RESEARCH ARTICLE



Distribution patterns of established alien land snail species in the Western Palaearctic Region

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Abstract

Established alien land snail species that were introduced into the Western Palaearctic Region from other regions and their spread in the Western Palaearctic are reviewed. Thirteen of the 22 species came from North America, three from Sub-Saharan Africa, two from the Australian region, three probably from the Oriental Region and one from South America. The establishment of outdoor populations of these species was usually first seen at the western or southern rims of the Western Palearctic. Within Europe, the alien species usually spread from south to north and from west to east. The latitudinal ranges of the alien species significantly increased with increasing time since the first record of introduction to the Western Palearctic. The latitudinal mid-points of the Western Palaearctic and native ranges of the species are significantly correlated when one outlier is omitted. There is a general trend of poleward shifts of the ranges of the species in the Western Palaearctic compared to their native ranges. There are three reasons for these shifts: (1) the northward expansion of some species in Western Europe facilitated by the oceanic climate, (2) the impediment to the colonisation of southern latitudes in the Western Palaearctic due to their aridity and (3) the establishment of tropical species in the Mediterranean and the Middle East. Most of the species are small, not carnivorous and unlikely to cause serious ecological or economic damage. In contrast, the recently introduced large veronicellid slugs from Sub-Saharan Africa and the giant African snail Lissachatina fulica could cause economic damage in irrigated agricultural areas or greenhouses in the Mediterranean and the Middle East.

Keywords

Europe, Gastropoda, introduced species, Middle East, Mollusca, North Africa, non-native

Introduction

An increasing number of species are being spread beyond their native ranges, usually by humans, sometimes intentionally, but often accidentally with commodities or travellers (van Kleunen et al. 2015; Seebens et al. 2017). The spread of species across biogeographical barriers results in global biogeographic homogenisation (McKinney and Lockwood 1999). The distributions of alien species are primarily explained by the prevailing climate and, to a lesser extent, by distance and trade relationships (Capinha et al. 2015). Alien species may disturb local ecosystems and may contribute to the extinction of native species (McKinney and Lockwood 1999; Clavero and Garcia-Berthou 2005). They may become pests and cause economic impacts (Pimentel et al. 2005; Vilà et al. 2010; Haubrock et al. 2021) and they may even be directly or indirectly harmful to human health as parasites, vectors or hosts (Hulme 2014). Therefore, the spread of alien species should be prevented; they should be monitored and, if necessary, controlled or eradicated (Butchart et al. 2010). However, for many taxa, especially invertebrates, we even lack an overview of the alien species and their distributions. Despite efforts to compile lists of alien species (e.g. DAISIE (2009)), a well-documented inventory of alien invertebrate species is not even available for Europe.

Molluscs are amongst the little-known taxa. In this paper, I focus on land snails. Land snail species play a variety of roles in ecosystems (Barker 2001). The greater majority of land snail species are detritivores, feeding on decaying plant material. They make an important contribution to decomposition, the nutrient cycle and soil formation (Meyer et al. 2013). Some also feed additionally or exclusively on living plant tissues (Godan 1983; Barker 2002). Others are facultative or obligate carnivores (Barker and Efford 2004). The different functional groups can pose different concerns if they are intentionally or unintentionally introduced into regions beyond their native ranges. Whereas the detritivores are of least concern, the herbivores may become agricultural and horticultural pests (Godan 1983; Barker 2002). Carnivorous land snails have been intentionally introduced in various regions as biological control agents for herbivorous snails. There are strong indications that they have not been effective in regulating the targeted pest snails (Cowie 2001; Gerlach et al. 2021). Instead, the introduction of carnivorous snails has often had fatal consequences for the native snail fauna. The extreme case is the Euglandina rosea (Férussac, 1821) species complex, known commonly as the rosy wolfsnail. This species complex has been introduced to many islands of the Pacific and Indian Oceans, as well as the Caribbean and southern and eastern Asia from the 1950s onwards as a biological control agent for the invasive giant African snail, Lissachatina fulica (Bowdich, 1822) (Griffiths et al. 1993; Civeyrel and Simberloff 1996; Lowe et al. 2000; Gerlach et al. 2021). However, the introduced Euglandina species prefer to prey on smaller native species than on L. fulica (Griffiths et al. 1993). The introduction of the Euglandina species has probably caused extinctions of at least 134 endemic land snail species (Régnier et al. 2009). Moreover, some land snails may act as intermediate hosts of pathogen species like the rat lungworm, *Angiostrongylus cantonensis* (Chen, 1935) (Grewal et al. 2003), which may cause meningitis (Kliks and Palumbo 1992; Prociv et al. 2000; Barratt et al. 2016). Therefore, it is important to compile available information about alien land snail species as a basis for decisions on further measures to control or eradicate introduced populations.

In this study, the distribution and spread of land snail species that were introduced into the Western Palaearctic Region from other regions and that have established selfsustaining outdoor populations within the Western Palaearctic is reviewed. Current knowledge about the timing of introduction of the species into the Western Palaearctic Region and their spread within the region is summarised from the scattered literature. The latitudinal ranges of the established alien species in the Western Palaearctic Region are compared with the latitudinal extent of their native ranges.

Methods

Records of land snail species introduced to the Western Palaearctic Region from other regions after 1492 that have established self-sustaining outdoor populations and their distribution in the Western Palaearctic were compiled from literature, GBIF.org (2022) and the online collection database of the Steinhardt Museum National Natural History Collections (https://smnh.tau.ac.il/en/research/collectionsdatabase/). Introductions of species that occur only in greenhouses, plant nurseries or in flowerpots were not considered. Whether populations occurred outdoors is usually stated in publications, but is often less clear in datasets retrieved from GBIF. org (2022). It was not possible to further restrict the outdoor habitats where the introduced species occurred; i.e. they may be restricted, for example, to permanently irrigated, anthropogenic habitats like gardens. The Western Palaearctic as considered here includes Europe, the Azores, Madeira, Canary Islands (but not Cape Verde), Africa north of the Sahara, the Caucasus region and the Middle East eastwards to western Iran (but not the Arabian Peninsula, which forms a transitional zone to the Ethiopian region). Only the first reports of established outdoor populations of introduced species at the country level are compiled. With the exception of the Macaronesian archipelagos, islands are not listed separately from the countries to which they belong.

Data on the native ranges of the alien species were mainly taken from GBIF.org (2022), Hubricht (1985) and additional papers listed under the respective species. The boundaries of the native ranges are often fuzzy, as species also expand beyond their native ranges in the regions where they originated.

Latitudinal limits, latitudinal extent and latitudinal mid-point of the native range of each species and its range in the Western Palearctic were calculated as described by Guo et al. (2012).

Results

List of established alien land snail species in the Western Palaearctic Region

Laevicaulis alte (Férussac, 1822) (Veronicellidae; Fig. 1A)

Origin: Tropical Africa (Forcart 1953).

First record for the Western Palaearctic Region: Egypt, 2018 (Ali and Robinson 2020).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Egypt.

References for identification: Forcart (1953).

Remarks: *Laevicaulis alte* has been spread by humans throughout the tropics (Robinson 1999; GBIF.org 2022). Given that most *Laevicaulis* species are restricted to Africa, it has been assumed that *Laevicaulis alte* originated in Africa (Forcart 1953). The species has only recently been found in the Western Palaearctic (Ali and Robinson 2020), but was already known for a longer time from anthropogenic habitats in the transitional zone to the Ethiopian region in the southern Arabian Peninsula (El-Alfy et al. 1994; Neubert 1998).

Laevicaulis stuhlmanni (Simroth, 1895) (Veronicellidae; Fig. 1B)

Origin: Eastern Democratic Republic of the Congo, Uganda, Rwanda, Burundi, Kenya, Tanzania (Forcart 1953; Verdcourt 2006).

First record for the Western Palaearctic Region: Egypt, 2016 (Ali 2017a, b). Western Palaearctic distribution (Suppl. material 1, Fig. 2): Egypt, Libya. References for identification: Forcart (1953).

Remarks: This East African species was reported from a garden in Cairo (Ali 2017a, b). Samples from Libya initially identified as *Laevicaulis striatus* (Simroth, 1896) (Liberto et al. 2021) were later also identified as *L. stuhlmanni* (Ali et al. 2022).

Allopeas clavulinum (Potiez & Michaud, 1838) (Achatinidae; Fig. 1C)

Origin: Oriental Region?

First record for the Western Palaearctic Region: Israel, 2011 (Mienis et al. 2012). Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1946); Kerney et al. (1983); Horsák et al. (2020).

Remarks: The delimitation of this species is unclear (see Horsák et al. (2020)). Some considered *A. mauritianum* (Pfeiffer, 1853) to be a synonym of *A. clavulinum* (Kerney et al. 1983; Griffiths and Florens 2006; Horsák et al. 2020), while others considered them distinct species (Pilsbry 1946; Gittenberger and van Bruggen 2013). *Allopeas clavulinum* is a common greenhouse species (Kerney et al. 1983; Horsák et al. 2020). Its association with ornamental plants can easily result in its introduction to countries with suitable environmental conditions. It has also been spread by humans throughout the tropics (Robinson 1999). Its origin is sometimes given as East Africa (Kerney et al. 1983; Robinson 1999; Griffiths and Florens 2006), although it is not known from mainland East Africa (Connolly 1925; Verdcourt 2006). Molecular genetic investigations may help to reveal the geographic origin of the species. Although *A. clavulinum* and its presumed synonym *A. mauritianum* (Pfeiffer, 1853) were originally described from the Mascarene Islands, it should be re-considered whether it originated in Southeast Asia, where the species is widespread, but usually considered introduced (Nurinsiyah and Hausdorf 2019).

Allopeas gracile (Hutton, 1834) (Achatinidae; Fig. 1D)

Origin: Oriental Region?

First record for the Western Palaearctic Region: Iraq, 2008 (Naser 2010).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Canary Islands, Iraq. References for identification: Pilsbry (1946); Horsák et al. (2020).

Remarks: Allopeas gracile has been distributed throughout the tropics by humans (Pilsbry 1946; Robinson 1999). For a long time, it has been supposed that *A. gracile* originated in the Neotropics (Pilsbry 1946; Solem 1964; Neubert 1998; Robinson 1999; Brodie and Barker 2011). However, Christensen and Weisler (2013) argued for an Old World origin of *A. gracile* because there are several Quaternary and archaeological records of *A. gracile* from southern Asia, the Middle East, Africa and Pacific islands, but none from the Americas.

Allopeas gracile has been recorded from irrigated agricultural land in Iraq (Naser 2010), a typical habitat for introduced tropical species for which the climate in the Mediterranean and Middle East is warm enough, but usually too dry. It has also been recorded from nurseries in Egypt (Ali and Robinson 2020) and Israel (Vaisman et al. 2020). It is unclear whether specimens of *A. gracile* from an alluvial sediment in Spain (identified as *Subulina octona*; Quiñonero-Salgado and López-Soriano (2020)) originated from an outdoor population or from a greenhouse. It can be expected that *A. gracile* will colonise irrigated outdoor habitats in these and additional Mediterranean countries.

Lissachatina fulica (Bowdich, 1822) (Achatinidae; Fig. 1E)

Origin: East Africa (Bequaert 1950; Mead 1961).

First record for the Western Palaearctic Region: Israel, 2010 (Mienis 2010).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Bequaert (1950).

Remarks: *Lissachatina fulica* is a tropical species that has been spread by humans throughout the tropics and has become a major pest (Mead 1961; Robinson 1999). In Israel, it occurs in gardens that are regularly irrigated during the dry season (Mienis 2010).

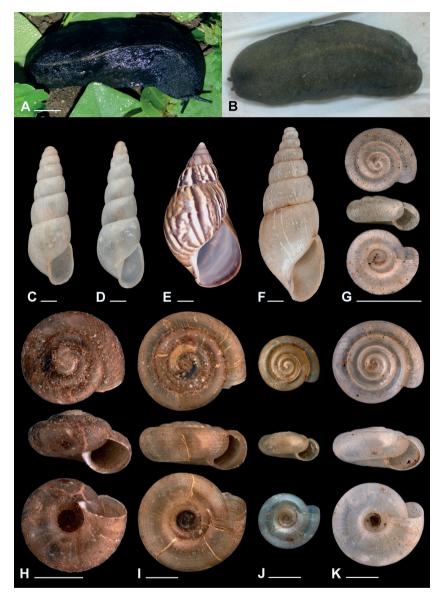


Figure I. Alien land snail species in the Western Palaearctic Region A Laevicaulis alte (Férussac, 1822), Egypt, Abu Rawash (reproduced from Ali and Robinson (2022), courtesy of R. F. Ali) B Laevicaulis stuhlmanni (Simroth, 1895), Egypt, El Zamalek (reproduced from Ali et al. (2022), courtesy of R. F. Ali)
C Allopeas clavulinum (Potiez & Michaud, 1838), Netherlands, Delft, botanical garden (ZMH 50896)
D Allopeas gracile (Hutton, 1834), Canary Islands, Tenerife, Santa Cruz de Tenerife, Parque García Sanabría (ZMH 122731) E Lissachatina fulica (Bowdich, 1822), Colombia, Tolima, Honda (ZMH 76101)
F Paropeas achatinaceum (Pfeiffer, 1846), Indonesia, Java, Pacitan, Poko (ZMH 133068) G Discocharopa aperta (Möllendorff, 1888), Indonesia, Java, Karangpaci, Green Canyon (ZMH 133063) H Paralaoma servilis (Shuttleworth, 1852), Spain, Vilanova de la Muga (ZMH 99005) I Helicodiscus parallelus (Say, 1821), USA, Salem (ZMH 45981) J Lucilla scintilla (Lowe, 1852), Austria, Wildon, debris of Kainach River (ZMH 89156) K Lucilla singleyana (Pilsbry, 1889), Russia, Armavir, debris of Urup River (ZMH 100266). Scale bars: 10 mm (A, E); 1 mm (C–D, F–K).

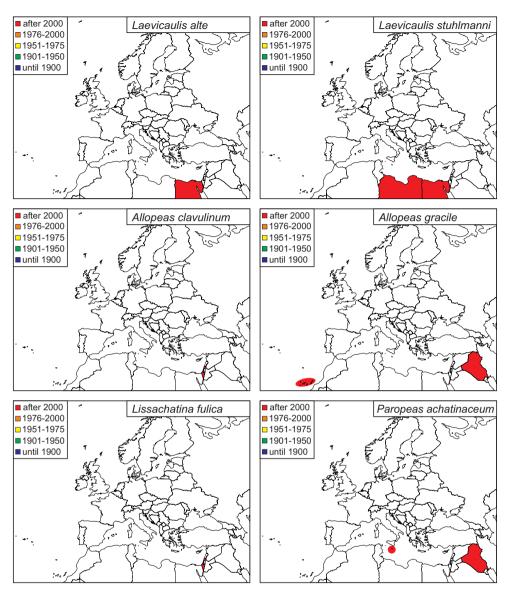


Figure 2. Maps showing the distributions of established alien land snail species in the Western Palaearctic Region and the period of the first records at the country level. Base map courtesy of Vemaps.com (https://vemaps.com/).

Paropeas achatinaceum (Pfeiffer, 1846) (Achatinidae; Fig. 1F)

Origin: Oriental Region.

First record for the Western Palaearctic Region: Iraq, 2017 (Hussein et al. 2018). Western Palaearctic distribution (Suppl. material 1, Fig. 2): Iraq, Malta. References for identification: Horsák et al. (2020).

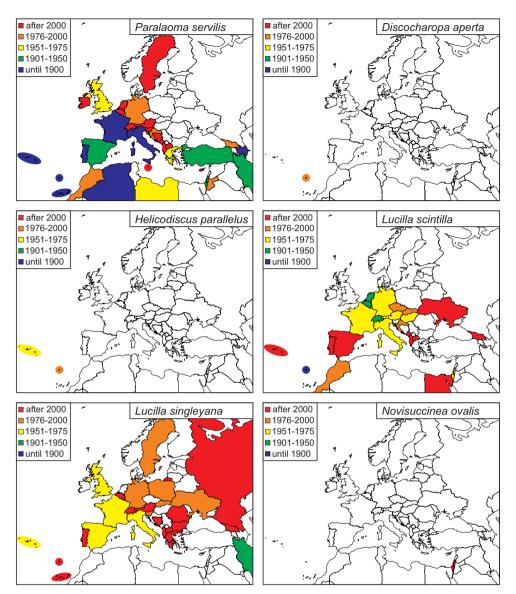


Figure 2. Continued.

Remarks: *Paropeas achatinaceum* is a Southeast Asian species that had probably already spread to Mauritius, Sri Lanka and Japan at the end of the 19th century (Boettger 1891 as *O. clavulinum* non Potiez & Michaud, 1838, according to Germain (1921), as *O. javanicum* (Reeve, 1849)). In the early 20th century, it was introduced to various Pacific Island groups (Brook 2010). In the Americas, it was established in Florida in 2001 (Robinson & Slapcinsky 2005) and in Guadeloupe in 2011 (GBIF.org 2022). All

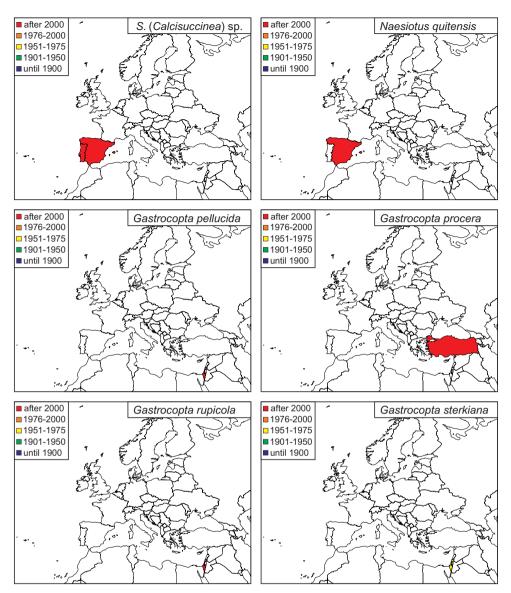


Figure 2. Continued.

of these introductions occurred on islands or coastal regions, which is consistent with Naggs' (1994) statement that *Paropeas achatinaceum* "has notably failed to penetrate inland on any major land mass". In contrast, the first record from the Western Palae-arctic in Baghdad, Iraq (Hussein et al. 2018), is the most inland occurrence. The record of this species at high altitudes in Nepal (Budha et al. 2015) is even more surprising and should be checked.

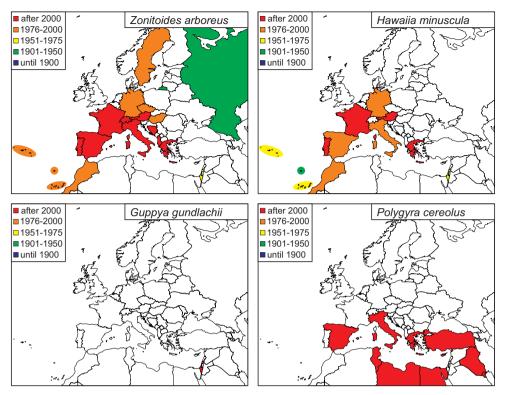


Figure 2. Continued.

Paralaoma servilis (Shuttleworth, 1852) (Punctidae; Fig. 1H)

Origin: Australia, New Zealand.

First record for the Western Palaearctic Region: Madeira, 1831 (Lowe (1831); as *Helix pusilla* Lowe, 1831).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Algeria, Andorra, Austria, Azerbaijan, Azores, Belgium, Bosnia and Herzegovina, Canary Islands, Croatia, Cyprus, France, Georgia, Germany, Greece, Iran, Ireland, Israel, Italy, Jordan, Libya, Madeira, Malta, Montenegro, Morocco, Netherlands, North Macedonia, Palestine, Portugal, Slovenia, Spain, Sweden, Switzerland, Turkey, United Kingdom.

References for identification: Kerney et al. (1983).

Remarks: Although *Paralaoma servilis* and several of its synonyms were originally described from different regions of the Western Palaearctic in the 19th century, it turned out to be an introduced species. It is now known from all continents, except Antarctica. *Paralaoma servilis* originated in New Zealand or/and Australia, where most of the other *Paralaoma* species occur and from where it is known from Pleistocene (Price and Webb 2006) and Holocene deposits (Jones 1984; McFadgen 1997; Brook 1999; Brook and Goulstone 1999).

Discocharopa aperta (Möllendorff, 1888) (Charopidae; Fig. 1G)

Origin: From the Philippines and Indonesia to Australia and the Society Islands (Solem 1982).

First record for the Western Palaearctic Region: Madeira, 1983 (Gittenberger and Ripken 1983).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Madeira. References for identification: Solem (1982).

Remarks: *Discocharopa aperta* has been reported from Madeira only twice (Gittenberger and Ripken 1983; Seddon et al. 1986), but is more common on the island (M. Horsák, pers. comm.).

Helicodiscus parallelus (Say, 1821) (Helicodiscidae; Fig. 1I)

Origin: North America (Pilsbry 1948; Hubricht 1985).

First record for the Western Palaearctic Region: Azores, 1969 (Backhuys 1975). **Western Palaearctic distribution (Suppl. material 1, Fig. 2):** Azores, Madeira. **References for identification:** Pilsbry (1948); Kerney et al. (1983).

Remarks: *Helicodiscus parallelus* has been reported from greenhouses in many European countries (Kerney et al. 1983), but outdoor populations have been observed only in the Azores and in Madeira. Sysoev and Schileyko (2009: fig. 54F) figured a

shell probably of *Helicodiscus parallelus* as '*Helicodiscus singleyanus*'. The shell was collected in 1969 in Ukraine (Balashov and Gural-Sverlova 2012), but it was not stated whether this was from a greenhouse or from outdoors.

Lucilla scintilla (Lowe, 1852) (Helicodiscidae; Fig. 1J)

Origin: North America (Pilsbry 1948; Hubricht 1985; Horsák et al. 2009).

First record for the Western Palaearctic Region: Madeira, 1852 (Lowe 1852).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Austria, Azores, Belgium, Croatia, Czech Republic, Egypt, France, Georgia, Germany, Hungary, Israel, Italy, Luxembourg, Madeira, Montenegro, Morocco, Netherlands, North Macedonia, Portugal, Slovakia, Spain, Switzerland, Ukraine.

References for identification: Horsák et al. (2009).

Remarks: Falkner et al. (2002) suggested that *Lucilla scintilla* is a European native not conspecific with any North American species. In contrast, Horsák et al. (2009) considered both European *Lucilla* species to be non-native introductions of North American species and synonymised *Helicodiscus singleyanus inermis* Baker, 1929 with *Lucilla scintilla* (Lowe, 1852). Hotopp et al. (2010) accepted this synonymy and used the name *Lucilla scintilla* for the North American species. Older identifications of shells as *H. singleyanus* or *H. (singleyanus) inermis* in literature were partly based on other criteria than those established by Horsák et al. (2009) and have to be checked. Here, some older literature records of *H. singleyanus* and

H. (*singleyanus*) *inermis* are preliminarily re-assigned following the lists of countries in the IUCN Red List evaluations of *L. singleyana* by Allen (2017) and *L. scintilla* by Seddon (2018).

Lucilla singleyana (Pilsbry, 1889) (Helicodiscidae; Fig. 1K)

Origin: North America (Pilsbry 1948; Hubricht 1985; Horsák et al. 2009).

First record for the Western Palaearctic Region: Iran, 1912 (GBIF.org 2022).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Austria, Azores, Belgium, Croatia, Czech Republic, France, Georgia, Germany, Hungary, Israel, Italy, Luxembourg, Madeira, Montenegro, Morocco, Netherlands, North Macedonia, Portugal, Slovakia, Spain, Switzerland, Ukraine.

References for identification: Horsák et al. (2009).

Remarks: Concerning the delimitation of the *Lucilla* species and the classification of older literature records, see remarks under *Lucilla scintilla*. The first record of *Lucilla singleyana* in the Western Palaearctic dates back to the Mission to Persia of Jacques de Morgan (1889–1912). The sample from Ardabil in Iran was identified by J. Gerber in 2018 (GBIF.org 2022).

Novisuccinea ovalis (Say, 1817) (Succineidae; Fig. 3A)

Origin: North America (Pilsbry 1948; Hubricht 1985).

First record for the Western Palaearctic Region: Israel, 2001 (https://smnh.tau. ac.il/en/collecting/smnhtau-mo-59720).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel, Palestine. References for identification: Pilsbry (1948).

Remarks: The systematics of succineids is poorly understood and the distinctness and delimitation of *Novisuccinea* is questionable. The introduction of the North American *Novisuccinea ovalis* to Israel and Palestine is not well-documented. It should be checked whether the introduced species reported from Israel and Palestine (Roll et al. 2009; Vaisman and Mienis 2017) as *Novisuccinea ovalis* might, in fact, be the species reported as *Succinea (Calcisuccinea) luteola* Gould, 1848 from the United Arab Emirates (Feulner and Green 2003) and/or the species reported as *Succinea (Calcisuccinea)* sp. from the Iberian Peninsula (Holyoak et al. 2013). *Novisuccinea ovalis* (if that is what it is) is the only alien species that occurs in the western Palearctic south of its native latitudinal range (Fig. 4).

Roll et al. (2009) and Vaisman and Mienis (2016) reported another invasive succineid species from Israel and Palestine as *Novisuccinea horticola* (Reinhardt, 1877) from East Asia. In the Gaza Strip, the species was found in a hothouse. It is not known whether it also occurs outdoors in Israel or Palestine. *Novisuccinea horticola* (Reinhardt, 1877) is a synonym of *Novisuccinea lyrata* (Gould, 1859) (Ueshima 1995).

Succinea (Calcisuccinea) sp. (Succineidae; Fig. 3B)

Origin: North and Central America (Pilsbry 1948; Hubricht 1985).

First record for the Western Palaearctic Region: Spain, 2011 (Holyoak et al. 2013). **Western Palaearctic distribution (Suppl. material 1, Fig. 2):** Portugal, Spain. **References for identification:** Holyoak et al. (2013).

Remarks: It has not yet been possible to clarify the specific identity of the succineid species introduced to the Iberian Peninsula (Holyoak et al. 2013). Feulner and Green (2003) recorded an introduced population of *Succinea (Calcisuccinea) luteola* Gould, 1848 from the United Arab Emirates. *Succinea luteola* is widespread in southern USA and in Mexico. It is not unlikely that the species introduced in the Iberian Peninsula is the same as the one reported from the Arabian Peninsula.

Naesiotus quitensis (Pfeiffer, 1848) (Bulimulidae; Fig. 3C)

Origin: Ecuador (Parodiz 1979; Breure et al. 2022).

First record for the Western Palaearctic Region: Spain, 2018 (Ramos Sánchez et al. 2018).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Spain.

References for identification: Parodiz (1979); Ramos Sánchez et al. (2018).

Remarks: *Naesiotus quitensis* is endemic to Ecuador. It lives in humid temperate climates at 1700–2400 m a.s.l. in the Andes (Breure et al. 2022). In some areas of Ecuador, it is used as food (Gutiérrez Cantuña and Guainilla Maldonado 2018). It is, therefore, possible that it was intentionally introduced into Spain.

Gastrocopta pellucida (Pfeiffer, 1841) (Gastrocoptidae; Fig. 3D)

Origin: Southern North America (Pilsbry 1948; Hubricht 1985; Nekola and Coles 2010).

First record for the Western Palaearctic Region: Israel, 1993 (https://smnh.tau. ac.il/en/collecting/smnhtau-mo-40901/).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: *Gastrocopta pellucida* is a widespread species originally from Central America and southern North America, but it is apparently spreading northwards in North America (compare Hubricht (1985); Nekola and Coles (2010); GBIF.org (2022)).

Gastrocopta procera (Gould, 1840) (Gastrocoptidae; Fig. 3E)

Origin: Eastern North America (Pilsbry 1948; Hubricht 1985; Nekola and Coles 2010).
First record for the Western Palaearctic Region: Turkey, 2015 (Frank 2016).
Western Palaearctic distribution (Suppl. material 1, Fig. 2): Turkey.
References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: Frank's (2016: fig. 4) figure of *G. procera* from an irrigated hotel park on the south coast of Turkey shows the deeply inserted lower palatal fold lying parallel to the aperture as characteristic for *G. procera*. The identification was confirmed by J. Nekola (pers. comm.). For the *Gastrocopta* population from En Gedi in Israel, which was initially identified as *G. procera*, see *Gastrocopta sterkiana*.

Gastrocopta rupicola (Say, 1821) (Gastrocoptidae; Fig. 3F)

Origin: South-eastern North America, Caribbean, northern South America (Pilsbry 1948; Haas 1960; Hubricht 1985; Nekola and Coles 2010; GBIF.org 2022).

First record for the Western Palaearctic Region: Israel, 2004 (https://smnh.tau. ac.il/en/collecting/smnhtau-mo-72414/).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: *Gastrocopta rupicola* is the third American *Gastrocopta* species that has been introduced to Israel (Vaisman and Mienis 2011).

Gastrocopta sterkiana Pilsbry, 1917 (Gastrocoptidae; Fig. 3G)

Origin: Southwest of the USA (Pilsbry 1948; Hubricht 1985; Nekola and Coles 2010).
First record for the Western Palaearctic Region: Israel, 1972 (Mienis 1977).
Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.
References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: The introduced *Gastrocopta* population from En Gedi in Israel was initially identified as *G. procera* (Mienis 1977). Later, the *G. procera* complex was split into *G. procera* sensu stricto, *G. riparia* Pilsbry, 1916 and *G. sterkiana* Pilsbry, 1917 (Hubricht 1978; Nekola and Coles 2010). Based on the criteria given by Hubricht (1978) and Nekola and Coles (2010), the specimens from En Gedi can be identified as *G. sterkiana* because their lower palatal fold inserts moderately deep, lying at a 45° angle to the aperture axis rather than parallel to the aperture and many of them are higher than 2.4 mm. This identification was confirmed by J. Nekola (pers. comm.). The identifications of other *Gastrocopta* population from Israel that were identified as *G. procera* have to be checked.

Zonitoides arboreus (Say, 1817) (Gastrodontidae; Fig. 3H)

Origin: North and Central America (Pilsbry 1946; Hubricht 1985).

First record for the Western Palaearctic Region: Russia, 1907 (Lindholm 1911; as *Hyalina roseni* Lindholm, 1911).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Austria, Azores, Bosnia and Herzegovina, Canary Islands, Czech Republic, France, Germany, Greece, Hungary, Israel, Italy, Madeira, Morocco, Portugal, Russia, Spain, Sweden, Switzerland.

References for identification: Pilsbry (1946); Kerney et al. (1983).

Remarks: This species is common in greenhouses and nurseries (Kerney et al. 1983; Hausdorf 2019) and increasingly spreads from these into the wild. The first

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report of an outdoor population of *Zonitoides arboreus* in the Western Palaearctic was from a park in Moscow (Lindholm 1911). Although the species was observed in the park from 1907 to 1918 (Boettger 1929), there are doubts as to whether this was really a self-sustaining outdoor population. The animals came from greenhouses in the park (Boettger 1929) and it is possible that the outdoor population was only maintained by the continuous supply of live animals from the greenhouses. This hypothesis is supported by the fact that neither this population nor any other population of *Zonitoides arboreus* appears to still exist in Moscow (Tappert 2009). If we neglect the population in Moscow, the first established populations of the species in the Western Palaearctic were found in the Azores. From Egypt, only a record from a nursery is known (Ali and Robinson 2020), but it is likely that *Zonitoides arboreus* also occurs in agricultural land and gardens there.

Hawaiia minuscula (Binney, 1841) (Pristilomatidae; Fig. 3I)

Origin: North and Central America (Pilsbry 1946; Hubricht 1985).

First record for the Western Palaearctic Region: Madeira, 1938 (http://id.luomus.fi/MY.2183079).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Austria, Azores, Canary Islands, France, Germany, Greece, Israel, Italy, Madeira, Morocco, Portugal, Spain.

References for identification: Pilsbry (1946); Kerney et al. (1983).

Guppya gundlachii (Pfeiffer, 1840) (Euconulidae; Fig. 3J)

Origin: Southern North America and northern South America (Pilsbry 1946; Hubricht 1985).

First record for the Western Palaearctic Region: Israel, 2015 (Mienis et al. 2016; as *Euconulus praticola* (Reinhardt, 1883)).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1946).

Remarks: The occurrence of *Guppya gundlachii* in Israel is a new record for the Western Palaearctic Region. Mienis et al. (2016) misidentified specimens from Israel as *Euconulus praticola* (Reinhardt, 1883), a synonym of *Euconulus alderi* (Gray, 1840) (Horsáková et al. 2020). *Guppya gundlachii* differs from *Euconulus alderi* in the, on average, smaller, more depressed shell, with more distinct incised spiral lines at the bottom side. *Guppya gundlachii* is a globally expanding species. It has been introduced to New Guinea and adjacent islands (van Benthem Jutting 1964) and Java (Nurinsiyah and Hausdorf 2019). It is probably also established in mainland Southeast Asia, as Robinson (1999) reported regular interceptions of this species in shipments from Thailand. In South America, *Guppya gundlachii* has recently been reported for the first time from Peru (Wendebourg and Hausdorf 2019) and mainland Ecuador (Ramirez Perez and Hausdorf 2022). It is unclear whether the South American occurrences are also the result of introductions or whether they are part of the native range of the species. Robinson (1999) even considered the occurrences of *Guppya gundlachii* in North America as introduced.

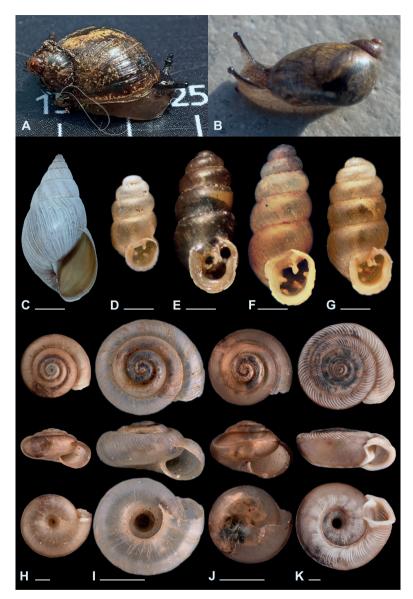


Figure 3. Alien land snail species in the Western Palaearctic Region A Novisuccinea ovalis (Say, 1817), Israel, Haifa (iNaturalist observation 118548596, courtesy of O. Shabbiel Lebber-Shabbat) B Succinea (Calcisuccinea) sp., Portugal, Seixal (iNaturalist observation 92683866, courtesy of N. Veríssimo P.) C Naesiotus quitensis (Pfeiffer, 1848), Spain, Madrid, Casa de Campo Park (reproduced from Ramos Sánchez et al. (2018), courtesy of J. López-Soriano) D Gastrocopta pellucida (Pfeiffer, 1841), Dominican Republic, Guaraguo (ZMH 51838) E Gastrocopta procera (Gould, 1840), Turkey, Evrenseki (reproduced from Frank (2016), courtesy of C. Frank) F Gastrocopta rupicola (Say, 1821), USA, Texas, San Marcos, Spring Lake Hills (iNaturalist observation 17346779, courtesy of B. Hutchins) G Gastrocopta sterkiana Pilsbry, 1917, Israel, En Gedi (ZMH 69886)
H Zonitoides arboreus (Say, 1817), Canary Islands, Tenerife, Bajamar (ZMH 145645) I Hawaiia minuscula (Binney, 1841), Canary Islands, Tenerife, Puerto de la Cruz (ZMH 99003) J Guppya gundlachii (Pfeiffer, 1840), Peru, Huánuco, reserva Panguana (ZMH 143639) K Polygyra cereolus (Megerle von Mühlfeld, 1816), Egypt, Cairo, El Zamalek (ZMH 75229). Scale bars: 5 mm (C); 0.5 mm (D–G); 1 mm (H–K).

Polygyra cereolus (Megerle von Mühlfeld, 1816) (Polygyridae; Fig. 3K)

Origin: Southern North America (Pilsbry 1940; Hubricht 1985).

First record for the Western Palaearctic Region: Spain, 2011 (Navarro Barrachina et al. 2012).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Cyprus, Egypt, Greece, Iraq, Italy, Kuwait, Libya, Spain, Tunisia, Turkey.

References for identification: Pilsbry (1940).

Remarks: *Polygyra cereolus* has been spread from southern North America into other continents only in the past decades: into Hawaii (Cowie 1996), Saudi Arabia (Neubert 1995, 1998), the United Arab Emirates (Feulner and Green 2003), Qatar (Al-Khayat 2010), the Lesser Antilles (Charles 2014) and the Greater Antilles (Charles and Lenoble 2020). It is also spreading northwards in the USA (compare Hubricht (1985) and GBIF.org (2022)). It has been intercepted on cargoes imported into the USA from Spain and Italy, as well as from Puerto Rico and the Dominican Republic long before introduced populations were recorded in these countries (Robinson 1999).

Timing of the introductions

Twenty-two land snail species have been introduced to the Western Palearctic Region and established outdoor populations there. There has been a continuous increase in the number of established alien species since the beginning of the 19th century (Fig. 5). The increase was slow in the 19th century and the first half of the 20th century and became exponential in the 1970s.

Latitudinal ranges of the established alien land snail species in the Western Palearctic and in their native region

The latitudinal mid-points of the Western Palaearctic ranges of established alien land snail species and of their native ranges are not significantly correlated. However, if *Naesiotus quitensis* is omitted, there is a significant correlation (Fig. 4, Table 1). The native range of this species at low latitudes in Ecuador implies that it is a tropical species. However, it lives at high altitudes in the Andes (1700-2400 m a.s.l.; Breure et al. (2022)), where the climate corresponds to the oceanic climate in Western Europe (Beck et al. 2018). The higher limit of the latitudinal ranges of 11 of the established alien species is higher in the Western Palaearctic than in their native region, whereas only a single species occurs in the Western Palaearctic at a latitude that is lower than the lower limit of its natural range. The ranges of ten alien species in the Western Palaearctic are entirely positioned within their native latitudinal limits. As upward shifts of the higher limits of the non-native ranges prevail, the latitudinal mid-points of the Western Palaearctic ranges also tended to be higher on average than those of the native ranges. The highest latitudinal limits of the ranges of the alien snails in the Western Palaearctic and of their native regions are significantly correlated, but their lowest limits and their latitudinal extents are not (Table 1). The latitudinal ranges of the alien species in the Western Palearctic significantly increased with increasing time since the first record of introduction (Pearson, $r^2 = 0.621$, $p < 10^{-4}$, Fig. 4).

Discussion

Number and timing of introductions

The present compilation lists 22 land snail species that were introduced into the Western Palearctic Region from elsewhere and established outdoor populations there. As in many other taxa (Roques et al. 2009; Seebens et al. 2017), the number of established alien land snail species increased exponentially (Fig. 5). The dynamics of the introduction of alien species into the Western Palearctic Region is also demonstrated by the fact that only nine of the 22 established alien species were listed in the last comprehensive list of introduced species in Europe (DAISIE 2009). Ten species were only introduced after the publication of this list (three previously introduced species were not listed).

Origin and spread of alien species

Land snails, like most invertebrates (Roques et al. 2009), are usually introduced unintentionally as contaminants of commodities, often agricultural products or ornamental plants (Cowie and Robinson 2003). Thus, the number of introduced invertebrate species is usually correlated with trade volume (Kobelt and Nentwig 2008; Roques et al. 2009). The largest share of imports into the Western Palaearctic comes from East Asia, followed by North America (Kobelt and Nentwig 2008). This is reflected in the highest number of introduced invertebrate species also coming from East Asia, followed by North America (Kobelt and Nentwig 2008; Roques et al. 2009). In contrast, no land snail species from temperate East Asia has yet become established in the Western Palaearctic until now. The reason for the lack of successful immigrants from East Asia is unclear. Given that the largest share of established alien plants in Europe is from temperate Asia (van Kleunen et al. 2015), there were obviously many opportunities for the introduction of East Asian land snails. Thirteen of the 22 established alien land snail species came from North America or adjacent areas. Two were from the Australian region or neighbouring island groups. Only recently did six species from tropical Sub-Saharan Africa or the Oriental Region establish populations in human-modified habitats in North Africa and the Middle East. One species from high altitudes of the Andes of South America was also only recently recorded.

The establishment of outdoor populations of most of these introduced land snail species began at the western or southern rims of the Western Palearctic (Figs 1, 3). The first populations of five of the introduced species, three from North America (*Helicodiscus parallelus, Lucilla scintilla* and *Hawaiia minuscula*), but also the two from the Australian region (*Paralaoma servilis* and *Discocharopa aperta*), were reported from the Macaronesian Islands. Perhaps some of these introductions date back to the time

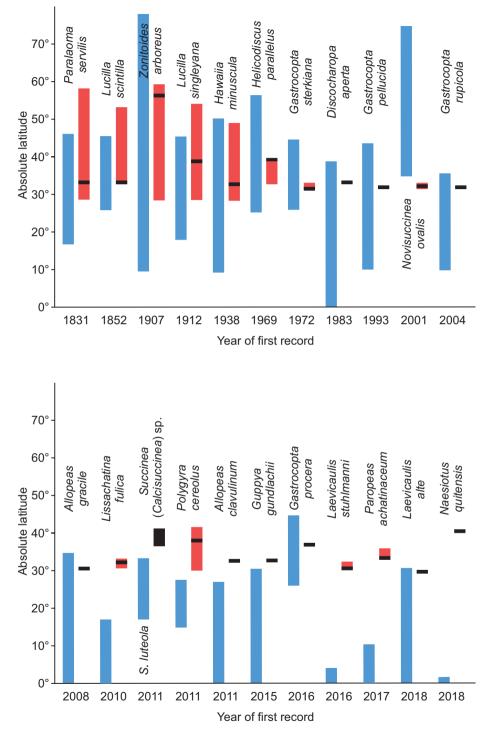


Figure 4. Comparison of the latitudinal distribution of established alien land snail species in their native range (blue) and in the Western Palaearctic Region (red), also showing the latitude at which a species was first recorded in the Western Palaearctic Region (black bar) and the year of the first record.

when the Macaronesian Islands were an important stop-over for sailing ships on their way to Europe. However, this may also be related to the higher susceptibility of island ecosystems to establishment of introduced species than mainland ecosystems (van Kleunen et al. 2015). The pattern of establishment changed in the second half of the 20th century. The first outdoor populations of 12 of the introduced species established during this period were found in North Africa and the Middle East, in Israel, Palestine, Egypt, Libya or Iraq. Israel become a hotspot of introduction. The reason may be the extensive economic trade between Israel and the USA and the transformation of large parts of the landscape of Israel into anthropogenic habitats and irrigated agricultural areas. The importance of Israel as a hotspot of introductions may be slightly exaggerated by the fact that there are malacologists in Israel who are able to record and recognise introduced species, whereas such expertise is lacking in many other countries in the Middle East and North Africa. Another recent pathway for the invasion of North American species into the Western Palearctic appears to be via Arabia. The North American species Succinea (Calcisuccinea) luteola and Polygyra cereolus were first recorded from the Arabian Peninsula (Neubert 1995, 1998; Feulner and Green 2003; Al-Khayat 2010) before Succinea (Calcisuccinea) sp. and Polygyra cereolus were found in the Mediterranean Region. The presumably Oriental Allopeas gracile, which is also widespread in southern North America, may also have been introduced into Iraq via Arabia. The introduction of these species could be due to the increased military and economic involvement of the USA in the region. In fact, Neubert (1995) supposed that Polygyra cereolus was introduced with military equipment from the USA for Operation Desert Storm at the beginning of the 1990s.

The change of the establishment patterns is correlated with the different ecology and origin of the naturalised species. Whereas most of the species introduced in the 19th century and the first half of the 20th century were temperate, mesophilic species, later more thermophilic species from southern North America arrived. These taxa established populations especially in warm, but often irrigated habitats in the Mediterranean. The newest arrivals are tropical species from Sub-Saharan Africa and the Oriental Region that can survive in the Mediterranean and Middle East outside greenhouses only in irrigated, anthropogenic habitats. This trend is probably favoured by climate change.

After their establishment at the periphery of the Western Palaearctic, many of the alien land snail species spread across Europe, usually from south to north and from west to east (Figs 1 and 3; with regard to the apparently exceptional *Zonitoides arboreus*, see remarks under the entry for this species). The continental climate in Eastern Europe is apparently challenging for alien land snail species, although large parts of North America, the main source area of the alien species, are also characterised by a continental climate. The lower levels of imports to Eastern European countries may also have contributed to the observed gradient, but can hardly explain that the gradient remained despite increasing trade between Western and Eastern Europe. A decreasing gradient of alien species towards Eastern Europe was also found in other invertebrate taxa (Roques et al. 2009: fig. 5.3).

Table 1. Correlations between mid-latitudes, highest and lowest latitudinal limits and latitudinal extents of the Western Palaearctic ranges of established alien land snail species and of their native ranges (considering absolute latitudes).

Correlations	r ²	P
Mid-latitudes	0.130	0.108
Mid-latitudes (without N. quitensis)	0.246	0.026
Highest latitudinal limits	0.197	0.044
Lowest latitudinal limits	0.003	0.810
Latitudinal extents	0.164	0.069

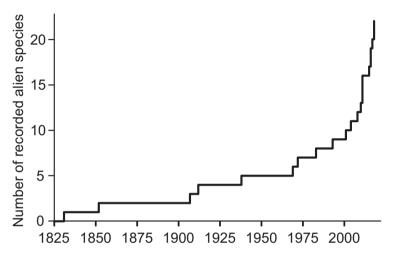


Figure 5. Cumulative number of recorded established alien land snail species in the Western Palaearctic Region.

The latitudinal ranges of the established alien land snail species in the Western Palearctic significantly increased with increasing time since the first record of introduction (Fig. 4). The latitudinal extent of their native ranges, a proxy for the ecological flexibility of the species, did not explain a significant part of the variation of the latitudinal extent of their ranges in the Western Palearctic (Table 1). This may indicate that many of the alien species have not yet colonised all the area that is potentially suitable for them rather than that their ecological requirements are irrelevant for invasion success.

The latitudinal mid-points of the Western Palaearctic ranges of established alien land snail species and of their native ranges are significantly correlated if *Naesiotus quitensis* is omitted (Fig. 4, Table 1) as in many other taxa (Guo et al. 2012). However, the latitudinal mid-points of the ranges in the Western Palaearctic tended to be higher than those of the native ranges on average. Eleven of the 22 alien species expanded into higher latitudes in the Western Palaearctic than in their native region (Fig. 4). Such poleward shifts of ranges in the non-native region were found by Guo et al. (2012) for several taxa on a global scale. Guo et al. (2012) discussed several possible mechanisms that may have contributed to such shifts. The main reason for the poleward shifts of the ranges of alien species in the Western Palaearctic is probably the arrangement of climate zones in the region, especially in comparison with eastern North America, the main source of the alien land snail species. Whereas subtropical and continental climate zones are latitudinally ordered in eastern North America, the arrangement of climate zones in Europe is more complicated (Beck et al. 2018). The oceanic climate of Western Europe allows species originating from the south to expand a long way north. On the other hand, species adapted to humid subtropical climates of south-eastern North America can hardly colonise similar latitudes in the Western Palaearctic where a much drier Mediterranean climate or even a desert climate prevails. Based on the observation that, on average, alien species have become naturalised at significantly lower latitudes on islands than on continents, Sax (2001) hypothesised that low latitude boundaries are usually set by biotic pressures. However, this is not the case in the Western Palaearctic where abiotic conditions, namely the aridity of the Mediterranean and the desert belt at the southern rim of the Western Palaearctic, are the main cause of the low latitude boundaries of the majority of alien as well as native species. Although the temperatures in the Mediterranean and the desert climate zones may be suitable for snails from the subtropical or even tropical climate zones, they can only colonise localities that are characterised by unusual high humidity. For example, Guppya gundlachii from Florida and Central America colonised artificially irrigated anthropogenic habitats in Israel. Similar habitats could also be colonised by tropical species like the *Laevicaulis* species and the giant African snail Lissachatina fulica from Sub-Saharan Africa. Thus, there are three reasons for the average poleward shifts of the ranges of alien land snail species in the Western Palaearctic compared to their native ranges (Fig. 4): (1) the northward expansion of some species in Western Europe facilitated by the oceanic climate, (2) the impediment to the colonisation of southern latitudes occupied in North and Central America due to the aridity in the southern Western Palaearctic and (3) the establishment of tropical species in artificially irrigated anthropogenic habitats in the Mediterranean and the Middle East north of their native ranges.

Potential impacts of established alien species

The land snail species that have been introduced to the Western Palearctic Region from elsewhere are generally restricted to anthropogenic habitats like most other introduced invertebrates (Roques et al. 2009). None of them is carnivorous. None of them is known to cause ecological damage or to be a pest in the field. *Zonitoides arboreus* is reportedly a pest of potted ornamental plants, which it damages especially by feeding on the roots (Godan 1983; Hollingsworth and Armstrong 2003). In the same way, it may cause root rot of sugar cane (Rands 1924). This may become a problem in greenhouses and plant nurseries where *Zonitoides arboreus* may become abundant. However, field populations of this species are rare and there are no reports of damage caused by it in the Western Palaearctic. Most of the alien snail species in the Western

Palaearctic are minute or small and are unlikely to cause serious economic damage. In contrast, the African *Laevicaulis* slugs, which were recently introduced to Egypt and Libya (Ali 2017a, b; Ali and Robinson 2020; Liberto et al. 2021) and the giant African snail *Lissachatina fulica*, may become pests in greenhouses and irrigated agricultural areas in the Mediterranean and the Middle East and should be extirpated or a least controlled. This is especially true for *Laevicaulis alte* and *Lissachatina fulica*, which have been spread globally in the tropics by humans (Robinson 1999). *Laevicaulis alte* and *Lissachatina fulica* were amongst the species with the highest negative total impacts in an assessment of alien land snails and slugs in Indonesia (Nurinsiyah and Hausdorf 2019) and also ranked high in an assessment of quarantine significance, based on the potential to damage natural ecosystems, agriculture or human health or commerce in the USA (Cowie et al. 2009).

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Supplementary material I

Supplementary file

Author: Bernhard Hausdorf

Data type: Occurrences (Excel document).

- Explanation note: Distribution of established alien land snail species in the Western Palaearctic Region. For each country to which a species has been introduced, the year of first record of outdoor populations (if not known, the year of first reference) and the reference are given. The author has no funding to report. The author has declared that no competing interests exist.
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