Mangalore, Karnataka, India
[2]Department of Biosciences, Mangalore University, Mangalagangotri, Karnataka, India

***Corresponding author:**
Department of Biosciences, Mangalore University, Mangalagangotri, Karnataka, India
E-mail: kandikere@gmail.com

Peer-Review History
Received: 20 February 2022
Reviewed & Revised: 23/February/2022 to 02/April/2022
Accepted: 05 April 2022
Published: May 2022

Peer-Review Model
External peer-review was done through double-blind method.

ABSTRACT

Millipedes are globally distributed most diversified soil fauna on the earth. Currently estimated species richness of Diplopoda is over 80,000, they are mainly confined to the tropical and subtropical regions. Pill-millipedes are of Gondwanan origin with large-bodied detritus feeders feeding on a variety of litter and surviving up to 12 years. There is little recent study on their phylogeny even though research on pill-millipedes is centaury old. The phylogenetic analysis revealed that pill-millipedes originated in the Pre-Jurassic era and they are microendemic in distribution. It is suggested that the richness of the litter strata in tropical or subtropical habitats helped the succession of pill-millipedes since Pre-Jurassic periods. Their microendemic nature and slow-moving nature severely hindered their distribution. They are under threat owing to human activities like deforestation and unconventional agricultural practices. Faunistic records showed many species are extinct and more emphasis should be focused on their conservation. Conservation of pill-millipedes is the need of the hour and connecting patchy forests, agricultural lands and reserve forests for conservation. The present review encompasses a general account of millipedes with diversity, phylogeny, distribution, endemism and conservation of pill-millipedes.

Keywords: Classification, conservation, distribution, endemism, phylogeny, threats

1. INTRODUCTION

According to Giller (1996), decomposition (up to 60–90%) of terrestrial primary production takes place in the soil as a main ecological service. Plant detritus (e.g., leaf, bark and woody litter) are often not utilizable immediately as many of the nutrients are locked up in highly complex physical structures. Such recalcitrant detritus decomposition is controlled by several edaphic factors (e.g., climate, litter quality and soil fauna) (Coûteaux et al., 1995; González and Seastedt, 2001; Zhang et al., 2008). Breakdown of the physical structure of the organic matter is necessary for transformation through microbial mineralization. Mechanical breakdown serves as a key factor necessary to increase microbial activities, which happens via limited routes and such a non-biological phenomenon through

DISCOVERY
SCIENTIFIC SOCIETY

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

natural seasonal weathering requires an extended time frame. This leads to the degradation of waxy outer surfaces of leaf and bark litter and the eventual breakdown of structural components into simpler constituents (Chapin et al., 2002). The climatic conditions and litter chemistry are the major regulators of plant litter decomposition (Meentenmeyer, 1978; Aerts, 1997). Climatic conditions in humid tropics have narrow variations, thus litter chemistry significantly plays an important role in determining the transformation of detritus by soil invertebrates as well as microbiota (Henegan et al., 1999; González et al., 2001).

One of the most efficient biological routes of mechanical breakdown of plant detritus is by detritivorous soil macroinvertebrates as an integral part of the soil ecosystem (e.g., earthworms, snails, insects, mites and millipedes). Arthropoda, the earth's major component of biological diversity has a dynamic role in ecosystem services especially the decomposition of plant-derived litter and humus formation (Plowman, 1990; Wilson, 1992; Stork, 1993; Golovatch et al., 1995; Giller, 1996). They fragment organic matter through grinding (increasing the surface area), mixing (with soil minerals) and enhancing channeling (improve the soil structure) (Nicholson et al., 1966; Webb, 1977; Hanlon, 1981; Coûteaux and Bottner, 1994). Such fragmentation results in an increase in surface to volume ratio of detritus and facilitates the growth of mineralizing microorganisms (e.g., bacteria and fungi). Even though various methods have been employed to understand litter decomposition in terrestrial ecosystems, Prescott (2005) argued that an accurate estimate of litter decomposition in forests depends on the fate of fecal material generated by the soil fauna as a product of litter breakdown. The fecal pellets of millipedes in temperate regions (*Glomeris marginata*) attract earthworms (*Octolasion lacteum* and *Lumbricus castaneus*), thus incorporating the fecal pellets into the soil and elevating carbon mineralization (Bonkowski et al., 1998; Scheu and Wolters, 1991). Stork and Eggleton (1992) proposed a sole index of soil quality by combining non-biological (chemical, hydrological and physical) with biological (microbial) criteria to account for the function of soil invertebrates with their diversity and species richness as keystone species. The activity of millipedes is governed by the chemistry of litter at wide narrow spatial scales and thus they are reliable indicators of qualities of soil (Warren and Zou, 2002). Interestingly, giant millipede *Seychelleptus seychellarum* (Spirostreptidae) endemic to Seychelles consumes litter of 73.6 kg/day has been considered a keystone species in Cousine Island (Lawrence and Samways, 2003).

2. MILLIPEDES

The fourth-largest class of Arthropoda is the Diplopoda, which belongs to the Devonian period as well as the largest terrestrial arthropods (after Hexapoda Crustacea and Chelicerata) (Bueno-Villegas et al., 2003; Sierwald and Bond, 2007; Shear and Edgecombe, 2010). Among 80,000 estimated species in all continents (except for the Antarctica), 12,000 described species are assigned to 2,947 genera in 145 families under 15 orders with three subclasses (Helminthomorpha, Penicillata and Pentazonia) (Hoffman 1980; WCMC, 1992; Heywood and Watson, 1995; Golovatch et al., 1995; Hoffman et al., 2002; Bueno-Villegas et al., 2003; Shelley, 2003; Sierwald and Bond, 2007). Millipedes are housed in 268 repositories in 143 countries (9 and 77 of them consist of over 20,000 and over 1,000 specimens, respectively). However, Asia, Africa, Central America and South America are deficient of millipede collections (Sierwald and Reft, 2004). Even though the class Diplopoda is the most diverse among terrestrial organisms, their morphology phylogeny and diversity are less studied compared to other arthropod groups (Sierwald and Bond, 2007).

According to Sierwald and Bond (2007), currently, eight orders of millipedes have been extinct (Amynilyspedida, Archidesmida, Arthropleurida, Cowiedesmida, Eoarthropleurida, Euphorberiida, Microdecemplicida and Pleurojulida). They are the oldest millipedes in the mid-Silurian (*Cowiedesmus eroticopodus*) and Lower Devonian (*Archidesmus macnicoli*) periods. In the Carboniferous period, several millipedes including pill-millipedes were recovered (e.g., order: Amynilyspedida) (Hannibal and Feldmann, 1981). A decline in fossil records was seen subsequently and several Spirobolida were described from Mongolia in the late-Cretaceous period (Kraus, 1974; Dzik, 1975). Amber-preserved millipedes have been collected belonged to the Oligocene period (Shear, 1981). Millipedes belonging to Callipodida, Choreumatida, Glomerida, Polyxenida and Polyzoniida are known from the Baltic amber (Sierwald and Bond, 2007).

Millipedes show a wide range of lifestyles, reproductive strategies and lifespan (1-11 years) (Carrel, 1990; Dangerfield and Telford, 1991). The extended lifespan has been linked with the consumption of poor quality dietary sources (Blower, 1985). Tropical millipedes possess a larger body size than their temperate equivalents (e.g., Julidae and Spirostreptidae; 2 g vs. 40 g) (Lawrence, 1984; Dangerfield and Telford, 1989). Similarly, increased body size of millipedes inhabiting high altitudes was reported Enghoff and Báez (1993). The larger body size is advantageous to tolerate increased moisture stress and enhance the burrowing ability (Manton, 1977; Baker, 1980). The size of the body is known to influence energy acquisition as well as utilization, which in turn, affects the decomposition rates of organic matter (Peterson and Luxton, 1982). Millipedes are rich in tropical and temperate forests, but some have adapted to extreme habitats (e.g., freshwater habitats, marine littoral habitats, deserts, tundra and caves) (Golovatch and Kime, 2009). Depending on the structural features, five morphotypes have been identified: i) Bristly millipedes or bark-dwellers

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

(Polyxenidae); ii) Pill-millipedes or rollers (Glomeridae and Sphaerotheriidae); iii) Bulldozers or rammers (Julidae); iv) Wedge or litter-splitters (Polydesmidae); v) Borers (Platydesmidae) (Kime and Golovatch, 2000). Millipedes contribute significantly to the turnover of organic matter in soil through fragmentation, ingestion and fecal pellet production. Mechanical fragmentation of plant detritus influences the rates of decomposition by conditioning suitable for microbial processing (Swift et al., 1979). Millipedes are known to be highly sensitive even to a single factor like litter thickness, and thus inventory of their richness and diversity helps to explicitly evaluate the negative or positive impacts on forestry or agricultural practices.

The order Glomerida consists up to 280 species in 33 genera, which has Holarctic distribution (Southern North America, Europe and North Africa, and Asia except for India) (Wesener, 2010; Shelley and Golovatch, 2011). On the contrary, the order Sphaerotheriida encompasses up to 343 species in 25 genera endemic to the Ethiopian, Oriental and Australian zoogeographic regions (Wesener, 2014). The following sections briefly review literature pertaining to pill-millipedes (order, Sphaerotheriida) distributed in various paleotropic regions.

3. DIVERSITY AND DISTRIBUTION

The order Sphaerotheriida consists of two families Sphaerotheriidae and Zephroniidae with two (Sphaerotheriinae and Arthrosphaerinae) and three (Zephroniinae, Castanotheriinae and Rajasphaerinae) subfamilies, respectively (Fig. 1). The subfamily Sphaerotheriinae consists of two tribes: Sphaerotheriini (two genera) and Cyliosomatini (three genera). The subfamily Arthrosphaerinae also consists of two tribes: Arthrosphaerini (one genus) and Zoosphaeriini (three genera). The family Zephroniidae consists of three subfamilies (Zephroniinae, Castanotheriinae and Rajasphaerinae). The subfamily Zephroniinae has two tribes: Zephroniini and Sphaeropoeini with nine and three genera, respectively. The subfamilies Castanotheriinae and Rajasphaerinae consist of three genera and one genus, respectively. Overall, the family Sphaerotheriidae encompasses 201 described species in 9 genera, while the family Zephroniidae has 142 described species in 16 genera. Species belonging to the order Sphaerotheriida are microendemic to the Ethiopian (130 species in 6 genera), Oriental (181 species in 16 genera) and Australian (32 species in 3 genera) zoogeographic regions (Wesener et al., 2010a; Wesener, 2014) (Fig. 2).

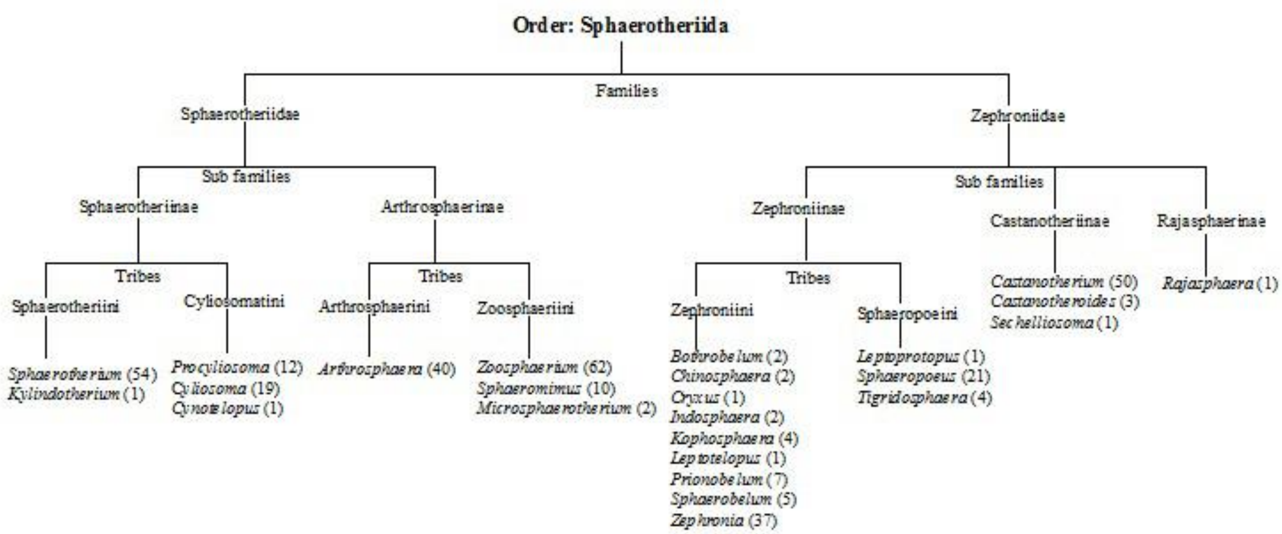

Figure 1. Current scheme of classification of the Order Sphaerotheriida (number of species in parentheses).

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

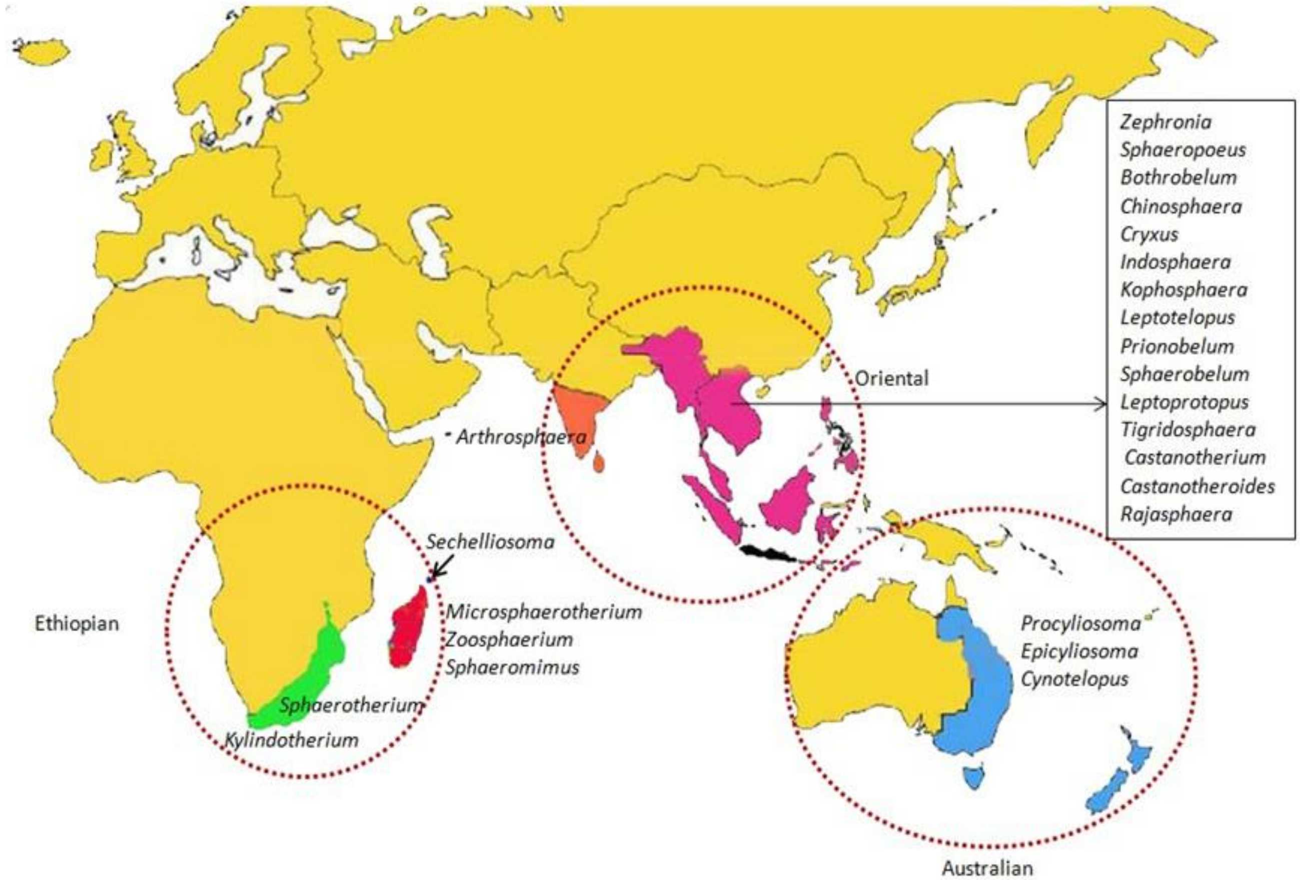

Figure 2. Distribution map of Sphaerotheriida in Ethiopian, Oriental and Australian zoogeographic regions.

3.1 *Sphaerotheriidae*

Individuals of the family Sphaerotheriidae are giant pill-millipedes with disjunct distribution predominantly in the Southern Hemisphere (South Africa, Madagascar and Indo-Australia) (Jeekel, 1974). Subsequently, wiped out in the intermediary geographic locations owing to hostile climatic circumstances. Currently, up to 201 nominal species in nine genera have been described from Southern Africa, Madagascar, India, Sri Lanka, Australia and New Zealand (Wesener et al., 2010a; Wesener, 2014).

Fifty-four species in the genus *Sphaerotherium* and one species *Kylindotherium leve* were recorded from South Africa (Wesener and Vanden Spiegel, 2009). Six species of *Sphaerotherium* are known from Northern South Africa (Redi et al., 2005). *Sphaerotherium punctulatum* and *S. giganteum* were broadly spread in post-mining transformed, naturally regenerated and mature dune forests, while the *Sphaerotherium* spp. 1, 2 and 3 were confined to the mature sites and another *Sphaerotherium* sp. was found in post-mining transformed and mature sites in South Africa.

Up to 62 species of *Zoosphaerium* (Pocock, 1895; Wesener et al., 2010b; Wesener, 2014), 10 species of *Sphaeromimus* (De Saussure and Zehntner, 1902; Wesener, et al., 2014) and two species of *Microsphaerotherium* (Wesener and Van den Spiegel, 2007) were explored from the Madagascar. According to Wesener and Sierwald (2005a), the genus *Sphaeromimus* shares certain characteristics with other genera like *Arthrosphaera* as well as *Zoosphaerium*. De Saussure and Zehnter (1897) showed the genus *Sphaeromimus* as a single male specimen (*Sphaeromimus musicus*) from the Malagasy of Madagascar. Later, two new species of *Sphaeromimus* (*S. inexpectatus* and *S. splendidus*) have been described by Wesener and Sierwald (2005a) from the patches of littoral forests (Mandena and Sainte Luce) of southern Madagascar. All three species of *Sphaeromimus* collected from the forests were restricted to semi-humid habitats (1,000 m asl). *Sphaeromimus inexpectatus* was restricted to patches of the littoral forest floor of Mandena (5-30 cm dry leaf litter covered with fruits). In Sainte Luce littoral rainforest, juveniles and adults of *S. splendidus* were found in 30-80 cm thick wet leaf litter. Recently, Wesener et al. (2014) discovered seven new species of *Sphaeromimus* (*S. andohahela*, *S. andrahomana, S. ivohibe*, *S. lavasoa*, *S. saintelucei, S. titanus* and *S. vatovavy*) in Madagascar. As these species are microendemic, human interference in such littoral forest patches and mining activities leads to extinction of these millipedes. Fascinatingly, the members of the genus

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

Zoosphaerium were also found in three collection sites along with *Sphaeromimus*. Despite geographic barriers (e.g., rivers and hills) amid the Sainte Luce and Mandena littoral rainforests, the annual precipitation drastically differs, which might have geographically restricted these pill-millipedes. From the native woodland (100 and 120 m asl) and at a low altitude (87 m asl) in the mixed woodland of Marianne (Seychelles), Hill et al. (2002) collected two individuals of *Cyliosomella furciparum*.

Table 1. Distribution of *Arthrosphaera* spp. on the Indian subcontinent.

Location code	Location	Pill-millipede	Reference
1	Adyanadka, Karnataka	*A. magna*	Ashwini (2003)
2	Agumbe, Karnataka	*Arthrosphaera* sp.; *A. lutescens*	Ashwini (2003); Kadamannaya (2008)
3	Alagarkovil hills, Tamil Nadu	*A. disticta*; *A. dalyi*	Achar (1986); Paulpandian (1966)
4	Annamalai hills	*A. davisoni*	Pocock (1899)
5	Bababudangiri hills, Karnataka	*A. carinata*	Attems (1936)
6	Basarikallu, Karnataka	*Arthrosphaera* sp.	Kadamannaya (2008)
7	Bombay, Maharashtra	*A. wroughtoni*; *A. atrisparsa*	Pocock (1899)
8	Chenganacherri, Kerala	*Arthrosphaera* sp.	Achar (1986)
9	Coimbatore, Tamil Nadu	*A. fumosa*	Pocock (1899)
10	Courtalam, Tamil Nadu	*A. gracilis*	Attems (1936)
11	Dharvad, Karnataka	*A. versicolor*	Kadamannaya (2008)
12	Ganjam, Orissa	*A. transitiva*	Attems (1936)
13	Kadaba, Karnataka	*A. dalyi*	Kadamannaya (2008)
14	Karkala, Karnataka	*A. magna*	Achar (1986)
15	Khandala hills, Maharashtra	*A. magna*; *A. davisoni*	Attems (1936); Achar (1986)
16	Kodaikanal, Tamil Nadu	*A. hendersoni*	Attems (1936)
17	Kollur, Karnataka	*Arthrosphaera* sp.	Ashwini (2003)
18	Kotagiri, Tamil Nadu	*A. marmorata*	Pocock (1899)
19	Kudremukh, Karnataka	*A. davisoni*	Kadamannaya (2008)
20	Kulthupuzha, Kerala	*A. lutescens*	Attems (1936)
21	Lonavala, Maharashtra	*A. magna*	Attems (1936)
22	Maddathoray, Tamil Nadu	*A. lutescens*	Attems (1936)
23	Madikeri, Karnataka	*A. fumosa*	Kadamannaya (2008); Achar (1986)
24	Madras, Tamil Nadu	*A. heterosticta*; *A. severa*; *A. inermis*; *A. pygostolis*	Pocock (1899), Attems (1936)
25	Marian shola, Palani hills, Tamil Nadu	*A. scholastica*	Attems (1936)
26	Nilgiri hills, Tamil Nadu	*A. thurstoni*	Pocock (1899)
27	Palani hills, Tamil Nadu	*A. dalyi*; *A. nitida*	Pocock (1899)
28	Parambikulam, Kerala	*A.craspedota*	Attems (1936)
29	Phonda Ghats, Maharashtra	*A. magna*	Attems (1936)
30	Rajahmundry, Andra Pradesh	*A. magna*	Attems (1936)
31	Sagara, Karnataka	*A. zebraica*	Chowdaiah (1966a)

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

32	Sakleshpur, Karnataka	*Arthrosphaera* sp.	Chowdaiah (1966a)
33	Salem, Tamil Nadu	*A. bicolor*	Pocock (1899)
34	Sampaje, Karnataka	*A. magna*	Ashwini (2003)
35	Shevaroy hills, Tamil Nadu	*A. magna*; *A.thurstoni*	Attems (1936); Pocock (1899)
36	Thirthahalli, Karnataka	*A. lutescens*	Achar (1986)
37	Thumbri, Karnataka	*A. carinata*	Ashwini (2003)
38	Travancore, Kerala	*A. inermis*	Attems (1936)
39	Ulvi, Karnataka	*A. craspedota*	Kadamannaya (2008)
40	Uppala, Karnataka	*A. hendersoni*	Kadamannaya (2008)
41	Varadalli, Karnataka	*A. zebraica*	Kadamannaya (2008)
42	Wayanad, Kerala	*A. nitida*	Achar (1986)

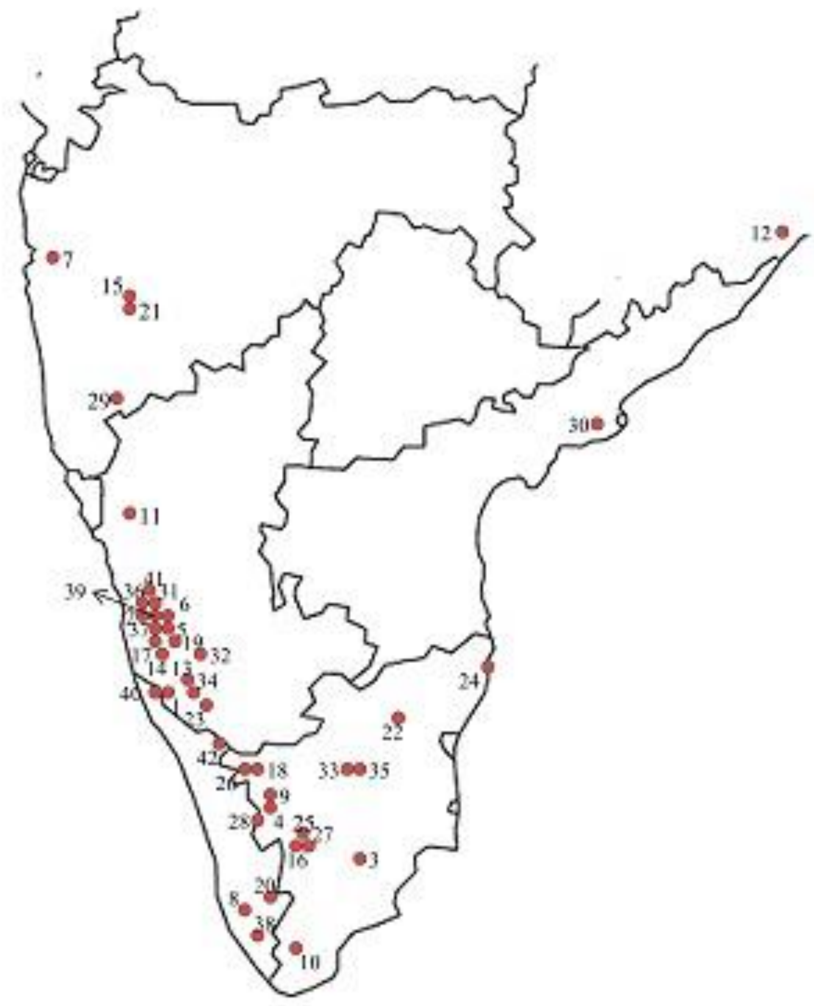

Figure 3. Distribution map of *Arthrosphaera* on the Indian Subcontinent (see location code in Table 1).

Sphaerotheriid millipedes are generally associated with tree species in Africa (Haacker and Fuchs, 1972). *Arthrosphaera brandti* was recorded in Amani (Tanzania) possibly introduced from Sri Lanka (Enghoff, 1977). Pocock (1899) published a monograph consisting of 27 species of *Arthrosphaera* based on the collections (Government Central Museum, Madras, India; Sri Lanka and

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

Burma). Subsequently, Attems (1936) gave an exhaustive report on the Indian diplopods and currently up to 40 species are found in the southern plateau in India as well as Sri Lanka (156 and 2,130 m asl) (Pocock, 1899; Attems, 1936; Chowdaiah, 1962, 1966a, b, c, 1969; Chowdaiah and Kanaka, 1974; Achar 1986; Janardanan and Ramachandran, 1983; Ashwini, 2003; Kadamannaya, 2008) (Table 1; Fig. 3). They are residents of regions with sufficient rainfall in the Western Ghats as well as Eastern Ghats forests of peninsular India (Maharashtra, Karnataka, Kerala, Tamil Nadu and Andhra Pradesh states). Some *Arthrosphaera* is common in the high altitudinal regimes of the Western Ghats (1,430-2,130 m asl) (e.g., *A. carinata*, *A. dalyi*, *A. davisoni*, *A. fumosa*, *A. hendersoni*, *A. nitida, A. scholastic* and *A. disticta*) (Attems, 1936; Achar, 1986; Sridhar and Ashwini, 2011; Ambarish and Sridhar, 2016, Ambarish and Sridhar, 2018). *Arthrosphaera magna* is extensively spread in the foothills of coastal regions of three states (Maharashtra, Karnataka and Tamil Nadu states) (156–450 m asl) (Attems, 1936; Achar, 1986; Ashwini and Sridhar, 2008). About five *Arthrosphaera* species *w*ere found in the Western Ghat forests in the one-time survey in nine localities each of forests and plantations (Kadamannaya et al., 2010). Seasonal survey (monthly) in the forests and adjoining plantations situated in the foothills of the Western Ghats showed extensive activities of pill-millipedes with high richness and biomass in mixed plantations managed by organic manure than in natural forests (Ashwini and Sridhar, 2006; Kadamannaya et al., 2010). The coastal regions (120-150 m asl) showed scanty distribution possibly owing to low forest cover, deficient litter strata and soil erosion (Ashwini, 2003). In the litter strata of the coastal *Acacia* plantation close to Uppala (Kerala State; ~10 km inside to the west coast), a few young *Arthrosphaera magna* were found. Similarly, *Arthrosphaera hendersoni* was plentiful in mixed plantations close to Uppala (Kadamannaya et al., 2010). Among the 10 species of *Arthrosphaera* found in Sri Lanka (*A. brandti*, *A. corrugata, A. dentigera, A. inermis, A. leopardina, A. noticeps, A. pilifera, A. rugosa, A. rugulosa and A. versicolor*) only *A. inermis* is common to India and Sri Lanka (Attems, 1936).

Australian Zoogeographic regions are dominated by pill-millipedes of the tribe Cyliosomatini. The pill-millipedes of Australia was explored by Silvestri (1917) by reporting 11 species of *Procyliosoma* and 15 species of *Epicyliosoma*. Jeekel (1986) recorded single species in the genus *Cynotelopus* from the Australian continent. Historically, the investigation of the pill-millipedes of New Zealand was revised by Silvestri (1917) and the pill-millipedes of New Zealand were placed under two genera: *Cyliosoma* and *Procyliosoma*. Holloway (1956) further revised the Sphaerotheriidae of New Zealand and authenticated five major species in the genus *Procyliosoma* (*Procyliosoma delacyi delacyi, P. delacyi striolatum, P. leiosomum, P. tuberculatum tuberculatum* and *P. tuberculatum westlandicum*). However, he also reported four additional species of *Procyliosoma* plentiful in decaying leaves as well as rotten logs in New Zealand forests (700 m asl). Meads and Fitzgerland (2001) found *P. tuberculatum* on Mokoia Island in New Zealand. *Sphaerotherium* species were also reported from New Zealand (*S. angulatum*, *S. leiosomum* and *S. novae-zealandiae*) (Holloway, 1956). Another endemic is Sphaerotheriid *Epicyliosoma excavatum* has recorded in Queensland as well as New South Wales (Jeekel, 1986).

3.2 *Zephroniidae*

Pill-millipedes belonging to the order Zephroniidae dominated in Southeast Asia and up to 142 nominal species have been described in 16 genera. Several species in the tribe Zephroniini and Sphaeropoeini were found in Southeast Asia (Wesener and Vanden Spiegel, 2009; Wesener, 2014). Recently four species such as *Tigridosphaera bimaculata, T. evansi, T. globusmagicus and T. zonata* have been reported by Jeekel (2001). The genus *Rajasphaera* consists of only one species (*Rajasphaera montana*) known from Borneo Island (Attems, 1935). Likewise, the genus *Sechelliosoma* also possesses single species (*Sechelliosoma forcipatum*) in the islands of Seychelles (Mauriès, 1980). *Zephronia siamensis* has been recognized in Kosichang-Chantaboon, Thailand (Hirst, 1907; Engohff, 2005). Similarly, *Zephronia moderata* as well as *Z. tivia* were found in Java and Sumatra, respectively (Chamberlin, 1945). *Prionobelum joliveti*, a new species has been described from Hainan (China) in comparison with *Zephronia hainani* by Mauriès (2001). Recently, Wongthamwanich et al. (2012) described another new species of the pill-millipede belonging to the genus *Sphaerobelum* based on molecular analysis from Northern Thailand.

4. ENDEMISM

Hopkin and Read (1992) opined that owing to limited mobility resulted in a high degree of speciation as well as the evolution of a large number of endemic millipedes. Unlike other fauna, millipedes have a narrow range and disjunct pattern of endemism. For instance, the East African coastal forests are well known for the diversity of endemic millipedes (Hoffman, 1993; Burgess, 1998). According to Hamer and Slotow (2002), a large number of described millipedes (243 species: ~50%) is known from single localities less than 10 km separation. In South Africa, the millipede's endemism has been divided into four classes: i) Site endemics (<10 km); ii) Local endemics (<70 km); iii) Regional endemics (<150 km); iv) South African endemics (inside the country) (Hamer and Slotow, 2002). This approach is judicious instead of following the area occupied based on the occurrence or lack of a species from one locality or between two or more localities. Endemic millipedes have numerous precise ecological and life-history characteristics like

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

poor powers of dispersal, restricted to sporadic habitats, strongly seasonal, only active during wet periods with low levels of fecundity (Harvey, 2002). Examination of millipedes having limited dispersal abilities is highly valued to follow their evolution and biogeographic history (Wesener et al., 2010a).

Wesener and Sierwald (2005a, b) described the endemism of *Sphaeromimus* and *Zoosphaerium* in Madagascar owing to limited abilities of dispersal. *Sphaeromimus inexpectatus* is microendemic in a patch of the littoral forest floor of Mandena (5-30 cm cover of dry leaf litter). In Sainte Luce littoral rainforest, juveniles and adults of *S. splendidus* were also microendemic and restricted (wet leaf litter thickness, 30-80 cm). Wesener (2009) emphasized endemism in Madagascar and stated that 26 out of 55 species of *Zoosphaerium* are geographically endemics and 42 species are ecosystem endemics.

Attems (1936) also opined that *Arthrosphaera* has a limited range of distribution (endemic to a single location) in Peninsular India. Such endemic and restricted distribution in Southern India as well as Sri Lanka, denote highly amiable soil edaphic factors for their inhabitation. The presence of more than one *Arthrosphaera* species was not seen despite inventorying 70 sites in 14 Western Ghat forests and plantations (Ashwini and Sridhar, 2008). Such a pattern of endemism with restricted distribution was also seen in one *Zoosphaerium* and two *Sphaeromimus* in the forest patches of Madagascar (Wesener and Wägele, 2007). Nevertheless, 2-3 species were noted within 200 m transects in the Western Ghat forests (Kadamannaya et al., 2010). The Western Ghat forests can be divided into different pill-millipede distributional zones (Ashwini, 2003; Kadamannaya, 2008): i) High altitude Kodagu (Madikeri) and Kudremukh (Basrikallu) regions are known for *A. fumosa* and *A. davisoni*, respectively; ii) The Western Ghat foothill regions are dominated by either *A. dalyi* (Kadaba and Uppinangadi) or *A. magna* (Karkala and Adyanadka); iii) Forests of Sagar and Shimoga are dominated by *A. disticta* (Shankaraghatta) and *A. zebraica* (Ulvi) (Western Ghats), respectively; iv) One of the gigantic *Arthrosphaera* sp. was confined to three Western Ghat locations (Hulikal, Kollur and Nittur).

5. THREATS AND CONSERVATION

It is necessary to understand various threats, possible conservation measures and futurology of pill-millipedes in peninsular India. Highly populated pill-millipedes are facing natural and human threats often in their habitats. The predators like mongoose, crow, wild boars and ants attack these millipedes often as their food source (Khadka et al., 2022). Mass cultivation of exotic plantations especially *Acacia*, *Casuarina, Eucalyptus, Grevillea* and *Tectona* in the Western Ghats has a major impact on the habitat destruction of *Arthrosphaera*. Litter generated from the exotic plantations is not easily degradable, not palatable due to rich phenolics or volatile compounds and changes the soil conditions unfavorable for pill-millipedes. The floors with exotic vegetation will affect the chemistry as well as the water-holding capacity of soil leading to interference feeding, egg laying, juvenile activities and molting of pill-millipedes. However, limited plants along with heterogeneous natural vegetation as forestry practice may not be a major threat to the invasion and survival of these millipedes. The road killing of pill-millipedes is a major issue of human interference. Construction of roads, dams and railway tracks demands a major area of virgin forests, which are the stabilized habitats of protection of pill-millipedes. Forest fragmentation, encroachment and use of chemicals in agriculture are the additional potential threats to the survival and activities of these endemic pill-millipedes.

Pill-millipedes mainly require moist and shredded litter strata for inhabitation and are thus traditionally considered important for forest-dwelling invertebrates. Surprisingly, most of the organically managed plantations of the foothill parts of Western Ghats are invaded by pill-millipedes. Unlike fast-moving and migrating arthropods, pill-millipedes are ground-dwelling with limited mobility need special restoration and conservation measures of their habitats. Specific conservation measures need to be implemented for pill-millipedes imply that such measures restore and protect much associated fauna of the ecosystem. The current fragmentary knowledge on the lifestyle and endemism of pill-millipedes hampers planning their restoration and conservation. One of the positive signs of restoration comes from the invasion of organically managed heterogeneous plantations by the species of *Arthrosphaera* in the foothills regions of the Western Ghats. Ecological restoration is an important issue in the conservation of several threatened soil fauna. Basic ecological knowledge of a specific target species is necessary for successful population restoration and supporting their new population (Bullock et al., 1996). Many threatened invertebrates rely on habitat restoration for their long-term security, thus restoration of existing local fauna has been considered an important approach in conservation and management strategies (New, 2009). Restoration measures have been proposed for threatened millipedes in Seychelles and Seychelles Island (Lawrence et al., 2012). Similarly, pill-millipedes should be considered for conservation on priority in the Western Ghats because of their long history of Gondwanan origin and active role in organic matter recycling. An ecological network has been projected for the conservation of Gondwanan giant pill-millipedes of Western Ghats by following the basic approaches proposed by Pryke and Samways (2012) (Fig. 4). The current landscape of Western Ghats reveals that most of the forests (including the sacred groves) are fragmented by roads and social forestry (monoculture or multiculture plantations). The ecological networks are necessary for those

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

forests under threat from agricultural activities and other anthropogenic pressures. The ecological network consists of corridors almost in a linear fashion sufficient to connect the patchy forest habitats. The corridor should mimic the wild habitats for the normal movement of millipedes and other fauna. The network connects the fragmented forest regions with other protected areas like scared groves and virgin forests in most parts of the Western Ghats.

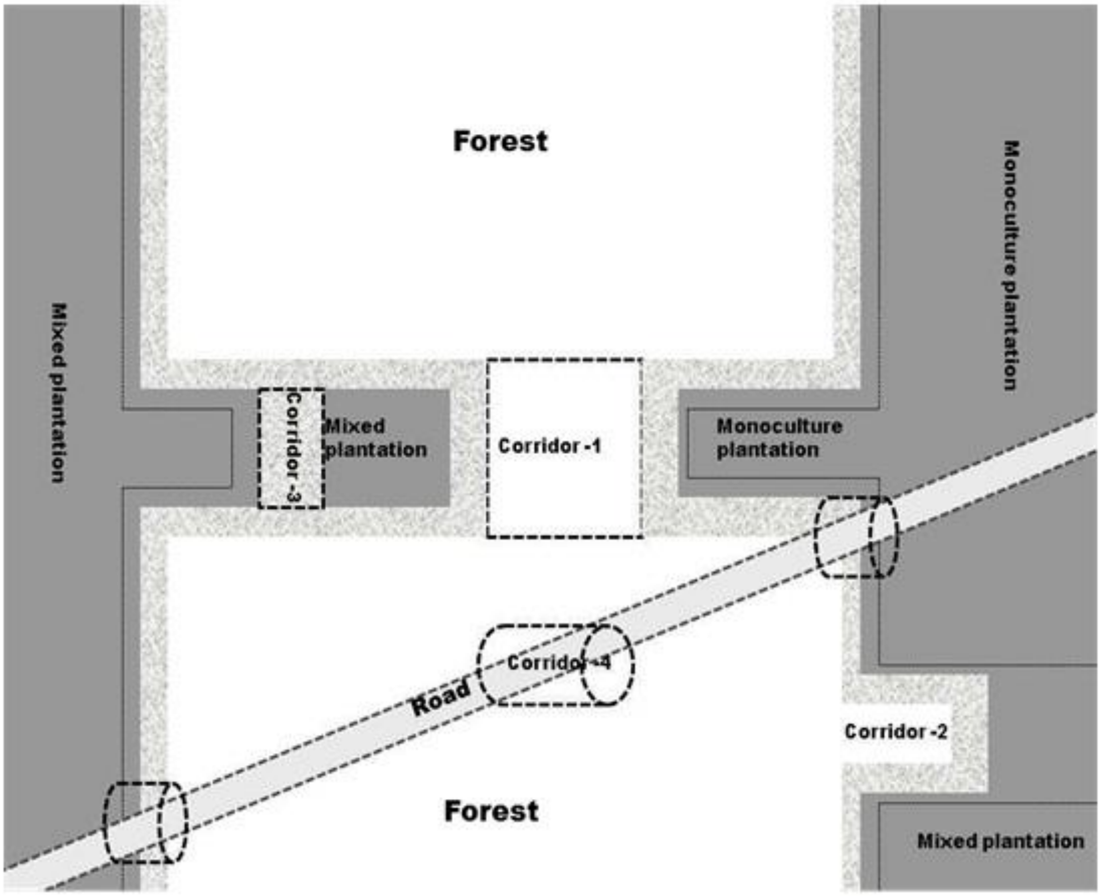

Figure 4. The illustration of possible ecological network corridors to connect fragmented forests and foothill plantations of the Western Ghats of India for conservation of threatened pill-millipedes (plain area, forest reserve and protected areas; gray shade, mixed and monoculture plantations (i.e. hub for pill-millipedes); dotted area, buffer zone. Corridor 1, connects forests to prevent human interference; Corridor 2, connects forests and plantations with interference by human inhabitation; Corridor 3, establishes a connection between patchy mixed plantations and buffer zone connections; Corridor. 4, to construct passage across the road/subways to connect fragmented forests and plantations for free movement of pill-millipedes (passage should mimic the natural habitat) (after Pryke and Samways, 2012).

Besides networking, various strategies could be implemented at local and regional scales for ecofriendly conservation and utilization of pill-millipedes of the west coast and Western Ghats of India:

i. Survey maps should be constructed for different locations of the west coast and Western Ghats (forests and plantations) consisting of pill-millipedes to earmark as 'pill-millipede banks' for restoration.
ii. Additional efforts should be invested to trace the distribution of pill-millipedes on ethnic knowledge of local people on the west coast and the Western Ghats.
iii. Organic farming should be practiced, the use of agricultural chemicals in pill-millipede invaded plantations should be curtailed, and heterogeneity of plantations and organic matter accumulation on the floor should be maintained.
iv. Activities of pill-millipedes will be during the monsoon period, which continues till post-monsoon, thus population expansion should be considered during such period to improve successful restoration.
v. Practice of urban organic waste utilization through pill-millipede compost round the year helps to meet the manure requirements at household or local or regional levels.

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

vi. Creating awareness and providing guidelines to local people for conservation and reap the advantage of ecological services of millipedes and earthworms to maintain the ecological balance.

vii. If large-scale cultivation is possible, the use of millipedes' byproducts in industries or for research (e.g., chitin and pharmaceuticals) should be supported.

6. OUTLOOK

Pill-millipedes belonging to the Order Sphaerotheriida are the important soil biotic component of the forest ecosystem in paleotropics. They serve as important indicators of soil quality and fertility. They are facing many threats due to human interference and need conservation strategies to utilize their ecosystem services. Conflicts between wildlife and human interests have increased in the recent past due to population explosion and anthropogenic pressures on wildlife habitats, especially the forest ecosystem. Ecological impacts of roads and traffic are important environmental issues for environmental managers and ecologists (Spellerberg, 2002). Such landscape alterations have a dramatic negative impact on the wildlife habitats. Western Ghats regions of India are experiencing extensive changes during the last century due to the development of plantations as well as townships. Fragmentation by roads severely affected the South African coastal forest dunes (Northern KwaZulu-Natal), especially by the mining and post-mining activities (Weiermans and Aarde, 2003). Millipede sensitivity serves as an authentic fingerprint of drastic climatic changes caused by human interference, especially litter chemistry at restricted spatial scales (1 m to 10 m) compared to earthworms (Warren and Zou, 2002; Jean-François, 2009). Climate change towards desiccation especially by vegetation clearing has a major threat to the decline of the millipede population in Australia (Moir et al., 2009). Goodman and Benstead (2005) opined that the priority of conservation depends on two important criteria like estimates of species diversity and levels of endemism. Unfortunately, the biological exploration of millipedes in the tropics is still in its infant stage in spite of their high biodiversity and heterogeneity.

Habitat preservation and restoration become utmost importance to conserve pill-millipedes and in turn soil fertility (Bonham et al., 2002; Snyder and Hendrix, 2008; Lawrence et al., 2012). Considerations and specific strategies need to be implemented to develop corridors for wildlife including millipedes during roadways through forests. In the west coast and Western Ghat plantations, two plantation practices are followed: i) Making basins for each plant/tree to apply organic manure and rows of bunds/trenches to enable water as well as manure application (e.g., *Areca*, coconut and coffee plantations), which has resulted in the migration of pill-millipedes from forests to plantations; ii) A significant association was found between the biomass of *Arthrosphaera* in the Western Ghats against soil organic carbon (Ashwini and Sridhar, 2008); in forest floors of foothill of the Western Ghats region (e.g., Mundaje, Gundya and Sampaje) consist of rocks and boulders with the increased population of *Arthrosphaera* owing to retention of sufficient organic matter in their terrain; large scale conversion or disruption of natural terrain exerts negative pressure on the habitat preference of pill-millipedes.

Pill-millipedes' sensitivity to ecological fluctuations at narrow spatial scales qualifies them to employ as reliable indicators of superior soil quality or superior habitat for their restoration. Preservation of native tree classes in the surroundings of the plantations produces mixed leaf litter suitable feedstock for pill-millipedes. Even though *ex situ* annual active periods of pill-millipedes are narrower than the rest of the soil fauna, they process a large quantity of organic matter and generate a huge amount of fecal pellets leading to improvement of soil fertility. There are many knowledge gaps on the pill-millipedes of paleotropics. Assessment of the diversity and ecological functions of pill-millipedes especially in Australian and Oriental Zoogeographic regions have been neglected. Understanding the precise conditions required for their activity and survival will be valuable for conservation as well as to consider them as indicator species. Studies on their behavior will be helpful to rear in the laboratory or controlled conditions in view of transforming organic solid wastes into manure. It is necessary to integrate morphological, cytological, biochemical and molecular strategies to strengthen pill-millipede taxonomy and phylogeny.

Funding

Department of Science and Technology, New Delhi, India [DST/INSPIRE Fellowship/2011/(294): Award # IF110540] to Cheviri N. Ambarish.

Acknowledgements

The authors are indebted to the Department of Biosciences, Mangalore University for providing the necessary facilities to pursue studies on pill-millipedes of the Western Ghats. We are thankful to Dr. S. Mahadevakumar, Karnataka State Open University, Mysore for his helpful suggestions.

Conflicts of interests

The authors declare that there are no conflicts of interests.

Data and materials availability

All data associated with this study are present in the paper.

REFERENCES AND NOTES

1. Achar, K.P. (1986) Analysis of male meiosis in seven species of Indian pill-millipede (Diplopoda: Myriapoda). *Caryologia*, 39, 89-101.
2. Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos*, 79, 439-449.
3. Ambarish, C N. & Sridhar K.R. (2018) occurrence, distribution and morphological description of 11 species of endemic giant pill-millipedes of the genus *Arthrosphaera* (Diplopoda: Sphaerotheriida: Arthrosphaeridae) in Southern India. *Proc. Zool. Soc.*, 71, 1-8.
4. Ambarish, C.N. and Sridhar, K.R. (2016) Pattern of distribution of endemic pill-millipedes in the southwestern India. *Proc. Zool. Soc.*, 69, 229-236.
5. Ashwini, K.M. & Sridhar, K.R. (2006) Seasonal abundance and activity of pill millipedes (*Arthrosphaera magna*) in mixed plantation and semi–evergreen forest of southern India. *Acta Oecol.*, 29, 27-32.
6. Ashwini, K.M. & Sridhar, K.R. (2008) Distribution of pill millipedes (*Arthrosphaera*) (Family: Sphaerotheriidae) and associated soil fauna in the Western Ghats and west Coast of India. *Pedosphere*, 18, 749-757.
7. Ashwini, K.M. (2003) *Ecological Studies on Indian Pill Millipede, Arthrosphaera magna*. Ph.D. Dissertation, Mangalore University, Mangalore, India.
8. Attems, C. (1935) Myriopoden von Sumatra. *Arch. Hydrobiol.*, 14, 114-142.
9. Attems, C. (1936) Diplopods of India. *Mem. Indian Mus.*, 11, 133-167.
10. Baker, G.H. (1980) The water and temperature relationships of *Ommatoiulus moreleti* (Diplopoda: Julidae). *J. Zool.*, 190, 97-108.
11. Blower, J.G. (1985) *Millipedes*. Linnean Society Synopses of the British Fauna (New Series), # 35, E.J. Brill/Dr. W. Backhuys, London.
12. Bonham, K.J., Mesibov, R. & Bashford, R. (2002) Diversity and abundance of some ground–dwelling invertebrates in plantation vs. native forests of Tasmania, Australia. *For. Ecol. Manage.*, 158, 237-247.
13. Bonkowski, M., Scheu, S. & Schaefer, M. (1998) Interactions of earthworms (*Octolasion lacteum*), millipedes (*Glomeris marginata*) and plants (*Hordelymus europaeus*) in a beech wood on a basalt hill: implications for litter decomposition and soil formation. *Appl. Soil Ecol.*, 9, 161-166.
14. Bueno-Villegas, J., Sierwald, P. & Bond, J.E. (2003) Diplopoda. In: Bousquets, J.L. & Morrone, J.J. (eds) pp. 569-599. *Biodiversidad, Taxonomia y Biogeografia de Artrópodos de México*, Pardova, Italy.
15. Bullock, J.M., Hodder, K.H., Manchester, S.J. & Stevenson, M.J. (1996) *Review of Information, Policy and Legislation on Species Translocation*. JNCC Report # 261. Species Conservation Branch, Peterborough, UK.
16. Burgess, N.D. (1998) Coastal forests of eastern Africa: Status, endemism patterns and their potential causes. *Biol. J. Linn. Soc.*, 64, 337-367.
17. Carrel, J.E. (1990) Chemical defence in the pill millipede *Glomeris marginata*. In: Minelli, A(ed), Proceedings of the 7th International congress of Myriapodology, E.J. Brill, Leiden, pp. 157-164.
18. Chamberlin, R.V. (1945) On some diplopods from the Indo-Australian archipelago. *Am. Mus. Novitates*, 1282, 1-43.
19. Chapin, F.S., Matson, P.A. & Mooney, H.A. (2002) *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York, pp. 26-32.
20. Chowdaiah, B.N. & Kanaka, R. (1974) Cytological studies in six species of pill–millipedes (Diplopoda–Myriapoda). *Caryologia*, 27, 55-64.
21. Chowdaiah, B.N. (1962) *Cytological Studies of Some Indian Diplopoda (Myriapoda)*. Ph.D. Dissertation, University of Mysore, India.
22. Chowdaiah, B.N. (1966a) Chromosome studies in two species of pill–millipedes (Diplopoda–Myriapoda). *Caryologia*, 19, 135-141.
23. Chowdaiah, B.N. (1966b) Cytological investigations on some Indian Diplopoda (Myriapoda). *Nature*, 210, 847.
24. Chowdaiah, B.N. (1966c) Cytological studies of some Indian Diplopoda - I (Myriapoda). *Cytologia*, 31, 294-301.
25. Chowdaiah, B.N. (1969) A note on the occurrence of chromatid bridges in the male of *Arthrosphaera* sp., a pill–millipede. *Current Science*, 7, 169-170.
26. Coûteaux, M.-M. & Bottner, P. (1994) Biological interactions between fauna and the microbial community, In: Ritz, K., Dighton, J. & Giller, K.E. (eds), *Beyond the*

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

Biomass: Compositional and Functional Analysis of Soil Microbial Communities Compositional and Functional Analysis of Soil Microbial Communities, Wiley, pp. 159-172.

27. Coûteaux, M.M., Bottner, P. & Berg, B. (1995) Litter decomposition, climate and litter quality. *Tr. Ecol. Evol.*, 10, 63-66.
28. Dangerfield, J.M. & Telford, S.R. (1991) Seasonal activity patterns of Julid millipedes in Zimbabwe. *J. Trop. Ecol.*, 7, 281-285.
29. Dangerfield, J.M. and Telford. S.R. (1989) Are millipedes important for soil fertility?. *Zimbawe Sci. News*, 23, 66-68.
30. De Saussure, H. & L. Zehnter. (1897) Atlas de Phistoire naturelle des Myriapodes. *Histoire Physique, Naturelle et Politique de Madagascar* 27, 1-12.
31. De Saussure, H. & Zehntner, L. (1902) Myriapodes de Madagascar. In: Grandidier (ed). *Histoire physique, naturelle et politique de Madagascar* 27. Alfred Grandidier, Paris.
32. Dzik, J. (1975) Sprobolid millipedes from the late Cretaceous of the Gobi desert, Mongolia. *Palaeontol. Polonica*, 33, 17-24.
33. Enghoff, H. & Báez, M. (1993) Evolution and habitat patterns in endemic millipedes of the genus *Dolichoiulus* (Diplopoda: Julidae) on the Canary Islands. With notes on distribution patterns of other Canarian species swarms. *Biol. J. Linn. Soc.*, 49, 277-301.
34. Enghoff, H. (1977) *Arthrosphaera brandti* (Humbert), a giant pill-millipede found in Tanzania, probably introduced from Sri Lanka (Diplopoda: Sphaerotheriidae). *Rev. Zool. Bot, Sr.*, 91, 997-999.
35. Enghoff, H. (2005) The millipedes of Thailand (Diplopoda). *Steenstrupia*, 29, 87-103.
36. Giller, P.S. (1996) The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiver. Conser.*, 5, 135-168.
37. Golovatch, S.I. & Kime, R.D. (2009) Millipede (Diplopoda) distributions: A review. *Soil Organ.*, 81, 565-597.
38. Golovatch, S.I., Hoffman. R.L, Adis, J. & de Morais, J.W. (1995) Identification plate for the millipede orders populating the Neotropical region south of central Mexico (Myriapoda: Diplopoda). *Stud. Neotrop. Fauna Environ.*, 30, 159-164.
39. González, G. & Seastedt, T.R. (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology*, 82, 955-964.
40. González, G., Ley, R.E., Schmidt, S.K., Zou, X. & Seastedt T.R. (2001) Soil ecological interactions: Comparisons between tropical and subalpine forests. *Oecologia*, 128, 549-556.
41. Goodman, S.M. & Benstead, J.P. (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39, 73-77.
42. Haacker, U. & Fuchs, S. (1972) Tree climbing in pill-millipedes. *Oecologia*, 10, 191-192.
43. Hamer, M.L. and Slotow, R.H. (2002) Conservation application of existing data for South African millipedes (Diplopoda). *Afr. Entomol.*, 10, 29-42.
44. Hanlon, R.D.G. (1981) Some factors influencing microbial growth on soil animal faeces, II. Bacterial and fungal growth on soil animal faeces. *Pedobiologia*, 21, 264-270.
45. Hannibal, J.T. & Feldmann, R.M. (1981) Systematics and functional morphology of Oniscomorph millipedes (Arthropoda: Diplopoda) from the Carboniferous of North America. *J. Palaeontol.*, 55, 730-746.
46. Harvey, M.S. (2002) Short-range endemism in the Australian fauna: some examples from non marine environments. *Inverte. Syst.*, 16, 555-570.
47. Henegan, L., Coleman, D.C., Zou, X., Jr. Crossley, D.A. & Haines, B.L. (1999) Soil macroarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. *Ecology*, 80, 1873-1882.
48. Heywood, V.H. & Watson, R.T. (1995) *Global Biodiversity Assessment*. United Nations Environment Programme, Cambridge University Press.
49. Hill, M.J., Matyot P., Vel, T.M., Parr, S.J. & Shah, N.J. (2002) *Marianne*. National Museum of Natural History Smithsonian Institution, Washington DC. *Attoll Res. Bull.*, 495, 157-176.
50. Hirst, A.S. (1907) On four new pill–millipedes from the Malay Peninsula and Siam. Annual Magazine Natural History 7th Series # 20, 215-219.
51. Hoffman, R.L. (1980) *Classification of the Diplopoda*. Muséum d'Histoire Naturelle, Genève, Switzerland.
52. Hoffman, R.L. (1993) Biogeography of East African montane forest millipedes. In: Lovett, J.C. & Wasser. S.K. (eds), *Biogeography and Ecology of the Rain Forests of Eastern Africa*, Cambridge University Press, Cambridge. pp. 103-115.
53. Hoffman, R.L., Golovatch, S.I., Adis, J. & de Morais, J.W. (2002) *Diplopoda*. In: Adis, J. (ed), Arachnida and Myriapoda, Pensoft, Sofia-Moscow, pp. 501-533.
54. Holloway, B.A. (1956) Revision of the New Zealand pill millipedes (Oniscomorpha, Sphaerotheridae). *Trans. Royal Soc. New Zeal.*, 84, 431-446.
55. Hopkin, S.P. & Read, H.J. (1992) *The Biology of Millipedes*. Oxford University Press, Oxford.
56. Janardanan, K.P. & Ramachandran, P. (1983) Observations on two new species of cephaline gregarines (protozoa: Sporozoa) of the genus *Stenoductus* Ramachandran, 1976 from Sphaerotheriid millipedes in Kerala, India. *Arc. Protistenkunde*, 127, 405-412.
57. Jean–François, D. (2009) Ecology of millipedes (Diplopoda) in the context of global change. *Soil Org.*, 81, 719-733.

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

58. Jeekel, C.A.W. (1974) The taxonomy and geography of the Sphaerotheriida (Diplopoda). *Symp. Zool. Soc. London*, 32, 41-52.
59. Jeekel, C.A.W. (1986) Millipedes from Australia, 10: Three interesting new species and a new genus (Diplopoda: Sphaerotheriida, Spirobolida, Polydesmida). *Beaufortia*, 36, 35-50.
60. Jeekel, C.A.W. (2001) A bibliographic catalogue of the Asiatic Sphaerotheriida (Diplopoda). *Myriapoda Memoranda*, 3, 5-38.
61. Kadamannaya, B.S. (2008) *Studies on Pill Millipedes of Western Ghats and West Coast of India*. Ph.D. Dissertation, Mangalore University, Mangalore, India.
62. Kadamannaya, B.S., Sridhar. K.R. & Sreepada, K.S. (2010) Assemblage and distribution of pill millipedes and earthworms in relation to soil edaphic features in the Western Ghats and the west coast of India. *Front. Agric. China.*, 4, 243-250.
63. Khadka BB, Pathak A, Khanal S, Paudel P. (2022). Trend of common crane (*Grus grus*) visit in Chitwan National Park of Nepal. *Species*, 23(71), 94-98
64. Kime, R.D. & Golovatch, S.I. (2000) Trends in the ecological strategies and evolution of millipedes (Diplopoda). *Biol. J. Linn. Soc.*, 69, 333-349.
65. Kraus, O. (1974) On the morphology of Palaeozoic Diplopids. *Symp. Zool. Soc. London*, 32, 13-22.
66. Lawrence, J.M. & Samways, M.J. (2003) Litter breakdown by the Seychelles giant millipede and the conservation of soil process on Cousine Island, Seychelles. *Biol. Conser.*, 113, 125-132.
67. Lawrence, J.M. (1984) *The Centipedes and Millipedes of Southern Africa: A Guide*. A.A. Balkema, Cape Town and Roterdam.
68. Lawrence, J.M., Samways, M.J., Kelly, J.A. & Henwood, J. (2012) Population dynamics of a threatened giant millipede: implications for restoration. *Inverte. Biol.*, 132, 46-51.
69. Manton, S.M. (1977) *The Arthropoda*. Oxford University Press, Oxford.
70. Mauriès, J.-P. (1980) Contributions álétude de la faune terrestre des îles granitiques de l_archipel des Séchelles. *Rev. Zool. Afr.*, 94, 138-168.
71. Mauriès, J.-P. (2001) Sur l'identité de *Zephronia hainani* Gressitt, 1941, à propos de la description d'un nouveau Prionobelum (Diplopoda, Sphaerotheriida, Sphaeropoeidae) de Haïnan, Chine. *Zoosystema*, 23, 131-142.
72. Meads, M.J. & Fitzgerald, B.M. (2001) *List of invertebrates on Mokoia Island, Lake Rotorua*. Conservation Advisory Science Notes No. 343, Department of Conservation, Wellington.
73. Meentenmeyer, V. (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*, 59, 465-472.
74. Moir, M.L., Brennan, K.E.C. & Harvey, M.S. (2009) Diversity, endemism and species turnover of millipedes within the south–western Australian global biodiversity hotspot. *J. Biogeogr.*, 36, 1958-1971.
75. Nicholson, P.B., Bocock, K.L. & Heath, O.W. (1966) Studies on the decomposition of the faecal pellets of a millipede *Glomeris marginata* (Villers). *J. Ecol.*, 54, 755-766.
76. Paulpandian, A.L. (1966) A note on the respiration of the pill-millipede *Arthrosphaera dalyi* (Pocock). *Current Science*, 35, 178-179.
77. Petersen, H. & Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos, 39*, 287-388.
78. Plowman, K.P. (1990) Forest–floor decomposers. In: Webb, L.J. & Kikkawa, J. (ed) *Australian Tropical Rainforests: Science-Values-Meaning*, CSIRO Publications, East Melborne, pp. 98-104.
79. Pocock, R.I. (1895) Descriptions of new genera of Zephroniidae, with brief preliminary Diagnoses of some new Species. *Ann. Mag. Nat. Hist.*, 16, 409-415.
80. Pocock, R.I. (1899) A monograph of the pill–millipedes (Zephroniidae) inhabiting India, Ceylon and Burma. *J. Bom. Nat. Hist. Soc.*, 12, 269-285.
81. Prescott, C.E. (2005) Do rates of litter decomposition tell us anything we really need to know? *For. Ecol. Manage.*, 220, 66-74.
82. Pryke, J.S. & Samways, M.J. (2012) Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. *J. Appl. Ecol.*, 49, 591-600.
83. Redi, B.H., van Aarde, R.J. & Wasener T.D. (2005) Coastal dune forest Development and the regeneration of millipede communities. *Restor. Ecol.*, 13, 284-291.
84. Scheu, S. & Wolters, V. (1991) Influence of fragmentation and bioturbation on the decomposition of 14C–labelled beech leaf litter. *Soil Biol. Biochem.*, 23, 1029-1034.
85. Shear, W.A. & Edgecombe, G.D. (2010) The geological record and phylogeny of the Myriapoda. *Arthro. Str. Develop.*, 39, 174-190.
86. Shear, W.A. (1981) Two fossil millipedes from the Dominican amber (Diplopoda: Chytodesmidae, Siphonophoridae). *Myriapodologica*, 1, 51-54.
87. Shelley, R. M. & Golovatch, S.I. (2011) Atlas of myriapod biogeography. I. Indigenous ordinal and supra-ordinal distributions in the Diplopoda: Perspectives on taxon origins and ages, and a hypothesis on the origin and early evolution of the class. *Insecta Mundi*, 0158, 1-134.
88. Shelley, R.M. (2003) A revised, annotated, family–level classification of the Diplopoda. *Arthropoda Selecta*, 11, 187-207.

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS

89. Sierwald, P. & Bond, J.E. (2007) Current status of the Myriapod Class Diplopoda (millipedes): Taxonomic diversity and phylogeny. *Ann. Rev. Entomol.*, 52, 401-420.
90. Sierwald, P. & Reft, A.J. (2004) The millipede collections of the world. *Fieldiana*, 103, 1-100.
91. Silvestri, F. (1917) Materiali per una revisione dei Diplopoda Oniscomorpha. II. Specie di Sphaerotheridae delle regioni australiana e neozelandese a me note. Bollettino del Laboratorio di Zoologia Generale e Agraria della Facoltà agraria in Portici 12, 61-85.
92. Snyder, B.A. & Hendrix, P.F. (2008) Current and potential roles of soil macroinvertebrates (earthworms, millipedes, and isopods) in ecological restoration. *Restor. Ecol.*, 16, 629-636.
93. Spellerberg, I. (2002) *Ecological Effects of Roads*. Science Publishers Inc. USA.
94. Sridhar, K.R. & Ashwini, K.M. (2011) Diversity, restoration and conservation of millipedes. In: Pullaiah T. (ed) *Biodiversity in India*, Volume # 5, pp. 1-38. Regency Publications, New Delhi.
95. Stork, N.E. & Eggleton, P. (1992) Invertebrates as determinants and indicators of soil quality. *Am. J. Alt. Agric.*, 7, 38-47.
96. Stork, N.E. (1993) How many species are there? *Biodiver. Conser.*, 2, 215-232.
97. Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, Oxford.
98. Warren, M.W. & Zou, X. (2002) Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. *For. Ecol. Manage.*, 170, 161-171.
99. WCMC (World Conservation Monitoring Centre). (1992) *Global Biodiversity: Status of the Earth's Living Resources*. Chapman and Hall, London.
100. Webb, D.P. (1977) Regulation of deciduous forest litter decomposition by soil arthropod faeces. In: Mattson, W.J. (ed), *The Role of Arthropods in Forest Ecosystem*, Springer–Verlag, Heidelberg, pp. 57-69.
101. Weiermans, J. & van Aarde, R.J. (2003) Roads as ecological edges for rehabilitating coastal dune assemblages in northern Kwazulu-Natal, South Africa. *Restor. Ecol.*, 11, 43-49.
102. Wesener, T. & Sierwald, P. (2005a) The giant pill–millipedes of Madagascar. *Proc. California Acad. Sci.*, 56, 557-599.
103. Wesener, T. & Sierwald, P. (2005b) New giant pill-millipede species from the littoral forest of Madagascar (Diplopoda, Sphaerotheriida, *Zoosphaerium*). *Zootaxa*, 1097, 1-60.
104. Wesener, T. & VandenSpiegel, D. (2007) *Microsphaerotherium ivohibiense*, a new genus and species of Giant–Pill Millipedes from Madagascar (Diplopoda, Sphaerotheriida, Arthrosphaerinae). *J. Afr. Ttrop. Zool.*, 3, 153-160.
105. Wesener, T. & VandenSpiegel, D. (2009) A first phylogenetic analysis of Giant Pill–Millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. *Cladistics*, 25, 545-573.
106. Wesener, T. & Wägele, J.-W. (2007) Giant pill–millipede (Deplopoda: Sphaerotheriida) in the littoral forest fragments of Southeastern Madagascar, In: Ganzhorn, J.U., Goodman, S.M. & Vincelette, M. (Eds) *Biodiversity, Ecology, and Conservation of Littoral Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin*), SI/MAB Series # 11, Smithsonian Institution, Washington DC. pp. 147-153.
107. Wesener, T. (2009) Unexplored richness: Discovery of 31 new species of giant pill–millipedes endemic to Madagascar, with a special emphasis on microendemism (Diplopoda, Sphaerotheriida). *Zootaxa*, 2097, 1-134.
108. Wesener, T. (2010) Revision of the American Pill Millipedes: *Onomeris* and *Trichomeris* (Diplopoda, Glomerida, Glomeridae). *Zootaxa*, 2725, 28-40.
109. Wesener, T. (2014) A new phylogenetic analysis of the Sphaerotheriida (Diplopoda) with a revision of the Australian giant pill–millipedes. *Invert. System.*, 28, 196-213.
110. Wesener, T., Bespalova, I. & Sierwald, P. (2010b) Madagascar's living giants: Discovery of five new species of endemic giant pill–millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae: *Zoosphaerium*). *Afr. Invertebr.*, 51, 133-161.
111. Wesener, T., Le, D.M.T. & Loria, S.F. (2014) Integrative revision of the giant pill-millipede genus *Sphaeromimus* from Madagascar, with the description of seven new species (Diplopoda, Sphaerotheriida, Arthrosphaeridae). *Zoo Keys*, 414, 67-107.
112. Wesener, T., Raupach, M.J. & Sierwald, P. (2010a) The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Mol. Phylo. Evol.*, *57*, 1184-1193.
113. Wilson, E.O. (1992) The Diversity of Life. Harvard University Press, Harvard.
114. Wongthamwanich, N., Panha, S., Sierwald, P., Wesener, T. & Thirakhupt, K. (2012) A new species of the giant pill–millipede genus *Sphaerobelum* Verhoeff, 1924 from northern Thailand, with an extensive description and molecular characters (Diplopoda: Sphaerotheriida: Zephroniidae). *Zootaxa*, 3220, 29-43.
115. Zhang, D., Hui, D., Luo Y. & Zhou G. (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J. Pl. Ecol.*, 1, 85-93.

ISSN 2278–5469 EISSN 2278–5450 I OPEN ACCESS