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A vagrant clone in a peregrine species: Phylogeography, high clonal diversity and geographical distribution in the earthworm *Aporrectodea trapezoides* (Dugès, 1828)

Rosa Fernández*, Ana Almodóvar, Marta Novo, Mónica Gutiérrez, Darío J. Díaz Cosín

Departamento de Zoología y Antropología Física, Facultad de Biología, Universidad Complutense de Madrid, Calle José Antonio Novais, 2, 28040 Madrid, Spain

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ABSTRACT

The peregrine lumbricid *Aporrectodea trapezoides* is originally from the Palaearctic region but is distributed worldwide. Little is known about its clonal diversity or the existence of a pattern of biogeographical diversification of clones. This study aimed to explore the evolutionary history of *A. trapezoides* by analysing the mitochondrial (COI and COII) and nuclear (28S rRNA and histone H3) DNA sequences of individuals collected in 11 different countries. High clonal diversity was found for this species, with thirty-seven clones clearly divided into two distinct lineages (I and II). The marked biogeographical boundary between these lineages corresponds to the line separating the Eurosiberian and Mediterranean climates in North Spain. Clone 1 was shared by one-third of the earthworms. While this clone was found in most of the sampled localities, the rest of the clones showed geographically-restricted distributions. This clone may have originated in the Mediterranean area of Central Spain. As it was obviously introduced in Australia and it was found in locations occupied by members of both lineages, we hypothesise that it may have also been introduced in other countries and that it could be a general-purpose genotype able to adapt to a wide range of niches.

1. Introduction

Earthworms are of particular phylogenetic and biogeographical interest because they are an ancient group with little mobility and are mostly confined to their areas of origin. Due to their restriction to small areas at all stages of their life cycle and their susceptibility to extreme environmental conditions (i.e., desiccation), their distributions can reflect past palaeogeographic events.

In contrast, in relatively recent times a few earthworm species have become widespread due to two main factors. First, human movement across the globe has caused their unintentional transportation in connection with agriculture and commerce. Secondly, in recent decades, the phenomenon of biological improvement in soils via the stimulation or introduction of earthworms has started to attract the attention of scientific research. During this period, many studies have shed light on the importance of these species in pedogenesis and their effect on the recycling of nutrients, the maintenance of soil fertility, soil structure and plant productivity (i.e., Brun et al., 1987; Edwards and Bohlen, 1996), leading to several introduction projects. For example, Huhta (1979) introduced *Aporrectodea caliginosa* into coniferous forests in Finland with encouraging results. Several other instances of earthworm introduction in Dutch polders (i.e., Van Rhee, 1969; Hoogerkamp et al., 1983; Hoogerkamp, 1984), peat areas in Ireland (Curry and Bolger, 1984; Curry and Boyle, 1987), American mine spoil sites (Dunger, 1969; Vimmerstedt and Finney, 1973; Hamilton and Vimmerstedt, 1980) or New Zealand pastures (Stockdill, 1982) were reported to have yielded very positive results.

Peregrine species are those distributed far from their regions of origin. The term was first used with regard to earthworms by Michaelsen (1903), who described the wide distribution of some earthworm species and their presence in geographically remote localities. Peregrine species are also anthropochorus and allochthonous. Most peregrine earthworms are supposed to share several characteristics: small size, parthenogenetic reproduction often accompanied by polyploidy (Gates, 1972), high fecundity, resistant cocoons, wide environmental or feeding tolerances and rapid rates of spread (Lee, 1985, 1987).

Aporrectodea trapezoides is categorised as a peregrine earthworm. It is a very widely distributed species. It is also one of the five species commonly sold and used as fishing bait in North America (Blakemore, 2006). It is usually the dominant species in

* Corresponding author. Tel.: +34 913944953.
E-mail address: romafg@bio.ucm.es (R. Fernández).

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Mediterranean soils, both in terms of biomass and in terms of the number of individuals, and it is often the only species present because it can adapt to a wide range of extreme environmental conditions. Both its wide geographical distribution and its high reproductive rate (Fernández et al., 2010) make *A. trapezoides* a key species in global soil management.

Like *A. trapezoides*, some other peregrine species are also parthenogenetic, and several studies have examined their genetic diversity. It has emerged that some species have low clonal diversity, with a low number of clones (i.e., only one or two clones found in the case of *Octolasion cyaneum* and *Octolasion tyrtaeum*; Terhivuo and Saura, 2003; Heethoff et al., 2004), whereas other species have a very large number (i.e., 20 clones out of 50 earthworms in the case of *Aporrectodea rosea*, Terhivuo and Saura, 2006).

The present study examined the genetic variation (mtDNA COI and COII and the nuclear 28S rRNA and H3 regions) and phylogeographic relationships of several populations of *A. trapezoides* collected worldwide. The aim of this study was to ascertain i) the clonal variability within the species, and ii) whether distinct lineages exist and, if so, how different they are.

2. Materials and methods

2.1. Earthworm sampling

A total of 178 specimens of *A. trapezoides* were collected by digging and manual sorting in 47 different locations (Fig. 1, Table 1) from Spain, France, Portugal, Italy, Greece, Turkey, Algeria, Egypt

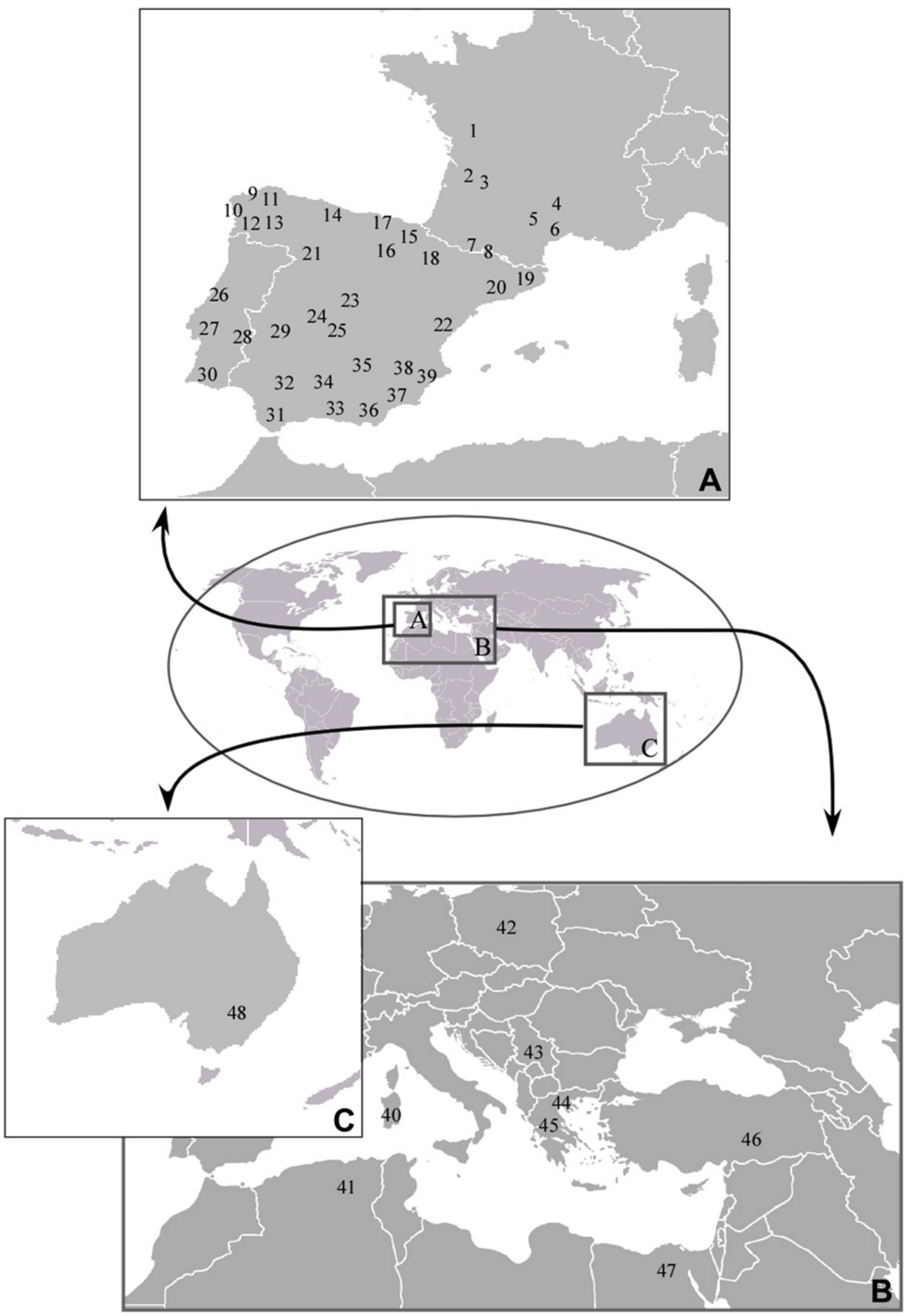

Fig. 1. Map of the sampled populations. See Table 1 for details.