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Distribution and natural history of *Plutonium zwierleini* (Chilopoda: Scolopendromorpha) in Sicily (Italy)

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Abstract

Plutonium zwierleini is a large plutoniumid centipede of great evolutionary interest, occurring with isolated populations along the western Mediterranean area, from Spain to Italy. Due to its rarity and the extreme paucity of available records, *P. zwierleini* is among the least known Mediterranean chilopods, and scarce information is currently available on its ecology and natural history. Based on an extensive sampling effort carried out in Sicily between 2022 and 2023, we here provide additional occurrence localities for the species across Sicily, and new insights into its ecology. Overall, 29 novel Sicilian records of *P. zwierleini*, scattered across 21 localities, were collected thus increasing its known Sicilian distribution area by 117%, and the number of localities by 110%. The species was found in a wide range of habitats such as open areas, woods, buildings, and caves, characterizing *Plutonium zwierleini* as a habitat generalist, whose fine ecological *preferenda* need to be further explored. Moreover, to explore the diet and behaviour of the species, some specimens were kept in captivity. The captive individuals fed mostly on dead or poorly mobile soft-bodied prey and inert food, without ever displaying predatory behaviour; this suggests that, contrarily to what is currently assumed, *P. zwierleini* might be a scavenger rather than a predator. The potential distribution of *Plutonium zwierleini* in Sicily was inferred based on georeferenced occurrence records and climatic variables. The implemented MaxEnt model forecasts the possible occurrence of *P. zwierleini* on the whole island, with the single exception of its south-easternmost part, possibly due to the local pattern of precipitation seasonality. We hope that the present work might pave the way for further surveys aimed at a better understanding of the ecology of *Plutonium zwierleini* and the collection of new data in the other regions inhabited by this secretive species.

Keywords: *Centipede*, *feeding behavior*, *species distribution model*, *soil fauna*, *cryptozoans*

Introduction

Rarity is a recurring attribute among species (Lennon et al. 2004; McCreadie & Adler 2008 and references therein), however its meaning can take different forms. The rarity of a species is often defined based on various conditions, not always simultaneously present (Rabinowitz 1981; Longton & Hedderson 2000). Collecting and analysing ecological (Sazima & Carvalho-Filho 2003; Faraone et al. 2021), distributional (McCreadie & Adler 2008; Vecchioni et al. 2022) and phylogenetic (Cai et al. 2007; Faraone et al. 2020) data on rare or elusive species usually require strong efforts, nevertheless it is a great opportunity to delve into various aspects of their

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natural history and provide a sound basis for conservation and management measures.

Within the chilopod order Scolopendromorpha, the relatively poorly known family Plutoniumidae currently includes two genera: the genus *Theatops* Newport, 1844, with six extant and one extinct species with highly disjointed distribution ranges scattered throughout the Holarctic (Shelley 1997; Di et al. 2010; Edgecombe et al. 2023), and the genus *Plutonium* Cavanna, 1881, with the only species *Plutonium zwierleini* Cavanna, 1881. Within the Plutoniumidae family, *P. zwierleini* has a highly distinctive feature: spiracles are present in every body segment from the second to the penultimate one, in contrast to the alternate segment distribution observed in all the other Scolopendromorpha species (Schileyko & Pavlinov 1997; Shelley 1997; Fusco 2005; Bonato et al. 2017). This feature, which can be observed only in *P. zwierleini* and in the distantly related Geophilomorpha within the Chilopoda, was previously considered a plesiomorphy of the genus, but it is now rather considered an autoapomorphic character of the species (Shelley 1997; Edgecombe et al. 2023). The species is heavily armed, equipped both with the strong and venomous forcipules typical of Chilopoda, and with blade-edged claws on its terminal non-ambulatory enlarged legs. Its peculiar morphology (i.e., blindness, shape of posterior legs, and tracheal system) seems to be adaptive for inhabiting deep fissures (Manton 1965). Such an endogeic habit could at least partly explain the paucity of currently available records for the species, which should thus be ascribable to its low detectability. In fact, *P. zwierleini*, despite being one of the largest and most striking European chilopods, and often considered potentially harmful to humans, is among the least known and most enigmatic Mediterranean centipede species, and it is an extremely rare taxon both due to the extreme paucity of available observations and its restricted and fragmented distribution (Bonato et al. 2017).

Plutonium zwierleini is to date known from relatively few and scattered observations from Italy and Spain: in the time frame comprised between its description (Cavanna 1881) and 2015, only 25 records had been collected, of which about 44% from the last two decades of the nineteenth century (Shelley 1997; Bonato et al. 2017). Later on, Bonato et al. (2017) updated the knowledge and distribution of the species by adding 19 additional records, obtained through an accurate census in the museum collections and by Citizen Science approach. The data reported by Bonato et al. (2017) allowed to identify four different distribution clusters: 1, Sicily (13 records, 10 localities) 2, Southern Italy, Tyrrhenian coasts, mostly on the Sorrento Peninsula (11 records, nine localities) 3, Sardinia (15 records, 14 localities) 4, Southern Iberian Peninsula, Peribaetic system (two records, two localities).

Due to the scarce and fragmentary available information, it is currently not possible to characterize the ecology and habitat preferences of *Plutonium zwierleini*, which has been found in both hypogean and epigean biotopes within variable contexts such as woods, cultivated fields, pastures, caves, urban settlements and inside buildings between sea level and 1200 m a.s.l (Bonato et al. 2017). Similarly, very little is known of other aspects of its natural history, such as its feeding behaviour. Scolopendromorpha are mostly active opportunistic foragers, which feed largely on other invertebrate and vertebrate animals (Guizze et al. 2016 and references therein) and, occasionally, on carrion and vegetal matter (Heymons 1901; Guizze et al. 2016). A single observation of predation in the wild is known for *P. zwierleini* and was documented in Sardinia, where a large adult individual was observed preying on a young cave salamander, *Speleomantes supramontis* (Lanza et al., 1986) (Sanna et al. 2018): similarly to documented cases in captive-reared *Theatops* sp. (UnicoCelula 2012; Furball677 2016a, 2016b), the centipede used its terminal legs as functional forcipules to pierce the prey (Manton 1965; Shelley 1997; Lewis 2010).

The phylogenetic relationship between *Plutonium zwierleini* and other species within the Plutoniumidae family is not fully resolved yet. The few available morphological and molecular analyses of Plutoniumidae mostly retrieve *Theatops* as a paraphyletic group with the monotypic genus *Plutonium* nested within it (see Bonato et al. 2017; Edgecombe et al. 2023, and references therein) so that a taxonomical revision of the family is pending and a more comprehensive taxonomical and geographical coverage of the genetic diversity of plutoniumid species is often advocated (Bonato et al. 2017; Edgecombe et al. 2023). Moreover, since sequence data are currently available for a single *P. zwierleini* specimen (Bonato et al. 2017), no information is to date available on the intraspecific genetic diversity and the phylogeography of the species.

Given the high evolutionary interest of the species within the Chilopoda and of the scarce information currently available on its distribution, ecology, we aimed to address these main goals: (1) providing additional records of *P. zwierleini* across Sicily, the region where its type locality occurs, (2) predicting its distribution across geographic space using bioclimatic environmental data, and (3) offering some insights into the natural history of this secretive taxon, including habitat preferences and feeding behaviour.

Materials and methods

Sampling and distribution data

Sampling was conducted in Sicily in some of the localities where *Plutonium zwierleini* was reported to occur following Bonato et al. (2017), and in new randomly selected sites. The selection was arbitrary, given that the habitat preferences of *P. zwierleini* have not to date been precisely delineated, with the species being observed in a diverse array of habitats, including both hypogeal and epigeal environments (Bonato et al. 2017). Throughout the fieldwork period spanning from December 2022 to June 2023, a total of 61 sampling sessions were conducted across 53 distinct locations (Figure S1). These sites were broadly categorized into open habitats, including pastures, garrigues, and grasslands (71.2%), as well as natural and artificial woods (28.8%). The average altitude of the sampled localities was 529.4 ± 414.9 (20–1570) m a.s.l. [mean ± SD (range)]. Latitude and longitude for each locality were determined with a geographical positioning system (GPS) receiver. In addition, at each sampled site we recorded local environmental characteristics and identified the occurring Scolopendromorpha taxa at the finer possible taxonomic level through visual inspection. Maps showing the sampling sites and *P. zwierleini* distribution were produced using QGIS software v. 3.30.2 (QGIS Development Team 2016, http://www.qgis.org).

Field sampling involved daytime active searches, by examining potential shelters under natural (e.g., rock crevices, logs, and vegetal detritus) and artificial structures (e.g., bituminous sheets and wooden boards). At each site, 1–4 researchers conducted surveys, dedicating 10 minutes to 3 hours, depending on the extension of the area and shelter density. At sites where *Plutonium zwierleini* was found, the number of findings/hours *per* researcher was calculated as a detection rate.

The body length of each collected specimen was measured with a digital calliper with a 0.05 mm precision from the anterior margin of the head to the tip of the ultimate tergite.

Five *P. zwierleini* voucher specimens were deposited in the collection of the Zoology Section "La Specola", Natural History Museum, University of Florence (Italy) with the collection numbers (MZUF): 379–383 (Table I). The other specimens are currently stored at the Dept. STEBICEF of the University of Palermo, under the responsibility of the author FPF.

In addition to field surveys, we employed Citizen Science (see also Faraone et al. 2017; Haklay et al. 2021), leveraging collaborative contributions from users in a zoology-oriented Facebook group "Fauna Siciliana" (https://www.facebook.com/groups/faunasiciliana) and records shared by colleagues. Contributors supplied location data, providing information on additional sites where *Plutonium zwierleini* occurs in Sicily (Table I). For each observation recorded through social networks, we meticulously checked the original files and pictures, the species identification, and the location provided by the users themselves. Therefore, new records were validated only when documented by voucher specimens and/or photographs taken in the field showing diagnostic characters of *P. zwierleini*. Only validated reports are here reported.

In order to estimate the extent of the distribution of *Plutonium zwierleini* in Sicily we used the Minimum Convex Polygon (MCP) method, as implemented in the QGIS software.

Species distribution model and spatial analysis

To predict the distribution of *Plutonium zwierleini* across Sicily using environmental data, we employed correlative species distribution models (SDMs). For this elusive species, we used georeferenced data for 19 out of the 21 localities listed in Table I, since only toponyms without reference to coordinates are known in the literature (see Bonato et al. 2017 and references therein). Among all available methods (Valavi et al. 2021), we utilized the Maximum Entropy Modeling (Maxent) algorithm, chosen for its demonstrated suitability as the minimum performance threshold is achieved with as few as 15 observations (Støa et al. 2019). We applied the "max_spec_sens" threshold (Hijmans 2023), representing the point at which the combined sensitivity (true positive rate) and specificity (true negative rate) are maximized. Bioclimatic data was collected from the WorldClim database, encompassing all the available 19 variables (Fick & Hijmans 2017).

Although subterranean habitats differ from aboveground areas, previous research has shown that each of these variables can significantly influence belowground conditions (Mammola & Leroy 2018). We initially considered all the 19 variables, however, as many were highly correlated (Figure S2), a variance inflation analysis (VIF) (Marquardt 1970) was

Table I. Novel records of *Plutonium zwierleini* in Sicily. The acronyms reported in the reference column refer to author names. The detection rate, DR, was calculated as the number of findings/hours per researcher.

Code	Locality - Province	Date	Latitude N	Longitude E	Habitat	Elevation (m a.s.l.)	N.	MZUF	DR	Reference
1	Catania - Catania§	Oct 2002	37.511	15.080	House inside urban area	49	1			A Marletta+
2	Castelbuono - Palermo§	20 Sep 2016	37.947	14.050	Rural house	290	1			M Paonita+
3	Monte Pellegrino - Palermo§	15 Oct 2016	38.170	13.352	Eucalypt reforestation	411	1			A Dentici+
4	Castelvetrano - Trapani§	18 May 2018–19 Feb 2023	37.692	12.760	Arable field margin	~110	6	380	0.17	AB, FPF, GS
5	Villafrati - Palermo	5 Jul 2018	37.910	13.488	Backyard in a suburban house	524	1			G Surdo⋆
6	Gravina di Catania - Catania§	Nov 2018	37.552	15.071	House inside urban area	301	1			P Galasso+
7	Catania - Catania	1 Apr 2019	37.511	15.087	Urban area	30	1			N Pavone⋆
8	Gravina di Catania - Catania	22 Jul 2019	37.551	15.073	Urban area	280	1			D Calabretta⋆
9	Mussomeli - Caltanissetta	21 Aug 2019	37.617	13.738	Backyard of a rural house	411	1			M Spoto⋆
10	Agrigento - Agrigento§	20 Nov 2020	37.329	13.587	Rural house	219	1			J Wojtkow+
11	Milo - Catania§	7 Dec 2020	37.735	15.135	Hypogean habitat	480	1			GN
12	Monreale - Palermo	15 Mar 2021	38.082	13.293	House inside urban area	285	1			S Costa+
13	Belpasso - Catania§	23 Jun 2021, 21 Jul 2022	37.604	14.998	Hypogean habitat	615	1			GN
14	Cefalù - Palermo	22 Nov 2021	38.024	14.011	Backyard of a rural house	180	1			K Cespa⋆
15	Zafferana Etnea - Catania§	18 Jan 2022	37.688	15.069	Hypogean habitat	1164	2			GN
16	Nicolosi - Catania§	21 Jul 2022	37.630	15.036	Hypogean habitat	820	1			GN
17	Alimena - Palermo§	30 Dec 2022	37.695	14.128	Pasture	844	1	379	0.50	FM, GG
18	Near Ficuzza - Palermo§	1 Mar 2023, 13 Jun 2023	37.896	13.379	Oak wood margin	566	2	381	0.33	CM
19	Piana degli Albanesi - Palermo§	12 Mar 2023, 26 Mar 2023	37.964	13.316	Pasture/Arable field margin	~726	2	382	0.50	FM, FPF, GG
20	Caccamo - Palermo§	6 Apr 2023	37.950	13.649	Pasture	176	1	383	0.33	FM, FPF
21	Caccamo - Palermo§	24 May 2023	37.915	13.619	Pine reforestation	180	1		0.50	FPF, LV

⋆Citizen science data; +personal communications; §collected specimen; MZUF, catalog numbers of the specimens deposited at Zoology Section "La Specola," Natural History Museum, University of Florence (Italy).

conducted using the "vif" function of the "usdm" package (Naimi 2017) to select a set of non-correlated variables. This process, ultimately, led us to analyse isothermality [ratio of the mean diurnal range (Bio 2) to the annual temperature range (Bio 7) multiplied by 100], temperature seasonality, mean temperature of driest quarter, precipitation seasonality, precipitation of warmest quarter, and precipitation of coldest quarter (Table S1). Seasonality variables provide a measure of change over the course of the year, with larger values indicating a greater variability in the selected variable. Pseudo-absence data were generated using 1000 random points across the region of interest. Then, we evaluated which climatic variables significantly affect the distribution of our studied species. Since we did not find spatial autocorrelation in our dataset (Moran's test for distance-based autocorrelation $p = 0.49$), we performed a general linear model with "glm" setting observations of presence/absence as dependent (outcome) variable and climate variables as independent (fixed) effects. We selected "binomial" as family distribution and conducted model diagnostic in "DHARMa" (Hartig 2022). All analyses have been performed in R v. 4.1.3 (R Core Team 2022).

Behavioural observations

Three live *Plutonium zwierleini* specimens, two individuals (44- and 102-mm body length) from the locality #4 and one individual (53-mm body length) from the locality #18 (Table I), were kept in captivity between February and August 2023 with the aim of observing their behaviour. The larger specimen was housed in a 30 cm long × 25 cm wide plastic box, whereas the smaller ones were housed individually in 20 × 15 cm similar enclosures. The lids of the boxes were finely perforated with 2–3 mm holes to allow air exchange. The bottom was filled with a layer of about 2 cm of loam, and a rock slab fragment was added as a shelter. Each box was kept at room temperature (18–28°C) at the *Dipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche* of the University of Palermo, with a natural daylight cycle, and misted with water once or twice a week to avoid dehydration. Various types of food were supplied once per week overnight inside the enclosures for 12 hours and the feeding response of the centipedes was recorded. Several different prey items, consisting of both alive and freshly dead small soil invertebrates and inert food (meat and fruits), were proposed. Three different responses have been registered: 1) Rejection (R), when the food item was totally ignored or avoided and found intact and in the same position after 12 hours, 2) Tasting (T), when the food item was briefly touched with the maxillae and mouth parts, and then ignored and/or found poorly damaged after 12 hours, and 3) Consumption (C), when the food item was entirely or almost entirely eaten.

In addition, we kept note of the observations previously collected on a 91 mm body length *Plutonium zwierleini* specimen from Sicily kept in captivity in 2019 by the authors AB and GS.

Results

Sampling and distribution

We here provide 29 novel Sicilian records of *Plutonium zwierleini* spanning from 2002 to 2023 and scattered across 21 localities (Table I).

Ten *Plutonium zwierleini* specimens were found in six out of the 52 sampled localities (11.5%, see Table I and Figure 1). Five additional specimens were collected in 2022 through non-targeted hypogean sampling sessions using pitfall traps as detailed in Nicolosi et al. (2023), placed from 1 to 26 m from cave entrances (#11, #13, #15, #16; see also Table I). Eight of the localities where we directly found *P. zwierleini* are new for the species (Table I), whereas locality #10 is close (~1.4 km) to the "Ficuzza" village (Province of Palermo), already mentioned by Attems (1930). Although they fall within the same municipality, localities #20 and #21 were considered as different sites since they are located 4.7 kilometres apart, characterized by different habitats, and separated by a large dam reservoir. In every location where a targeted sampling session revealed the presence of *P. zwierleini*, its coexistence with other Scolopendromorpha was observed. *Scolopendra cingulata* Latreille, 1829, *S. oraniensis* Lucas, 1846, and Cryptopidae were syntopically found with *P. zwierleini* in localities #19, #20, #21; *S. cingulata* and *S. oraniensis* in #4; *S. cingulata* and Cryptopidae in #18; *S. cingulata* in #17. Furthermore, the presence of *S. cingulata*, *S. oraniensis*, and Cryptopidae was also verified in the non-targeted site #15.

Two published *Plutonium zwierleini* localities, "Monte Gorna" and "Monte Pagano" (see Bonato et al. 2017), were surveyed without success. More than one observation was collected in localities #4 (three specimens during our 2023 fieldwork), #10 (two specimens in 2023) and #19 (two specimens in 2023, see Table I and Figure 2). The detection rate of the species in the localities where it was found ranged from 0.17 to 0.50 records/hour per person (see Table I for further details).

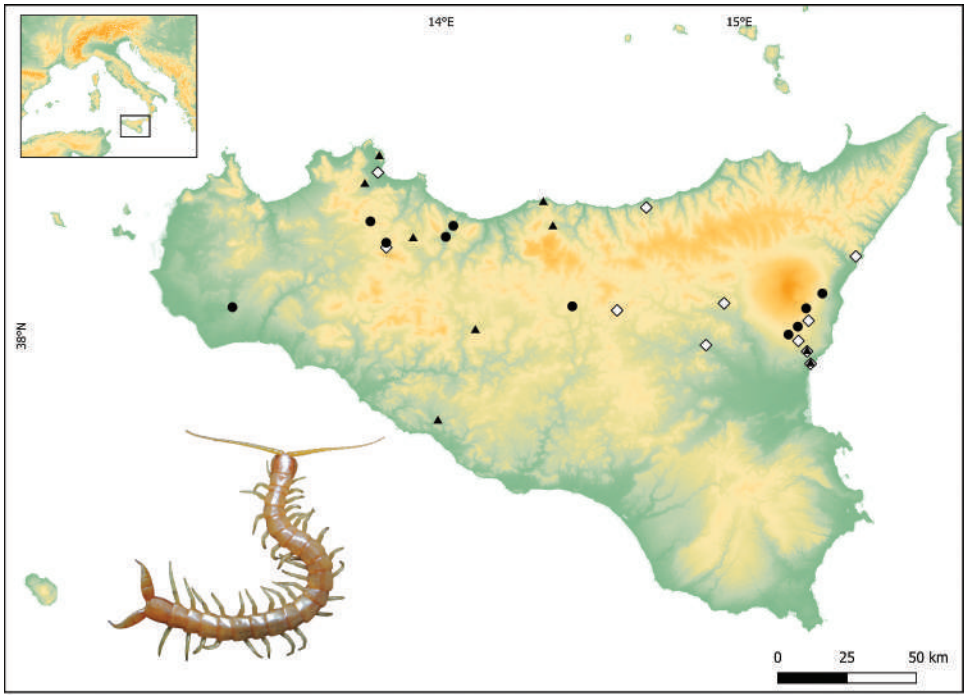

Figure 1. Occurrence localities of *Plutonium zwierleini* in Sicily. Black circles indicate novel sites where the centipede was directly observed by the authors; Black triangles report data from citizen science and personal communications; White diamonds represent bibliographic records of the species obtained from Bonato et al. (2017). See Table I for more information on the novel occurrence localities of the species.

Figure 2. Four of the *Plutonium zwierleini* individuals collected in the field and photographed in a controlled environment. (a) 44 mm total length from Castelvetrano (Trapani province, locality #4); (b) 63 mm total length from Piana degli Albanesi (Palermo province, locality #19); (c) 102 mm total length from Castelvetrano (Trapani province, locality #4); (d) 114 mm total length from Castelvetrano (Trapani province, locality #4).

Ten further observations of *Plutonium zwierleini* were collected through the Citizen Science approach (Table I). Six of the localities were new, whereas #6 and #8 confirmed the occurrence of the species in "Gravina di Catania" and #1 and #"7 in "Catania", i.e., two sites already mentioned by Bonato et al. (2017).

These new records expand the extent of occurrence (based on the MCP method) of *Plutonium zwierleini* in Sicily by approximately 117%, from 5990 ca. square kilometres, calculated by merging all the bibliographic localities (Shelley 1997; Bonato et al. 2017 and references therein), to 12991 ca. square kilometres, roughly 51% of the island surface.

The novel *Plutonium zwierleini* localities range from about 30 (#7) to 1164 m a.s.l. (#15) [412 ± 294 (30–1164) m a.s.l.]. As in other cases described in literature (Bonato et al. 2017), the habitats exhibit quite a variability, and can be both epigeal and hypogean (see records #11, #13, #15, and #16, Table I). Nevertheless, four out of the six localities derived by targeted samplings shared similar features, which are open areas such as pastures and uncultivated land with scattered rocks (Figure 3). All the Citizen Science observations originated from human settlements and highly anthropized areas. Five centipedes were in fact found inside houses in rural and urban context (Table I). In particular, specimens from localities #2 and #12 emerged from the drain pipes of a sink and a shower indoor, respectively, while at locality #14 *P. zwierleini* was found in an outdoor utility sink in a backyard.

We found that the highest probability of occurrence of our studied species, inferred from our continuous predictions of habitat suitability (Figure S3) transformed into binary predictions, includes the whole surface of Sicily except a large section of its south-eastern part (Figure 4), as also supported by presence data shown in Figure 1. Of all the analysed climate variables, the general linear model pointed out that only precipitation seasonality plays a significant ($p < 0.03$) and negative (-0.32 ± 0.15 SE) role in predicting the occurrence of *P. zwierleini* (Figure 4) and shows the higher contribution value in the Maxent model (Table S2). As such, the likelihood of occurrence is greatest in areas where precipitation variations across the year are limited. Surprisingly, no temperature variables significantly affect the likelihood of occurrence.

Behavioural observations

The three captive *Plutonium zwierleini* individuals showed highly secretive habits. Most of the time was spent under the shelters. The activity took

Figure 3. Four of the *Plutonium zwierleini* habitat in Sicily. (a) Near Ficuzza, Monreale (Palermo province, locality #18); (b) Piana degli Albanesi (Palermo province, locality #19); (c) Caccamo (Palermo province, locality #20); (d) Alimena (Palermo province, locality #17).

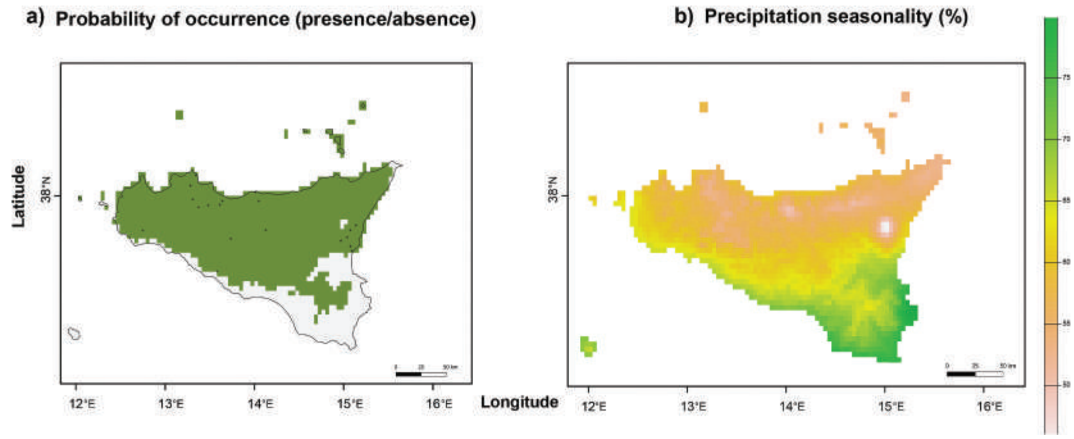

Figure 4. (a) Predicted presence (green) and absence (grey) occurrence distribution from the "max_spec_sens" threshold evaluation model; (b) Precipitation seasonality variation (%) across the region. The 19 observations are marked with a cross in panel "A".

place almost exclusively at night and consisted of exploring the enclosures, feeding, and self-cleaning. Scarce and occasional superficial digging activity was observed. As observed in other Chilopoda (Lewis 1981), grooming behaviour is frequently performed by means of the maxillary complex, especially on the antennae and along the sides of the body trunk and each leg, lingering on each segment. It was also observed that all specimens drank from the water droplets on the sides of the enclosure after misting. Although our three captive *P. zwierleini* fed regularly, no increase in body length was detected in the two smallest individuals during the captivity period (respectively 140 and 199 days), while a growth of only 4 mm (3.9% of the whole length) was recorded in 199 days in the largest centipede. No moulting episodes or evidence were documented in a time interval of 199 days, likely due to the slow growth rate (see Brunhuber 1970) or, alternatively, to the consumption of the exuviae, a phenomenon already known for Chilopoda (Lewis 1981; McMonigle 2014). When alarmed, all specimens raised the last tergite upright and spread the terminal legs wide, displaying their pincer-like extremity. If stimulated, they did not hesitate to bite the forceps or the gloves, like other Scolopendromorpha (Lewis 1981), to pierce with the last two legs, and to emit an unpleasant smell, similar but less intense to that of the Julidae (Diplopoda).

Overall, 16 food types have been proposed (Figure 5). No live items were accepted for all prey categories, except Formicidae larvae, which were readily accepted both alive and dead from all the *Plutonium zwierleini* specimens, and slugs, which were eaten sporadically (Table S3). Most preys were accepted only when dead, especially soft-bodied or poorly sclerotized invertebrates. Caterpillars (Lepidoptera) whereas woodlice (Oniscidae) were totally ignored by all centipedes. Among the inert foods, only the raw chicken meat was readily accepted and consumed by all specimens, while raw beef and fruits (banana) were only briefly tasted, with no evidence of actual feeding. A specimen from site #4 kept in captivity in 2019 also accepted live Lumbricidae (G. Signorello, *unpublished data*). Tactile contact with fast-moving prey (mainly arthropods) caused an immediate escape reaction in all individuals, even several hours after the introduction of live meals into the plastic boxes.

Although observed in the field in a Sardinian population (Sanna et al. 2018), the use of the terminal legs during predation and feeding was never observed in our *Plutonium zwierleini* individuals, as well as in other captive Sicilian and peninsular Italian specimens (L. Cavigioli, J. Wojtkow, L. D'Aniello, *pers. comm.*).

Meal duration was highly variable, apparently based on food type and size. Some food items were tasted for a few seconds whereas, in other cases, very large meals (scarabaeid larvae, chicken meat) were consumed by the largest specimen, without interruption, up to 2 hours and 45 minutes. After each meal, the centipedes generally remained inactive under the shelter from three to six days.

Discussions

Distribution and ecology

The results from this study show that the distribution of *Plutonium zwierleini* in Sicily is significantly broader than previously documented. The new data increase the Sicilian extent of occurrence of the

Figure 5. Foraging in captive *Plutonium zwierleini*. (a) Staphylinidae larvae; (b) Lumbricidae; (c) *Scolopendra cingulata*; (d) Banana; (e) Gryllidae; (f) Raw chicken meat.

species. To date, there is still no past and present evidence of the presence of *P. zwierleini* from north-eastern and south-eastern Sicily (cf. Bonato et al. 2017), i.e., from the Peloritani mountains and Hyblean area; however, the latter area has only been marginally investigated in the frame of our fieldwork (Table I and Figures 1 and S1). Accordingly, a low probability of presence in south-eastern Sicily is also supported by the low values based on the maximum entropy of the climatic niche (Figure 4). The species distribution modelling aligns with our novel observations and is consistent with records obtained from the literature spanning from 1881 to 2017 (Figure 1) (Bonato et al. 2017 and references therein).

Our results confirm that *Plutonium zwierleini* can be found in a wide range of biotopes, from natural sites, as oak woods, and caves, to extremely anthropized ones, such as buildings and urban areas. In anthropized areas, the repeated finding of this species inside or near drain pipes appears particularly interesting, but it is difficult to understand whether these circumstances are due to an effective use of hydraulic systems as biotopes or shelters, as it happens in other myriapods (Acosta 2003; Short & Huynh 2013), or if these animals simply get trapped there.

The syntopy of *Plutonium zwierleini* with other scolopendromorphs was observed in all sites, especially with medium to large-sized species (*Scolopendra* spp.), which were always abundant. This might indicate the absence of competitive exclusion between these large centipedes, perhaps in the context of particularly favourable biotopes for Scolopendromorpha.

With regard to bioclimatic variables, the wide extent of areas with high suitability values (Figure 4) indicates a wide spectrum of climatic conditions where the species could potentially be present (Figure 4). Specifically, we found that the presence of *Plutonium zwierleini* seems to be limited by the seasonality of rainfall. These conditions could increase the risk of flooding, soaking or, conversely, excessive soil drying, serving as potential disruptive factors for chilopods (Uetz et al. 1979; Lewis 1981; Ivask et al. 2019; Menta & Remelli 2020).

The comprehensive data derived from our fieldwork corroborate that *Plutonium zwierleini* is a species characterized by a relatively low detectability, as it was identified in 11.5% of the sampled localities. This centipede shows a low detection rate when compared with the other large chilopod present in Sicily, the Mediterranean banded centipede, *Scolopendra cingulata*, which was recorded in

79.2% of the sampled areas. The outcome of the species distribution models, based on bioclimatic variables, does not align with the hypothesis of a patchy or localized distribution of *P. zwierleini* in the Sicilian territory (Figure 4). Therefore, two alternative, not mutually exclusive, hypotheses emerge warranting future investigation with appropriate methodologies: (1) *P. zwierleini* exhibits low-density populations. Low local abundance is recognized as a factor that negatively influences the detectability of a species within a study area (Royle & Nichols 2003; Walsh et al. 2018). Indeed, low-density likely contributes to low detectability across various taxa, including predatory endogeic chilopods (Peretti et al. 2022); (2) *P. zwierleini* adopts predominately endogeic habits. Subterranean chilopods, as well as other cryptozoans (e.g., Kopecký & Tuf 2013), may have specific patterns of epigean activity, often constrained to limited time frames coinciding with periods of optimal external conditions (Lewis 1981; Tuf et al. 2006). Although, our sampling effort does not allow us to reveal a clear seasonal pattern of epigeal activity, we observed a reduced occurrence of the species during the warmest months, possibly due to increased aridity and temperature of the superficial soil layers (see Lewis 1981). Alternatively, they may surface in response to unpredictable events such as heavy rain and flooding, altering soil conditions (Lewis 1981). Therefore, it is possible that *P. zwierleini* primarily resides in deep soil layers thus rendering its occurrence under stones and in epigean habitats and subsequent detection rare or occasional.

Behaviour

A substantial part of the life history information on cryptozoic fauna is drawn from observations in captivity (Monge-Nájera et al. 1993; Punzo 2005; Fremlin & Taylor 2022). This reliance on captive observations stems from the elusive nature of cryptozoans and the inherent challenges associated with observing their behaviours *in situ*. This also extends to other Chilopoda taxa (Lewis 1981; McMonigle 2014; Guizze et al. 2016), where a significant portion of field records is based on opportunistic and isolated observations (Lewis 1981; Molinari et al. 2005; Noronha et al. 2015; Bonato et al. 2021).

Our data show distinctive feeding habits in captive *Plutonium zwierleini* individuals, setting them apart from other chilopod species examined under identical conditions. While the latter generally exhibit predatory behaviour using a combination of sit-and-wait and active foraging strategies (Lewis 1981; Lewis et al. 2010; McMonigle 2014; Guizze et al. 2016), our *P. zwierleini* specimens exhibited avoidance of live prey, except for soft-bodied and low-mobility preys such as ant larvae and slugs, and mostly consumed dead preys and inert food. The fast response observed in *P. zwierleini* upon detecting and consuming Formicidae larvae suggests that this resource might fall within its natural trophic spectrum, which aligns with expectations based on its relatively frequent occurrence under stones. Throughout the study period, sporadic instances of vegetable tasting, notably banana, were also observed (Table S3 and Figure 5), which is consistent with observations in several centipede species, where fruits and vegetables are briefly consumed, especially in prolonged absence of other resources (Lewis 1981; McMonigle 2014).

Although scavenging is widely reported in many chilopods (Wang 1945; Lewis 1981; Lewis et al. 2010), also under captivity condition (Lewis 1981; McMonigle 2014), it is generally considered as an optional habit that occurs in active opportunistic predators. Quite unexpectedly, our controlled environment observations suggest that *Plutonium zwierleini* predominantly exhibits a necrophagous-like behaviour. Conversely, the only feeding record of *P. zwierleini* in the field (Sanna et al. 2018) described a predatory behaviour on a living vertebrate, using terminal legs as forceps (as observed in *Theatops* spp., see above). This behaviour was never observed in our captive specimens, supporting what was previously suggested by Lewis (2010) on the doubtful predatory functional use of the terminal legs.

However, despite what was inferred from our observations, we cannot rule out that the stress induced by the captivity conditions might have affected the feeding behaviour of our centipedes.

Conclusions

Despite its large size and evolutionary interest, *Plutonium zwierleini* is one of the least known taxa among the Mediterranean Scolopendromorpha. The present study allows to get a better insight on the distribution and ecology of the species, but also opens some challenging questions.

The dearth of information currently available about the natural history of this centipede is traditionally ascribed to its rarity and the consequent exceptional paucity of records throughout its wide west-Mediterranean distribution area, ranging from the southern Iberian Peninsula to peninsular Italy. Current study proves that, at least in Sicily, the species is less rare than expected and that dedicated surveys allow to collect valuable information and samples in a reasonable time span. Novel data collected in the frame of this survey increased its known geographic distribution range on the island by 117%, and the number of localities by 110% compared to those available in the literature (cf. Bonato et al. 2017 and references therein). Collected occurrence data confirmed that this centipede is a generalist species, whose fine ecological *preferenda* should, however, be explored with dedicated studies regarding microhabitat features. Furthermore, its frequent syntopy with other large centipede species suggests that exploring the ecological and behavioral aspects of multi-species Scolopendromorpha coexistence is a worthwhile area for further, in-depth investigations.

The diet composition of wild *P. zwierleini* inhabiting different habitats (e.g., caves *vs.* pasture lands) should be desirably investigated, possibly through NGS (cf. Bortolin et al. 2018; Bonato et al. 2021). Nevertheless, observations carried out on captive specimens allowed us to get some insights on the feeding behaviour of the species, suggesting that *P. zwierleini* might be a scavenger rather than a predatory species. This is somewhat at odds with the few observations available in nature for this species (Sanna et al. 2018) and those available in captivity for the closely related genus *Theatops* (UnicoCelula 2012; Furball677 2016a, 2016b), although we cannot rule out an effect of the stress induced by their restrained conditions.

Eventually, molecular analyses including *Plutonium zwierleini* samples from the entire distribution range of the species are needed to shed light on the taxonomy of the Plutoniumidae, clarifying the relationships between the genera *Plutonium* and *Theatops*, and to account for the phylogeography of the species and the possible presence of cryptic species currently lumped under this binomen. We hope that the present work might pave the way for such studies and encourage the collection of new distributional and ecological data on *Plutonium* populations in the other regions inhabited by this charming and enigmatic species.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Data availability statement

The data used for this work are available from the corresponding author on reasonable request.

Supplementary material

Supplemental data for this article can be accessed online at https://doi.org/10.1080/24750263.2024.2324118

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