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Millipedes and centipedes (Myriapoda: Diplopoda, Chilopoda) in Swiss heated greenhouses, with seven species new for Switzerland

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Abstract: The international plant trade provides opportunities for the introduction of exotic species into tropical greenhouses around the world. The millipede and centipede fauna of greenhouses is barely known in Switzerland. We conducted a survey in greenhouses of nine botanical gardens and other institutions across Switzerland. We captured and identified 1390 individuals belonging to 14 millipede species and 43 individuals belonging to 9 centipede species. Most millipede individuals recorded (80.3%) were non-native as were the species (8/14). Most centipede individuals (55.3%) were non-native, but not the majority of the species (4/10). The species composition varied strongly among greenhouses with species originating from different parts of the world. Seven species already known from greenhouses in other European countries are reported for the first time in Switzerland. These are the millipedes *Cylindrodesmus hirsutus* Pocock, 1889, *Poratia obliterata* (Kraus, 1960), *Paraspirobolus lucifugus* (Gervais, 1836) and the centipedes *Mecistocephalus guildingii* Newport, 1843, *Tygarrup javanicus* Attems, 1929, *Lamyctes* (*Lamyctes*) *coeculus* (Brölemann, 1889b), and *Cryptops* (*Cryptops*) *doriae* Pocock, 1891. The relevance of these findings is discussed.

Keywords: Artificial habitats - botanical gardens - hothouses - invasive species - non-native species - passive dispersal - soil fauna - urban biodiversity.

INTRODUCTION

Millipedes (Diplopoda) and centipedes (Chilopoda) are two diverse groups of arthropods belonging to subphylum Myriapoda. Millipedes comprise around 11 000 described species worldwide (Enghoff *et al.*, 2015), while centipedes comprise around 3300 (Edgecombe & Giribet, 2007; Bonato & Zapparoli, 2011; Bonato *et al.*, 2016). In general, millipedes are mostly detritivores whilst centipedes are venomous predators. Myriapods are predominantly soil or ground-dwelling organisms but some species have adapted to other habitats and live in aerial parts of trees or show amphibious habits (Golovatch & Kime, 2009; Tsukamoto *et al.*, 2021). Millipedes and centipedes are usually found in humid and sheltered microenvironments in forests, mainly amongst leaf-litter, under tree bark or beneath stones (Golovatch & Kime, 2009; Voigtländer, 2011). However, some species are able to live in extreme environments such as deserts, high mountains, caves or littoral habitats (Demange, 1958; Barber, 2009a; Golovatch, 2009; Gobbi *et al.*, 2020). Millipedes and centipedes are present in all continents except Antarctica. Four of the five extant centipede orders (Scutigeromorpha, Lithobiomorpha, Geophilomorpha, and Scolopendromorpha) have very wide distributions, but the fifth one (Craterostigmomorpha) with only two known species, is only found in Tasmania and New Zealand (Bonato & Zapparoli, 2011). On the other hand, millipede orders tend to have smaller distribution ranges, making them a suitable group for biogeographical studies (Enghoff, 2015) and most millipede species have small distribution areas (Golovatch & Kime, 2009). Nevertheless, several millipede and centipede species have increased their distribution range by being transported by human means, settling in areas where they are not native and, in some cases, even becoming invasive (Stoev *et al.*, 2010).

International trade of cultivated plants and soil material allow the colonization of European plant nurseries and greenhouses, from where these species may have subsequently spread (Stoev *et al.*, 2010). In Europe, introduced myriapods seem to pose only a minor problem for the native biodiversity and human economic activities

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(Stoev *et al.,* 2010). Wittenberg (2005) agrees on this, but also states that the knowledge on introduced Myriapods in Switzerland is so scarce that no comprehensive list could be provided. However, some species such as the invasive *Oxidus gracilis* (C.L. Koch, 1847) have become a pest in several European countries (Stoev *et al.,* 2010; Gilgado, 2020) but their effect on native biodiversity has not yet been studied (Iniesta *et al.,* 2020). *Oxidus gracilis* was first reported in Switzerland by Bigler (1913) from greenhouses and it is currently the second most abundant inhabitant of urban private gardens in the city of Basel (Braschler *et al*., 2020).

Since heated greenhouses and plant nurseries are most likely hotspots for exotic myriapods in Europe, their examination is a prerequisite for the prevention of future invasions. These artificial environments provide a very special set of conditions such as higher and more stable temperature and humidity, and the presence of non-native plant species, compared to other synanthropic outdoor habitats in Europe (Decker *et al.,* 2014). Decker *et al.* (2014) provide an overview of the literature with millipede and centipede records in greenhouses of Europe, but since then several new findings have been reported (see for example Tuf *et al*., 2018; Dolejš *et al*., 2019; Damasiewicz & Leśniewska, 2020; Gregory & Lugg, 2020; Gregory, 2021). In Switzerland, the literature with greenhouse myriapods records is scarce (Bigler, 1913; Holzapfel, 1932; Pedroli-Christen, 1993; Golovatch *et al*., 2001a). Regarding millipedes, only four non-native species have been reported in Swiss greenhouses: *Amphitomeus attemsi* (Schubart, 1934), native to South America (Golovatch *et al.*, 2001a); *Cylindroiulus truncorum* (Silvestri, 1896a), of Mediterranean origin (Holzapfel, 1932; Pedroli-Christen, 1993); *Oxidus gracilis*, an east Asian species (Bigler, 1913; Holzapfel, 1932; Pedroli-Christen, 1993); and *Poratia digitata* (Porat, 1889) of neotropical origin (Holzapfel, 1932; Pedroli-Christen, 1993). When the first records of *C. truncorum* and *O. gracilis* were made, they were limited to greenhouses (Bigler, 1913; Holzapfel, 1932; Pedroli-Christen, 1993), but they are currently widespread in other urban habitats in Switzerland (Vilisics *et al*., 2012; Braschler *et al*., 2020; Gilgado, 2020). Regarding centipedes, only four European native species, namely *Lithobius melanops* Newport, 1845, *Cryptops* (*Cryptops*) *hortensis* (Donovan, 1810), *Stenotaenia linearis* (C.L. Koch, 1835) and *Schendyla nemorensis* (C.L. Koch, 1837) have been reported from Swiss greenhouses (Holzapfel, 1932). These species live in the wild in Switzerland (Stöckli, 2009; Bonato *et al*., 2016).

In the present work we present an updated list of the millipede and centipede species inhabiting heated greenhouses of Switzerland and provide new records for seven non-native species.

MATERIAL AND METHODS

We were granted permission to sample in heated greenhouses of nine institutions across Switzerland (Table 1): the Botanical Garden of Basel University, Basel Zoo, Botanical Garden of the University of Bern, Conservatory and Botanical Garden of the City of Geneva, Botanical Garden of St. Gallen, Botanical Garden of the University of Fribourg, Botanical Garden of the University of Zurich, the Jurassica Botanical Garden (Porrentruy), and the Papiliorama Tropical Garden in Kerzers. The greenhouses were visited between June and December 2019. In each greenhouse two methods for invertebrate sampling were used: active search and pitfall trapping. At localities where more than one greenhouse was present (Porrentruy, Geneva, Zurich, and Fribourg), we used both sampling methods in the greenhouse that had the highest air temperature and humidity, and only applied active search in the other one. Active search was carried in each greenhouse by the same two members of the team (J.D.G and I.B.) for 30 minutes. We visually searched for millipedes and centipedes, which were captured with forceps and placed in vials with 70% ethanol. The active search targeted millipedes and centipedes on the ground, in leaf litter, under deadwood, stones, plates, pots, etc., and on the bark or plant stems. The pitfall consisted of plastic cups (5.8 cm in diameter each) half filled with propylene glycol and covered by a plastic plate to prevent water or leaves to fall in. We distributed eight pitfall traps throughout the soil area of the main greenhouse of each locality, hiding them as much as possible from the view of the visitors. The traps worked for seven days. Captured specimens were sorted in the lab and transferred to 70% ethanol.

Specimens were identified by J. D. Gilgado (Diplopoda) and D. Cabanillas (Chilopoda) by comparison of external morphology and/or sexual characters, by using keys of identification (Titova, 1981; Eason, 1982; Bonato *et al*., 2009, 2014; Mitić *et al*., 2012; Enghoff *et al*., 2013; Lewis, 2013) and the original descriptions or redescriptions of the species known to inhabit Switzerland (Pedroli-Christen, 1993; Stöckli, 2009; Gilgado 2020) or greenhouses of Europe (Kime & Enghoff, 2011, 2017; Decker *et al*., 2014). Specimens were prepared for long-term storage in ethanol and a voucher collection is deposited in the Naturhistorisches Museum Basel. Photos were taken using a KEYENCE VHX-6000 and a Panasonic Lumix DMC-FZ200 camera equipped with a Raynox DCR-250 macro lens.

TAXONOMIC PART

A total of 1390 individuals belonging to 14 millipede species and 47 individuals of 10 centipede species were identified (Table 2). Of them, 1116 millipede individuals (80.3%), belonging to 8 species (57.1%) and 26 centipede individuals (55.3%) belonging to 4 species (40%) were

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Table 1. Names, location, and dates of visit of the greenhouses examined. The asterisk indicates additional active captures (not standardized).

Institution	Locality, Canton	Greenhouse	Code	Coordinates	Date 1	Date 2
Basel Zoo	Basel, Basel-Stadt	Altes Vogelhaus (Old bird house)	BZV	47°32’53.56”N, 7°34’43.13”E	3.10.19	10.10.19
Botanical Garden of St. Gallen	St. Gallen, St. Gallen	Tropischer Regenwald (Tropical rainforest)	SGR	47°26’24.12”N, 9°24’24.44”E	2.10.19	9.10.19
		Tropische Nutzpflanzen (Tropical cultures)*	SGN	47°26’24.50”N, 9°24’25.15”E	2.10.19	9.10.19
Botanical Garden of the University of Basel	Basel, Basel-Stadt	Tropenhaus (Tropical house)	BAT	47°33’31.06”N, 7°34’54.36”E	26.6.19	3.7.19
		Viktoriahaus (Victoria greenhouse)*	BAV	47°33’32.75”N, 7°34’54.06”E	20.03.19	
Botanical Garden of the University of Bern	Bern, Bern	Palmenhaus (Palm house)	BEP	46°57’8.99”N, 7°26’44.26”E	4.12.19	11.12.19
Botanical Garden of the University of Fribourg	Fribourg, Freiburg	Forêt tropicale (Tropical forest)	FRF	46°47’35.42”N, 7°9’18.17”E	23.10.19	30.10.19
		Plantes utiles tropicales (Tropical useful plants)*	FRP	46°47’33.70”N, 7°9’21.26”E	23.10.19	30.10.19
Botanical Garden of the University of Zurich	Zurich, Zurich	Tropischer Tieflandregenwald (Tropical lowland forest)	ZUT	47°21’28.45”N, 8°33’42.59”E	5.12.19	12.12.19
		Tropischer Bergwald (Tropical mountain forest)*	ZUB	47°21’28.49”N, 8°33’41.14”E	5.12.19	12.12.19
Conservatory and Botanical Garden of Geneva	Geneva, Geneva	Serre Tropicale Principale (Main Tropical Greenhouse)	GEP	46°13’31.44”N, 6°8’43.07”E	15.10.19	22.10.19
		Jardin d’hiver (Winter garden)*	GEH	46°13’33.61”N, 6°8’44.97”E	15.10.19	22.10.19
Jurassica Botanical Garden	Porrentruy, Jura	La Petite Serre Tropicale (The small tropical greenhouse)	JUP	47°24’48.78”N, 7°4’36.89”E	7.11.19	14.11.19
		La Grande Serre Tropicale (The large tropical greenhouse)*	JUG	47°24’48.88”N, 7°4’36.60”E	7.11.19	14.11.19
Papiliorama	Kerzers, Fribourg	Jungle Trek	PAP	46°59’24.05”N, 7°12’4.14”E	12.9.19	19.9.19

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Table 2. Summary of the number of captured individuals of each species by greenhouse. An asterisk indicates that the species is a new record for Switzerland, (+) indicates that the locality was sampled during additional visual search. Abbreviations of the greenhouse names as in Table 1.

Class Diplopoda				Locality (Institution/greenhouse)															
Order				BZV	SG		BA			BE	FR		ZU		GE		JU		PAP
Family	**Species**	**Origin**	**Total**		SGR	SGN (+)	BAT	BAT (+)	BAV (+)		FRF	FRP (+)	ZUT	ZUB (+)	GEP	GEH (+)	JUP	JUG (+)	
Julida Blaniulidae	*Blaniulus guttulatus* (Fabricius, 1798)	Native	**98**	—	2	—	—	—	—	—	4	4	—	87	—	—	1	—	—
	Choneiulus palmatus (Němec, 1895)	Native	**81**	1	—	—	—	—	—	—	6	3	13	5	—	—	33	20	—
	Nopoiulus kochii (Gervais, 1847)	Native	**86**	—	—	—	—	—	—	—	—	—	7	42	1	—	30	6	—
Julida Julidae	*Cylindroiulus latestriatus* (Curtis, 1845)	Native	**2**	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
	Cylindroiulus salicivorus Verhoeff, 1908	Italy	**3**	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—
	Cylindroiulus truncorum (Silvestri, 1896a)	Mediterranean	**202**	6	—	6	1	—	—	7	—	—	11	12	135	22	—	2	—
Polydesmida Haplodesmidae	*Cylindrodesmus hirsutus* Pocock, 1889*	Indonesia or Melanesia	**317**	—	—	—	280	—	—	—	—	—	35	—	—	—	—	—	2
Polydesmida Oniscodesmidae	*Amphitomeus attemsi* (Schubart, 1934)	South America	**153**	3	—	10	—	—	—	5	17	2	43	1	49	10	3	10	—
Polydesmida Paradoxosomatidae	*Oxidus gracilis* (C.L.Koch, 1847)	East Asia	**362**	6	—	1	10	1	—	1	132	—	67	13	74	22	1	34	—
Polydesmida Polydesmidae	*Brachydesmus superus* Latzel, 1884	Native	**8**	—	—	—	—	—	—	—	—	8	—	—	—	—	—	—	—
	Propolydesmus testaceus (C.L.Koch, 1847)	Native	**1**	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Polydesmida Pyrgodesmidae	*Poratia digitata* (Porat, 1889)	Neotropical	**3**	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
	Poratia obliterata (Kraus, 1960)*	Neotropical	**9**	—	—	—	—	—	—	6	—	—	3	—	—	—	—	—	—
Spirobolida Spirobolellidae	*Paraspirobolus lucifugus* (Gervais, 1836)*	South America	**65**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	65

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Table 2. Continued.

Class Chilopoda				Locality (Institution/greenhouse)															
Order				BZV	SG		BA			BE	FR		ZU		GE		JU		PAP
Family	**Species**	**Origin**	**Total**		SGR	SGN (+)	BAT	BAT (+)	BAV (+)		FRF	FRP (+)	ZUT	ZUB (+)	GEP	GEH (+)	JUP	JUG (+)	
Geophilomorpha Geophilidae	*Geophilus flavus* (De Geer, 1778)	Native	**1**	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Geophilomorpha Mecistocephalidae	*Mecistocephalus guildingii* Newport, 1843*	Amphi-atlantic	**11**	—	—	—	—	—	—	—	—	—	—	—	7	4	—	—	—
	Tygarrup javanicus Attems, 1929*	South Asia	**5**	—	—	1	—	—	—	—	—	—	—	—	—	2	—	1	1
Lithobiomorpha Henicopidae	*Lamyctes coeculus* (Brölemann, 1889)*	Unclear	**9**	—	—	—	—	—	—	—	—	3	1	—	5	—	—	—	—
Lithobiomorpha Lithobiidae	*Lithobius forficatus* (Linnaeus, 1758)	Native	**15**	—	—	—	—	2	—	3	—	—	—	—	4	—	6	—	—
	Lithobius melanops Newport, 1845	Native	**2**	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Scolopendromorpha Cryptopidae	*Cryptops anomalans* Newport, 1844	Native	**1**	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
	Cryptops doriae Pocock, 1891*	Palaeotropical	**1**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	Cryptops hortensis (Donovan, 1810)	Native	**1**	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
	Cryptops parisi Brölemann, 1920	Native	**1**	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—

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non-native. This corresponds to 50% of the total number of species recorded and to 79.3% of the total number of individuals captured. Seven species are reported in Switzerland for the first time.

First records for the Swiss Fauna

Class Diplopoda de Blainville in Gervais, 1844
Order Polydesmida Pocock, 1887
Family Haplodesmidae Cook, 1895
Genus *Cylindrodesmus* Pocock, 1889
***Cylindrodesmus hirsutus* Pocock, 1889**
Fig. 1

Material examined: NMB; 115 females, 9 juveniles; Switzerland, Basel-Stadt, Botanical Garden of the University of Basel, Tropenhaus, 47°33’31”N, 7°34’54”E, 270 m; 03.07.2019; J.D. Gilgado and I. Bobbitt leg. – 151 females, 5 juveniles; same data but in the collection of J.D.G. – NMB; 31 females, 2 juveniles; Switzerland, Zurich, Botanical Garden of the University of Zurich, Tropischer Tieflandregenwald, 47°21’28”N, 8°33’42”E, 438 m; 12.12.2019; J.D. Gilgado and I. Bobbitt leg. – 2 females; same data but in the collection of J.D.G. – NMB; 2 females; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59’24”N, 7°12’4”E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg.

Distribution: According to Recuero (2018), who compiled all the records of the species, it is currently a pantropical species appearing in many greenhouses in Europe (see also Dolejš *et al*., 2019). It may be originally native to Indonesia or Melanesia (Golovatch *et al*., 2001b).

Remarks: It is a small, white, or pinkish white species, with a hairy appearance. Some populations of this species include males (Read, 2008), but others are parthenogenetic and thus composed only by females (Golovatch *et al*., 2000). All the individuals collected in Switzerland were females or juveniles. More detailed information about its morphology can be found in Read (2008), Golovatch *et al.* (2000) and Golovatch *et al.* (2001b).

Family Pyrgodesmidae Silvestri, 1896b
Genus *Poratia* Cook & Cook, 1894
***Poratia obliterata* (Kraus, 1960)**
Fig. 2

Material examined: NMB; 1 subadult male, 2 females, 1 juvenile; Switzerland, Bern, Botanical Garden of the University of Bern, Palmenhaus, 46°57’9”N, 7°26’44”E, 520 m; 11.12.2019; J.D. Gilgado and I. Bobbitt leg. – 2 females; same data but in the collection of J.D.G. – NMB; 1 female; Switzerland, Zurich, Botanical Garden of the University of Zurich, Tropischer Tieflandregenwald, 47°21’28”N, 8°33’42”E, 438 m; 12.12.2019; J.D. Gilgado and I. Bobbitt leg. (Table 2). – 2 juveniles; same data but in the collection of J.D.G.

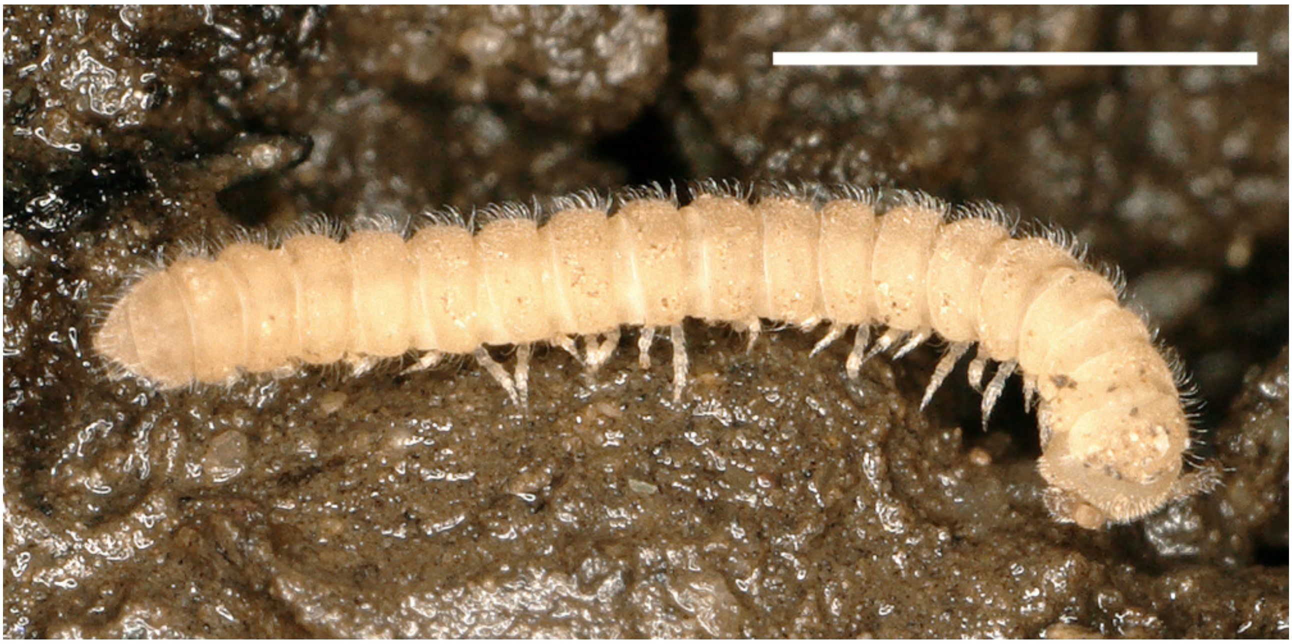

Fig. 1. Living specimen of *Cylindrodesmus hirsutus* from the Tropenhaus of the Botanical Garden of the University of Basel. Scale bar: 2 mm.

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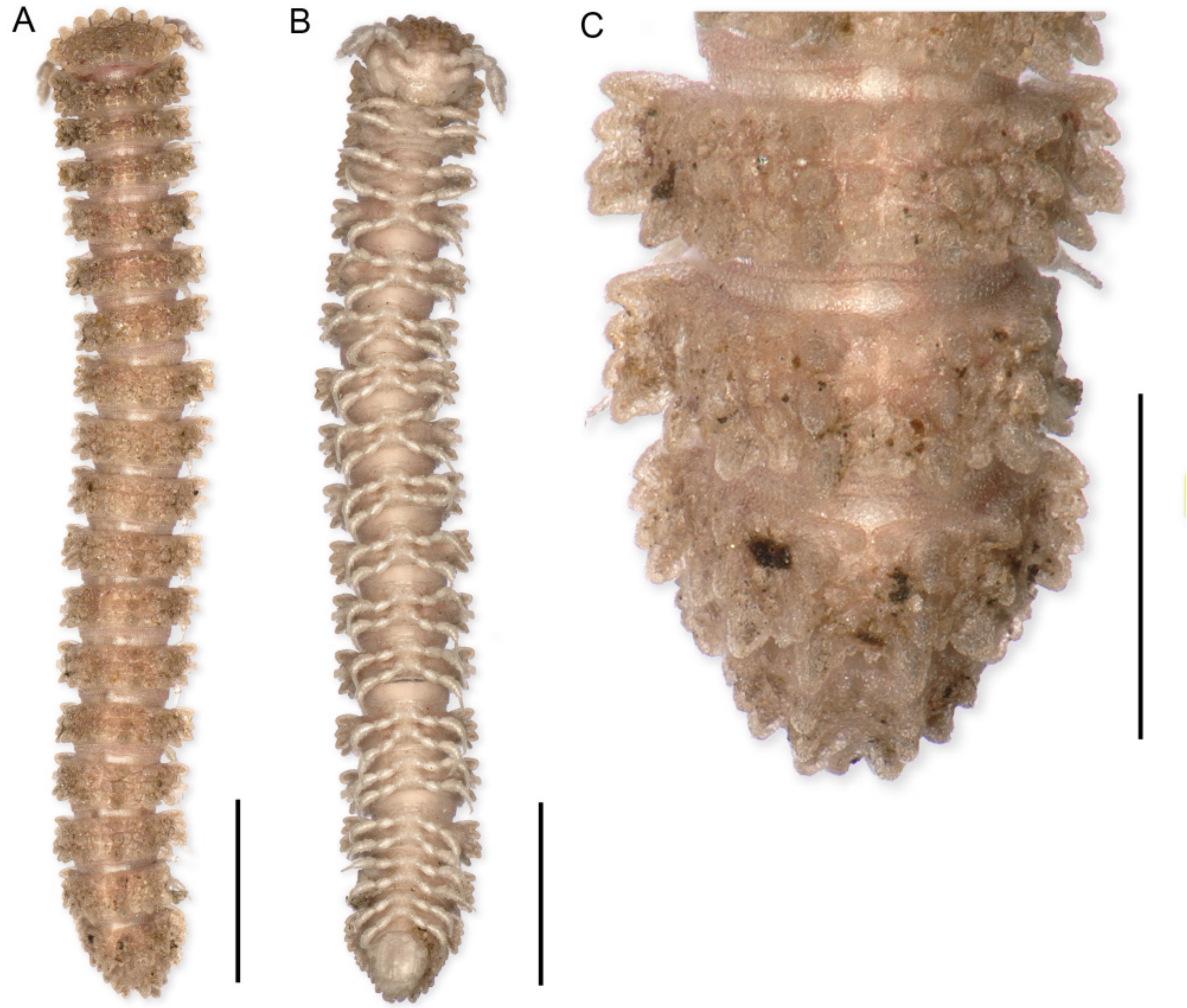

Fig. 2. *Poratia obliterata* from the Botanical Garden of the University of Bern. (A) Dorsal view. (B) Ventral view. (C) Detail of the last body rings. Scale bars: A, B, 1 mm; C, 0.5 mm.

Distribution: This species is found in the wild in Peru, Brazil and Colombia, and in Costa Rica (Golovatch & Sierwald, 2001). In Europe, the species has been recorded in greenhouses in Kiel, Germany (Wilck, 2000; Decker *et al*., 2014) and in Paris, France (Golovatch & Sierwald, 2001).

Remarks: It is very similar to *Poratia digitata*, also known in greenhouses of botanical gardens of Europe, but it can be distinguished by the number of rings (20 in *P. obliterata* and 19 in *P. digitata*) and the number of lateral lobulations in paraterga of ring 16-18(19) (always 4 in *P. obliterata* and mostly 3 in *P. digitata*) (Golovatch & Sierwald, 2001). All the individuals collected in Switzerland were females or juveniles.

Order Spirobolida Bollman, 1893
Family Spirobolellidae Brölemann, 1913
Genus *Paraspirobolus* Brölemann, 1902
***Paraspirobolus lucifugus* (Gervais, 1836)**
Fig. 3

Material examined: NMB; 17 males, 10 females, 7 juveniles; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg. – 20 males, 11 females; same data but in the collection of J.D.G. (Table 2).

Distribution: This originally South American species has been found in greenhouses in England (Read, 2008), Denmark (Enghoff, 1975a) and Germany (Decker *et al*., 2014). In Germany, it was found in six different locations.

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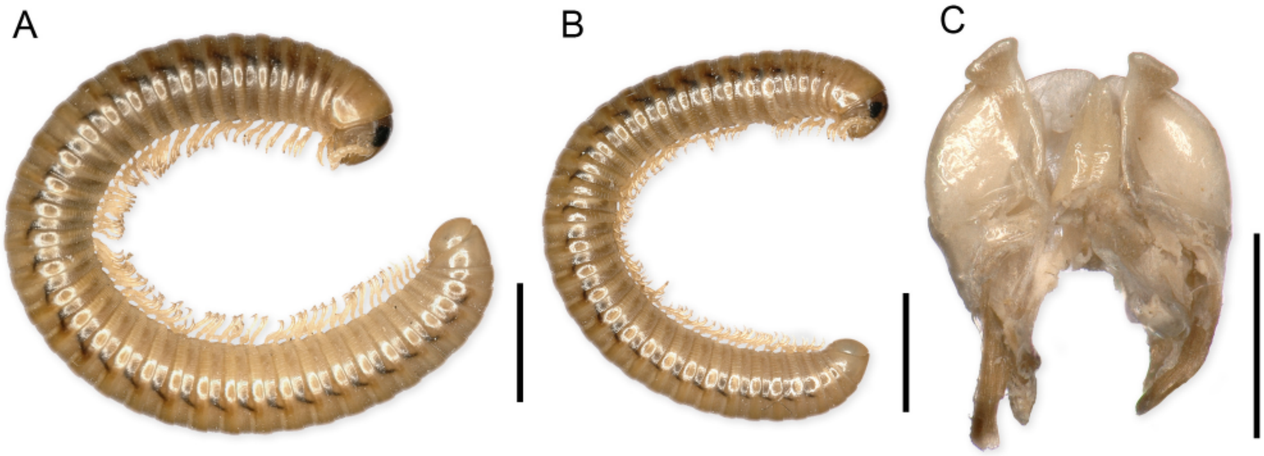

Fig. 3. *Paraspirobolus lucifugus* from the Papiliorama. (A) Adult female. (B) Adult male. (C) Gonopods. Scale bars: A, B, 2 mm; C, 0.5 mm.

Remarks: A description of the species can be found in Read (2008). Both males and females were collected in the present work. As a curiosity, this is one of the few known bioluminescent myriapods (Rosenberg & Meyer-Rochow 2009; Oba *et al.,* 2011).

Class Chilopoda Latreille, 1816
Order Geophilomorpha Pocock, 1896
Family Mecistocephalidae Bollman, 1893
Genus *Mecistocephalus* Newport, 1843
***Mecistocephalus guildingii* Newport, 1843**
Fig. 4

Material examined: NMB; 2 males, 4 females; Switzerland, Geneva, Conservatory and Botanical Garden of Geneva, Serre Tropicale Principale, 46°13'31"N, 6°8'43"E, 389 m; 22.10.2019; J.D. Gilgado and I. Bobbitt leg. – 1 male, 2 females, 2 juveniles; same data but in Jardin d'hiver, in the collection of D.C. (Table 2).

Distribution: *M. guildingii* is an amphi-Atlantic species that inhabits Atlantic islands and coastal or tropical mainland sites from the Americas to West Africa (Bonato *et al*., 2009). According to Bonato *et al*. (2009), *M. guildingii* is present in at least the Greater and Lesser Antilles, Bermuda Islands, Florida, Panama and Brazil in the Western Atlantic, but also in Madeira, the Cape Verde archipelago, Gambia, and Liberia in the Eastern Atlantic. Additionally, *M. guildingii* has been reported from coastal localities of the Pacific Ocean, specifically from Puerto Vallarta (Bonato *et al*., 2009) and the Botanical Garden of Culiacán Rosales in Mexico (López-Bonel *et al*., 2019). Zodinpuii *et al*. (2019) also reported *M. guildingii* from forests and cultivations of Mizoram in the northeast of India but this record seems highly uncertain and therefore needs verification. This species has been introduced to Europe, namely in France, Germany, and United Kingdom, where it is confined to hothouses (Latzel, 1895; Brölemann, 1930; Barber, 2008; Tillier, 2018).

Remarks: This species could be confused with *Mecistocephalus maxillaris* (Gervais, 1837) in European greenhouses. However, the two species can be distinguished by examining the proportion between the length of the areolate clypeus and the plagulae. In *M. guildingii*, the areolate clypeus is twice the length of the plagulae, whilst in *M. maxillaris* both structures are of the same length (Bonato *et al*., 2009). Both males and females of *M. guildingii* were detected in Swiss greenhouses.

Genus *Tygarrup* Chamberlin, 1914
***Tygarrup javanicus* Attems, 1929**
Fig. 5

Material examined: NMB; 1 female, 1 juvenile; Switzerland, Geneva, Conservatory and Botanical Garden of Geneva, Jardin d'hiver, 46°13'31"N, 6° 8'43"E, 389 m; 22.10.2019; J.D. Gilgado and I. Bobbitt leg. – 1 female; Switzerland, St. Gallen, Botanical Garden, Tropische Nutzpflanzen, 47°26'24"N, 9°24'24"E, 662 m; 09.10.2019; J.D. Gilgado and I. Bobbitt leg.; in the collection of D.C. – NMB; 1 female; Switzerland, Jura, Porrentruy, Jurassica Botanical Garden, La Grande Serre Tropicale, 47°24'48"N, 7°4'36"E; 430 m; 14.11.2019; J.D. Gilgado and I. Bobbitt leg. – NMB; 1 female; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg. (Table 2).

Distribution: *Tygarrup javanicus* is probably native to southeastern Asia, originally described from the island of Java in Indonesia (Attems, 1929), with later

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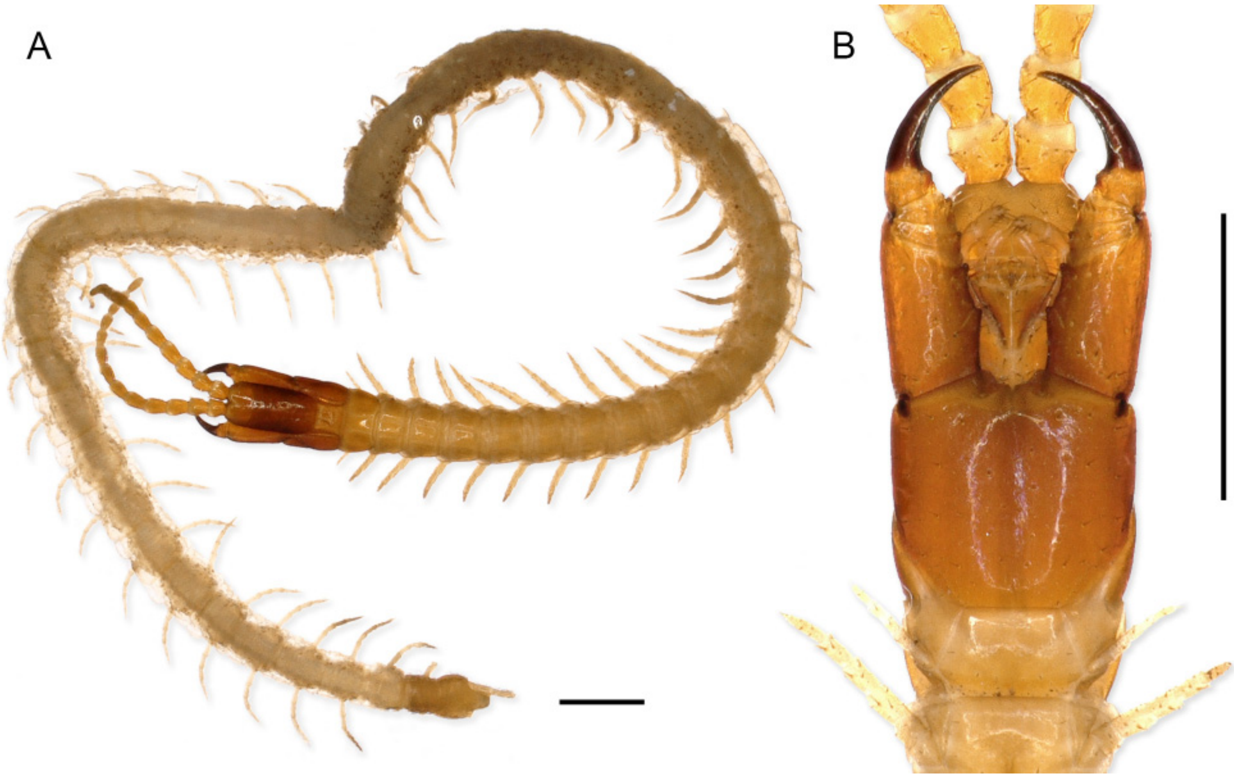

Fig. 4. *Mecistocephalus guildingii* from the Conservatory and Botanical Garden of Geneva. (A) Dorsal view. (B) Head in ventral view. Scale bars: 1 mm.

Fig. 5. *Tygarrup javanicus* from the Papiliorama, Kerzers. Dorsal view. Scale bar: 1 mm.

records in the Seychelles, Cambodia, Vietnam, and Mauritius (Demange, 1981; Titova, 1981; Bonato & Minelli, 2010). This species was presumably introduced to the Hawaiian islands (Bonato *et al*., 2004) and also to Europe. The species has been recorded in Austria, Czech Republic, Germany, Poland, Russia, Slovakia, and United Kingdom, where it is only capable of living in heated greenhouses (Lewis & Rundle, 1988; Christian, 1996; Barber, 2009b, c; Decker *et al*., 2014; Tuf *et al*., 2018; Nefediev, 2019; Damasiewicz & Leśniewska, 2020).

Remarks: Complete data about its morphology can be consulted in Bonato *et al*. (2004). All adult specimens from Swiss greenhouses were sexed as females.

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Order Lithobiomorpha Pocock, 1895
Family Henicopidae Pocock, 1901
Genus *Lamyctes* Meinert, 1868
Subgenus *Lamyctes* Meinert, 1868
***Lamyctes* (*Lamyctes*) *coeculus* (Brölemann, 1889b)**
Fig. 6

Material examined: NMB; 1 female; Switzerland, Zurich, Botanical Garden of the University of Zurich, Tropischer Tieflandregenwald, 47°21'28"N, 8°33'42"E, 438 m; 12.12.2019; J.D. Gilgado and I. Bobbitt leg. – NMB; 2 females, 1 juvenile; Switzerland, Fribourg, Botanical Garden of the University of Fribourg, Plantes utiles tropicales, 46°47'35"N, 7°9'18"E; 631 m; 30.10.2019; J.D. Gilgado and I. Bobbitt leg. – NMB; 3 females; Switzerland, Geneva, Conservatory and Botanical Garden of Geneva, Serre Tropicale Principale, 46°13'31"N, 6°8'43"E, 389 m; 22.10.2019; J.D. Gilgado and I. Bobbitt leg. – 2 females; same data but in the collection of D.C. (Table 2).

Distribution: The family Henicopidae is native to the Southern Hemisphere, although the origin of *L. coeculus* is uncertain. This species was first detected in a greenhouse in Italy (Brölemann, 1889a) and subsequently reported from greenhouses in Sweden, France, Illinois (U.S.A.), Finland, Denmark, United Kingdom, Germany, and the Asian part of Russia (Lohmander, 1923; Brölemann, 1930; Auerbach, 1952; Lehtinen, 1960; Enghoff, 1975b; Barber, 2009c; Decker *et al*., 2014; Nefediev *et al*., 2016). This species has been recently recorded in new greenhouses of France (Tillier, 2018) and the United Kingdom (Gregory & Lugg, 2020). *Lamyctes coeculus* has been reported outdoor in Australia, Hawaii, the Galapagos Islands, Mexico, Argentina, Cuba, the Canary Islands, Democratic Republic of Congo, Tanzania, Madagascar, La Réunion and Palestine (Negrea *et al*., 1973; Enghoff, 1975b; Matic *et al*., 1977; Peck, 1990; Enghoff & Eason, 1992; Shear & Peck, 1992; Negrea & Matic, 1996; Zapparoli & Shelley, 2000; Edgecombe & Giribet, 2003; Edgecombe, 2004; Cupul-Magaña, 2011, 2015). It has been also recorded in Venezuela, but no collecting data were provided (Turk, 2009). Currently, this species could have a subcosmopolitan distribution and be widely extended all over the world, possibly due to anthropochory and thelytoky (Enghoff, 1975b; Edgecombe & Giribet, 2003; Enghoff *et al*., 2013).

Remarks: Worth mentioning another blind henicopid species which could potentially inhabit European

Fig. 6. *Lamyctes coeculus* from the Conservatory and Botanical Garden of Geneva. (A) Dorsal view. (B) Lateral view of head and first segments of trunk. Scale bars: A, 1 mm; B, 0.5 mm.

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greenhouses and be confused with *L. coeculus* (Enghoff *et al*., 2013): *Lamyctes* (*Lamyctes*) *hellyeri* Edgecombe & Giribet, 2003, which differs in having a higher number of antennal articles (29-33 vs. 24 in *L. coeculus*) and the presence of a distal spinose projection on the tibiae of legs 12 (Edgecombe & Giribet, 2003). All examined specimens of *L. coeculus* from Swiss greenhouses were sexed as females.

Order Scolopendromorpha Pocock, 1895
Family Cryptopidae Kohlrausch, 1881
Genus *Cryptops* Leach, 1814
Subgenus *Cryptops* Leach, 1814
***Cryptops* (*Cryptops*) *doriae* Pocock, 1891**
Fig. 7

Material examined: NMB; 1 juvenile; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg. (Table 2).

Distribution: *Cryptops doriae* is natively found in tropical areas of Asia and Australia, namely in the Seychelles, Kazakhstan, Uzbekistan, Nepal, India, Burma, Laos, Vietnam, Cambodia, Philippines, Pahang (Malaysia), Sumatra and Java (Indonesia), Tonga, and Papua New Guinea (Pocock, 1891; Silvestri, 1894a; Attems, 1907, 1938; Lewis, 1999, 2007a, 2010; Schileyko, 2001, 2007; Schileyko & Stoev, 2016; Khanna, 2008; Nguyen *et al*., 2019; Dyachkov, 2020; Dyachkov & Nedoev, 2021). Additionally, *C. doriae* has been detected in European greenhouses in the United Kingdom (Lewis, 2007b) and in Germany (Decker *et al*., 2014).

Remarks: *Cryptops doriae* can be readily distinguished from native species by the presence of one or two saw teeth on the ventral surface of the femora of the ultimate leg pair. The morphology of the species has been studied in depth by Lewis (2009, 2013).

DISCUSSION

With some variation among greenhouses, millipedes were generally much more abundant (1390 individuals) than centipedes (47 individuals). Despite the differences in abundance, the number of centipede species (10) was not much lower than that of millipedes (14), as few millipede species had very high abundances (Table 2). The reason for the higher abundance of millipedes may be related to their trophic level. Millipedes are mostly detritivores consuming decaying leaf litter (David, 2015), a frequently occurring resource in greenhouses. Centipedes are predators (Voigtländer, 2011) and their populations depend, among others, on the abundance of prey. Centipedes are also rapid runners often escaping the forceps of the samplers. However, this may not explain the difference of the 30 times higher abundance of millipedes.

The high numbers of non-native millipede and centipede species found are remarkable. Interestingly, seven of these species have not previously been recorded in Switzerland. However, their presence in greenhouses in Switzerland was expected, as these species were already

Fig. 7. *Cryptops doriae* from the Papiliorama. Dorsal view. Scale bar: 2 mm.

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found in greenhouses of other European countries (see for example Decker *et al*., 2014). In addition to the comments made on the new records, it is also worth mentioning the millipede *Cylindroiulus salicivorus* Verhoeff, 1908 (Table 2), an Italian species that is spreading outdoors across Europe (Read *et al*., 2002; Lee, 2006; Spelda, 2005; Kime & Enghoff, 2017) and has been only recently recorded in Switzerland from two urban private gardens in Basel (Gilgado, 2020). Conversely, the non-native centipede species found in the present work, *M. guildingii*, *T. javanicus*, *L. coeculus* and *C. doriae,* have never been never reported outdoors in Europe, most probably because they may not be able to survive in temperate climates.

There is increasing literature on non-native myriapods found in greenhouses in Europe (see for example Dányi & Tuf, 2016; Tuf *et al*., 2018; Dolejš *et al*., 2019; Damasiewicz & Leśniewska, 2020; Gregory, 2021). However, there are few comprehensive species lists for countries, an exception being Decker *et al*. (2014) for Germany. These authors used data from 46 greenhouses and re-surveyed 29 of them. Despite the higher number of greenhouses examined, Decker *et al.* (2014) reported a similar percentage of non-native species from different continents (34%) as found in our study (41.7%; Table 2). Most of the myriapod species found in Swiss greenhouses are also present in greenhouses in Germany. However, some native Western European species found in Swiss greenhouses were not recorded in German greenhouses, such as *Propolydesmus testaceus* (C.L. Koch, 1847), *Cryptops* (*Cryptops*) *anomalans* Newport, 1844 and *Cryptops* (*Cryptops*) *parisi* Brölemann, 1920*,* as well as some non-native species such as *C. salicivorus* (in Germany only known from parks or gardens) or *M. guildingii*. On the other hand, Decker *et al*. (2014) reported 10 non-native myriapoda species in German greenhouses that were not found in the present study. The apparent absence of these species in Switzerland might be due to the lower number of greenhouses examined, although preventive measures taken by some institutions, use of pesticides, or presence of predators such as birds, may also reduce the number of introduced species.

The results on millipedes and centipedes indicate that despite greenhouses harbouring a mix of native and non-native species, the latter are predominant. Native centipedes from this study are mostly eurioic species able to colonise and exploit new habitats. Amongst them, *L. forficatus* (Linnaeus, 1758), *L. melanops* and *C. hortensis* were previously recorded by Holzapfel (1932) in Swiss greenhouses and are also common in other European hothouses (Decker *et al*., 2014, Gregory & Lugg, 2020). The native millipedes recorded in our study are synanthropic species usually found in urban and suburban environments (Pedroli-Christen, 1993; Kime & Enghoff, 2011, 2017; Vilisics *et al*., 2012; Braschler *et al*., 2020). The non-native species found have various original distribution areas (Table 1), but those from tropical or subtropical areas are the most abundant, most probably favoured by the higher temperature and humidity in the greenhouses.

Several hypotheses have been proposed to explain the introduction and survival of alien centipedes in greenhouses, for example small body size that allows them to be passively transported with pot-plants and the presumable reproduction by thelytoky (Enghoff, 1975b; Golovatch, 2009; Stoev *et al*., 2010). These explanations could firmly support the presence and expansion of *L. coeculus* and *T. javanicus* throughout European greenhouses since they are small-sized species and only females have been ever detected in Europe (Enghoff, 1975b; Tuf *et al*., 2018). Other biological features such as high fertility, short development time and early maturity have been proposed to explain the ability of non-native millipedes and centipedes to survive in greenhouses (Golovatch, 2009; Tuf *et al*., 2018).

It is also possible that the absence of seasonal variations in environmental conditions negatively affects native millipede species in greenhouses, as some temperate species are adapted to seasonal variations in light, temperature and humidity in order to complete their life cycle (Fujiyama, 1996; David *et al*., 2003). Most of the non-native species coming from tropical areas have little potential to settle in the wild in Europe but some species from subtropical or temperate climates seem to spread into synanthropic habitats in Central Europe (Gilgado, 2020). This could be due to a lower number of competing species, absence of natural predators and parasites, etc. (Tilman, 1999). Thus, greenhouse managers should do their best to prevent the introduction of non-native soil-dwelling arthropods into their greenhouses and their later escape into the wild.

Regarding millipedes, the last comprehensive checklist for Switzerland made by Pedroli-Christen (1993) contains 127 taxa (125 species, two of them with two subspecies each), including those living indoors. Several new records have been made ever since: Bogyó *et al*. (2013) added *Polydesmus rupicursor* Verhoeff, 1907, Golovatch *et al*. (2001a) added *Amphitomeus attemsi*. Gilgado (2020) added *Cylindroiulus britannicus* (Verhoeff, 1891), *C. salicivorus*, *C. vulnerarius* (Berlese, 1888), *Heteroiulus intermedius* (Brölemann, 1892), *Anamastigona pulchella* (Silvestri, 1894b) and *Macrosternodesmus palicola* Brölemann, 1908. These records in the literature, added to the three new records in greenhouses reported in this study, result in a total of 136 millipede species for Switzerland. However, a revision is needed, because the validity of some of the species listed is discussed (Pedroli-Christen 1993). According to the checklist provided by Stöckli (2009), 62 centipede species have been reported from Switzerland (but precise data for two of them has not been published yet), although the author estimates that the number could reach 90 species for the country. The present study provides four new records for the Swiss

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centipede fauna and adds seven species to the catalogue of centipedes able to live in Swiss greenhouses. Despite this progress, more centipede species could potentially be detected in further studies, for example *Polygonarea silvicola* Lawrence, 1955, *M. maxillaris*, *Pectiniunguis pauperatus* Silvestri, 1907 or *Lamyctes (Metalamyctes) africanus* (Porat, 1871), since they have been previously reported from other European greenhouses (Andersson *et al*., 2005; Stoev *et al*., 2010; Enghoff *et al*., 2013; Dányi & Tuf, 2016; Iorio, 2016).

In conclusion, our work provides the first comprehensive list of millipedes and centipedes in Swiss heated greenhouses (Table 2). Our results show a high share of non-native species from different regions of the world and provides seven new records for Switzerland. Not all exotic species reported in greenhouses of other European countries were found, probably because the small number of greenhouses examined and/or prevention measures taken in Swiss greenhouses. The present work suggests that the managers of these greenhouses should keep working on the prevention of introduction of exotic invertebrates.

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