ON ABUNDANCE AND PHENOLOGY OF GEOPHILOMORPHA (CHILOPODA) FROM CENTRAL AMAZONIAN UPLAND FORESTS

Joachim Adis¹, Alessandro Minelli², José Wellington de Morais³, Luis A. Pereira⁴, Francesco Barbieri² & José Maria G. Rodrigues³

 ¹ Max-Planck-Institute for Limnology, Tropical Ecology Working Group, Postfach 165, D-24302 Plön, Germany
² Dipartimento di Biologia, Università degli Studi di Padova, Via Trieste 75, I-35121 Padova, Italy
³ Instituto Nacional de Pesquisas da Amazônia (INPA), C.P. 478, 69.O11-970 Manaus/AM, Brazil
⁴ Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s.n., 1900 La Plata, Argentina

Abstract. The 629 Geophilomorpha collected within 12 months in the soil (0–7 cm depth) of a primary upland forest $(24 \pm 16 \text{ individuals/m}^2/\text{month} \text{ on average})$ and of a secondary upland forest $(94 \pm 28 \text{ ind./m}^2/\text{month} \text{ on average})$ near Manaus (Brazil) comprised 7 and 8 terricolous species respectively. Only 3 species were common to both forest types. In the primary forest, the Schendylidae (3 spp.) represented 57%, and in the secondary forest, the Geophilidae (4 spp.) 82% of all geophilomorphs. The correlation found between the monthly abundance of *Hyphydrophilus adisi* (Geophilidae) and the humidity of the soil indicated that this eudominant and most probably plurivoltine species of the secondary forest (71 ± 29 ind./m²/month on average) is scrophilous. Additional studies showed that the Geophilomorpha represented 0.1–0.3% of the total arthropods extracted from the soil (0–14 cm depth) in three different upland forest types in Central Amazonia. Between 65% and 91% (48–72 ind./m²/month) of the total geophilomorphs were obtained from the upper 7 cm of the soil during the dry scason and 44–100% (29–91 ind./m²/month) during the rainy scason, compared to the subsoil (7–14 cm depth). Accepted 20 December 1996.

Key words: Abundance, phenology, Geophilomorpha, Amazon, Neotropics.

INTRODUCTION

Terrestrial arthropods of Central Amazonian forests have been investigated for several years (cf. Adis & Schubart 1984) in a scientific cooperation between the National Institute for Amazonian Research (INPA) at Manaus/Brazil and the Tropical Ecology Working Group at the Max-Planck-Institute for Limnology in Plön/Germany (Projeto INPA/Max-Planck). Data on abundance and phenology of Geophilomorpha sampled during 12 months in a primary and a secondary upland forest are now available, as their taxonomic evaluation has been completed (cf. Pereira *et al.* 1994, 1995, and unpubl.).

STUDY AREA AND METHODS

Geophilomorpha were collected between 1981 and 1983 in the course of ecological studies on Central Amazonian arthropods from two previously investigated and fully described forest types, all within 30 km of Manaus: (1) primary upland forest at Reserva Florestal A. Ducke (= Reserva Ducke; 2°55'S, 59°59'W) on the Manaus-Itacoatiara highway (AM-010 at km 26; cf. Penny & Arias

1982), (2) secondary upland forest at Rio Taruma Mirím (03002'S, 60017'W), a tributary of the Rio Negro, where the vegetation was previously cut but unburned (cf. Adis 1992). Both forests are subject to a rainy season (December-May: average precipitation 1550mm) and a "dry" season (June-November: average precipitation 550mm), but each month has some rain events; cf. Ribeiro & Adis (1984). The yellow latosoil of the primary and secondary upland forests supported a 2-3 cm-thick humus layer, interspersed with fine roots, and a thin surface covering of leaf-litter. One ground photo-eclector (emergence trap) and one arboreal photo-eclector for trunk ascents (funnel trap) were installed in both forests from December 1981 to December 1982 (cf. Adis & Schubart 1984). The distribution of geophilomorphs in the soil was studied between September 1982 and August 1983 (Morais 1985, Rodrigues 1986). Twelve soil samples were taken once a month from each forest type at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm) which was driven into the soil by a mallet. The combined area of 12 samples represented 0.42 m². Each sample

of 7 cm depth was then divided into two subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of Kempson (Adis 1987). The monthly collection data of geophilomorphs from the two soil layers in relation to changing conditions of precipitation, temperature and humidity of the air near the forest floor as well as moisture content, temperature and pH of the soil were statistically evaluated with a linear correlation test (Cavalli-Sforza 1972) using the original field data (cf. Morais 1985, Rodrigues 1986). In addition, the presence of geophilomorphs in tree crowns of the primary upland forest was tested by fogging canopies with pyrethrum (with and without synergist) during the dry and rainy seasons (July 1977, August 1991, February & August 1992, July 1994; Adis et al. 1984, 1997). The taxonomic work for this paper was done by L. Pereira, A. Minelli and F. Barbieri. Geophilomorphs sampled were classified as juveniles and adults according to the degree of differentiation of the gonopods and the sexual secondary characters of the last pair of legs. For adults from the primary forest, sex was also determined according to the sexual secondary characters of the last pair of legs and the shape of the gonopods.

RESULTS

A total of 124 Geophilomorpha was collected in the primary upland forest and 505 in the secondary upland forest. Out of these, 96% could be identified to species and developmental stages.

About 98% of all Geophilomorpha were obtained from the forest soil. In the primary forest they represented 0.3%, and in the secondary forest 0.5% of the total Arthropoda (Chilopoda: 0.4 and 0.6% respectively) extracted from soil samples within 12 months (Acari & Collembola omitted; cf. Morais 1985, Rodrigues 1986). Their abundance in 0-7 cm soil depth was four times higher than that of the Scolopendromorpha (Fig. 1). An average of 24 ± 16 individuals/m² was recorded in the primary forest and 94 ± 28 ind./m² in the secondary forest per month (Table 1). About 80% of the geophilomorphs in the primary forest, and 46% in the upland forest inhabited the organic layer (Fig. 2: 0-3.5 cm) compared to the mineral subsoil (3.5-7 cm depth). Only 5% of all specimens in the primary forest, but 21% in the secondary forest were represented by immatures. Sex ratio (adult males to females) in the primary forest was 1:1.2. The total catch of geophilomorphs

collected during the dry season and the rainy season was similar: 58% versus 42% in the primary forest and 54% versus 46% in the secondary forest respectively.

The Geophilomorpha obtained from the two upland forests near Manaus represented eight new species and the new genus Hyphydrophilus. Only Ribautia (Schizoribautia) centralis (Silvestri, 1907) was known. The qualitative and quantitative Sørensen index of species similarity between the two sites (cf. Magurran 1988) was 40% and 12% respectively. All species are considered terricolous. Only during the rainy season was one adult specimen obtained both in the arboreal photo-eclector (Ityphilus crabilli Pereira, Minelli & Barbieri, 1994) and the ground photo-eclector (Ityphilus demoraisi Pereira, Minelli & Barbieri, 1994) of the primary upland forest, but none from the canopy. In the secondary upland forest, eight adults of I. crabilli were captured in the arboreal funnel trap during the rainy season as well. In this species, mature spermatozoa were observed in males and spermathecae filled with spermatozoa in females during the dry season only (Aug. & Oct.; cf. Pereira et al. 1995). No geophilomorphs were obtained with the emergence trap on the ground.

Four out of the nine species obtained in the primary and secondary upland forest occurred in Central Amazonian inundation forests as well: *Hyphydrophilus adisi* Pereira, Minelli & Barbieri, 1994, *Ityphilus crabilli, Ribautia* (S.) centralis, and Schendylurus continuus Pereira, Minelli & Barbieri, 1995 (cf. Pereira et al. 1994, 1995; Morais et al., in press).

In the soil of the primary forest, the Schendylidae (3 species) represented 57% of all geophilomorphs, the Geophilidae (2 species) 34%, and the Ballophilidae (2 species) 9%. Four species were dominant (Table 1) and 3 species occurred in the secondary forest as well: *Pectiniunguis ducalis* Pereira, Minelli & Barbieri, 1995, *Ribautia (R.) proxima* Pereira, Minelli & Barbieri, 1995, and *Ityphilus crabilli*. No significant correlation was found between the vertical distribution of species in the soil and the local abiotic factors.

In the soil of the secondary forest, the Geophilidae (4 species) represented 82% of all geophilomorphs, the Schendylidae and the Ballophilidae (2 species each) 9% repectively. *Hyphydrophilus adisi* Pereira, Minelli & Barbieri, 1994 (Geophilidae) (max. length 19 mm) was eudominant and the only species significantly more abundant (χ^2 -test: P < 0.05)

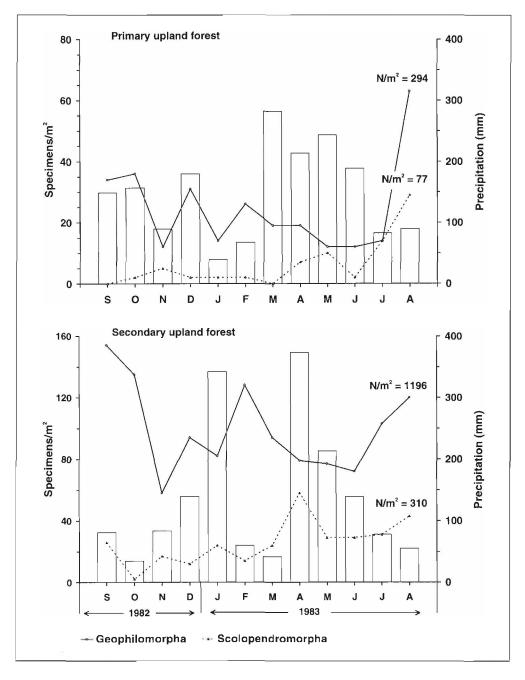


FIG. 1. Distribution of Geophilomorpha and Scolopendromorpha in the soil. Samples taken monthly at 0–7 cm depth between September 1982 and August 1983 in two upland forests near Manaus, Brazil. Total catch = 100% in each forest type; N = total number of specimens. Total precipitation per month given between sampling dates (= at the end of each month in the primary upland forest and in the middle of each month in the secondary upland forest). The low rainfall observed in early 1983 was due to a strong El Niño-event (cf. Adis & Latif 1996).

in the mineral subsoil (3.5-7 cm: 62%) than in the organic layer (0-3.5 cm depth; cf. Table 1, Fig. 2). About 77% of the total 354 specimens collected could be identified to their developmental stages. Of these, 96% represented adults (Fig. 3). Sex ratio (adult o' to 9) was 1.3:1.0. There was no distinct reproductive period and adults (both sexes) as well as juveniles were found throughout the year (Fig. 3). These results indicate a plurivoltine mode of life, which has not yet been reported for geophilomorphs. The monthly abundance of adults was negatively correlated with the humidity of the soil of the previous month in the organic layer (0-3.5 cm: r = -0.5962, P < 0.5, n = 12) and positively in the mineral subsoil (3.5-7 cm: r = +0.5545, P < 0.10, n = 12). During the dry season, about 64% of H. adisi (adults and juveniles) were obtained from the

upper 3.5 cm of the soil, whereas during the rainy season about 61% of all specimens were found in the mineral subsoil. These data indicate that *H. adisi* is xerophilous.

DISCUSSION

According to Pereira *et al.* (in press), the current knowledge of Neotropical Geophilomorpha is mostly restricted to the taxonomic description of about 300 species. Of these, about 90 species, representing the genera *Schendylops, Pectiniunguis* and *Ribautia.* are only known from localities along major rivers like the Amazon and Orinoco, where they may have evolved (cf. Erwin & Adis 1982, Adis & Schubart 1984, Adis, in press). In addition, several other species seem to be endemic to non-flooded upland areas postulated

TABLE 1. Average abundance (N/m^2) and dominance (%) of Geophilomorpha species in the soil of two upland forests near Manaus, Brazil. Samples taken monthly at 0–3.5 and 3.5–7 cm soil depths between September 1982 and August 1983.

		Primary upland forest			
Species (Family)			N/m ² per month		
		0-3.5 cm	3.5–7.0 cm	07.0 cm	0–7.0 cm
Schendylurus oligopus	(Sch.)	6.3± 6.3	0.2±0.7	6.5± 6.3	27.1
Pectiniunguis ducalis	(Sch.)	4.3± 3.8	1.2±1.9	5.5± 4.3	22.0
Ribautia (R.) ducalis	(Geo.)	2.7± 2.9	1.4±1.2	4.1± 2.9	18.6
Ribautia (R.) proxima	(Geo.)	1.9± 1.4	1.7±2.4	3.6± 2.6	15.4
Ityphilus crabilli	(Bal.)	1.7± 2.4	0.2±0.7	1.9± 3.1	8.5
Schendylurus continuus	(Sch.)	1.8± 2.2	-	1.8± 2.2	7.6
Iryphilus demoraisi	(Bal.)	0.2± 0.7	-	0.2± 0.7	0.8
Total		18.9±12.9	4.7±4.8	23.6±16.3	100.0
		Primary upland forest			
Species (Family)		N/m ² per month			%
		0-3.5 cm	3.5–7.0 cm	0–7.0 cm	0–7.0 cm
Hyphydrophilus adisi	(Geo.)	25.0±13.7	46.0±20.4	71.0±29.4	74.4
Ityphilus crabilli	(Bal.)	7.7± 5.9	0.7± 1.5	8.4± 6.3	8.8
Pectiniunguis geayi	(Sch.)	5.8± 4.6	1.0± 1.6	6.8± 4.9	7.1
Ribautia (R.) proxima	(Geo.)	1.0± 1.6	2.2± 3.2	3.2± 3.3	3.4
Ribautia (S.) centralis	(Geo.)	2.2± 2.4	1.0± 1.0	3.2± 2.6	3.4
Pectiniunguis ducalis	(Sch.)	0.7± 1.5	0.1± 0.6	0.8± 1.7	1.9
Macronicophilus n.sp.	(Geo.)	0.2± 0.6	0.6± 0.9	0.8± 1.3	0.8
Ityphilus cf. guianensis	(Bal.)	0.2± 0.6	-	0.2± 0.6	0.2
Τοτα		42.8±16.8	51.6±17.5	94.4±27.5	100.0

Bal. = Ballophilidae, Geo. = Geophilidae, Sch. = Schendylidae

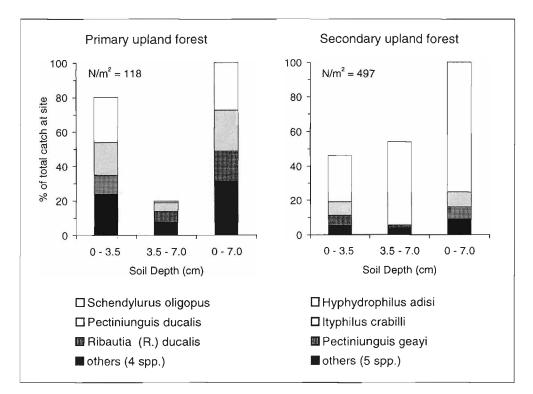


FIG. 2 Distribution of Geophilomorpha in the soil according to depth in two upland forests near Manaus, Brazil. Total catch = 100% in each forest type. Samples taken monthly at 0–3.5 and 3.5–7 cm soil depths between September 1982 and August 1983. N = total number of specimens.

as Pleistocene refugia (cf. Prance 1982). Historical events, hardly understood, and the lack of long-term ecological studies may explain in part that out of 16 species of Geophilomorpha obtained in five different forest types near Manaus, 15 were new to science (cf. Pereira *et al.* 1994, 1995, and unpubl.). Against this background, in the following we compare our results with some information available from the literature on the ecology of Geophilomorpha from the Neotropics and in general.

Comparable data on the abundance and vertical distribution of the soil fauna in three different upland forest types of Central Amazonia were obtained by Adis and collaborators (cf. Adis *et al.* 1987a, b; 1989a, b). Arthropods were collected to a soil depth of 14 cm during rainy and dry seasons and extracted with the Kempson method as described above. Between 84% and 92% of all arthropods were found to inhabit the top 7 cm when Acari and Collembola were included in the total catch numbers, and 76-84% when they were omitted:

The first study was conducted in 1985/86 in a secondary upland forest on yellow latosoil at the INPA campus in Manaus, where the vegetation was previously cut but unburned (Adis *et al.* 1987a, b). Geophilomorpha represented 0.2-0.3% (Chilopoda: 0.2-0.4%) of the total arthropods when Acari and Collembola are included (dry season: 50.448 ind./m², rainy season: 63.850 ind./m²), and 0.7-1.2% (Chilopoda: 0.8-1.3%) when they are omitted from the total catch numbers (dry season: 11.934 ind./m², rainy season: 17.886 ind./m²). About 77% (62.6 ind./m²; dry season) and 44% (91.4 ind./m²; rainy season) of the total Geophilomorpha were obtained from the upper 7 cm of the soil compared to the lower soil layers (7-14 cm depth).

The second study was made in 1988 in a primary forest on whitesand soil, about 45 km north of

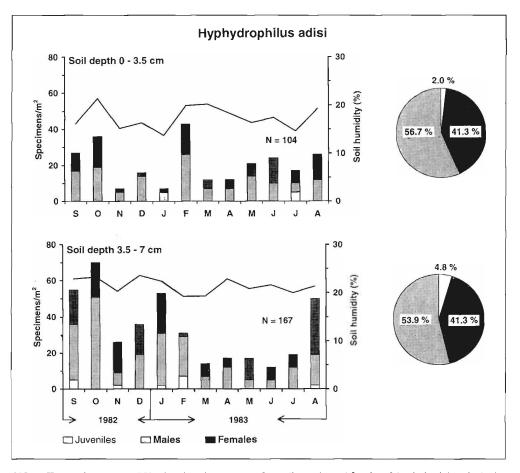


FIG. 3. Temporal occurrence (N/m2) and total percentage of juveniles, males and females of *Hyphydrophilus adisi* in the soil of a secondary upland forest near Manaus, Brazil. Samples taken monthly at 0–3.5 and 3.5–7 cm soil depths between September 1982 and August 1983. N = total number of specimens identified to developmental stages (see text for details).

Manaus (Adis *et al.* 1989a, b). Geophilomorpha represented 0.1-0.2% (Chilopoda: 0.3-0.4%) of the total arthropods when Acari and Collembola are included (dry season: 57.703 ind./m², rainy season: 74.255 ind./m²), and 0.4-0.7% (Chilopoda: 1.2-1.6%) when they are omitted from the total catch numbers (dry season: 14.119 ind./m², rainy season: 15.023 ind./m²). About 65% (72.2 ind./m²; dry season) and 83% (48.1 ind./m²; rainy season) of the total Geophilomorpha were obtained from the upper 7 cm of the soil compared to the lower soil layers (7-14 cm depth).

The third study was conducted in 1987 in the primary upland forest on yellow latosoil at Reserva

Ducke (Adis *et al.*, unpubl.). Geophilomorpha represented 0.1% (Chilopoda: 0.2–0.3%) of the total arthropods when Acari and Collembola are included (dry season: 38.727 ind/m², rainy season: 25.905 ind./m²), and 0.2–0.5% (Chilopoda: 0.6%) when they are omitted from the total catch numbers (dry season: 11.005 ind./m², rainy season: 11.741 ind./m²). About 91% (48.1 ind./m²; dry season) and 100% (28.9 ind./m²; rainy season) of the total Geophilomorpha were obtained from the upper 7 cm of the soil compared to the lower soil layers (7–14 cm depth).

All these data indicate that abundances of Geophilomorpha [as well as of Chilopoda and total

Arthropoda] in formerly cut and unburned upland secondary forests on latosoil of Central Amazonia are higher (94-207 ind./m²) than in primary upland forests on latosoil and whitesand soil (24-111 ind./m2). One of the reasons might be the much higher availability of potential food, particularly mites, springtails & termites (cf. Morais 1985, Rodrigues 1986, Adis 1988). However, in secondary upland forests which were formerly cut but burned, abundances of Chilopoda and total Arthropoda are generally lower within the first 15 years compared to primary forests; see Ribeiro (1994) for Central Amazonia, Pozo & Blandin (1991) for Western Ecuador. Lavelle & Pashanasi (1989) for Peruvian Amazonia. It remains to be clarified whether Hyphydrophilus adisi in Central Amazonia represents a potential bioindicator for disturbed forest formations (secondary forests, inundation forests; cf. Table 1; Pereira et al. 1994).

Total abundances of Geophilomorpha in Central Amazonian upland forests (24–207 ind./m² in 0–14 cm soil depth) are comparable to population densities of geophilomorphs in European deciduous forests, which range between 50 and 200 ind./m² (Dunger 1993). Comparable quantitative data are available from two further studies in which arthropods were obtained by means of the Kempson extraction method:

In the soil of a mixed oak forest (*Quercus robur*) in the valley of the river Inn at Tirol (Austria), the average abundance of Geophilomorpha extracted from a total soil depth of 18-21 cm was 58.7 ind./m² (Chilopoda: 228.7 ind./m²) which corresponded to 0.6% (Chilopoda: 2.3%) of the total soil macrofauna collected during 12 months (Meyer *et al.* 1984). Average biomass of the geophilomorphs was 49 mg dw/m², which represented about one-third of the average biomass of the total Chilopoda (186 mg dw/m²).

In the soil of a beech forest (*Fagus sylvatica*) on limestone near Göttingen (northern Germany), the average abundance of Chilopoda (Geophilomorpha: 7 spp., Lithobiomorpha: 3 spp.) extracted from a total soil depth of 6 cm during one year amounted to 187 ind./m² (Poser 1988a, b). Average biomass of the geophilomorphs was 62 mg dw/m², which represented about one-fourth of the average biomass of the total Chilopoda (265 mg dw/m²). The three geophilomorph species (*Geophilus insculptus* Attems, 1895, *Geophilus (Brachygeophilus) truncorum* Bergsoe & Meinert, 1866 (Geophilidae), and *Strigamia acu-* *minata* (Leach, 1815) (Linotaeniidae) represented about 60% of the total Chilopoda collected.

The depth to which geophilomorphs occur in the soil of the Central Amazonian upland forests is unknown. First studies below 14 cm soil depth in a primary forest on yellow latosoil, and on whitesand soil 45 km north of Manaus, showed that soil layers 20-30 cm in depth were dominated by social insects, in particular Isoptera, and that Geophilomorpha occur here as well (Harada & Bandeira 1994a, b, and unpubl.). In Costa Rica, "Chilopoda" were located during the rainy season at 15-20 cm soil depths in a forest (38 ind./m²) and in a coffee plantation (25 ind./m²). They represented 0.2% (125 ind./m²) and 0.1% (87 ind./m2) respectively of the total arthropods collected to a depth of 20 cm (Serafino & Merino 1978). European geophilomorphs have been found down to 1.8 m depth (Szekelyhidy & Loksa 1979), and females of Geophilus flavus (Degeer, 1778) (= Necrophloeophagus longicornis (Leach, 1815) (Geophilidae) and Pachymerium ferrugineum (C.L. Koch, 1835) (Geophilidae) penetrate to a soil depth of 50-70 cm for oviposition (Dunger 1993). The thin and elongate body form is regarded as one of the reasons why colonization of deeper soil layers in Chilopoda has been restricted to the Geophilomorpha, which therefore were able to survive fires in the Mediterranean ecosystem of cork-oak forests (Quercus ilex and Q. suber; Saulnier & Athias-Binche 1986). This may be important with respect to the rapidly increasing slash-and-burn impact on primary upland forests in the (Neo-)tropics. On the other hand, Schendyla nemorensis (C.L. Koch, 1836) (Schendylidae) and Clinopodes flavidus C.L. Koch, 1847 (Geophilidae) predominated at a soil depth of 10 cm in an oak forest (Q. petraea) in Hungary (Szekelyhidy & Loksa 1979). Other geophilomorph species even prefer deciduous forest litter (cf. Matic 1991 for a forest in Romania).

The occurrence and vertical distribution of Geophilomorpha in the soil is attributable to microclimatic conditions in the habitat, to availability of prey and to the type of biotope. Our data indicate that some species in Central Amazonian upland forests are xerophilous. For example, some specimens of I. crabilli moved to the lower trunk region during the rainy season in the primary and secondary upland forest investigated. The vertical distribution of *H. adisi* in the secondary upland forest was correlated with low humidity in the soil. In the neighboring inundation forest, adults pass inundation of 5–7 months duration on tree trunks (Adis *et al.*, in press). This was also observed for *R*. (*S.*) *centralis* and *S. continuus* in a mixedwater inundation forest near Manaus (Morais *et al.*, in press). Both species inhabit the soil of nonflooded upland forests as well (Table 1). However, several European and Asian species are considered hygrophilous and pass dry summer periods in lower soil layers, some even in a quiescent state (cf. Weil 1958, Kheirallah 1977, Dunger 1993).

Fluctuations in the vertical distribution and abundance of Geophilomorpha may also be related to brooding periods in females, which take care of eggs and juveniles. In European Geophilidae, this may take up to 3 months (cf. Weil 1958; Vaitilingham 1960; Lewis 1961, 1981; Dunger 1993). In Pachymerium ferrugineum from Finland, maturity was reached after two years and life span in females was at least three years (Palmen & Rantala 1954). For Neotropical geophilomorphs, the duration of the brooding period in females, the time of maturation and mobility in immatures, as well as the life span of species is unknown. The low number of juveniles obtained in our soil extractions indicate, that their activity in the soil was low, even in more dominant species like H. adisi (Fig. 3).

The vertical distribution of Geophilomorpha in the soil may also be related to their prey preference (spectrum and size). Geophilus insculptus inhabits the mineral soil of beech forests on limestone in northern Germany, where it prefers to feed on lumbricid earthworms, enchytraeids and larvae of dipterans. Strigamia acuminata is found in the upper organic layer of the soil, where it prefers to prey on juliform millipedes, enchytraeids and larvae of dipterans. Both predators select big prey with low mobility on which they feed in groups (Weil 1958; Poser 1988a, b). Geophilidae from an oak forest of the Russian steppe were reported to be polytrophic facultative predators but showed a food selectivity which depended on the size of earthworms offered as prey (Sergeeva et al. 1985). Besides earthworms, geophilomorphs in the soil of a grassland in north Wales (United Kingdom) attacked slugs, diplurans and adult carabids (Gunn & Cherrett 1993). Geophilomorpha observed in non-tillage maize fields in North Carolina (USA) feed on first and second instar larvae of the chrysomelid pest beetle Diabrotica undecimpunctata howardi (Brust 1991). Some of the foraging geophilomorphs, which in the tropics are paralyzed by ants and serve as prey (e.g., Masuko 1990), may effectively use cyanogenetic and other

secretions as a chemical defence (Jones *et al.* 1976, Hopkin & Anger 1992).

Terricolous geophilomorphs inhabit many natural biotopes worldwide (e.g.; Auerbach 1951; Lewis 1962, 1980, 1981; Eason 1964; Negrea et al. 1970; Price 1975; Summers & Uetz 1979; Koch & Majer 1980; Petersen & Luxton 1982; Flogaitis 1984; Andersson 1985; Fründ 1987; Minelli & Iovane 1987; Rybalov 1990; Wytwer 1990, 1992; Kretschmer & Schauermann 1991; Barber 1992; Klinger 1992; Kos 1992, 1996; Vicente & Serra 1992; Dunger 1993; Radea 1993; Voigtländer 1995a; Lesniewska 1996; Ribarov 1996) as well as those modified and used by man (e.g., Albert 1982; Ghabbour et al. 1988; Paoletti 1988; Paoletti et al. 1988; Dunger & Voigtländer 1990; Zapparoli 1992, 1996; Glück et al. 1995; Voigtländer 1995b; Wytwer 1995, 1996). According to our studies, geophilomorphs of Central Amazonia inhabit primary and secondary upland forests as well as inundation forests in the valley of the Amazon River and in the lower basin of the Negro River near Manaus. They have not yet been found in the soil of man-made pastures (0-14 cm depth) adjacent to upland forests. One reason might be the low humidity and high temperature of the soil around noon, particularly during the dry season (Adis & Franklin, unpubl.).

ACKNOWLEDGEMENTS

We wish to acknowledge the valuable support received from PD Dr. Wolfgang J. Junk, Head of the Tropical Ecology Working Group at the Max-Planck-Institute (MPI) for Limnology in Plön/Germany, during this study. We thank Dr. Dick Jones (King's Lynn/United Kingdom), Dr. John Lewis (Taunton/ United Kingdom) and Dr. Sergei Golovatch (Moscow/Russia) for their valuable comments on the manuscript. Berit Hansen (MPI Plön) is thanked for making the drawings. Dr. Johann Bauer, MPI for Biochemistry (Martinsried/ Germany), kindly provided the backsearch of literature on Geophilomorpha, covering the last 30 years.

REFERENCES

- Adis, J. 1987. Extraction of arthropods from Neotropical soils with a modified Kempson apparatus. J. Trop. Ecology 3: 131–138.
- Adis, J. 1988. On the abundance and density of terrestrial arthropods in Central Amazonian dryland forests. J. Trop. Ecol. 4: 19–24.

- Adis, J. 1992. Überlebensstrategien terrestrischer Invertebraten in Überschwemmungswäldern Zentralamazoniens. Verh. naturwiss. Ver. Hamburg (NF) 33:21–114.
- Adis, J. In press. Terrestrial invertebrates: Survival strategies, group spectrum, dominance and activity patterns. *In* Junk, W.J. (ed.). The Central Amazon floodplain. Ecology of a pulsing system. Ecological Studies 126. Heidelberg.
- Adis, J., & M. Latif. 1996. Amazonian arthropods react to El Niño. Biotropica 28: 403–408.
- Adis, J., & H.O.R. Schubart. 1984. Ecological research on arthropods in Central Amazonian forest ecosystems with recommendations for study procedures. Pp. 111–144 in Cooley, J.H., & F.B. Golley (eds.). Trends in ecological research for the 1980s. NATO Conference Series, Series I: Ecology, Vol. 7. New York.
- Adis, J., Lubin, Y.D., & G.G. Montgomery. 1984. Arthropods from the canopy of inundated and terra firme forests near Manaus, Brazil, with critical considerations on the pyrethrum-fogging technique. Stud. Neotrop. Fauna Environ. 19: 223–236.
- Adis, J., Morais, J.W. de, & H.G. de Mesquita. 1987a. Vertical distribution and abundance of arthropods in the soil of a Neotropical secondary forest during the rainy season. Stud. Neotrop. Fauna Environ. 22: 189–197.
- Adis, J., Morais, J.W. de, & E.F. de Ribeiro. 1987b. Vertical distribution and abundance of arthropods in the soil of a Neotropical secondary forest during the dry season. Trop. Ecol. 28: 174–181.
- Adis, J., Morais, J.W. de, Ribeiro, E.F., & J.C. Ribeiro. 1989a. Vertical distribution and abundance of arthropods from white sand soil of a Neotropical campinarana forest during the rainy season. Stud. Neotrop. Fauna Environ. 24: 193–200.
- Adis, J., Ribeiro, E.F., Morais, J.W. de, & E.T.S. Cavalcante. 1989b. Vertical distribution and abundance of arthropods from white sand soil of a Neotropical campinarana forest during the dry season. Stud. Neotrop. Fauna Environ. 24: 201–211.
- Adis, J., Paarmann, W., Fonseca, C.R. da, & J.A. Rafael. 1997. Knock-down efficiency of natural pyrethrum and survival rate of arthropods obtained by canopy fogging in Central Amazonia. Pp. 67–81 *in* Stork, N.E., Adis, J., & R.K. Didham (eds.). Canopy arthropods. London.
- Adis, J., Barbieri, F., Minelli, A., & L.A. Pereira. In press. Behavioral and morphological adaptations of Geophilomorpha centipedes in a periodically inundated Amazonian forest. Stud. Neotrop. Fauna Environ.
- Albert, A.M. 1982. Species spectrum and dispersion patterns of chilopods in three Solling habitats. Pedobiologia 23: 337–347.
- Andersson, G. 1985. The distribution and ecology of centipedes in Norrland, Sweden (Chilopoda). Bijdr. Dierk. 55: 5–15.

- Auerbach, S.I. 1951. The centipedes of the Chicago area with special reference to their ecology. Ecol. Monogr. 21: 97–124.
- Barber, A.D. 1992. Distribution and habitat in British centipedes (Chilopoda). Pp. 339–352 in Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology (Innsbruck 1990). Ber. nat.-med. Verein Innsbruck, Suppl. 10.
- Brust, G.E. 1991. A method for observing below-ground pest-predator interactions in corn agroecosystems. J. Entomol. Sci. 26: 1–8.
- Cavalli-Sforza, L. 1972. Grundzüge biologisch-medizinischer Statistik. Stuttgart.
- Dunger, W. 1993. Chilopoda. Pp. 1047-1094 in Gruner, H.-E. (ed.). Lehrbuch der Speziellen Zoologie. Bd. I: Wirbellose Tiere. 4. Teil: Arthropoda (ohne Insecta). Stuttgart.
- Dunger, W., & K. Voigtländer. 1990. Succesion of Myriapoda in primary colonization of reclaimed land. Pp. 219-227 in Minelli, A. (ed.). Proceedings of the 7th International Congress of Myriapodology. Leiden.
- Eason, E.H. 1964. The centipedes of the British Isles. London.
- Erwin, T.L., & J. Adis. 1982. Amazonian inundation forests. Their role as short-term refuges and generators of species richness and taxon pulses. Pp. 358-371 in Prance, G.T. (ed.). Biological diversification in the tropics. V. Int. Symp. Assoc. Trop. Biol. (Caracas 1979). New York.
- Flogaitis, E. 1984. Le peuplement de macroarthropodes édaphiques d'une foret tempérée mixte: Composition, phénologie et organisation spatiale. Pedobiologia 27: 1–14.
- Fründ, H.C. 1987. Spatial distribution of Chilopoda in an old beech forest. Pedobiologia 30: 19–29.
- Ghabbour, S.I., da Fonseca, J.C., & S.H. Shakir. 1988. Characteristics of soil mesofauna in agro-ecosystems of the Mariut region Egypt. Rev. Bio-Mathemat. 102: 26–40.
- Glück, E., Spelda, J., & J. Blank. 1995. Destruentencoenosen von Windwurfflächen. Veröff. PAÖ 12: 143–154.
- Gunn, A., & J.M. Cherrett. 1993. The exploitation of food resources by soil meso- and macroinvertebrates. Pedobiologia 37: 303–320.
- Harada, A.Y., & A.G. Bandeira. 1994a. Estratificação e densidade de invertebrados em solo arenoso sob floresta e plantios arbóreos na Amazônia central durante a estação seca. Acta Amazonica 24: 103–118.
- Harada, A.Y., & A.G. Bandeira. 1994b. Estratificação e densidade de invertebrados em solo argiloso sob floresta e plantios arbóreos na Amazônia central durante a estação seca. Bol. Mus. Par. Emílio Goeldi, sér. Zool. 10: 235–251.

- Hopkin, S.P., & H.S. Anger. 1992. On the structure and function of the glue-secreting glands of *Henia vesuviana* (Newport, 1845) (Chilopoda: Geophilomorpha). Pp. 71-79 *in* Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology (Innsbruck 1990). Ber. nat.-med.Verein Innsbruck, Suppl. 10.
- Jones, T.H., Conner, W.E., Meinwald, J., Eisner, H.E., & T. Eisner. 1976. Benzoyl cyanide and mandelonitrile in the cyanogenetic secretion of a centipede. J. Chem. Ecol. 2: 421–429.
- Kheirallah, A.M. 1977. The ecology of millipedes and centipedes in the southern highlands of Saudi-Arabia. Pakistan J. Zool. 9: 177–182.
- Klinger, K. 1992. Diplopods and chilopods of conventional and alternative (biodynamic) fields in Hesse (FRG). Pp. 243–250 in Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology Innsbruck 1990). Ber. nat.-med. Verein Innsbruck, Suppl. 10.
- Koch, L.E., & J.D. Majer. 1980. A phenological investigation of various invertebrates in forest and woodland areas in the south-west of Western Australia. J.R. Soc. West-Australia 63: 21–28.
- Kos, I. 1992. A review of the taxonomy, geographical distribution and ecology of the centipedes of Yugoslavia (Myriapoda, Chilopoda). Pp. 353–360 in Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology (Innsbruck 1990). Ber. nat.-med. Verein Innsbruck, Suppl. 10.
- Kos, I. 1996. Centipedes (Chilopoda) of some forest communities in Slovenia. Pp. 635–646 in Geoffroy, J.-J., Mauriès, J.-P., & M. Nguyen Duy-Jacqueminn (eds.). Acta Myriapodologica. Mém. Mus. natn. Hist. nat. 169.
- Kretschmer, K., & J. Schauermann. 1991. Zur Arthropodengemeinschaft zweier Naturwälder im Forstamt Sellhorn. Berichte. Norddeutsche Naturschutzakademie 4: 150–156.
- Lavelle, P., & B. Pashanasi. 1989. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). Pedobiologia 33: 283–291.
- Lesniewska, M. 1996. Centipedes of Poznan town (Poland). Pp 221–224 in Geoffroy, J.-J., Mauriès, J.-P., & M. Nguyen Duy-Jacquemim (eds.). Acta Myriapodologica. Mém. Mus. natn. Hist. nat. 169.
- Lewis, J.G.E. 1961. The life history and ecology of the littoral centipede *Strigamia* (= *Scolioplanes*) maritima (Leach). Proc. 2001. Soc. Lond 137: 221–248.
- Lewis, J.G.E. 1962. The ecology, distribution and taxonomy of the centipedes found on the shore in the Plymouth area. J. mar. biol. Ass. U.K. 42: 655–664.

Lewis, J.G.E. 1980. The relative abundance of myriapods in the Gunung Mulu National Park, Sarawak. Ent. mon. Mag. 116: 219–220.

Lewis, J.G.E. 1981. The biology of centipedes. Cambridge.

Magurran, A.E. 1988. Ecological diversity and its measurement. London.

- Masuko, K. 1990. Behaviour and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). Insectes Sociaux 37: 31–57.
- Matic, Z. 1991. Chilopods in the scientific reserve of the Retezat National Park. Studia Univ. Babes-Bolay (Biologia) 36: 49–54.
- Meyer, E., Schwarzenberger, I., Stark, G., & G. Wechselberger. 1984. Bestand und jahreszeitliche Dynamik der Bodenmakrofauna in einem inneralpinen Eichenmischwald (Tirol, Oesterreich). Pedobiologia 27: 115–132.
- Minelli, A., & E. Iovane. 1987. Habitat preferences and taxocenoses of Italian centipedes (Chilopoda). Boll. Mus. civ. Stor. nat. di Vencza 37 (1986): 7–34.
- Morais, J.W. de 1985. Abundância e distribuição vertical de Arthropoda do solo numa floresta primária não inundada. M.Sc.-thesis, CNPq/INPA/FUA. Manaus.
- Morais, J.W. de, Adis, J., Berti-Filho, E., Pereira, L.A., Minelli, A., & F. Barbieri. In press. On abundance, phenology and natural history of Geophilomorpha (Chilopoda, Myriapoda) from a mixedwater inundation forest in Central Amazonia. Ent. scand. Suppl.
- Negrea, S., Darabantu, C., & Z. Matic. 1970. Contribution à l'étude des géophilomorphes (Chilopoda) cavernicoles de Roumanie. Pp. 411-420 *in* Orghidan, T. (ed.). Livre du centenaire Emile G. Racovitza (1868-1968). Editions de l'Academie de la Republique Socialiste de Roumainie, Bucharest.
- Palmén, E., & M. Rantala. 1954. On the life-history and ecology of *Pachymerium ferrugineum* (C.L. Koch) (Chilopoda, Geophilidae). Ann. Zool. Soc. 'Vanamo' 16: 1–44.
- Paoletti, M.G. (1988). Soil invertebrates in cultivated and uncultivated soils in northeastern Italy. Redia 71: 501–563.
- Paoletti, M.G., Iovane, E., & M. Cortese 1988. Pedofauna bioindicators and heavy metals in five agroecosystems in north-east Italy. Rev. Ecol. Biol. Sol. 25: 33–58.
- Penny, N.D., & J. Arias. 1982. Insects of an Amazon forest. New York.
- Pereira, L.A., Minelli, A., & F. Barbieri. 1994. New and little known geophilomorph species from Amazonian inundation forests near Manaus, Brazil (Chilopoda: Geophilomorpha). Amazoniana 13: 163–204.
- Pereira, L.A., Minelli, A., & F. Barbieri. 1995. Description of nine new centipede species from Amazonia and related matters on Neotropical geophilomorphs (Chilopoda: Geophilomorpha). Amazoniana 13: 325–416.

- Pereira, L.A., Foddai, D., & A. Minelli. In press. Zoogeographical aspects of Neotropical Geophilomorpha. Ent. scand. Suppl.
- Petersen, H., & M. Luxton 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 287–388.
- Poser, T. 1988a. Aufteilung der Ressourcen innerhalb der Chilopodengemeinschaften eines Kalkbuchenwaldes. (Zur Funktion der Fauna in einem Mullbuchenwald 12). Verh. Ges. Ökol. 17: 279–284.
- Poser, T. 1988b. Chilopoda as arthropod predators in a beech wood. Pedobiologia 31: 261–281.
- Pozo, X.S. del, & P. Blandin. 1991. Les peuplements de macroarthropodes édaphiques à différentes étapes de la reconstitution de la fôrer mésothermique en Équateur occidental. Rev. écol. Biol. Sol. 28: 435–442.
- Prance, G.T. 1982. Forest refuges: evidence from woody angiosperms. Pp. 137-157 in Prance, G.T. (ed.). Biological diversification in the tropics. V. Int. Symp. Assoc. Trop. Biol. (Caracas 1979). New York.
- Price, D.W. 1975. Abundance and vertical distribution of microarthropods in the surface layers of a Californian pine forest soil. Hilgardia 42: 121–148.
- Radea, C. 1993. Environmental factors that influence the temporal variation of predatory macroarthropods in the organic horizon of a Mediterranean pine forest. Biologia Gallo-hellenica 20: 249–258.
- Ribarov, G. 1996. Check-list, distribution and habitat in Bulgarian centipedes. Pp. 235–241 in Geoffroy, J.-J., Mauriès, J.-P., & M. Nguyen Duy-Jacquemim (eds.). Acta Myriapodologica. Mém. Mus. natn. Hist. nat. 169.
- Ribeiro, M.O. de A. 1994. Abundância, distribuição vertical e biomassa de artrópodos do solo em uma capoeira na Amazônia Central.M.Sc.-thesis, INPA/UFAM. Manaus.
- Ribeiro, M. de N.G., & J. Adis. 1984. Local rainfall variability – a potential bias for bioecological studies in the Central Amazon. Acta Amazonica 14: 159–174.
- Rodrigues, J.M.G. 1986. Abundância e distribuição vertical de Arthropoda do solo, em capoeira de terra firme. M.Sc.Thesis, CNPq/INPA/FUA. Manaus.
- Rybalov, L.B. 1990. Comparative characteristics of soil macrofauna of some tropical savannah communities in Equatorial Africa: preliminary results. Trop. Zool. 3: 1–11.
- Saulnier, L., & F. Athias-Binche. 1986. Modalités de la cicatrisation des écosystèmes méditerranéens après incendie: Cas de certains arthropodes du sol. 2. Les myriapodes édaphiques. Vie Milieu 36: 191–204.
- Serafino, A., & J.F. Merino. 1978. Poblaciones de microartrópodos en diferentes suelos de Costa Rica. Rev. Trop. Biol. 26: 139–151.
- Sergeeva, T.K., Kudryashova, I.V., & L.P. Titova. 1985. Seasonal aspects of feeding of gcophilids (Chilopoda,

Geophilomorpha) in the oak forests of the southern forest-steppe, USSR. Zool. Zh. 64: 1377–1383.

- Summers, G., & G.W. Uetz. 1979. Microhabitats of woodland centipedes in a streamside forest. Am. Midl. Nat. 102: 346–352.
- Székelyhidy, E.H., & Loksa, I. 1979. Oniscoiden-, Diplopoden- und Chilopoden-Gemeinschaften im Untersuchungsgebiet "Sikfökűt-Projekt" (Ungarn). Opuc. Zool. Budapest 14: 151–174.
- Vairilingham, S. 1960. The ecology of the centipedes of some Hampshire woodlands. M.Sc.-thesis, Univ. of Southampton.
- Vicente, M.C., & A. Serta. 1992. Étude des communautés de myriapodes de pâturages supraforestiers Pyrénéens (Huesca, Espagne) (Chilopoda, Diplopoda). Pp. 219–230 in Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology (Innsbruck 1990). Ber. nat.-med. Verein Innsbruck, Suppl. 10.
- Voigtländer, K. 1995a. Diplopoden und Chilopoden aus Fallenfängen im Naturschutzgebiet "Dubringer Moor" (Ostdeutschland/Oberlausitz). Abh. Ber. Naturkundemus. Görlitz 68: 39–42.
- Voigtländer, K. 1995b. Diplopoden und Chilopoden in immissionsgeschädigten Kiefernforsten im Raum Bitterfeld. Hercynia, NF 29: 269–289.
- Weil, E. 1958. Zur Biologie der einheimischen Geophiliden. Z. angew. Entomol. 42: 173–209.
- Wytwer, J. 1990. Chilopoda of linden-oak-hornbeam (*Tilio-Carpinetum*) and thermophilous oak forests (*Potentillo albae-Quercetum*) of the Mazovian Lowland. Fragm. Faunistica 34: 75–94.
- Wytwer, J. 1992. Chilopoda communities of the fresh pine forests of Poland. Pp. 205–211 *in* Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology (Innsbruck 1990). Ber. nat.-med. Verein Innsbruck, Suppl. 10.
- Wytwer, J. 1995. Faunistical relatioships between Chilopoda of forest and urban habitats in Mazowia. Fragm. Faunistica 38: 87–133.
- Wytwer, J. 1996. Chilopoda of urban greens in Warsaw. Pp. 213–220 in Geoffroy, J.-J., Mauriès, J.-P., & M. Nguyen Duy-Jacquemim (eds.). Acta Myriapodologica. Mém. Mus. natn. Hist. nat. 169.
- Zapparoli, M. 1992. Centipedes in urban environments: Records from the city of Rome (Italy). Pp. 231–236 in Meyer, E., Thaler, K., & W. Schedl (eds.). Advances in Myriapodology. Proc. 8th Int. Congr. Myriapodology (Innsbruck 1990). Ber. nat.-med. Verein Innsbruck, Suppl. 10.
- Zapparoli, M. 1996. Distribution patterns and qualitative composition of the centipede fauna in forestal habitats of mainland Greece. Pp. 599–605 *in* Geoffroy, J.-J., Mauriês, J.-P., & M. Nguyen Duy-Jacquemim (eds.). Acta Myriapodologica. Mém. Mus. natn. Hist, nat. 169.