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A study of the association of *Ondoteus armiger* (Scopoli, 1772) (Coleoptera: Geotrupidae) with the European rabbit

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ABSTRACT

Ondonteus armiger (Scopoli, 1772) (Coleoptera: Scarabaeoidea: Geotrupidae) is the smallest European representative of the secretive Bolboceratinae sub-familly. Numerous authors have reported or observed a likely association with the European rabbit *Oryctolagus cuniculus* (Linnaeus, 1758), (Mammalia: Leporidae). In order to ascertain this assumption, pit-fall trapping was carried-out in Western Europe (France, England), and a detailed literature study was carried out on the distribution of both species and reported association between the two species and/or other mammals. Results are presented along with new biological information for *O. armiger*.

Keywords: *Ondonteus armiger*, *Oryctolagus cuniculus*, Bolboceratinae, Hypogeous fungi, *Glomus* sp., *Endogone lactiflua*.

1. Introduction

Odonteus armiger (Scopoli, 1772) is the smallest European representative of the Geotrupidae family (Coleoptera: Scarabaeoidea). In older works (e.g. [1-3]), it also appeared under the specific name *mobilicornis* (Fabricius, 1775), due to the male's mobile cephalic horn, and the light coloured varieties were described as a separated species: *testaceus* (Fabricius, 1775). Although the accepted genus is now *Odonteus* Samouelle 1819 [4], the species also appears under the genus *Bolboceras* Kirby 1819, *Bolbocerus* Kirby 1829 and *Odontaeus* Dejean 1821, please see the discussion associated with the ICZN ruling for further details [5-10]. The bolboceratids group status is also a debated topic with some authors considering it forms a separate family [11-12]. However, in the most recent analysis of Coleoptera families, Bouchard *et al.* [13] re-placed them as a sub-family of the Geotrupidae.

O. armiger is the only European representative of a genus that also includes ten North American [14] and two Asian species [15-16]. It is widely distributed throughout Europe (except Northern Europe and meridional parts of Mediterranean countries) to the Urals and Caucasus [12, 17]. Like most members of the Bolboceratinae, its biology is poorly known. At First [1-3, 18-19], it was assumed to be a coprophagous insect, partly by analogy to the biology of the Geotrupinae and partly because it had been found under different excrements (see Table 1). However, Mulsant [3] was suspecting it could be feeding on animal or vegetal decomposing matter. It was not only until the beginning of the 20th Century [31-33] that a link with hypogeous fungi was made. Many western European authors [24-30] also made a connection with the European rabbit, *Oryctolagus cuniculus* (Linnaeus, 1758). Warlet [24] and Paulian [25] even claim that *O. armiger* is uniquely dependent on fungi developing in rabbit warrens, Paulian [25] refereeing to it as an "indirect coprophagous".

In order to ascertain this relationship, trapping was carried out at entrances of rabbit burrows at localities where *O. armiger* was observed or had previously been reported. We also examined the literature to establish any reported connection with other mammals and examined the historical and current distribution range of both species.

2. Methods and Materials

Un-baited pitfall traps were placed at the entrance of rabbit burrows located within 500m of known location (i.e. directly observed or captured) or near locations with previously published observations of *O. armiger*. The same number of control traps was placed in the same area as far as possible from the rabbit burrows. Live specimens were marked using paint dots and released. Traps were set-up for a period of two weeks to 5 months,

between the months of May and September. The locations, year and total duration of trapping, total number of traps and number of captures are given in Table 1. In addition, surroundings were searched for burrows dug by *O. armiger* and burrows were carefully exposed. Attempts were made for adults caught in the wild to reproduce in captivity (60l indoor terrarium) and for wild caught larvae to be raised in either a 60l indoor terrarium or outdoor using a 90l wooden crate with bottom drainage holes and a top made from a 4×4mm^2 galvanised welded mesh sheet. Larvae can be identified using [34-35]; detailed drawings have also been published [36].

Records were obtained from the State Museum of Natural History Collections (Lviv, Ukraine), Schmalhausen Institute of Zoology of the National Academy of Science collections (Kyiv, Ukraine), Taras Shevchenko National University of Kyiv collections (Kyiv, Ukraine), National Museum of Natural History collection (Kyiv, Ukraine), private collections (B. Vasko, M.E. Miquel, U. Schmidt, J.-C. Miquel, O. Hillert) and internet forums (entomology and macrophotography). For seasonal distribution records across two months were included in the second months.

Associations with rabbits and other mammals were searched in the published literature and the internet using scientific names and common names in English, French, German, Spanish and Italian as keywords.

3. Results and Discussion

3.1. Records in Association with Rabbits and Distribution

Apart from Warlet [24] and Paulian [25], all other associations between *O. armiger* and rabbits published in the scientific literature can be categorised as weak: they refer to captures or observations in localities where rabbits were particularly abundant or rabbit dejections present in close proximity, or make reference to such observations.

Paulian [25] seems to refer to Warlet's work without directly citing it. Warlet [24] makes a clear direct connection between the two species as he has captured large numbers of specimen using light traps in warrens, and found larvae and adults while excavating burrows. He concluded that *O. armiger* lives inside rabbits burrows with both adults and larvae feeding on mycelium that develops on droppings, vegetable material, hairs or even dead kits inside the corridors and chambers of burrows. However, he also states that larvae were in fact found on mycelium growing on partly decaying roots crossing the burrows that he excavated.

In our study, only in one location (see **Table 2**) did the traps placed at burrow entrances lead to the capture of a significantly higher number of specimens than the control traps. This particular warren is located on the edge of clearings inside a wood dominated by oaks and other deciduous tree. Following the information in [24], Tauzin ([26] and personal communication) has captured *O. armiger* in large numbers using UV light traps in the warrens at the edge of the forest of Fontainebleau (Seine-et-Marne, France) and those near the wood of Verrières (Bièvres, Essone, France) during the months of June and July in the 1990s. As we did not use light but just passive trapping, this might explain the lower number of captures in our study compared to those reported by both Warlet [24] and Tauzin [26].

3.2. Distribution of Rabbits and O. armiger

Further to his direct observations, Warlet [24] mainly advances an argument based on matched distribution of the two species. However, he only refers to Western European countries: Spain, France, Belgium, Netherlands, England, Germany and the North of Italy.

Although, this argument can be dismissed conclusively with little effort, it is worth spending time on the distribution of the two species. First, it is worth looking in more detail at the European rabbit, its origin and distribution. As the only animal domesticated in Western Europe, the current range of the rabbit in the wild, both in Europe and worldwide, has greatly been determined by human activities and direct introductions [37-39]. It is now accepted [40-41] that rabbits can be arranged into two sub-species groups: *O. cuniculus algirus* (Haeckel, 1874) and *O. cuniculus cuniculus* (Linnaeus, 1758). The first one is of small size (less than 1kg) and its range is now limited to North Africa (likely historical introduction according to Dobson [42]), some Mediterranean islands (introduced [38]) and the Iberian peninsula (native). This subspecies is considered to be the true wild rabbit and had a native range going no further than the Loire Valley in the North, and Alps in the East [43]. The second sub-species is larger (up to 2kg in the wild) and also includes all the domestic breeds. It occupies the rest of the rabbit range throughout Europe, Australia, Chile and numerous islands [38, 44]. It probably originated through selection by the Romans and should be considered as the feral rabbit [45]. In the native range of the rabbit, *O. armiger* only occurs in Northern Spain and France (**Figure 1**). This would make *O. armiger* an introduced or adventive species throughout most of its range.

In France, rabbits were originally only found south of the Loire valley [43]. They were introduced in other parts of the country during the Middle Ages, however, warren rights were restricted by Royal ordinances and warrens were enclosed and controlled. They are scarcely no mention of rabbits in the wild until Napoleon III declared it to be hunting game that can range freely. It quickly spread throughout the country due to the establishment of private hunts in the 19th and early 20th century [43, 60]. In France, *O. armiger* is widely distributed and since the original cartography of the species by Lumaret [49] records for a further ten départements have been added and we are providing data for five others (see **Figure 1**). It is also worth noting that *O. armiger* is reported to be less abundant in the native range (south west and Midi) than in the introduced range of the rabbit [49].

The history of the rabbit in England is similar to that of Northern France. It was introduced by the Normans and, throughout the Middle Ages, warrens were closely guarded and regulated commercial enterprises [61-62]. The agricultural revolution had the combined effect of making more land profitable for agriculture, making warren less profitable, and creating suitable habitat and food resources throughout the year for feral rabbits [63]. However, rabbits were still uncommon in the wild through the 18th century in large parts of the country [62]. In Britain, *O. armiger* is mainly distributed in Southern England with some records from Wales (**Figure 1**). The species has always been considered to be very rare [19, 64-65], however, records have been published and are still being published at regular intervals [27, 29, 57-59, 67-69]. The oldest record dates back from the end of the 18th Century, a specimen captured in or around 1895 by Lady Wilson [19].

In Germany, the history of the rabbit is similar to France and England; it was introduced through trade between monasteries in the early Middle Age and feral populations gradually expended in the 17th and 18th centuries [39, 43]. Rabbits are still absent from the

extreme south of the country [44] where *O. armiger* can be found [70].

In continental Italy, although the rabbit was an early introduction by the Roman, its range is still limited to two main areas in the North and some local populations [71]. Although mainly present in the North and centre of the country, the range of *O. armiger* is more extensive [72] than the one of the rabbit. Recent records ([73], **appendix 1**) in the regions of Marche, Venetto or Bologna are also outside the range of the rabbit.

The situation in many Central and European countries is even clearer. In neighbouring Slovenia, *O. armiger* is widely distributed and relatively common [74], whereas rabbits are absent [44]. In Eastern Europe, rabbits and *O. armiger* are both present in Poland, Ukraine, Moldova, Romania and parts of Russia. However, rabbits are always recent introductions that are still occurring for hunting game, and at the exception of Poland, the distribution of the rabbit is often local and limited. However, even in Poland, the rabbit was only introduced in the 19th century [39]. It is still relatively rare and absent from the southeast where *O. armiger* occurs commonly [75]. Furthermore, some Polish records predate the introduction of rabbits [76]. In Ukraine, the rabbit is only well established in two zones with potentially some local populations due to more recent introductions in other parts of the country [39, 44] whereas *O. armiger* is more widely distributed (**Figure 2**). It has been reported from the Steppes and right-bank Ukraine, where it has been found in manure and river sediments, and is likely to be present throughout the country [23, 77]. In total, according to the Fauna Europae database (version 2.6, 2013) [78], *O. armiger* is present in 16 countries and 5 Russian regions where rabbits are absent: Albania, Andorra, Belarus, Bosnia and Herzegovina, Estonia, European Turkey, Kosovo, Finland, Latvia, Liechtenstein, Lithuania, Macedonia, Montenegro, Russia (Central, East, North, North West, Kalingrad Region), San Marino, Serbia and Slovenia. However, some of the records in the database are inaccurate, for example the rabbit has been introduced as hunting game in parts of Russia and the Baltic states [39] and *O. armiger* is not present in Ireland or Portugal [47].

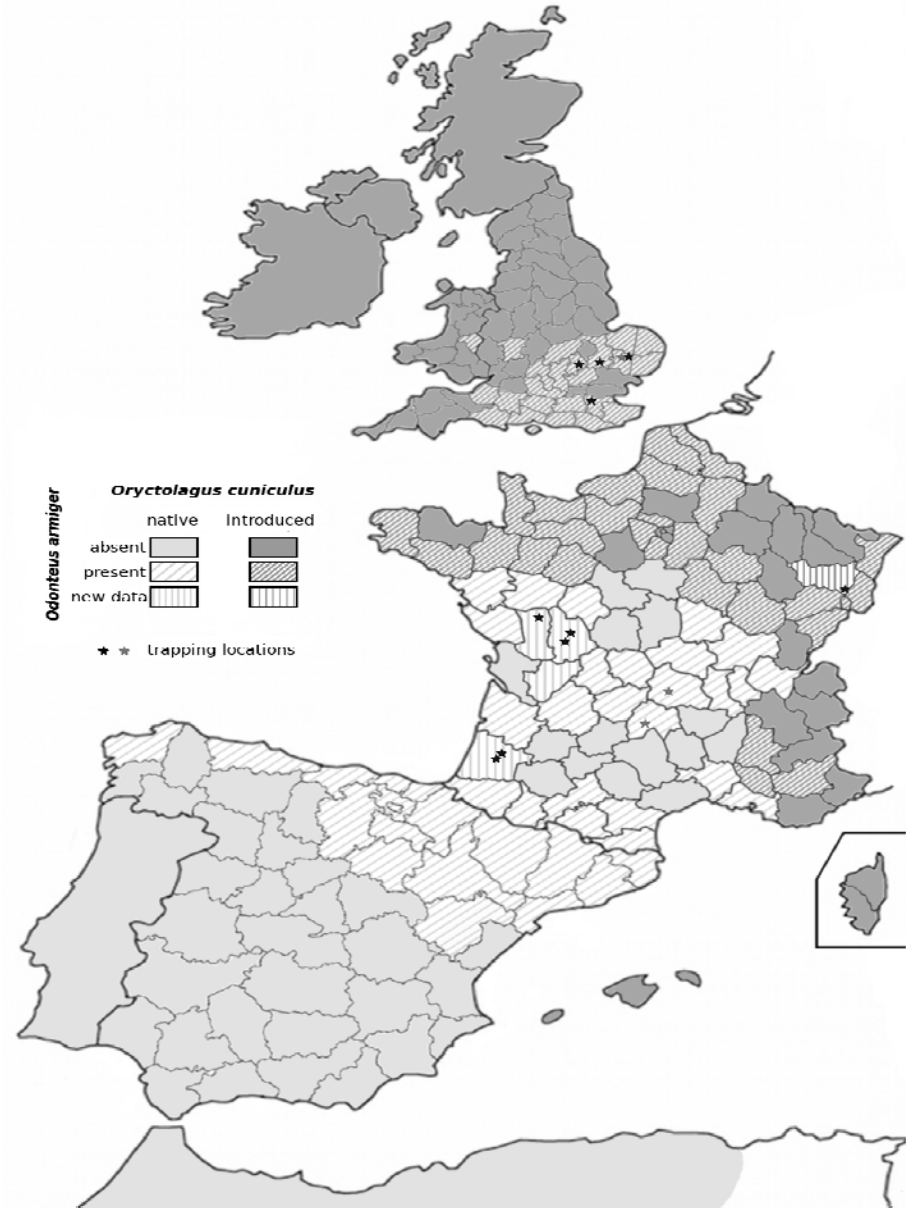

Fig 1: Distribution of *O. armiger* and *O. cuniculus* in the British Isles, France and the Iberian Peninsula. Native range (light grey) of *O. cuniculus* after [43], please note that the limit is approximated to include complete Départements in France. Distribution of *O. armiger* in Spain after [46-48], in France after [28, 30, 49-56] and Britain after [19, 27, 29, 57-59]. Trapping locations in grey where chosen near previously published data. In black, traps placed within 500 m radius of observed locations.

Fig 2: Distribution of *O. armiger* (from records) and *O. cuniculus* in Ukraine (from [39, 44]).

3.3. Association with Other Mammals

The literature clearly demonstrates that *O. armiger* is present in large parts of Europe where rabbits do not live or where rabbits are recent introductions and that although the species can be found with rabbits, this is not a necessary association. One could argue that *O. armiger* is associated with a related species or one with similar borrowing habits outside the rabbit distribution range. However, although, there are seven other native and one introduced species of Leporidae in Europe [79], they are not digging deep burrows like rabbits. The only other two animals with burrows that have been associated with *O. armiger* are the European red fox (*Vulpes vulpes* (Linnaeus, 1758)) and the European badger (*Meles meles* (Linnaeus, 1758)) [24]. Interestingly, Warlet [24] considered that the burrows were or might previously have been of mixed occupancy with rabbits to justify the presence of *O. armiger*.

3.4. Food habits of O. armiger

The established consensus between modern authors is that *O. armiger* feeds on fungi, especially underground species. In numerous references, it is suggested that it is associated with "hypogeous fungi", possibly truffles; more specific associations are given in **Table 3**. The adults have been found on aerial, underground and semi-underground fungi as well as mycelium, whereas the larvae have been found only on ryzhomorphic mycelium growing on tree roots. In our study, we found *O. armiger* feeding on a partly subterranean decomposing *Rhizopogon luteolus* Fr. The North American species *O. darlingtoni* (Wallis, 1928) has been reported in shallow burrows under a decomposing *Rhizopogon nigrescens* Coker & Couch [83] and also, feeding on fully subterranean *Rhizopogon pachyphloes* Zeller & Dodge on species [84]. We also found an adult male feeding on a decaying *Glomus microcarpum* Tul. & C. Tul. at the end of a straight burrow of approximately 9cm depth. Both *O. armiger* and *Bolbelasmus unicornis* (Schrank, 1789) have previously been reported from *Glomus macrocarpum* Tul. & C. Tul. [80]. We also found *Endogone lactiflua* Berk. at proximity of two other burrows in southern France but no borrow appeared to lead to them. Those fungi were accepted as food in captivity as well as roots sections covered in mycelium found near burrows. Adults refused any other species that were offered; including fresh or decomposing *Boletus* sp., *Calvatia* sp., *Lycoperdon* sp. and *Agaricus* sp. The latter are eaten in the wild in the steppes of Ukraine [23]. Interestingly, Fabre [85] reports that burrows of the related European species, *Bolbelasmus gallicus* (Mulsant, 1842), lead to hypogeous fungi (*Hydnocystis arenaria* Tul. & C. Tul., *Tuber requienii* Tul.). Whereas Rahola Fabra [86] never found any near the burrows in 20 years of observation at a different French location. This could indicate geographical variations in feeding habits of Bolboceratinae species.

3.5. O. armiger burrows and larvae

Out of all the twelve burrows dug at three different sites, only four were successfully excavated to their full length (**Figure 3**). Most burrows were found at a site with sandy soil rendering it difficult to dig burrows without damage due to collapse. Eleven burrows appeared to branch out laterally (two or three branches), the only definitely non-branching burrow was leading to a fungus (see previous section). In his study of *O. armiger*, Arens [32] describes vertical burrows, 24-70cm deep, that bends and increase in diameter to form a chamber where the egg lays. However, it does not mention multiple branches. The North-American species *O. darlingtoni* has similar branching burrows [14, 83] whereas some species of the related *Bolbocerasoma* and *Bolbelasmus* are known to have non-branching burrows [14, 83, 86]. In total, 16 end-of-burrow chambers were found, but neither egg nor larvae were found in them. The chambers were all empty; there was no presence of humus or fungus in the cell. Arens [32] did not find food in the cell either but in some cases, pieces of fungus and humus were found in the main tunnel. This differs from the habit of the three North American species of the genus with known larval habits; in those species, the parents pack humus in the cells for the larvae [83]. It has also been suggested [87], that some Bolbceratini add pieces of fungi to the humus. The related European species, *Bolbelasmus gallicus* also appears not to fill its burrows with food [86].

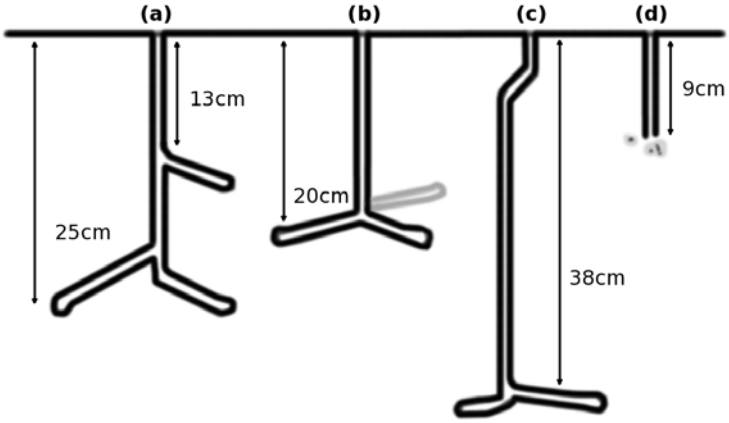

Fig 3: Schematics of the successfully excavated burrows. Diameter of the burrows c.a. 8mm and end of burrows up to 14mm in diameter.

In eight cases, the burrows were leading to close proximity of two roots covered with mycelium, and in three of those it was a large (over 5cm diameter) partly decaying root. Rahola Fabra [86] reported that *Bolbelasmus gallicus* digs burrows near roots and rootlets. As Warlet [24] found larvae feeding on mycelium growing on decaying tree stumps roots inside rabbits warren, it was therefore assumed that the larvae did not stay in the cell but where looking for food in close proximity. Based on this assumption sections of roots with mycelium were cut out and searched for sign of larval activity at one site in France (Sore, Landes). Larvae were found in the mycelium at the surface of the decaying wood. Three sections of roots with definite larvae activity (one with at least one larva, the other two with at least two larvae) were placed in indoor terrariums (2) or outside crate in soil collected from the area for rearing in the month of July. The soil was sandy and rich in humus (mixed pine and deciduous tree forest). A single female imago was obtained when the outside crate was inspected in December; no adults were obtained from the indoor terrariums. This probably indicates that either the larvae and/or their food require specific humidity and / or temperature conditions that were not met indoors. Howden [83] mentions that a larva of *Odonteus liebecki* (Wallis, 1928) he attempted to raise had likely been killed by too high a temperature. The imago was found in a lose casing made of sandy soil and small pieces of root material. Warlet [24] found imago in the wild in similar cases and around the same time of year. It also confirms that the adults over-winter as imago as previously suspected [23-24]. All our attempts for adults to reproduce in captivity failed, rendering it difficult to obtain more detailed information on the reproduction, egg and larva.

3.6. Biomes and activity period of O. armiger

In the records we obtained from 15 countries and 94 sites across Europe (see **appendix 1**), we found habitats ranging from open environments (fields, steppes), forest edges and clearings, and inside forest including trapping records from underbrush area. We have also found records from environments that had been extensively changed by human intervention in particular gardens and vineyard (Charentes, France).

This correlate well with previously published literature that includes reports of many different habitats including heathlands [29], meadows and grasslands [75, 86], chalky areas [22], steppes [23] forest edges and clearings [32, 48, 74-75], and forests [75]. There are also reports from gardens [89] and even a racehorse track [69]. In many countries, an overwhelming number of reports come from forest edges and forest clearings. However, this might be a bias due to the location of light traps not intended to capture *O. armiger* but to which the beetles came to. Indeed, the number of specimen reported at light is very high; most reports of single specimen are often at lights, and in the data we collected the proportion of specimens collected at light was 54% (39% if including our trapping data). According to Jessop [22], around 35% of records in England are at light. This proportion is much higher in some publications, for example around 90% of the specimens reported from the region of Limousin in France [51]. However, there is clear evidence that the beetles also live within wooded areas away from any clearings. We have found records in France, Italy and Ukraine from pitfall traps in thick forest underbrush or caught at lights well inside forests (**appendix 1**).

Although its attraction to light has been well reported, it appears that the beetles can also exhibit photophobic behaviour. During an extensive study of the species in the Czech Republic and Slovakia, that is soon to be published, it was observed that when swarming (up to 50 beetles) just after sunset, beetles would drop to the ground or fly away when exposed to lights ([90] and personal communication).

The range of reported biomes might indicate that *O. armiger* does not depend on a single species or genus of underground fungus but is feeding on various species. There seems to be a particular attraction to mycorrhizal fungi of the genus *Endogone* and *Glomus*; both known to occur in a variety of biomes from sand dunes to forests.

The distribution of Bolboceratini species has been linked to the nature of soil [91] and this is likely to play a role in the localised nature of the species throughout its extensive range.

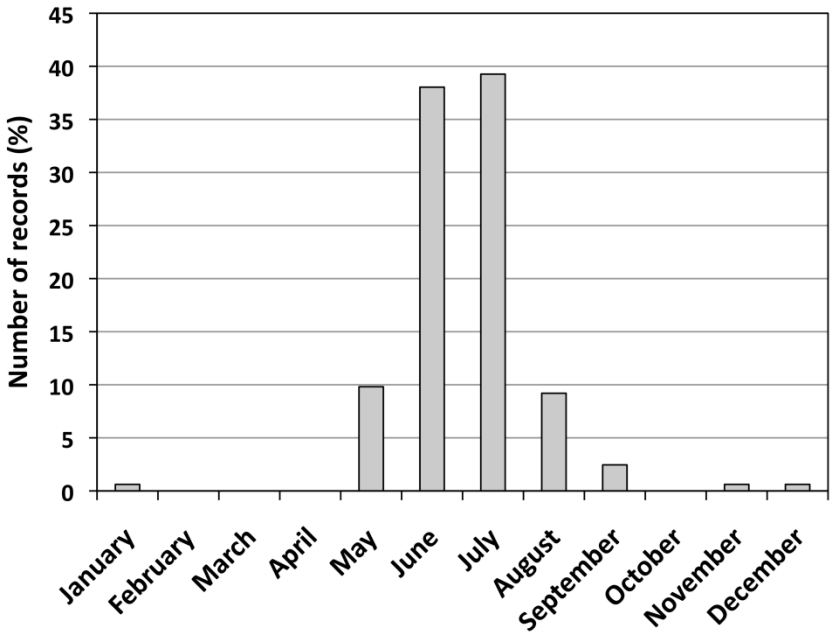

Fig 4: Temporal distribution of the records of *O. armiger* from 15 countries and 94 sites.

The analysis of the collected data (**Figure 4**) confirmed that *O. armiger* is primarily a summer species with over 77% of all records occurring in June and July. The activity period is between May and August (over 96% of records) but can sometimes extend to the early part of September (2%); all records from this month are males. They are odd records of single examples outside this period, for example found dead in January or an example raised in captivity from a larva collected during the summer. The summer peak of activity correlates well with previously published data [22, 32, 49, 72, 75, 82]. It has also been suggested that later sporadic records, for example until October in Ukraine [23], might correspond to a second generation.

4. Conclusion

Based on the biology of *Ondonteus armiger* and its distribution, there is enough evidence to reject the hypothesis of a unique association with the European rabbit. However, it seems than *O. armiger* can exploit the favourable environment created in some warrens. Both adults and larvae appear to feed on fungi: the adults have been found on a range of species, with a preference for decomposing subterranean species, while the larvae appear to feed on mycelium on tree roots. The species can exploit a large range of open and wooded habitats. This widespread species is local but not necessarily rare, appearing to be abundant in some cases. Its location and density is most likely linked to the availability of its underground food source. Considering the variety of habitat it is probably not link to a single species or genus of fungus. The parents appear to not provide humus to the larvae, at least not for its full development cycle. However, due to its secretive life and despite observations conducted for over 20 years, its full life cycle could not be fully established. Although larvae are difficult to obtain in the wild, a more detailed study of the larval habits is feasible and would help clarify the matter.

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6. References

1. Curtis J. Bolboceras armiger Plate 259 [plus 2 unnumbered pages of text] 1829. in: Curtis J. British entomology; being illustrations and descriptions of the genera of insects found in Great Britain and Ireland. 1824-1840. London.
2. Stephens JF. Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions, Volume 7 Mandibulata (III), Baldwin and Cradock, London, 1830, 19 pl, 374 pp.
3. Mulsant ME. Lamellicornes, Histoire Naturelle des Coléoptères de France, Maison, Paris, 1842, 650pp, 3 pl.
4. ICZN. Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera): not conserved; priority maintained for Odonteus Samouelle, 1819 (June). Opinion 2138 (Case 3097). Bulletin of Zoological Nomenclature 2006; 63(1):62-64.
5. Jameson ML, Howden HF. Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera): proposed precedence over Odonteus Samouelle, 1819 (June). (Case 3097). Bulletin of Zoological Nomenclature 2002; 59(4):246-248.
6. Krell F-T, Ziani S, Ballerio A. Comment on the proposed precedence of Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera) over Odonteus Samouelle, 1819 (June). (Case 3097). Bulletin of Zoological Nomenclature 2003; 60(4): 303-311.
7. Krell F-T, Ziani S, Ballerio A. Comment on the proposed precedence of Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera) over Odonteus Samouelle, 1819 (June).(Case 3097). Bulletin of Zoological Nomenclature 2004; 61(2):110-113.
8. Smith A. Comment on the proposed precedence of Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera) over Odonteus Samouelle, 1819 (June). (Case 3097). Bulletin of Zoological Nomenclature 2004; 61(2):113-114.

9. Ratcliffe BC. Comment on the proposed precedence of Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera) over Odonteus Samouelle, 1819 (June). (Case 3097). Bulletin of Zoological Nomenclature 2004; 61(1):43.
10. Alonso-Zarazaga MA. Comment on the proposed precedence of Bolboceras Kirby, 1819 (July) (Insecta, Coleoptera) over Odonteus Samouelle, 1819 (June). (Case 3097). Bulletin of Zoological Nomenclature 2005; 62(2):84.
11. Scholtz CH, Browne DJ. Polyphyly in the Geotrupidae (Coleoptera: Scarabaeoidea): a case for a new family. Journal of Natural History 1996; 30(4):597-614.
12. Král D, Löbl I, Nikolajev GV. Bolboceratidae in Löbl I., Smetana A. (ed.): Catalogue of Palaearctic Coleoptera, Apollo Books, Stenstrup, 2006, 3: 283-313.
13. Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CH et al. Family-group names in Coleoptera (Insecta). Zookeys 2011; 88:1-972.
14. Wallis JB. Revision of the Genus Odontaeus, Dej. (Scarabeidae, Coleoptera). The Canadian Entomologist 1928; 60:119-128,151-156,168-176.
15. Mittal IC. New record of genus Odontaeus Klug with a new species from Oriental region. Journal of Entomological Research 1998; 22(4):385-386.
16. Carpaneto GM, Mignani R. A new species of the genus Odonteus (Coleoptera: Geotrupidae) from northern Pakistan. Zootaxa 2005; 968:1-10.
17. Nikolaev GV. Plastinchatousije zhuki (Coleoptera, Scarabaeoidea) Kazakhstana i Central Asia, Nauka, Alma-Ata, 1987, 232pp.
18. Calwer CG. Käferbuch. Naturgeschichte der Käfer Europas. Verlag von Krais & Hoffmann, Stuttgart, 1858, 49 pl, 788pp.
19. Fowler WW. The Coleoptera of the British Islands, volume IV Lamellicornia – Serricornia – Longicornia – Phytophaga, London,1890, 411pp.
20. Saunders CJ. A note on Odontaeus armiger Scop. The Entomologist's Monthly Magazine 1936; 72:178.
21. Arrow GJ. Horned beetles. A study of the Fantastic in Nature. W. Junk, The Hague, 1951, 14 pl., 154 pp.
22. Jessop L. Dung beetles and chaffers Coleoptera: Scarabaeoidea. Handbooks for the Identification of British Insects, vol 5, part 11. RES London, 1985, 53 pp.
23. Martynov V. A Review of fauna and ecology of Scarabaeid beetles (Coleoptera, Scarabaeoidea) of South-Eastern Ukraine. The Kharkov Entomological Society Gazette 1997; 5:22-73.
24. Warlet JM. Odontaeus armiger Scop. (Coléoptère Scarabeidea - Famille des Geotrupidae). Linneana Belgica 1983; 9:135-138.
25. Paulian R. Les Coléoptères à la conquète de la terre. Boubée, Paris, 1993, 224 pp.
26. Tauzin P. [Bolboceras armiger] Odonteus armiger. Le Monde des Insectes, 2004. http://www.insecte.org/forum/viewtopic.php?f=1&t=927&hilit=armiger, last accessed 24/10/2013.
27. Leech MJ. Odontaeus armiger Sp. (Col. Scarabaeidae) in Northamptonshire. The Entomologist's Record and Journal of Variation 1964; 76:296.
28. Denux O. Récente découverte du Geotrupidae Odontaues armiger (Scopoli, 1772)(Coleoptera) en Bourgogne, dans le département de la Nièvre. Le Coléoptériste 2007; 10(2):79-81.
29. Scott D, Scott J. Odontaeus armiger (Scopali 1772) [sic!] Coleoptera: Geotrupidae at Astley Burf. Worcestershire Records 2008; 24:11.
30. Chabrol L. Coléoptères rares ou remarquables du Limousin. Bulletin de la Société Linnéene de Bordeaux 1998; 26(1):37-40.
31. Bedel L. Faune des Coléoptères du bassin de la Seine: Scarabaeidae. Tome IV, 1er Fascicule, Société Entomologique de France, Paris, 1911, 164pp.
32. Arens LE. K biologii Odontaeus armiger Scop. (Coleoptera). Izvestya Petrogrogradskogo Nauchnogo Instituta Imeni P. F. Lesgafta 1922; 5:241-246.
33. Comon R. Catalogue des coléoptères du département de l'Yonne. Bulletin de la Société des Sciences Historiques et Naturelles de l'Yonne 1932; 86:123-126.
34. Van Emden FI. Larvae of British Beetles. II. A Key to the British Lamellicornia Larvae. The Entomologist's Monthly Magazine 1941; 77:117-127,181-192.
35. Medvedev SI. Ličinki plastinčatousych žukov fauny SSSR. Akademiya Nauk SSSR, Moskow/Leningrad, 1952, 344pp.
36. Verdú JR, Galante E, Lumaret J-P, Cabrero-Sañudo FJ. Phylogenetic analysis of Geotrupidae (Coleoptera, Scarabaeoidea) based on larvae. Systematic Entomology 2004; 29(4):509-523.
37. De Vos A, Manville RH, Van Gelder RG. Introduced mammals and their influence on native biota. Zoologica 1956; 41:163-194.
38. Flux J, Fullagar P. World distribution of the rabbit Oryctolagus cuniculus on islands. Mammal Review 1992; 22:151-205.
39. Long JL. Introduced Mammals of the World: Their History, Distribution and Influence. CSIRO Publishing, Collingwood, Australia, 2003, 559pp.
40. Biju-Duval C, Ennafaa H, Dennebouy N, Monnerot M, Mignotte F, Soriguer, RC et al. Mitochondrial DNA evolution in Lagomorphs: origin of systematic heteroplasmy and organization of diversity in European rabbits. Journal of Molecular Evolution 1991; 33(1):92-102.
41. Ferrand N, Branco M. The evolutionary history of the European rabbit (Oryctolagus cuniculus), pp 207-235 in Weiss, S; Ferrand, N. (editors) Phylogeography of Southern European Refugia. Springer, Berlin, 2007, 377pp.
42. Dobson M. Mammal distributions in the western Mediterranean: the role of human intervention. Mammal Review 1998; 28(2):77-88.
43. Rogers PM, Arthur CP, Soriguer RC. The rabbit in Continental Europe. In: The European Rabbit The History and Biology of a Successful Colonizer (Ed. by H.V. Thompson & GM. King), Oxford University Press, Oxford, 1994, pp 22-63.
44. Smith AT, Boyer AF. Oryctolagus cuniculus. 2008. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Last accessed on 08 October 2013.
45. Gibb JA. The European Rabbit Oryctolagus cuniculus. In: Rabbits, Hares and Pikas - Status Survey and Conservation Action Plan (ed. by Chapman JA, Flux JEC) IUCN. Gland, 1990, pp 116-120.
46. Lopez-Colon JI, Bahillo De La Pueble P. Registros en el País Vasco de Odonteus armiger (Scopoli, 1772). Boletin de la Sociedad Entomológica Aragonesa 1997; 19: 55.
47. Martin-Piera F, Lopez-Colon JI. Fauna Iberica 14: Coleoptera Scarabaeoidea 1. CSIC, Madrid, 2000, 526 pp.
48. Amarante Rodríguez B. Primera cita de Bolboceras armiger (Scopoli, 1772) (Coleoptera: Geotrupidae) para Galicia (N.O. Península Ibérica). Arquivos Entomolóxicos 201; 7:113-114.

49. Lumaret, JP. Atlas des Coléoptères Scarabéides Laparosticti de France. Inventaire de Faune et de Flore, 1, SFF/MNHN, Paris, 1990, 420 pp.
50. Bachelard P. Capture d'Odontaeus armiger (Scop.) dans le Puy-de-Dôme (Coléoptères Geotrupidae). Arvensis 1998; 10:11.
51. Chabrol L, Chambord R, Gransagne C, Pantacchini C. Bolboceras armiger (Scopoli, 1772) en Limousin (Coleoptera Geotrupidae). Le Coléoptériste 2009; 12(1): 28-30.
52. Charrier S. Clé de determination des Coléoptères Lucanides et Scarabéides de Vendée et de l'Ouest de la France. Le Naturaliste Vendéen 2002; 2(1):61-93.
53. Meurgey F. Odontaeus armiger (Scopoli) nouvellement signalé en Loire-Atlantique (Coleoptera, Geotrupidae). Bulletin de la Société des Sciences Naturelles de l'Ouest de la France 2003; 25(1):39-41.
54. Drouet E, Favretto J-P, Cama A, Lambert B. Aperçu de la faune lépidoptérologique de Belle-île-en-Mer (Morbilhan, France) (Lepidoptera, 2003). Bulletin de la Société des Sciences naturelles de l'Ouest de la France 2005; 27(2): 83-92.
55. Mériguet B, Zagatti P. Domaine régional du Grand Voyeux (Congis-sur-Thérouanne - Seine-et-Marne). Inventaire entomologique - AEV-OPIE, 2006, 49 pp.
56. Coache A. Première citation de l'Odontaeus armiger (Scopoli, 1772) dans le département des Alpes-de-Haute-Provence (Coleoptera, Geotrupidae, Bolboceratinae). Le Coleoptériste 2007; 10(2):123-124.
57. Eeles WJ. Odontaeus armiger (Scop.) (Col., Scarabaeidae) in South Oxon. Entomologist's Monthly Magazine 1961; 97:236.
58. Ansorge E. Odontaeus armiger Scopoli Coleoptera, Scarabaeidae at Chalfont Saint Peter, Bucks. The Entomologist's Gazette 1972; 3:280.
59. Chuter K. Odontaeus armiger (Scopoli) (Geotrupidae) and others in Kent 2002 and 2003. Coleopterist 2004; 13(1):4.
60. Callou C. Modifications de l'aire de répartition du lapin (Oryctolagus cuniculus) en France et en Espagne, du Pleistocène à l'époque actuelle. État de la question. Anthropozoologica 1995; 21: 95-114.
61. Veale EM. The rabbit in England. The Agricultural History Review 1957; 5(2):85-90.
62. Bailey M. The Rabbit and the Medieval East Anglian Economy. The Agricultural History Review 1988; 36(1):1-20.
63. Sheail J. Rabbits in post medieval England. Journal of Historical Geography 1978; 4(4):343-355.
64. Joy NH. 1932. A practical handbook of British beetles. Classey, Oxon, 1932, 622pp.
65. Britton EB. Coleoptera Scarabaeoidea (Lucanidae, Trogidae, Geotrupidae, Scarabaeidae). Handbooks for the Identification of british Insects, volume V, part 11, London, 1956, 29pp.
66. Grensted LW. Odontaeus armiger Scop. (Col., Scarabaeide) in Hants. The Entomologist's Monthly Magazine 1939; 75:174.
67. Cooter J. Rev. H. S. Gorham and some 19th Century Records. The Entomologist's Record and Journal of Variation 1979; 91:197-204
68. Nash DR. Notes on the Suffolk list of Coleoptera: seventeen species new to the Suffolk list, six deletions and recent significant records. Transactions of the Suffolk Natural Society 2007; 43: 75-89.
69. Dobson RM, Hancock EG. Historical review of a cabinet of Coleoptera from Thomas George Bishop's collection connected with James Francis Stephens. The Glasgow Naturalist 2008; 25(1):9-14.
70. Reichholf JH. Lichtfallenfunde des klapphornkäfers Odontaeus armiger im niederbayerischen Inntal. Mitteilungen der Zoologischen Gesellschaft Braunau 1993; 5(17/19):389-390.
71. Spagnesi M. Coniglio Selvatico – Oryctologus cuniculus (Linnaeus, 1758) in Spagnesi, M.; De Marinis, A. M. (editors) Mammiferi d'Italia, Quaderni di Conservazione della Natura, 14, Ministera Dell'Ambiente / Instituto Nazionale per la Fauna Silvatica Alessandro Ghigi, 2002, 309 pp.
72. Carpaneto GM, Piattella E. Sulla distribuzione di Bolboceras armiger in Italia. Giornale Italiano di Entomologia 1989; 4:167-172.
73. Piatella E. Contribution to the knowledge of scarab beetles of Vincheto di Celarda Nature Reserve (Coleoptera: Scarabaeoidea), in: Hardersen S, Mason F, Viola F, Campedel D, Lasen C & Cassol M (eds.), Research on the natural heritage of the reserves Vincheto di Celarda and Val Tovanella (Belluno province, Italy), Quaderni Conservazione Habitat, 5, Arti Grafiche Fiorini, Verona, 2008, pp 117-124.
74. Brelih S, Kajzer A, Pirnat A. Gradivo za favno hroščev (Coleoptera) Slovenije. 4. prispevek: Polyphaga: Scarabaeoidea (= Lamellicornia). Scopolia 2010; 70: 1-386.
75. Byk A., Mokrzycki T, Dworakowski M, Bidas M. Rozmieszczenie Odonteus armiger (Scopoli, 1772)(Coleoptera: Scarabaeoidea: Bolboceratidae) w Polsce z uwagami o jego bionomii. Wiadomości Entomologiczne 2012; 31(2):100-112.
76. Burakowski B, Mroczkowski M, Stefańska J. Chrząszcze Coleoptera, Scarabaeoidea, Dascilloidea, Byrrhoidea i Parnoidea, Katalogu Fauny Polski XXIII (9). Warsaw, 1983, 194 pp.
77. Vasko B. Fauna and ecology of Lamellicornia beetles (Coleoptera: Scarabaeoidea) of the Right-Bank Ukraine. The Kharkov Entomological Society Gazette 2010; 18(1):4-86.
78. Fauna Europaea. 2013. version 2.6, http://www.faunaeur.org, last accessed 24/10/2013.
79. Chapman JA, Flux JEC. Rabbits, Hares and Pikas - Status Survey and Conservation Action Plan. IUCN, Gland, 1990, 172pp.
80. Bratek Z, Papp L, Merkl O, Takács V. Főld alatti Gombákon rovarok. Mikológiali Közlemények 1992; 31(1-2):55-66.
81. Forshage M. Svenska namn pĺ inhemska bladhorningar. Entomologisk Tidskrift 2000; 121(3):99-118.
82. Nádai L. A Bolboceratinae alcsalád magyarországi fajainak lelőhelyadatai (Coleoptera, Scarabaeoidea: Geotrupidae). Folia Historico Naturalia Musei Matraenis 2006; 30:205-210.
83. Howden HF. The biology and taxonomy of the North American beetles of the subfamily Geotrupinae with revisions of the genera Bolbocerosoma, Eucanthus, Geotrupes, and Peltotrupes (Scarabaeidae). Proceedings of the United States National Museum 1955; 104:151-319.
84. Sim RJ. Scarabæidæ, Coleoptera; observations on species unrecorded or little-known in New Jersey. Journal of the New York Entomological Society1930; 38: 139-147.
85. Fabre JH. Souvenirs entomologiques. Edition définitive illustrée. Delagrave, Paris, 1925.
86. Rahola-Fabra P. Biologie de Bolbelasmus gallicus (Mulsant, 1842) (Coleoptera: Geotrupida: Boloboceratinae) dans le département du Gard (Languedoc, sud de la France). Elytron 2003-2004; 17-18: 37-46.
87. Howden H.F. Subfamilia Geotrupinae in Morón, MÁ. Atlas de los escarabajos de México: Coleoptera: Lamellicornia.

Familias Scarabaeidae, Trogidae, Passalidae y Lucanidae. Argania Editio, Barcelona. 2003, 227 pp.
88. Janssens A. Faune de Belgique. Insectes Coléoptères Lamellicornes. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, 1960, 411pp.
89. Telnov D. Swarming observation of Odonteus armiger (Scopoli, 1772) (Coleoptera: Geotrupidae). Latvijas Entomolgs 2012; 51:150-152.
90. Juřena D. in Gigli M. Odonteus armiger (Scopoli, 1772) – Bolboceratidae 28.V.2013- Italia- RM, Bosco di Manziana. Forum Entomologi Italiani, http://www.entomologiitaliani.net/public/forum/phpbb3/viewtopic.php?f=166&t=44900&hilit=odonteus+armiger&start=15, May 2013.
91. Howden H, Howden A, Holloway G. Digging down under: Australian Bolboceratini, their habits and a list of species (Coleoptera: Scarabaeoidea: Geotrupidae). Zootaxa 2007; 1499: 47-59.

Appendix 1: Records of *Odonteus armiger*

Armenia: 1♂ (v. *testaceus* Muls.)-Tavush, Haghartsin Monastery, alt. 1344m, [pitfall trap], 30-VI-2010, leg. D. Prunier⁄**Austria:** 1♂2♀-Radnig, Gaital, 21-30.VII.1981, leg. M. Woelky⁄1♂-Tirol, Baumkirchen, 6.VIII.1993, leg. Egger⁄1♂-Vienna⁄**Bulgaria:** 1♂1♀-Tschamkorja, M. Hilf, 1911, coll. Leonhard⁄**Czech Rep.:** 4♂5♀-SE Moravia, Ječmeniště env., alt. 150m, 5–6.VII.2013, leg. O. Hillert⁄1♂1♀-Nová Lhota env., Vápenky, garden/dry grass, 15.VI.2006, [UV ligth trap, time 22:10], leg. P. Mückstein⁄1♂1♀-Milovice, Bohemia, VI.2009, leg. L. Fiala⁄1♂-Strážné, meadow, alt 780m, VI.1987, [at lights], leg. J. Vaněk⁄1♂-Víchová nadJizerou, meadow –southern slope- surrounded by woods, alt. 480m, 8.VI.2011, [Malaise trap], leg. J. Vaněk⁄**England:** 1♀-Marston Moretaine, Bedfordshire, 04.VII.1998, [dead in spider web], leg J. Garcia⁄1♂2♀-Cambridgeshire, South Cambridge/Trumpington, (1♂) 28.VI.2012 [in flight], 21-28.VII.2012(1♀) [pitfall trap, rabbit burrow], 7-10.VI.2013 (1♀) [pitfall trap], leg. M. Miquel⁄1♂-Kent, St Mary Cray, Kynaston Wood, [at lights], 18.VII.2004, leg. M. Miquel⁄1♀-Thetford Forest, near Brandon, West Suffolk, [drown in puddle], 28.VI.1997, leg. J. Garcia⁄**France:** 1♀-Dordogne, Bordeaux, town garden, VII.1982, [at lights], leg. J-C Miquel⁄9♂6♀-Landes, Sore, Barthe, 2.IX.1984 (1♀), [at lights], leg. J-C Miquel, VII.1987(1♂), [at lights], VI.1989 (1♂2♀) [pitfall trap], VII.1989 (1♂2♀) [pitfall trap], VI.1992 (1♀) [pitfall trap], VII.1992 (1♂), [pitfall trap], 26.XII.1995 (1♀), [ex-larva, VII.1995], VI-1990 (1♂), [pitfall trap], 3-12.VII.1990 (1♂) [pitfall trap], 1-15.VII.1992 (1♂), [pitfall trap], 14-21.V.1997 (1♂), [pitfall trap], 15-28.V.1998 (1♂), [pitfall trap], leg. Miquel M. & J-C⁄1♂-Landes, Sore, small deep valley, thick underbrush,1-12.VII.1991, [pitfall trap – malt vinegar], leg. Miquel M. & J-C ⁄1♂-Landes, Pissos, Leyre, VI,1992, [in flight], leg. Miquel J-C⁄3♂3♀-Meurthe-et-Moselle, St-Amond Forest, Grand Rinchard Wood, Favières, alt. 420-460m, mixed deciduous trees, 2-3km inside forest, 14.VII.1978 (1♂1♀), 26.VII.1978 (1♂), 28.VII.1978 (2♀), 30.VII.1978 (1♂), [at lights], leg. Neid J. (further captures in 1979 & 1980)⁄1♀-Yvelines, Velizy-Villacoublay, near Etang du Trou aux Gants, [in flight], VI-1980, leg. J-C Miquel⁄2♂1♀-Deux-Sèvres, Rigné, mixed deciduous trees wood, 23.VI.1996 (1♂), [in flight], 29.VI.1996 (1♂), [feeding on Glomus microcarpum], 3.VIII.2009 (1♀), [at lights], leg. Miquel M.⁄1♂-Charentes, Mosnac, Chez Sandons, vineyard, 9.VII.1994, [at lights], leg. Miquel M.⁄8♂4♀-Vienne, Bois de St Pierre, Smarves, 27.V.1989 (1♂), [drown in puddle], VI.1990 (1♂1♀), [pitfall traps entrance rabbit burrow], VII.1990 (2♂), [pitfall traps entrance rabbit burrow], VI.1992 (2♀), [pitfall traps entrance rabbit burrow], VII.1992 (1♂), [pitfall traps entrance rabbit burrow], VIII.1992 (1♂), [pitfall traps entrance rabbit burrow], 11-26.VI.1994 (1♂), [pitfall traps entrance rabbit burrow], 26.VI-2.VII.1994 (1♀), [pitfall traps entrance rabbit burrow], 15-29.V.1993 (1♂), [pitfall trap], leg. Miquel M. &J-C⁄3♂4♀-Vienne, Nouaillé-Maupertuis les Bordes, 1♀ 11-28.VII.1991 [pitfall trap – malt vinegar], 1♂ V.1992, 1♀ 12-25.VI.1993, 1♂ VII.1993, 1♀ 1-6.VII.1994, 1♀ 16-23.VII.1994 [pitfall trap], 1♂ 17.VII.1997 [at lights], leg. M. & J-C Miquel⁄1♂1♀-Vienne, Champot, forêt de Moulière, ♀ 2-15.VI.1993 [pitfall trap – malt vinegar], ♂ 7-22.VIII.1993 [pitfall trap], leg. Miquel J-C & M⁄2♂-Vosges, Le Ménil, field near wood, alt c.a. 750m, 23.VIII.2010 [in flight], 28.VIII.2010 [pitfall trap], leg. M. Miquel⁄2♂-Vosges, Le Ménil, Forest/field border, alt. c.a. 920m, 02.IX.2010 [at lights], leg. M. Miquel⁄**Germany:** 1♀-Brandenburg, Schöneiche bei Berlin, 27.VII.2010, leg. O. Hillert⁄1♂-Berlin Hessenwinkel, 19.VII.2001, leg O. Hillert⁄1♂-Berlin Wilhelmshagen, 15.I.1998, [found dead], leg. Klöditz⁄1♂-Haag in Oberbayern, Bavaria, 19.VII.1951, leg. H. Damarz⁄2sp.– Bavaria, Unterfranken, Dornheim, 28-VI-1972, leg. H.J. Mager⁄1sp.-Bavaria, Unterfranken, Schwebheim, 1980, leg. Buck⁄1♀-Spandau, Berlin Spandau, 22.VI.?⁄1sp.-Bavaria, Bamberg, Unterhaid, 1980, leg. Buck⁄1sp.-Bayrischer Wald, Oberpfalz, Spiegelau/Langdorf, 16.VI.1974, leg. Apfelbacher⁄5sp.-Bavaria, Unterfranken, Dornheim, 15.VII.1966, [at lights], leg. U. Eitschberger⁄2sp.–Bavaria, Unterfranken, Winterhausen, 15.VIII.1977, leg. H.J. Mager⁄2sp.-Bayerische Wald, Bavaria, Spiegelau/Langdorf, 05.VIII.1979, [at light], 14.V.1973, leg. Apfelbacher⁄1sp.-Bavaria, Bayreuth, Weidenberg, 25.VIII.1968, [at lights], leg. G.Rößler⁄1sp.-Bavaria, Oberfranken, Untersteinach, Weinberg, 11.VIII.1972, [at lights], leg G. Rößler⁄1♀-Baden-Württemberg, Botanical gardens of the Stuttgart-Hohenheim University, 16.VI.2013, [at lights], leg. A. Haselboeck⁄**Hungary:** 1♂-Ujpest, Ungarn⁄1♀-Gammel, Budapest⁄**Italy:** 1♂-Emilia-Romagna - BO, Castel d'Aiano – Roffeno 6.VII.2013, [at lights], leg. Colacurcio L.⁄1♀-Lazio, Roma, Bosco di

Manziana, 28.V.2013, [at lights], leg. M. Gigli.(1♂-Toscana, GR, Scansano, [at lights], leg. Longo Turri G.(1♀-Sasso Marconi (BO) - Palazzo Rossi, 27.VIII.2010, [at lights], leg. Colacurcio L.(1♂2♀-Marche, Pesaro, V.2010, [in empty fish tank left outdoors], leg. Paglialunga M.(1♀-Emilia-Romagna, RA, Palazzuolo sul Senio, [at lights], leg. ?(1♂1♀- Tuscany - SI, loc. Casone, Wood (mainly oak with developed shrub undergrowth), V-VII.2010, [pitfall trap] ,leg. Bettacchioli G. & M.?(1♂1♀-Pratoni del Vivaro, Rocca di Papa, Roma, garden at edge of woodland, 9-VI-2008 (♀), 11-VI-2008 (♂), [at lights], leg. P Mazzei(**Lithuania:** 1♀-Ringovės Mound, Vilkijos env., Kauno district, 31.VII.2009, leg. Ferenca(1♂-Tervydonia , Šakių district, 08.VI.2009, leg. Steiblys(**Poland:** 2♂1♀-Rogów, 5.VI.1933 (♂), 11.VI.1934 (♂),12.V.1934 (♀), leg. W. Steciow(**Romania:** 1♀ (v. *testaceus* Muls.)-Dobrogea, Ciucurova env., 30.VI.1998, leg. Mertlik J.(1♀-Balcani, Bacău, VII-1991, leg. Leard(**Russia**: 1♂1♀ (v. *testaceus* Muls.)-Samara reg., Stavropol distr., "Zhigulevskij" reserve, 7.VI.2002, [at lights], leg. Kurochkin A.(1♂-Moscow, 14.VII.1994(**Serbia**: 2♂-Fruška Gora - Popovica, leg. Farkaš G.(**Ukraine:** State Museum of Natural History Collections (Lviv, Ukraine): 2♂1♀ & 2♂1♀(v. *testaceus* Muls.)- Pistyń [Kosovo area, Ivano-Frankivsk distr.], Coll. Grölle(2♀-Golosko, Lviv env., 4.VI.?, leg. Verhvatskij(1♀-Golosko, Lviv env., 13.VI.?(1♀-Kryvchyci, Lviv env., 9.VII.?(1♀-Klepariv, Lviv env., 12.VI.?, Leg. Zan`ko(1♂-Monastyryska, Ternopil reg., 2.VII.?(4♂1♀-Worochta, Yaremcha distr., Ivano-Frankivsk reg., coll. A. Stökl(1♀-Piznanka, Husiatynskyi distr., Ternopil reg., 27.V.?(1♀-Znesinnja, Park, Lviv, 22.VII.?(1♀-Pribin, Peremyshljany distr., Lviv reg.(1♂1♀-Ivano-Frankivsk(2♀-Sichów, Lviv reg., coll. A. Stökl(1♀-Turze vill., Stary Sambir distr., Lviv reg., 1908(2♂-Lviv(1♀-Pasiki, Pasiki-Zubritski vill., Pustomyty distr., Lviv reg., 1.VII.? (1♂1♀- Gaji, Velyki Gaji vill., Ternopil reg. & distr., VII.1909 (1♂), 10.VIII.? (1♀)(1♀-Zvenyhorod [Buchach distr., Ternopil reg., 5.VII.?(other collections: 1♂- Novoarkhangelsk urban village, Novoarkhangelsk distr., Kirovograd reg., 18.VII.2007, [at lights], leg. Reminnyi Yu.(1♂1♀-Kamennyje Mogily reserve, Volodarskij distr., Donetsk reg., 18.VI.1997, [at lights], leg. Martynov V.?(1♂-left Kuyalnik coastal lake shore, near Odessa, [in sediments], 9.IX.1995, leg. Gontarenko A.(1♂1♀-80km North of Odessa, Berezovka vill. env., Berezovsky forest, [pitfall trap], 18.VI-15.VII.1999, leg. Gontarenko A. (v. *testaceus* Muls.)(1♂4♀-Kiev, Lysa Hora park, 24.V.1998 (1♂), 14.VI.1998 (1♀), [pitfal trap], leg. Uspensky G., (1♀) 1-15.VII.2000 [pitfall trap], leg. Nazarenko Yu., 5.VIII.2007 (1♀), 25.VI.2007 (1♀),[pitfall trap], leg. Gerasimov R.(2♂-Lugansk reg., Melovskoj distr., "Streltzovskaya Steppe" reserve, [at lights], 1-5.VI.2006 (1♂), 21.VI.2008 (1♂), leg. Prokhorov A.(6♂5♀-Dnepropetrovsk-city, "Tunel`naja Balka" park, 16-19.VI.2008 (3♂4♀), 13.VI.2012 (3♂1♀), [4 in flight, rest at lights], leg. Sukhenko A.(1♂-Kiev reg., Makarov distr., Novoselki vill. env., 6.V.2013, [at lights], leg. Nesterov M(1♂(v. *testaceus* Muls.) -Podolian Tovtry (W Ukraine), Ternopil reg., Pidvolochysk distr., between Chagari-Zbarazhki & Shevchenkove vill., steppe sites, 6.V-7.VI.2012, leg. Panin R.(1♀-Crimea, Sudak distr., near Veseloje vill., (Crimean Mt.), 2.V.1994, [caught in flight], leg. Sidorenko V.(1♀-Donetsk reg., Sverdlovskij distr., "Provalskaya Steppe" reserve, near Kalinovskaya, 7.VI.2007, [at lights], leg. Prokhorov A.(1♀-Bukovina, Chernivtzi reg.(2♀-Chernivtzi reg., Kitsman distr., Stavchany vill., 24-25.VI.1959 [at lights], leg. S. Medvedev(2♀(1♀ v. *testaceus* Muls.)-Chernivtzi reg., Zastavna distr., near Zastavna-city, 20.VIII.1975, [at lights], leg.nat.coll.(1♀-Transkarpatians reg., West Ukraine, near Rakhiv, 14.VII.1998, leg. Simutnik S. (v. *testaceus* Muls.)(1♀- Lugansk-sity, 20-30.V.2010 [at lights], leg. Landik V.(2♀ (*v. testaceus* Muls.)–NW Ukraine, Volynj reg., Kovel distr., vill., forest, Turija river, [at lights], 20.VI.2013 and 27.XI.2012, leg. P. Vojko(1♀ (*v. testaceus* Muls.)–Poltava battle fields, Kiev dist., clearing in mixed forest, [in flight (night)], 29.V.2011, leg. E. Ribalchenko(

Table 1: Reported animal links

Species	Relationship	References	Observations
Worms	comatose beside worm-holes after application of worm-killer	[20]	Based on this, Arrow [21] assumed that *O. armiger* was not digging its own burrows!
Cattle	under dung/ dry dung	[3,22-23]	Reported by many other authors
Sheep	in droppings	Foudras in [3, 22]	Reported by many other authors
Humans	in faeces	Kingelmann in [3]	
Toads	prey	Vaillant, Perret, both in [3]	
Rabbits	in burrows	[24-26], this study	Paulian [25] seem to refer to Warlet [24]
	near droppings/burrows	[27-30]	
Red Foxes	in burrows	[24]	Warlet [24] assumed a mixed burrow occupancy with rabbits
Badgers	in burrows	[24]	Warlet [24] assumed a mixed burrow occupancy with rabbits

Table 2: Locations, years and duration of trapping. Letters in the "*O. armiger* burrows" column correspond to the diagram of fully excavated burrows in Figure 3.

Location			Number of traps	Year (duration)	Number of Captures		Excavated *O. armiger* burrows
Country	Départment/ Vice-County	Locality			Rabbit burrows	Controls	
France	Cantal	Saint Martin-Valmeroux / Salers	6	1989 (2 weeks)	0	0	
	Deux-Sèvres	Rigné	4	2009 (2 weeks)	0	0	2 (c,d)
	Landes	Sore (Barthe)	10	1988-99 (21 months)	0	11 (1 recapture)	9 (a,b)
	Landes	Vallée de la Leyre / Pissos	2	1994-95 (2 months)	0	0	
	Puy-de-Dôme	La Bourboule	4	1990 (2 weeks)	0	0	
	Vienne	Smarves (Bois de St Pierre)	10	1989-94 (25 months)	9	1	
	Vienne	Nouaillé-Maupertuis (Les Bordes)	10	1992-96 (12 months)	0	5	1
	Vienne	Champot	6	1993 (4 months)	0	1	
	Vosges	Le Ménil	4	2010 (2 weeks)	0	1	
England	Bedfordshire	Marston Moretaine	4	1999 (2 months)	0	0	
	Cambridgeshire	Cambridge	4	2012-13 (8months)	1	1	
	Kent	St Mary Cray (Kynaston Wood)	4	2004-05 (5 months)	0	0	
	West Suffolk	Thetford Forest Park	6	1998 (2 months)	0	0	
	West Suffolk	Brandon	4	1998 (2 months)	0	0	

Table 3: Reported Fungus associations in the literature and this study. Reference only referring to "underground fungi" or "truffles" without citing a precise species or genus are not included.

Fungus	*O. armiger* stage	References	Observations
Agaricus sp.	Adult	[23]	In decaying fungi. Not eaten in captivity in this study.
Endogone lactiflua	Adult	This study	In captivity. Fungi found near *O. armiger* burrows. Seem to prefer decaying specimen.
Glomus macrocarpum	Adult	[80]	Also *Bolbelasmus unicornis*.
Glomus microcarpum	Adult	This study	One male in burrow.
Rhizopogon luteolus	Adult	This study	One male found feeding on a large partly decaying specimen along two *Anoplotrupes stercorosus.*
Sclerodorma sp.	Adult	[81]	
Tuber sp.	Adult	[82]	
Mycelium	Larva	[24], this study	Thick mycelium growing on partly decaying roots inside rabbit warrens [24] or on roots near *O. armiger* burrows (this study).