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Islands, saurians and parasites

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A review and discussion of the results obtained after more than 40 years of research on parasites of insular saurian reptiles in some areas of the Mediterranean and the Atlantic has been carried out. Twenty-seven species and subspecies belonging to seven different genera of lizards were analysed, revealing the existence of diverse helminth communities, related to different biotic and abiotic characteristics of the hosts and habitats. The biogeographical and evolutionary particularities of the endemic parasites found are detailed and commented, as well as the peculiarities of the helminth fauna of the hosts in relation to their type of feeding or their age and size. The capacity and opportunity of saurian hosts in the dispersal of parasite species and the importance of parasites as bioindicators are also analysed.

Key words: ecology; endemism; evolution; islands; parasites; saurians.

In the last 40 years, a line of research on reptile parasites has been consolidated in the Laboratory of Animal Parasitology of the Faculty of Biological Sciences of the University of Valencia, and numerous works have been developed about different aspects of the parasite-host (in this case, parasite-reptile) relationships. Many of these investigations have aimed at hosts that inhabit islands, which incorporate an additional interest taking into account the ecological particularities exhibited by these territories and their eventual inhabitants.

Island ecosystems present the highest rates of both unique biodiversity and species extinctions (Whittaker *et al.*, 2017). Even though the number of species is typically low compared to the mainland, the number of endemics in islands is usually high (Whittaker *et al.*, 2017; Pinho *et al.*, 2022). On the other hand, low gene flow among islands, together with lower predation pressures and more limited food resources than in mainlands, promote the occurrence of unusual biological characteristics, such as diet specialization (Schluter, 1988; Pérez-Mellado & Corti, 1993; Roca, 1999) and gigantism (Pregill, 1986; Greer, 2001).

The islands of central Mediterranean harbour several lizard species, including some which are endemic of macro- and micro-insular systems (Roca *et al.*, 2006a). For example, lacertid lizards of the genus *Podarcis* Wagler, 1830 probably evolved in the Mediterranean Basin (Harris & Arnold, 1999; Arnold *et al.*, 2007) and are today widespread across both mainland and island ecosystems of the region

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(Alcover, 1988). Likewise, both Mediterranean and Atlantic islands are particularly rich in endemic saurians that have established populations in these places according to different routes of settlement (Alcover, 1988; Brandley *et al.*, 2010). Often, insular reptiles exhibit peculiar feeding habits such as herbivory, omnivory or cannibalism, and consequently they play a variety of roles as seed dispersers, pollinators or even top predators in some cases (Miranda, 2017).

From a global perspective and in comparison with parasitic faunas of fish, mammals or birds, it can be considered that the helminth communities of reptilian hosts are generally impoverished, isolationist, with low abundance and species richness (Aho, 1990; Roca *et al.*, 2012a). However, there are many different aspects related to the considered group of reptiles (Roca, 1999) and also to the characteristics of the ecosystems where each group inhabits (Roca *et al.*, 1990; Sanchis *et al.*, 2000; Martin & Roca, 2004a).

In insular ecosystems, several ecological peculiarities can give rise to particular helminth faunas in reptile hosts. Thus, (i) reproductive isolation leads to the emergence of new host species and subspecies, which opens up new possibilities for new parasitic species (and subspecies); (ii) a lower predation pressure and a higher population density of hosts with respect to the continent can increase the intensity of parasitisation; (iii) the low trophic availability of arthropods on islands may impel reptile hosts to expand their diet to include the consumption of plants (Roca, 2004). In this insular context, host-parasite associations could arise through descendance, when each host species inherits the association from its ancestor, or by colonisation, when the parasite switches to a new host lineage or species different from the host ancestor (Banks & Paterson, 2005). Rather than tracking their host with perfect fidelity, parasites may switch lineages, speciate independently of their host, go extinct, fail to colonise all the descendants of a host lineage, or fail to speciate when the host does (Jorge *et al.*, 2011). On the other hand, events other than co-speciation, such as geographical differentiation (Callejón *et al.*, 2010), may generate "false" congruent host and parasite phylogenies (Clayton *et al.*, 2003). In fact, several events could shape the current distribution of the parasite-host associations, resulting only rarely in a perfect match between both phylogenies (Page, 2003).

All the described circumstances show the interest of the study of the parasitic fauna of these insular saurians, because (i) sometimes they evidence some unusual characteristics of the parasite life cycles that may shed light on the processes that led to parasitism in vertebrate populations; and (ii) both parasites and hosts have often been isolated for long periods, thus providing a scenario of better understanding of the details of their interaction (Roca *et al.*, 2009).

The present work aims to highlight some relevant circumstances of four decades of study of the insularity-saurian-parasites relationship. These include aspects related to the endemicity of hosts and parasites, feeding habits of the hosts and their importance in the helminth fauna, or the role that host saurian can play on dispersion and / or concentration of

Table 1: Numbers and locations of the sampled hosts. WM = Western Mediterranean; EM = Eastern Mediterranean; EA = Eastern Atlantic; WA = Western Atlantic.

Hosts	**Number of sampled specimens**	**Location**
Podarcis pityusensis (Boscá, 1883)	564	Eivissa and Formentera (WM)
Podarcis lilfordi (Günther, 1874)	541	Menorca (WM)
Podarcis liolepis (Geniezt *et al*., 2014)	14*	Columbretes (WM)
Podarcis erhardii (Bedriaga, 1882)	200	Aegean Islands (EM)
Podarcis milensis (Bedriaga, 1882))	77	Milos (EM)
Podarcis tiliguerta (Gmelin, 1789)	17	Corsica (WM)
Podarcis muralis (Laurenti, 1768)	73	Tuscan Archipelago (WM)
Podarcis sícula (Rafinesque, 1810)	77	Tuscan Archipelago (WM)
Gallotia galloti galloti (Oudart, 1839)	27	Tenerife (EA)
Gallotia galloti palmae (Boettger & Müller, 1914)	27	La Palma (EA)
Gallotia caesaris caesaris (Lehrs, 1914)	318	El Hierro (EA)
Gallotia caesaris gomerae (Boettger & Müller, 1914)	21	La Gomera (EA)
Gallotia stehlini (Schenkel, 1801)	33	Gran Canaria (EA)
Gallotia atlantica atlantica (Petters & Doria, 1882)	52	Lanzarote (EA)
Gallotia atlantica laurae Castroviejo, Mateo et Collado, 1985	18	Lanzarote (EA)
Gallotia atlantica mahoratae Bischoff, 1985	42	Fuerteventura (EA)
Gallotia simonyi (Steindachner, 1889)	83**	El Hierro (EA)
Gallotia bravoana Hutterer, 1985	620**	La Gomera (EA)
Chalcides sexlineatus Steindachner, 1891	15	Gran Canaria (EA)
Tarentola boettgeri boettgeri (Joger & Bischoff, 1983)	38	Gran Canaria (EA)
Tarentola boettgeri hierrensis (Joger & Bischoff, 1983)	4	El Hierro (EA)
Tarentola gomerensis Joger & Bischoff, 1983	16	La Gomera (EA)
Tarentola mauritanica (Linnaeus, 1758)	98	Mallorca and Cabrera (WM)
Hemidactylus turcicus (Linnaeus, 1758)	42	Cabrera (WM)
Anolis grahami Gray, 1845	101	Bermuda WA)
Plestiodon longirostris Cope, 1861	152**	Bermuda (WA)
Chioninia coctei (Duméril et Bibron, 1839)	3*	Cabo Verde (EA)

*collection specimens, **faecal simples.

parasites, as well as their possible role as bioindicators.

MATERIALS AND METHODS

Hosts

Table 1 shows all the species and subspecies of saurian hosts analysed during 40 years of helminthological investigations. Eight belong to the genus *Podarcis* Wagler, 1830 (Sauria: Lacertidae), 10 to the genus *Gallotia* Boulenger, 1816 (Sauria: Lacertidae), four to the genus *Tarentola* Gray, 1825 (Sauria: Phyllodactylidae), one to the genus *Hemidactylus* Oken, 1827 (Sauria: Gekkonidae), one to the genus *Chalcides* Laurenti, 1768 (Sauria: Scincidae), one to the genus *Anolis* Daudin, 1802 (Sauria: Dactyloidae), one to the genus *Plestiodon* Duméril et Bibron, 1839 (Sauria: Scincidae), and one to the genus *Chioninia* Schmidt, 2004 (Sauria: Scincidae).

Figure 1: Island sites sampled in the Mediterranean. 1: Eastern Mediterranean; 2: Western Mediterranean.

Islands

The investigations were carried out in three major regions: Mediterranean islands (with two regions, Eastern and Western, Fig. 1); Canary Islands and the Cabo Verde archipelago (Eastern Atlantic) (Fig. 2); and Bermuda (Western Atlantic) (Fig. 2). Table 1 also details the location of the studied species.

As it happens in any island of volcanic origin, the Canary Islands start from a null biotic composition. From there, the colonization of the territory by species from more or less nearby continental lands, is a matter of time. Time and isolation play a role in allopatric speciation that will lead to the appearance of endemic species. This was the situation of the lizards established in the Canary Islands that are nowadays endemic species and subspecies (some of them more or less recently extinct, Mateo *et al.*, 2022). Arrival of lizards to the Canary islands probably took place in the Miocene, with an initial colonization of small lizards from Africa (López-Jurado & Mateo, 1995). Endemic lacertid lizards of the genus *Gallotia* appear as a monophyletic group with an east-west colonization pattern (Delgado, 2001); after the initial colonization, some species would become giants (Mateo *et al.*, 2022). The actual distribution of the geckoes of the genus *Tarentola* probably is consequence of several independent colonisations from the African continent and the extinction of some species (Nogales *et al.*, 1998). Skinks have colonized all the islands except La Palma. *Chalcides sexlineatus* lives only in Gran Canaria, where has originated two subspecies geographically separated (Delgado, 2001).

The Cabo Verde archipelago also has a volcanic origin, and its colonization was probably from continental Africa and / or from the dispersion of species from other islands of the Macaronesian region. We were able to do the helminthological study only from five museum specimens (Pinho *et al.*, 2022) of *Chioninia coctei* (Duméril et Bibron, 1839) (Sauria: Scincidae), a species considered extinct since the second half of the twentieth century (Pinho *et al.*, 2022). It is an endemism that lived in some islands and islets of this archipelago located about 500 km from the African Atlantic coast and that together with the Canary Islands and

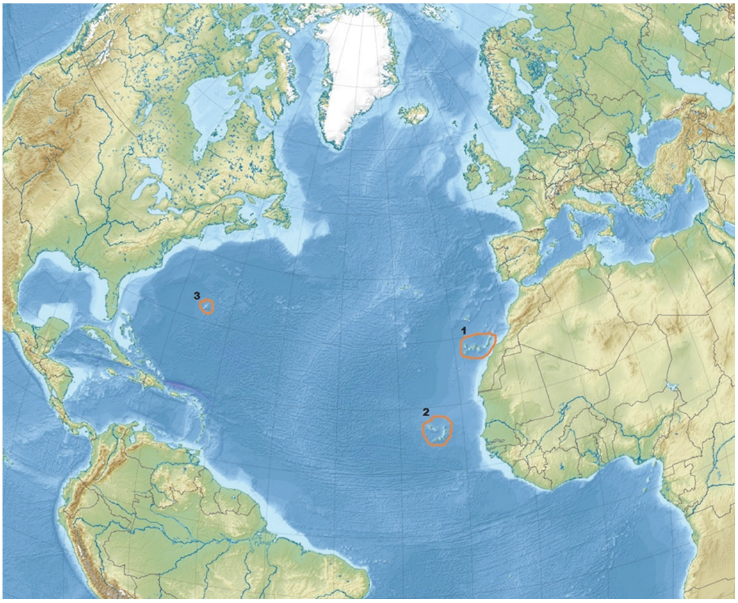

Figure 2: Island sites sampled in the Atlantic: 1: Cabo Verde archipelago; 2: Canary Islands; 3: Bermuda.

other archipelagos of the eastern Atlantic form the region of Macaronesia (Mateo *et al.*, 2022).

Bermuda is an isolated archipelago in the Atlantic, approximately 1000 km east of the United States. The islands are comprised mainly of lithified dunes formed during the Quaternary sea-level regressions (Herwitz, 1992), and its climate lies in the transition zone between tropical rainforest and humid subtropical climate. There, some saurian species have been established, one of them endemic, such as *Plestiodon longirostris* Cope, 1861 (Smith, 2005), and others introduced such as several species of the genus *Anolis* (Wingate, 1965), which is widely spread across the West Indies (Schwartz & Henderson, 1988; Hedges & Burnell, 1990).

The Balearic Islands are continental islands initially related to nearby continental lands. The current geological interpretation seems to indicate that these islands come from the east continuity of the Penibética mountain range, contracted and folded during the lower Miocene, which has been called the Balearic promontory. It is not known exactly when the first ruptures of this promontory occurred, but they led to the appearance of the islands. The current phase of the islands was reached after a series of long transformations that covered two different geological periods, the Pliocene and the Quaternary (Colom, 1988). The islets surrounding the main islands have been separated from them during more recent times (Hornero, 1991). Obviously the colonization of this type of (continental) islands is different from that of oceanic islands. Thus, in the Mediterranean, the endemic species have originated in the islands by meso-evolution and, in fact, when their ancestors reached the islands, they were no different from the continental species (Alcover, 1988). Now we find two endemic lacertid lizards, *Podarcis lilfordi* (Günther, 1874) and *Podarcis pityusensis* (Boscá, 1883), inhabiting respectively the Gymnesian and the Pityusic islands. Both are considered distinct but closely related species (Salvador & Pérez-Mellado, 1984; Mayol, 1985; Salvador, 1986a,b; Hornero, 1991; Pérez-Mellado, 2002a,b) belonging to the wide group of lizards from the West Mediterranean (Klemmer, 1957; Bischoff, 1973).

Methodology (hosts)

Since the early 1980s to the present time there have been some (and convenient) changes in scientific methodology regarding the handling (and eventual sacrifice) of animals. Most of the examined specimens, with the pertinent permit of the competent organizations (Ministry of Environment, Regional Councils, Insular Councils, or others) were processed properly providing us with a lot of good helminthological material for a complete scientific information. However, changes over time in legislation regarding animal handling, or particular circumstances of the various studied species, led to an adaptation of the methods of parasitological analysis. Thus, many studies opted for the capture of hosts and obtention of fresh faeces followed by the immediate release of the animal (Roca *et al.*, 2015). It is true that this methodology conditions the parasitological analysis since it is not possible to make a total count of the parasites found, nor can their specific determination be achieved (Roca *et al.*, 2015). However, the benefits of the technique are obvious and allow a relevant quantitative comparison that provides valuable information (Jorge *et al.*, 2013a). This was for example the cases of the species *Gallotia simonyi* (see Roca *et al.*, 1999a), *Gallotia bravoana* (see Roca, 2012) and *Plestiodon longirostris* (see Roca & García, 2021a). In the cases of *Podarcis liolepis* (see Roca, 2016) and *Chioninia coctei* (see Pinho *et al.*, 2022) the few analysed specimens were museum specimens loaned for study with the pertinent permission.

Methodology (parasites)

The collection and isolation of parasites from complete hosts is done by dissecting the host specimens and extracting all their organs that are placed in separate Petri dishes for thorough examination with the binocular stereoscope; helminths are individualized for posterior procedure. For processing the parasites (fixation, conservation and eventual staining and mounting on slides) we followed the steps commonly used in general helminthology. Thus, platyhelminths are usually fixed under pressure between slide and cover slide with Bouin liquid, and nematodes are fixed with hot 70% alcohol. Only platyhelminths are stained with aluminic carmine (Roca, 1985; Hornero, 1991).

For the analysis of faecal samples, we followed the quantitative and qualitative usual techniques (see Roca *et al.*, 1999; Roca, 2016), which provided us with information concerning the identification of eggs, larval forms and some adults that can be expelled in the process of defecation (Jorge *et al.*, 2013a).

The identification of the parasitic species was done through the microscopic study of the parasites, their description and relevant iconographic support, all with the aid of keys and specialized bibliography (Roca, 1985).

RESULTS AND DISCUSSION

Endemics

As indicated above, insularity causes, among other effects, a tendency towards the settlement of endemisms. MACARTHUR & WILSON (1967) stated that the number of species living in an island is the result of an equilibrium between those who colonized it and those who became extinct, although this balance between immigration and extinction is not the same in all islands and archipelagos, and will depend on many factors (MATEO *et al.*, 2022). One of the paths to speciation of parasites (see Introduction) is to follow the footsteps of their hosts. Therefore, it is not surprising that we find endemic species of parasites on their endemic hosts on various islands.

Pseudoparadistomum yaizaensis Roca, 2003 (Digenea: Dicrocoeliidae) (Fig. 3) is a flatworm identified for the first time in *Gallotia atlantica*. It is a genus and species endemic from a single location of Lanzarote Island, Yaiza village (ROCA, 2003). In fact, until its description, no species of dicrocoelid had been cited in the region of Macaronesia. Some species of the related genus *Paradistomum* Kossack, 1910 are distributed mainly in Asia and also in the European Mediterranean Basin (ROCA, 2003). So, the origin of this Canarian species is, for the moment, uncertain.

Spauligodon atlanticus Astasio, Zapatero, Ojeda et Solera, 1987 (Nematoda: Pharyngodonidae) was described as a specific parasite of lizards of the genus *Gallotia*, endemic from the Canary Islands (ASTASIO -ARBIZA *et al.*, 1987). This nematode shows a monoxenous (direct) life cycle (SÁNCHEZ, 1996), and so, gene flow among parasites

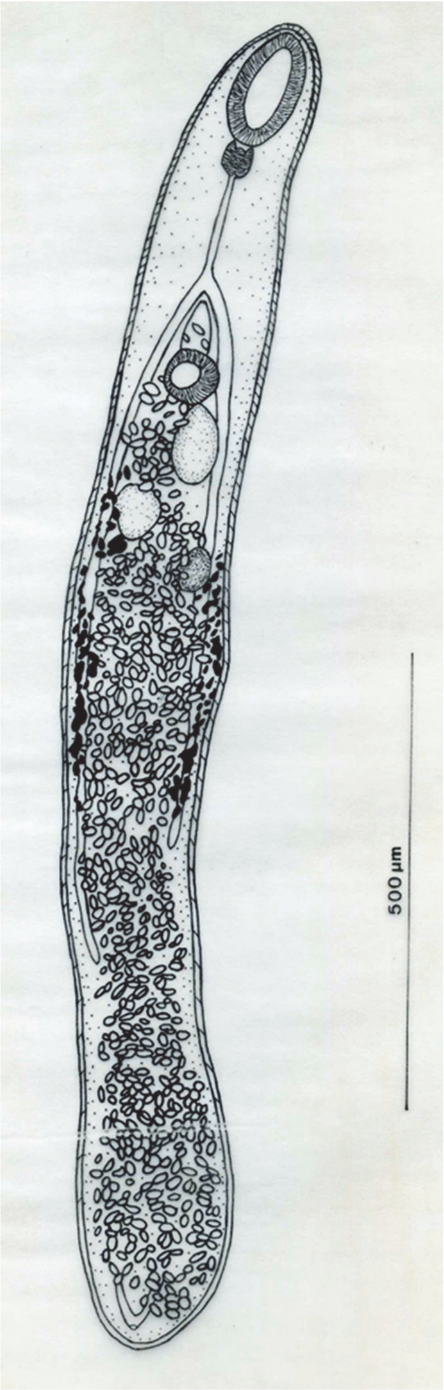

Figure 3: *Pseudoparadistomum yaizaensis*, gravid adult specimen, ventral view.

depends strictly on the movements and contacts between the hosts. However, *S. atlanticus* appeared to be a ″multihost″ parasite, parasitizing different species of the genus *Gallotia* (Jorge *et al*., 2011). Thus, it has been cited infecting all the investigated Canarian species and subspecies (Martin, 2005). However, a more recent genetic analysis revealed the phylogenetic and evolutionary complexity of this parasitic species revealing a colonization pattern that seems to fit that of the hosts. Jorge *et al*. (2013b) suggested that this could be another case of cryptic species. In fact, they demonstrated that it is a polyphyletic species including two highly divergent and not directly related lineages, one of them corresponding to the eastern islands and the other one to the western islands. More in-depth studies that combined molecular and morpho-anatomical techniques led to the description of the Western lineage as a new species, *Spauligodon occidentalis* Jorge, Perera, Carretero, Harris et Roca, 2013, distributed in the islands of El Hierro, La Gomera, La Palma and Tenerife (Jorge *et al*., 2013b).

The genus *Thelandros* Wedl, 1862 is widely distributed in all the biogeographic regions. The genus includes many cosmopolitan species but there are other species restricted to certain areas and / or hosts. Three of these species, *Thelandros tinerfensis* Solera, Astasio, Zapatero et Castaño, 1988, *Thelandros galloti* Astasio, Zapatero, Ojeda et González, 1988 and *Thelandros filiformis* Astasio, González, Castaño et Zapatero, 1989, were described from endemic hosts of the Canary Islands (Astasio-Arbiza *et al*., 1988, 1989; Solera-Puertas *et al*., 1988; Martin, 2005).

In São Vicente Island (Cabo Verde archipelago), a species of *Thelandros* was identified. This species had a great morphological coincidence with *T. tinerfensis* but had some molecular divergence (Sousa *et al*., 2017). Therefore, additional molecular markers and more samples are required to correctly determine the relationships with other *Thelandros* spp., allowing us to assess if this parasite represents a distinctive lineage specific to Cabo Verde, and to infer the prime host with whom this parasite colonized the archipelago (Sousa *et al*., 2017).

Also in the archipelago of Cabo Verde, on the island of São Nicolau, the endemic nematode *Spauligodon nicolauensis* Jorge, Carretero, Perera, Harris et Roca, 2012 has been identified from the hosts *Tarentola bocagei* Vasconcelos *et al*., 2011 and *Tarentola nicolauensis* Schleich, 1984. *Spauligodon nicolauensis* resembles *S. tarentolae*, a parasite of the geckoes from the Canary Islands (Jorge *et al*., 2012). According to available phylogenetic data (Carranza *et al*., 2000), the Cape Verdean *Tarentola* species originated from a colonization from the western Canary Islands, with São Nicolau being probably the first colonized island (Vasconcelos *et al*., 2010). Thus, *S. nicolauensis* may have originated via colonization by an ancestor of *S. tarentolae* brought by the ancestral species of Cape Verdean *Tarentola* (Jorge *et al*., 2012).

Strongyloides ophiusensis Roca et Hornero, 1992 (Fig. 4) is a strongylid nematode described from *Podarcis pityusensis* from Formentera Island and some islets surrounding it (Roca & Hornero, 1992). The genus *Strongyloides* Grassi, 1879 includes a great number of species parasitiz-

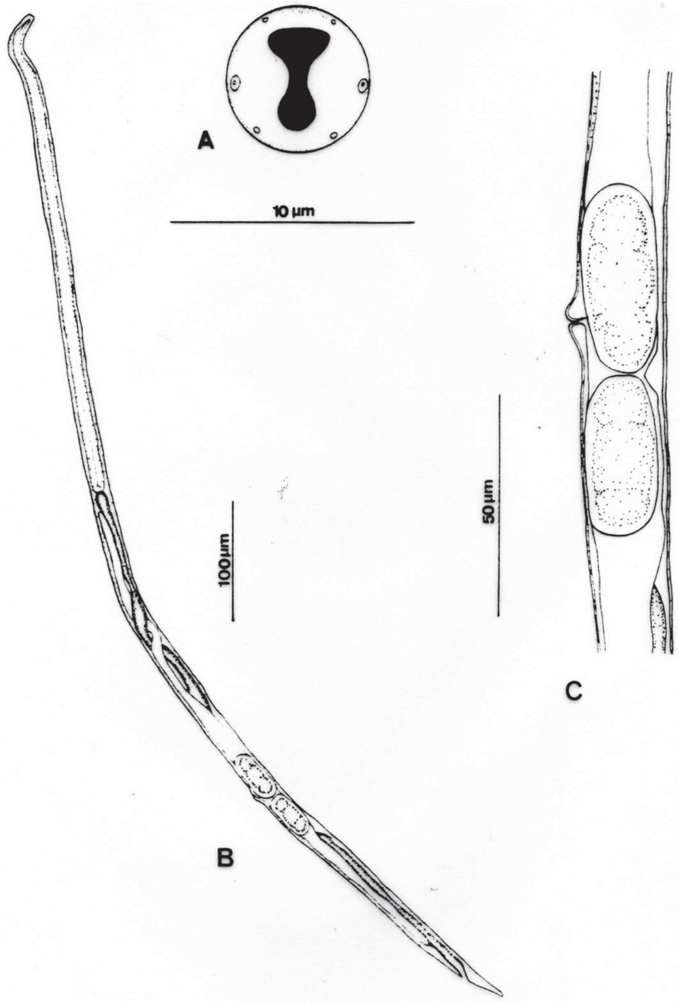

Figure 4: *Strongyloides ophiusensis*. A: cephalic end, apical view; B: gravid female, lateral view; C: eggs and vulva .

ing distinct amphibians, reptiles, birds, and mammals. The most similar species to this Balearic endemism is *Strongyloides mascomai* Navarro, Lluch et Izquierdo, 1989, described from *Pelophylax perezi* (Seoane, 1885) (Amphibia: Ranidae) from the east of the Iberian Peninsula (NAVARRO *et al.*, 1989). Given the origin of Balearic Islands closely related to the east of the Iberian Peninsula, it is possible to consider an allopatric speciation occurring in the insular location from the continental species, or to consider a common ancestor, since *Strongyloides* sp. has also been recorded from water snakes in the Iberian Pyrenees (GARCÍA-ADELL *et al.*, 1987).

Spauligodon cabrerae Castaño, Zapatero et Solera, 1988 was described from *Podarcis lilfordi* from Cabrera Island (CASTAÑO-FERNÁNDEZ *et al.*, 1988). The genus *Spauligodon* Skrjabin, Schikhobalova et Lagodovskaja, 1960 includes a great number of species having a wide geographic distribution. Some species have been recorded in areas close to the Balearic Islands, such as *S. extenuatus*, *S. auziensis*, *S. laevicauda* and *S. carbonelli* in Italy, Spain and North Africa (ROCA *et al.*, 1985, 1986; CASTAÑO-FERNÁNDEZ *et al.*, 1988; ROCA & FERRAGUT, 1989). However, to suggest the most zoogeographically coherent evolutionary aspects of this endemic nematode, taking into account the origin of the Balearic Islands (see above), we should look at the Iberian Peninsula, and more specifically at the east of the peninsula, where three species have been recorded: *S. auziensis*, *S. paratectipenis* and *S. saxicolae* (ROCA *et al.*, 1985, 1986). These three species have parasitized for a long time some saurians from Eastern Spain like *Podarcis hispanica*, *Tarentola mauritanica* and *Hemidactylus turcicus* (Roca *et al.*, loc. cit.). It is plausible to think that at the end of the separation of the Balearic promontory from the Iberian Penibetic Mountains, a process of allopatric speciation could have happened, which would explain the pattern observed in these nematode species. This situation would be favoured by the conjunction of isolation and plasticity of the genus *Spauligodon* (ROCA, 1993).

Insularity, herbivory and parasitism

Among reptiles, herbivory is a focus of interest in trophic ecology (POUGH, 1973). The cases of complete herbivory in terrestrial reptiles are the tortoises of the genus *Testudo* (and others) and some groups of lizards *sensu lato* (Squamata) (ROCA, 1999). These groups tend to be considered as non -specialists (POUGH, 1973) compared to other specialist groups such as chamaeleonids, varanids and anguids (Pough, loc. cit.).

Many species can be placed along a continuum "carnivory-omnivory-herbivory" (Fig. 5) and their diet can fluctuate along this continuum depending on various factors such as season, size, or availability of resources. Species usually considered herbivorous are, at best, facultative herbivorous, and more likely, simply omnivorous (ROCA, 1999). The variation in diet and its dependence on external factors is very evident in various populations of island lizards. PÉREZ-MELLADO (1989) and PÉREZ-MELLADO & CORTI (1993) pointed to seasonality, trophic availability, high density of individuals and the absence of

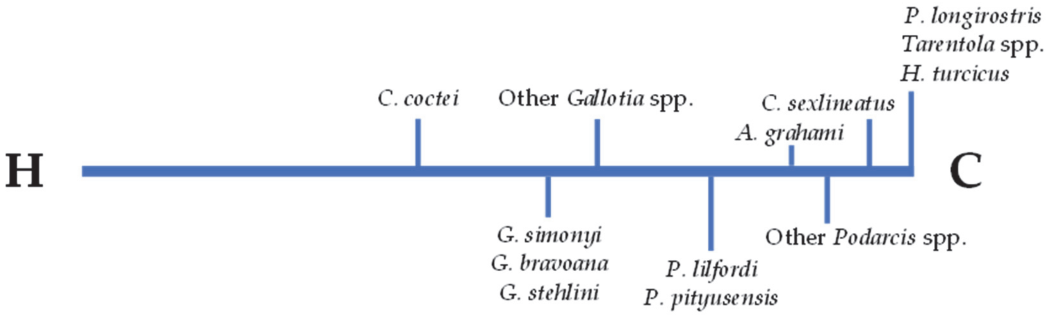

Figure 5: Relative position of the sampled hosts in the herbivory (H)-carnivory (C) continuum.

predators, as probable causes of pseudo-specialization (which does not involve morphological or physiological changes) that sometimes led to temporary stenophagy and a significant consumption of plant matter, in particular of the most energetic parts of plants, such as pollen, anthers and seeds (BROWN & PÉREZ-MELLADO, 1994).

Another interesting aspect of the parasitic ecology of reptiles is the relationship between parasitisation and feeding (ROCA & HORNERO, 1991). Herbivorous reptiles have larger and more diverse nematode faunas than carnivorous ones (BOWIE, 1974), and these helminth faunas are qualitatively different (ROCA, 1999). Thus, many nematode species characteristic of saurian reptiles belong to the superfamily Oxyuroidea Railliet, 1905, family Pharyngodonidae Travassos, 1919. PETTER (1966) and PETTER & QUENTIN (1976) distinguished two evolutionary lineages consistent with the fact that each of them had evolved in parallel in very different groups of hosts. The first lineage includes all Pharyngodonidae of carnivorous saurians, including the genera *Pharyngodon*, *Spauligodon*, *Skrjabinodon*, *Parapharyngodon* and *Parathelandros*. The second evolutionary lineage includes the Pharyngodonidae of herbivorous Iguanidae and Testudinidae, comprised by the genera *Tachygonetria*, *Mehdiella*, *Alaeuris*, *Thaparia*, *Ortleppnema*, *Ozolaimus*, *Travassozolaimus* and *Mamillomacracis*. The genus *Thelandros*, parasite of both carnivorous and herbivorous reptiles, shows affinities with the species of both lines; it would therefore seem logical to place *Thelandros* at the base of the two lineages of divergent evolution.

Among the inspected insular saurians, the species of the genera *Tarentola* and *Hemidactylus* are strictly insectivorous, and so they would be situated at this end within the herbivory-carnivory continuum (Fig. 5). Thus, the analysis of some *Tarentola* spp. from the Canary Islands showed no vegetable matter in the gut, and the observed nematodes corresponded to the lineage of carnivorous reptiles (ROCA, 1999; ROCA *et al.*, 1999b). *Tarentola mauritanica* and *Hemidactylus turcicus* from the Balearic Islands also showed helminth fauna of the insectivorous type (ROCA, 1993). *Chalcides sexlineatus* can be considered a fairly strict insectivore that actively seeks out prey, mostly little or non-flying soil arthropods (e.g. larvae, Hemiptera, isopods, beetles, spiders). Occasionally they also consume medium-sized snails and slugs, as well as some fleshy fruits and nectar (MATEO *et al.*, 2022). In both *Tarentola* spp. and *C. sexlineatus* from the Canary archipelago, the parasitic faunas conform to the pattern corresponding to carnivorous reptiles, that is, poor helminths and presence of Pharyngodonidae nematodes typical of reptiles with this type of diet (ROCA, 1993; ROCA *et al.*, 1999b, 2012b).

As noted above, many species of lizards of the genus *Podarcis* have evolved in the Mediterranean basin, both in insular and continental areas of Europe and Africa. In general, most species exhibit an insectivorous diet, but it is worth noting certain nuances that occur precisely in some island species. Thus, while the diet of several *Podarcis* spp. investigated in the eastern Mediterranean does not seem to contain significant amounts of plant matter (ADAMOPOULOS *et al.*, 1999), the Balearic species *P. lilfordi* and *P. pityusensis* are likely to incorporate appreciable amounts. In both species the consumption of plant parts is frequent (PÉREZ-MELLADO, 1989), and seems to be inversely related to trophic availability (PÉREZ-MELLADO & CORTI, 1993).

On the other hand, the two investigated species from the Bermuda archipelago, the scincid *Plestiodon longirostris* and the iguanid (*sensu lato*) *Anolis grahami* exhibit an insectivorous diet (CONYERS & WINGATE, 1996; LOSOS & DE QUEIROZ, 1997; STROUD *et al.*, 2017), although *A. grahami* has been observed ingesting flower nectar (Losos & de Queiroz, loc. cit.). These eminently insectivorous feeding habits are reflected in their helminth faunas that consist of few species with low prevalence and intensity of infection, including some oxyurid nematode typical of the phylogenetic lineage of carnivorous hosts (BUNDY *et al.*, 1987; ROCA & GARCÍA, 2021a,b).

The feeding trends of the Canarian lizards point towards a wide diversification both in the consumption of prey and in the inter and intraspecific trophic behaviour (pers. obs.). *Gallotia caesaris*, for example, is shown as a species that combines almost equally the consumption of arthropods with that of plant matter. It ingests a high number of animal taxa but also incorporates into its diet vegetable matter such as fruits and seeds, very energetic parts of plants (ROCA, 1999). This type of herbivory differs from that detected in *G. simonyi* (PÉREZ-MELLADO *et al.*, 1999), a giant lizard (and sympatric with *G. caesaris*), that eats less energetic plant parts (leaves, stems). This brings it closer than *G. caesaris* to the herbivory end of the continuum. In fact, the giant Canarian lizards (*G. simonyi*, *G. bravoana*, *G. stehlini*) tend towards a much more pronounced herbivory than that of their smaller island congeners (MATEO *et al.*, 2022).

The helminth fauna of the Canarian lizards also reflects the aforementioned trophic behaviour. Thus, medium-sized lizards show a certain tendency towards herbivory that is materialized in intensities and helminth diversity somewhat higher than other island species, as well as the presence of some oxyurid nematodes typical of tortoises, such as *Alaeuris* spp. and *Mehdiella* spp. (ROCA, 1999). Larger lizards exhibit even greater intensity and diversity of parasites and incorporate into their helminth fauna a greater number of species of oxyurids typical of herbivorous reptiles, such as *Alaeuris numidica* and some species of the genus *Tachygonetria* (MARTIN, 2005).

The species that is furthest from the extreme of carnivory is the giant Cape Verdean scincid, *C. coctei*. This recently extinct large saurian (ANDREONE & GAVETTI, 1998; MIRALLES *et al.*, 2010) shows a particular teeth morphology that has been regarded by several authors as evidence of an adaptative shift towards herbivorous or omnivorous diet (PERACCA, 1891; POMPANON *et al.*, 2012). Our recent studies on collection specimens support the adaptation towards the consumption of plant matter by *C. coctei*, identifying both items of this nature in their digestive systems and a very wide helminth fauna of oxyurid nematodes typical of herbivorous tortoises (PINHO *et al.*, 2022).

In short, insularity causes the appearance of peculiar adaptive characteristics in saurians, such as gigantism and perhaps the consequent adaptive change towards herbivory. Other characteristics of insular systems, such as the low trophic availability of arthropods, has pushed many species of island saurians towards this adaptive tendency of their feeding behaviour.

Spillover and spillback effects

Invasion ecologists have focused on the disease risks to native communities through "spillover" of infectious agents introduced with non-indigenous hosts, while overlooking a potentially more common mechanism of impact, that of "parasite spillback" (KELLY *et al.*, 2009). In Parasitology, the "spillover" effect is considered as the introduction of allochthonous parasites into autochthonous hosts, and the "spillback" effect consists in the functioning of the allochthonous invader as a compatible host for autochthonous parasites (DOMÉNECH *et al.*, 2016). Invasions can impact the parasite communities through both the introduction of exotic parasite species and effects of invading hosts on native parasite dynamics (TELFER & BOWN, 2012). The probability of spread of an exotic parasite and impacts of introduced species on native parasite dynamics depend on key parameters related to rates of encounter, transmission, mortality and recovery (Telfer & Bown, loc. cit.). Islands are excellent natural laboratories for the investigation of many ecological and evolutionary phenomena and also for the study of invasion phenomena, both in free-living (SERRA & TRAVESET, 2020) and in parasitic organisms (STROUD *et al.*, 2017).

The Caribbean Sea has been shown as a geographical area very conducive to phenomena of invasion and colonization. The large number of islands and islets and the affordable distance among them favours the movement of species between islands. Thus, anoles are predominantly arboreal iguanids (*sensu lato*), which occur throughout the tropical and subtropical Americas including the Caribbean region (BUNDY *et al.*, 1987). Of the large number of species of this genus living in this region, some are endemic to certain islands or islets and many others have spread through different islands of the area. Along with these hosts, many parasites that infect them have also had the opportunity to colonize new places (GOLDBERG *et al.*, 2005) even reaching regions somewhat further from the Caribbean area such as the Bermuda archipelago (GOLDBERG *et al.*, 1995) or very far away such as Hawaii (GOLDBERG & BURSEY, 2000).

The terrestrial herpetofauna of Bermuda is mainly constituted by four lizard species, the endemic Bermuda skink *Plestiodon longirostris* and the introduced anoles *Anolis grahami, A. loechi* and *A. roquet* (Polychrotidae) (BRANDLEY *et al.*, 2010). The two species of nematodes found parasitizing *P. longirostris* are common parasites in other Caribbean lizards that are widely distributed in this region, and, particularly, have been cited in Bermuda also in the introduced host *A. grahami* (ROCA & GARCÍA, 2021a). It is presumable that this host may have expanded their parasites ("spillover" effect) to the endemic *P. longirostris*, which is a competent host for these parasites ("spillback" effect), being this native species causing an amplification effect on the dynamics of these introduced parasites (ROCA & GARCÍA, 2021a,b).

Parasites as bioindicators

Parasites play a role as markers of environmental quality (Marcogliese, 2005) and they can also be indicators of environmental stress (Megía-Palma *et al.*, 2020). Recently, some intrinsic and extrinsic factors have been identified as predictors of the prevalence and abundance of ecto and endoparasites in a lizard community (Drechsler *et al.*, 2021).

During the course of all these years our research group has revealed the general patterns of parasitisation of peninsular and insular Spanish saurians and has also shown that there are some phenological and environmental factors that can influence the establishment of helminth communities in different species of reptiles. The presence of adult cestodes and nematodes with indirect life cycles that include arthropods as intermediate hosts may reinforce the evidence of insectivorous feeding habits in certain saurian hosts (Roca, 2021). According to the position they occupy in the carnivory-herbivory continuum (Fig. 5), adults of *Nematotaenia tarentolae* have been detected parasitizing *T. mauritanica* and *P. lilfordi* from Cabrera (Roca, 1996) and *P. pityusensis* from the Pityusic Islands (Roca & Hornero, 1994); and *Oochoristica* spp. has been recorded on different species of *Podarcis* from some Mediterranean islands (Roca & Hornero, 1994; Roca, 1995, 1996). The nematode *Physaloptera squamatae* (also with indirect life cycle) was found in Bermuda parasitizing *A. grahami* and *P. longirostris* (Roca & García, 2021a,b). In saurians with a greater tendency towards herbivory (*Gallotia* spp. and *C. coctei*), no adult cestodes with indirect life cycles have been found, although, as an exceptional case, the presence of *N. tarentolae* and *O. agamae* was recorded in the lacertid *G. stehlini* but with very low prevalence of infestation (3%) (Martin & Roca, 2004b). However, nematodes *Skrjabinelazia* spp. (also with indirect life cycle) have been found in the intestine of some Canarian lizards of the genus *Gallotia* (Martin & Roca, 2004a,b), suggesting that, despite the trend towards herbivory, these insular lizards may include animal prey, if they are available.

On the other hand, the presence of larval forms of cestodes, nematodes and acantocephalans in saurians suggests that they act as intermediate (or paratenic) hosts of life cycles in which adult helminths are parasites of birds or mammals, evidencing the prey character of these saurian hosts (Roca, 2021). Perhaps the saurians that best represent this character (prey) are the species of the genus *Tarentola*; both the Balearic and Canary species are parasitized by different species of cestode larval forms (Roca, 1995, 1996; Roca *et al.*, 1999b). Also, many species of Mediterranean and some Canarian lacertids harbour larval forms of nematodes and acanthocephalans, which also suggest that they can be common prey of mammals or birds.

Apart from feeding, other intrinsic factors such as age and size can condition the helminthological fauna of these hosts (Roca, 2021). Thus, the relationship between parasite infestation and host size is revealed as an indicator of the age of the host and, therefore, of the longer time for parasite recruitment (Roca *et al.*, 2006b). In fact, larger species, such as the giant lizards of the Canary Islands and the Cape Verdean scincid *C. coctei* harbour greater diversity and quantity of parasites than other smaller species.

Among the extrinsic factors, one of those that most affects the diversity of parasite fauna of saurian reptiles is the more or less humid or dry environment that these hosts occupy (DRECHSLER *et al.*, 2021). Thus, species that inhabit humid areas tend to reach higher values of richness and abundance of parasitic helminths than those that occupy drier habitats (ROCA, 2021). Trematodes with indirect, mixed aquatic-terrestrial life cycles including freshwater molluscs as first intermediate hots can be considered as indicators of the type of habitat occupied by many saurian species. Thus, in the Iberian Peninsula the presence of digenids is associated with saurian hosts living in humid zones, such as rivers or marsh areas (ROCA, 2021). Only two species of digenids have been recorded in the investigated insular saurians, *Paradistomum mutabile* in many species of Mediterranean lacertids and gekkonids (ROCA, 1993, 1995), and *Pseudoparadistomum yaizaensis* in *G. atlantica* from Lanzarote (ROCA, 2003). Interestingly, these two closely related species of trematodes appear to be typical of dry environments. Thus, *P. mutabile* has been cited mostly on islands and rarely in continental areas of impoverished territories. In fact, it has never been recorded in the Iberian Peninsula but is abundant in the Balearic Islands and islets (ROCA, 1993). The explanation for this apparent contradiction may be that the first intermediate host in the life cycle of this parasite (and probably in that of *P. yaizaensis*) is a land snail living in dry environments; TIMON-DAVID & TIMON-DAVID (1967) suggested that it could be a species of the genus *Helicella*. Perhaps, as in several species of the family Dicrocoeliidae (to which *P. mutabile* and *P. yaizaensis* belong), the cercariae emitted by the mollusc first intermediate host are covered with a mucous layer to resist desiccation (KENNEDY *et al.*, 1987), and given the character of certain heterogeneity in the feeding of the investigated Balearic and Canarian saurians, these hosts could directly ingest these mucus balls, thus incorporating the infesting larval forms (HORNERO, 1991).

Another interesting character is the effect of the insular surface. In a specific area with more or less uniform climate (as are the study sites of the present work), there is a relationship between the sampled area and the number of species living there (DARLINGTON, 1957). The situation is more complicated when we consider parasites. Generally larger islands show a greater number of parasitic species because a larger size means a greater diversity of habitats, so a greater number of free-living species as potential definitive or intermediate hosts, and consequently more opportunities for parasitic species (MAS-COMA *et al.*, 1987). We were able to carry out a comparative study in the Balearic archipelago whose islands and islets did not show differences in their habitats but rather a certain xeric uniformity. In addition, we only studied a single host, *P. lilfordi* in the Gymnesian and *P. pityusensis* in the Pityusic Islands. The result was the non-correlation between the size of the studied islands and islets and the helminth diversity (ROCA, 1996), as already pointed out by KENNEDY (1978) and DOBSON *et al.* (1992), who indicated that the local conditions of each island (and not the size) were the determining factors in the composition of parasitic faunas.

Recently, the use of the parasite-saurian host relationship has been proposed as a bioindicator of post-fire regeneration dynamics (Roca *et al.*, 2015). In the Mediterranean region, wildfires are a key process to understand the functioning of natural ecosystems (Pausas, 2012). Various species of saurians can be useful as biomarkers in post-fire regeneration processes, since they play an important role in the trophic chain and can also be seed dispersers (Roca *et al*, 2015). Due to their high ecological requirements, the parasites of these saurians can also be proposed as markers of this process of ecosystem regeneration (Fuentes *et al.*, 1998; Roca, 2021).

In all these years of parasitological research, fortunately there have not been many episodes of fires of great magnitude in the studied Mediterranean islands, however it is worth noting a few important fires in some of the Canary Islands, not to mention the very recent volcanic eruption of the island of La Palma. Although we did not had the opportunity to carry out field studies to determine the importance of saurians and their parasites in post-fire regeneration, our hypothesis, corroborated in the Iberian Peninsula (Roca *et al.*, 2015), is that after a fire (or lava flow) there will be changes in the parasite communities of the insular saurians as a result of the alterations in the habitat and soil structures, as well as in the availability of prey for reptiles (Álvarez-Ruiz *et al.*, 2021). Significant differences in the prevalence and intensity of infection of hosts in burned areas compared to unburned areas (control) can be expected in relation to post-fire regeneration processes (Roca *et al.*, 2015).

In reptiles, burned areas have communities more abundant in number of individuals (Rochester *et al.*, 2010; Santos & Cheylan, 2013). The aggregation of hosts would lead to a higher prevalence of parasites and a higher rate of parasite transmission (intensity) (Fuentes *et al.*, 2007). Thus, the saurian oxyurids with direct life cycles could be favoured by a high population density of their hosts (Arneberg, 2001). The recolonization capacity of parasites with direct life cycles will be higher than that of parasites with indirect life cycles, since the latter need intermediate hosts (insects and other arthropods) that in some cases could take longer to recolonize the burned area. Thus, at first, we would expect a higher prevalence of infection by monoxenous species, a situation that would tend to balance as time goes by if we consider that the post-fire habitat can produce an increase in the diversity and abundance of insects, the main prey of many reptiles (Roca *et al.*, 2015).

Bioethical considerations

All the animals used in our investigations have been treated ethically and in accordance, in each moment, with the applicable regulations in the handling of experimental animals.

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