The Ecology and Rapid Spread of the Terrestrial Slug *Boettgerilla pallens* in Europe with Reference to Its Recent Discovery in North America

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Abstract. The terrestrial slug *Boettgerilla pallens* Simroth, 1912, is reported from two sites on Vancouver Island, British Columbia, the first records for this Palearctic species in America. This paper describes how to recognize the species, and summarizes European studies of its ecology. It is unusually wormlike in appearance, lives mostly underground, and occurs in a very wide range of habitats. This century the species has spread remarkably far and fast across Europe from the Caucasus. This is demonstrated by a table of first occurrences in each country, and by three case studies of spread within Great Britain, Belgium, and north-west Austria. We predict that it will spread rapidly in North America, and may already occur more widely, but there is no evidence that it will become an important pest.

INTRODUCTION

European slug species have been extremely successful colonists in other continents (Chichester & Getz, 1969; Rollo & Wellington, 1975; Barker, 1979, 1989). *Arion subfuscus* (Draparnaud, 1805), for instance, had already been discovered at several localities in eastern North America in the first half of the 19th century, and evidence points to repeated introduction events (Chichester & Getz, 1969). In many North American localities European slugs now predominate over native slugs, in terms of both abundance and number of species. Some are economically important pests. However, some introduced species are usually still limited to synanthropic habitats.

This paper reports the first finding in America of another Palearctic slug species, *Boettgerilla pallens* Simroth, 1912. Within this century this species has spread from the Caucasus right across central and northwest Europe, which suggests that the invasion in North America could rapidly become equally extensive. We hope here to draw workers' attention to the possibility of this species occurring in their own neighborhood in the near future, if not already. Also workers in other continents should realize that it is a potential colonist.

The literature on *B. pallens* that we have consulted is in several languages and spread over many journals. We consider here only the most pertinent aspects of its biology and cite only a selected minority of the publications dealing with the species, since most report little more than its discovery in a new location. We describe how to recognize *B. pallens* and where to look for it, summarize what is known of its ecology, and then discuss in greater detail its rate and pattern of spread.

DISCOVERY IN BRITISH COLUMBIA

We discovered *B. pallens* on 14 July 1998 at two sites at the southern end of Vancouver Island, British Columbia, Canada: from beside a trail below Denison Road, Walbran Park, east side of Gonzales Hill, Oak Bay District Municipality (48°024.7'N, 123°019.0'W); and in Centennial Park, near Graham Creek, Central Saanich District Municipality (48°035.2'N, 123°025.5'W). Specimens have been deposited in the Royal British Columbia Museum, Victoria (catalogue number 998-00224-001) and in the Staatliches Museum für Naturkunde Görlitz, Germany (catalogue numbers p5495 and p5496).

The first locality is in a residential suburb adjacent to the city of Victoria, in scrubland at the back of gardens. The flora is a mixture of native and naturalized species, the latter presumably spread from the gardens. The second locality is 21 km away, in a rural area of suburban acreages and farmland. We found *Boettgerilla pallens* in a small wooded ravine dominated by Western Redcedar
(Thuja plicata), Douglas-fir (Pseudotsuga menziesii), and Bigleaf Maple (Acer macrophyllum). This site borders the developed portion of the park but is at least 100 m from the nearest habitation.

At the first locality we found six individuals, and at the second four individuals, so the species appeared to be well established at these sites. All specimens were roughly half grown, which is compatible with the usual timing of the life cycle in Europe (see below).

This discovery was preceded by a more widespread survey of non-marine Mollusca in British Columbia by RGF and TJB, but this has concentrated on snails (Forsyth, 1999). Subsequently, we specifically searched for slugs in several other synanthropic localities in Greater Victoria, in the city and suburbs of Vancouver, and elsewhere in mainland British Columbia, finding other introduced slugs but not B. pallens. However, as time was limited and the weather mostly rather dry, we cannot be confident that it does not occur more widely.

DESCRIPTION

Boettgerilla Simroth, 1910, is currently placed in its own family, Boettgerillidae Van Goethem, 1972. Three nominal species have been described—B. compressa Simroth, 1910, B. pallens, and B. vermiformis Wiktor, 1959—but the latter two names have been synonymized (Wiktor, 1972, 1973).

Boettgerilla pallens is a small to medium-sized slug, up to 50 mm long when extended. When active it is unusually slender and appears distictively wormlike (Figure 1). When contracted, it is of more normal proportions, and then the keel, which extends right up to the mantle edge, is more prominent. Full-grown animals are an un-speckled lead-grey color that fades to almost white in front of the mantle and on the lower flanks and sole. The sole may show a tinge of yellow, but the mucus is colorless. Juveniles are paler, and very young slugs look albino. Young B. pallens, when contracted, might be confused with a young Deroceras, although their long keel is still distinctive. The pneumostome, which in the adult stands out as slightly paler than the mantle, is only a little more than halfway back along the mantle. Two grooves extend from the top of the pneumostome, one forward and one back, but these can be difficult to see after preservation. Boettgerilla pallens has a thin internal shell, typically with an irregular outline. The genitalia are very distinct from those of other genera, particularly in respect of a spindle-shaped swelling along the vas deferens (e.g., see the figures in Van Goethem, 1972, or Colville et al., 1974; the latter includes a character for separating B. compressa).

ECOLOGY

Boettgerilla pallens occurs in a wide variety of habitats, including gardens, grassland, and both deciduous and coniferous woodland. It is also tolerant of a wide range of soil types, and of soil water content, calcium content, and pH (3.2–7.8; De Wilde et al., 1983). It is predominantly subterranean, mostly found within about 25 cm of the surface, but sometimes at depths of up to 60 cm (Gunn, 1992; Seidl & Seidl, 1997). Wiktor (1973) further stated that it can burrow holes like an earthworm. Fortunately for malacologists, a small proportion of the population can also be found by searching under stones, under rotting wood, and in leaf litter. The species is strongly photophobic, but a study using a rhizotron showed that the slugs underground are most active during the hours of daylight (Gunn, 1992).

In North Wales mating and egg laying occurred below ground during late summer and into autumn (Gunn, 1992). The juveniles started to develop grey coloration from early May, and adults could survive until December. These observations are compatible with casual observations from central Europe (Ant, 1966; Zeissler, 1981; Seidl & Seidl, 1997). However, Zeissler also proposed, on somewhat weak evidence, that in Romania possibly the development is delayed by hot dry sumers, so that slugs would not become adult until the following spring.

Gunn (1992) observed B. pallens feeding most often on earthworm feces, detritus, and soil surfaces. These slugs also ate decaying plant matter, fungal hyphae, carrion, and living roots. This agrees with Dax’s (1967) conclusions that they prefer roots to green plant material (based on feeding preferences in the laboratory and gut dissections of wild-collected specimens). Other supporting observations come from Schmid (1962), Zeissler (1964), Wiktor (1973), and von Proschwitz (1994). Boettgerilla pallens has also been reported to eat slug eggs (Wiktor, 1961; Fehcher & Falkner, 1990).

There is no evidence that this species has ever become a horticultural or agricultural pest, but its subterranean habits might make this difficult to establish, especially as in Europe other slug species known to be pests are normally also present. Individual B. pallens usually take only a few bites from any particular food item before moving on, which makes it less likely that the species would have a significant effect on root crops (Gunn, 1992; Seidl & Seidl, 1997).

HISTORY OF SPREAD

Boettgerilla pallens was first described from specimens collected in 1907 from natural habitats (shady montane forests) in the Caucasus, a mountain range forming the south-eastern border of Europe (Simroth, 1912). As this is also the only area where the sole other member of the family (B. compressa) is known, it is normally assumed that B. pallens has spread from there. Records of its occurrence in natural habitats in this region all lie in Abkhazia and western Georgia, on the south-western flank of the Great Caucasus (Likharev & Wiktor, 1980), but the
areas around have probably been too little studied to be sure of the full extent of its natural range.

In 1959 Wiktor described *B. vermiformis* (later synonymized with *B. pallens*) from Poland. This and his subsequent papers (Wiktor, 1960, 1961) drew attention to the possibility that it might be found elsewhere in Europe. There rapidly followed a rush of discoveries throughout much of Europe. Table 1 gives the dates of first collection in each country: 1949 is the earliest date outside the Caucasus, based on preserved German material identified subsequently (Schmid, 1966). *B. pallens* has also been reported from Turkey (Wiktor, 1994) and from other regions of the former USSR including Armenia, the Ukraine, the St Petersburg and Moscow regions of Russia, and from well east of the Caucasus (in Tadzhikistan, and from Chelyabinsk in Western Siberia) (Likharev & Wiktor, 1980).

The high rate of discovery in new countries in the 1960’s probably reflects the rate of spread of information rather than the speed of dispersal of the species. In order to judge how the species really spreads, we consider three cases where initially the species had not been recorded despite local malacologists being both actively involved in mapping and aware of this species’ existence.

In Great Britain many malacologists contribute to the mapping scheme administered by the Conchological Society of Great Britain and Ireland. The initial discovery of *B. pallens* in Britain in 1972 was well publicized in that society’s journals (e.g., Colville et al., 1974), and interest in mapping was also stimulated in the 1970’s by

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Figure 1

Adult specimens of *Boettgerilla pallens* from Europe. The specimen in the upper photograph (from Upper Lusatia, eastern Germany) is about 40 mm long. The lower photograph is a slightly dorsal view of a specimen freshly preserved in alcohol, where the scale has 1-mm divisions (collected from Leigh Delamere Motorway Services, Wiltshire, England). The keel here shows up most clearly where kinked near the tail, but it continues up to the mantle.
Table 1

Date of first collection of *Boettgerilla pallens* in each country where it has been found (as defined before post-1990 political changes, except for Ireland where the unit is the whole island). The references are not necessarily to the original publications, but do allow these to be traced. We have not found records for Italy, Greece, Bulgaria, Yugoslavia, Albania, Spain, or Portugal.

<table>
<thead>
<tr>
<th>Country</th>
<th>Date of collection</th>
<th>Reference</th>
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<tr>
<td>USSR</td>
<td>1907</td>
<td>Simroth, 1912</td>
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<tr>
<td>West Germany</td>
<td>1949</td>
<td>Schmid, 1966</td>
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<td>1956</td>
<td>Wiktor, 1959</td>
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<td>Schmid, 1963</td>
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</tr>
<tr>
<td>Switzerland</td>
<td>1960</td>
<td>Schmid, 1963</td>
</tr>
<tr>
<td>Belgium</td>
<td>1967</td>
<td>De Wilde et al., 1983</td>
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<tr>
<td>France</td>
<td>1968</td>
<td>von Proschwitz, 1994</td>
</tr>
<tr>
<td>Finland</td>
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The spread of *Boettgerilla pallens* in the British Isles as shown by new vice-county records. These have been published annually in the "Proceedings" section of the Journal of Conchology, and we add here Irish records given in Cawley (1998), and two records from our own recent fieldwork. Kerney’s (1999) map of occurrences in 10-km grid squares implies that the species occurs in at least a further 10 British vice-counties, but these unconfirmed records are not incorporated here. Dates given as, for instance, 1980–81 are counted as 1980. In Figure 2a the diameter of the dot correlates linearly with how long ago *B. pallens* has been known in that vice-county. For clarity, outlines of the vice-counties are shown straightened. The Channel Islands, and Orkney and Shetland are displaced in boxes. Figure 2b shows the increase in the cumulative number of these records for the 70 vice-counties in England and Wales.

After the initial discovery was publicized, it was not the case that many new sites were immediately reported; rather the number of vice-county records increased steadily throughout the late 1970’s and the 1980’s (Figure 2b). The rate of increase has fallen sharply in the 1990’s. This cannot be explained by the reduced number of vice-counties in which it remains to be discovered, but may be an artifact caused by recorders rarely visiting some vice-counties, by a general lowering of recording effort, or by a reduced tendency to report what is now a less “exciting” species (M. P. Kerney, personal communication).

Our second case study is Belgium where *B. pallens* was first discovered in 1967. The evidence is good that it did not occur at least before 1950 (De Wilde et al., 1983). A project systematically mapping terrestrial mollusks on a 10-km grid started in 1970. From 1973 onward the data showed that *B. pallens* was widespread through most of Belgium except for the north. Although the north...
was extensively sampled in the 1970's, only from 1981 onward did *B. pallens* appear there (De Wilde et al., 1983, 1986). In the south, although the localities already occurred over a wide area in the 1970's, De Wilde et al. (1983) stressed that on a more local scale the species became more densely distributed, and spread to a wider range of habitats.

The third case study is an extensive area in northwest Austria, which had been searched for slugs in 1994 and 1995 (Seidl & Seidl, 1997). Nevertheless, *B. pallens* was known from only 12 sites in this area until another search in 1997 which revealed 70 new localities in the same area. Seidl & Seidl concluded that the species was still spreading, especially because some of these new localities had been searched several times earlier.

All three case studies show rapid range expansion over a wide area, which suggests that dispersal was aided by human activities. This is supported by comments from several authors that the species was first found in synanthropic habitats or in more natural habitats adjacent to where garden waste had been dumped (e.g., Wiktor, 1973; De Wilde et al., 1983; von Froschwitz, 1994; Seidl & Seidl, 1997). It is easy to envisage that the subterranean habits of *B. pallens* facilitate its dispersal with garden plants distributed from commercial nurseries. The increasing distances that potted plants and root vegetables are transported probably explains why it is only in the last 50 years that it seems to have spread through Europe.

However, *B. pallens* is also found in natural, or at least near-natural, habitats far away from settlements (e.g., Schmid, 1966; De Wilde et al., 1983; Seidl & Seidl, 1997). This has led some authors to question the assumption that the species is an introduction in central Europe (Ant, 1966; Schmid, 1966). But even in Britain, where it is clearly an introduction, it is now found commonly in undisturbed habitats. So we presume that in central Europe the same process of colonization simply occurred at an earlier date before monitoring began (see also De Wilde et al., 1983; von Froschwitz, 1994).

**DISCUSSION**

What can this information from Europe suggest about the likely spread of *B. pallens* in North America? There are climatic and vegetational differences with Europe, but the species has shown itself very adaptable in these respects. Perhaps more important for a species that first colonizes synanthropic habitats are differences in human geography, such as in the distances between towns, the retailing of horticultural plants, or whether rubbish dumps occur adjacent to natural habitats. However, any such differences have not stopped other European species from becoming common in North America, at least in urban areas (Chichester & Getz, 1969; Rollo & Wellington, 1975). Because the long-distance spread of *B. pallens* in Europe seems to have been much assisted by man, neither the straits separating Vancouver Island from the mainland nor the Rocky Mountains look likely to be significant barriers to its dispersal eastward. What might prove more of a barrier is the border with the USA across which transport of soil and plants is restricted and actively controlled. If *B. pallens* succeeds in crossing this border, it is difficult to predict how much farther south it could spread before being limited by climatic factors. In Europe the species is not known from most of the countries to the south, bordering the Mediterranean, where the climate is generally hotter (Table 1); this might partly be explained by less faunistic work in these countries, but at least in Spain, Italy, and Greece research on terrestrial mollusks is not undeveloped.

It will be interesting to monitor how far and how quickly *B. pallens* spreads on Vancouver Island, to mainland British Columbia, and perhaps elsewhere. To do this it is most important to check now whether the species occurs already. In North America the occurrence of terrestrial mollusks, and particularly of introduced terrestrial slugs, has been far less studied than in Europe. It is not at all improbable that *B. pallens* is already common in other parts of North America as a result of independent introductions from Europe.

In Europe there is no evidence that *B. pallens* has been economically important. This will probably also hold true in North America, but there are fewer native slugs there, and maybe consequently fewer biological enemies of slugs, so its harmlessness cannot be guaranteed.

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**LITERATURE CITED**


DAXL, R. 1967. Ein Beitrag zur Biologie von *Boetigera ver-*


