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Alien non-marine snails and slugs of priority quarantine importance in the United States: A preliminary risk assessment

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Abstract: In 2002, the U.S. Department of Agriculture requested assistance from the American Malacological Society in the development of a list of non-native snails and slugs of top national quarantine significance. From a review of the major pest snail and slug literature, together with our own experience, we developed a preliminary list of gastropod species displaying significant potential to damage natural ecosystems or agriculture, or human health or commerce, and either entirely absent from the United States to our knowledge or restricted to narrow areas of introduction. Comments on the list from the worldwide malacological community were then solicited and led us to modify the original list. We then evaluated the taxa on this list by ranking them according to 12 attributes—seven biological variables and five aspects of human interaction—based on thorough review of the detailed literature. The ranked list that emerged from this risk assessment process included 46 taxa (species or species-groups) in 18 families. The highest ranked taxa were in the Ampullariidae, Hygromiidae, Cochlicellidae, Helicidae, Veronicellidae, Succineidae, Achatinidae, and Planorbidae. We validated the risk assessment model by scoring a suite of non-native snail and slug species already present in the United States. The list is not definitive but rather is offered as a framework for additional research. There remain important gaps in biological knowledge of many of the taxa evaluated, and rigorous reporting of economic impacts is extremely limited. We expect the prioritizing and listing of taxa to be dynamic, not only as these knowledge gaps are filled but also as environmental, agricultural, international trade, and societal factors change.

Key words: Gastropoda, invasive species, life-history, natural ecosystems, pests

Alien species are being moved around the world at unprecedented rates as a result of the globalization of trade and the increased ability of people to travel widely. These alien species have serious impacts on agriculture, the natural environment, commerce, and human health and well-being (Bright 1998, Cox 1999, Mack *et al.* 2000, Staples and Cowie 2001), and these effects may be complex (Didham *et al.* 2007). In the United States, annual costs associated with damage to the environment and to agriculture caused by alien species have been most recently estimated as US$120 billion (Pimentel *et al.* 2005). Combined costs for the United States (Pimentel *et al.* 2000), the United Kingdom, Australia, South Africa, India, and Brazil have been estimated as US$314 billion per year (Pimentel *et al.* 2001). Although the level of uncertainty is high, these estimates indicate that the problem is severe.

While much attention is paid to invasive plants (*e.g.*, Gordon *et al.* 2008), insects (Simberloff 1986), and pathogens (Palm 2001), with some notable exceptions (*e.g.*, zebra mussels (*Dreissena polymorpha* (Pallas, 1771)): Britton and McMahon 2005; apple snails (*Pomacea* spp.): Hayes *et al.* 2008; New Zealand mud snails (*Potamopyrgus antipodarum* (Gray, 1853)): Kerans *et al.* 2005, Hall *et al.* 2006), molluscs receive relatively little attention (Keller *et al.* 2007). Nonetheless, invasive molluscs can have important impacts on agriculture (Godan 1983, Henderson 1989, 1996, Barker 2002a), biodiversity (Coote and Loève 2003, Lydeard *et al.* 2004), and human health (Madsen and Frandsen 1989, Pointier *et al.* 2005, Hollingsworth and Cowie 2006, Boaventura *et al.* 2007, Hollingsworth *et al.* 2007) and can become major public nuisances (Civeyrel and Simberloff 1996).

Quarantine measures to limit the spread of invasive species include pre-introduction screening of species to assess their potential for invasiveness (Ruesink *et al.* 1995). Formal systems of weed risk assessment have been put into regulatory use widely for plants (Gordon *et al.* 2008), driven in part by the continuing demands of the global horticulture trade to move many species to new localities, with the horticultural industry playing probably by far the most important role in the introduction of invasive plants (Dehnen-Schmutz *et al.* 2007). Similar science-based risk assessment protocols based on the guidelines of the International Plant Protection Convention (IPPC) have been developed by Australia, New Zealand, and other countries for other major groups of organisms. There have been many assessments of individual species of concern (*e.g.*, Ruesink *et al.* 1995) and many jurisdictions have lists of prohibited species, but for the most part these have not been developed by applying objective, science-based, standardized protocols. Some countries have nascent protocols but have yet to implement them widely (*e.g.*, Mito and Uesugi 2004, Gederaas *et al.* 2007).

Many studies of various animal and plant groups, reviewed by Kolar and Lodge (2001) and Hayes and Barry (2008), have attempted to develop formal screening protocols by assessing potential risk based on suites of characters thought *a priori* to correlate with invasiveness, *e.g.*, in fish (Kolar and Lodge 2002), birds (Veltman *et al.* 1996, Duncan *et al.* 2001), and reptiles and amphibians (Bomford *et al.* 2008). The goals of such screening systems are primarily to provide an objective means of analyzing the legal, deliberate import of alien species. But they could also be used to allocate special attention to the interception of species transported inadvertently that are potentially invasive. However, increasingly it is being suggested that any species-level characteristics that might identify successful invaders are both taxon and location specific (Sakai *et al.* 2001, Hayes and Barry 2008), and general approaches to risk analysis of potential invasive species remain challenging (Stohlgren and Schnase 2006).

With some notable exceptions, most alien snails and slugs are transported inadvertently (Cowie and Robinson 2003). Quarantine agencies around the world routinely intercept numerous species of snails and slugs. Robinson (1999) listed those that were intercepted by U. S. quarantine officials between 1993 and 1998. The purpose of the present study was, on behalf of the American Malacological Society (AMS) and at the request of the U. S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine (USDA-APHIS-PPQ), to develop a much shorter list of the snail and slug species considered as top priority for prevention of their introduction and establishment in the United States. This list would then be used by USDA-APHIS-PPQ officials as a list of species of quarantine importance to the United States and upon which to focus their attention. A preliminary version of the list (Cowie 2002a) was submitted to the USDA; the present paper is a revised version based on further analysis and more extensive review of the literature.

MATERIALS AND METHODS

Scope

Species to be considered were species not present in the United States or, if present, only distributed highly locally and with the possibility of eradication or at least containment. A number of species found only in Hawaii, although widespread there, were considered containable with respect to invasion of the remainder of the United States and were therefore included. Only species falling under the jurisdiction of USDA-APHIS-PPQ were included, that is, pest species with the potential to cause damage to either agriculture or natural ecosystems. Marine species (the responsibility of the National Marine Fisheries Service) were excluded, as were species only affecting endangered species (the responsibility of the U. S. Fish and Wildlife Service). However, we treated these constraints fairly broadly because they are often inter-related and considered pest problems in four areas: agriculture (including livestock health), environment, human health, and commerce.

Initially, the charge from the USDA was to generate a list of 15 species, selected and prioritized using an explicit protocol. It soon became clear that a simple list of 15 species would not serve the interests of USDA-APHIS-PPQ adequately, for the following reasons. (1) Most snail and slug species are generalist herbivores. They do not in general exhibit the kind of precise host-specificity exhibited, for instance, by many of the insect pests upon which PPQ focuses greater attention. Congeners (and even less closely related species) are therefore likely to have similar feeding habits, and listing just one species would exclude other, related species that may not differ markedly in pest potential. (2) Detailed information regarding species-level differences in feeding preferences among related species is available for few taxa. Therefore, listing one and not others of a number of species in a group (*e.g.*, a genus) might again divert attention away from potential pests. (3) Distinguishing closely related species is difficult even for experts in the group and would be impossible for PPQ field personnel without extensive training, except in certain clear cases. (4) Limiting the list to just 15 species could result in a focus on only a few taxonomic groups that include multiple species considered potential pests while omitting species in other groups that might be equally problematic but for which information was limited. Conversely, selecting 15 well-known species from a range of larger groups might also have meant omitting other species in those groups that were potential pests. For these reasons, we decided to create a prioritized list of larger taxonomic groups (families) with a number of known or potential pests considered within each.

Development of an initial unranked list

Focusing primarily on species intercepted by USDA-APHIS-PPQ (Robinson 1999; D. G. Robinson, unpubl. data), we developed a preliminary list by scanning the literature on mollusc pests worldwide, including primarily Godan (1983), Henderson (1989, 1996), Barker (2002a), augmented by our own knowledge. Some well-known pests were immediately excluded from the list because they were already widely distributed in the United States, *e.g.*, *Deroceras reticulatum*

(Müller, 1774) (Barker 2002a), *Cornu aspersum* (Müller, 1774) (Dundee 1974, Roth and Sadeghian 2003). Other less well-known taxa were evaluated provisionally but omitted from the list, including, notably, the following.

Bradybaena similaris (Rang, 1831) (Bradybaenidae). This species is probably already too widespread in the United States, occurring in much of the southeast (Dundee 1974).

Otala lactea (Müller, 1774) (Helicidae). This species is a minor plant pest but is probably already too widespread in the United States, as it is known from southeastern states, Arizona, and a number of counties in California (Roth and Sadeghian 2003).

Theba Risso, 1826 (Helicidae). *Theba pisana* (Müller, 1774) is a serious pest (Baker 1989, 1991, 2002, Coupland 1996), currently confined to a small number of localities in southern California (Roth and Sadeghian 2003), and is included in the list. However, no other species in the genus appears to have pest potential as none is referred to in the pest snail literature.

Trochulus Chemnitz, 1786 (Hygromiidae). There is no clear evidence that these species have pest potential (D. G. Robinson, unpubl. data) and they are not mentioned widely in the pest snail literature.

Xerotricha Monterosato, 1892 (Hygromiidae). *Xerotricha conspurcata* (Draparnaud, 1801) is established in four or five counties in the San Francisco Bay area, and although USDA-APHIS-PPQ still takes action on it when intercepted, the agency decided some years ago not to address these infestations. We therefore excluded it and other *Xerotricha* spp. from our analyses.

Milax gagates (Draparnaud, 1801) (Milacidae). This species is a major pest in Europe and elsewhere (Barker 2002a) but is already probably too widespread in the United States, occurring in much of eastern North America, the Pacific Northwest, and California (Pilsbry 1948, Roth and Sadeghian 2003).

Gonaxis Taylor, 1877 (Streptaxidae). At least two species of *Gonaxis* have been introduced to Hawaii as putative biocontrol agents for *Achatina fulica* Bowdich, 1822 (Cowie 1997). However, although they have been implicated in the decline of native snail species, there is no evidence that they are a serious problem on the scale of that caused by the better known predator *Euglandina rosea* (Férussac, 1821) (Cowie 2001a). They are not listed by Robinson (1999) as having been intercepted and there is no intention of introducing them deliberately to the mainland United States.

Subulinidae. Too little is known of the pest potential of subulinids; they are rarely mentioned in the pest literature; and a number of species are already widespread in the United States (Robinson and Slapcinsky 2005).

Belocaulus angustipes (Heynemann, 1885) (Veronicellidae). This slug may not be important as a major plant pest but is known as a disease vector (Rueda *et al.* 2002), although it is probably already too widespread in the United States (D. G. Robinson, unpubl. data).

Aegopinella nitidula (Draparnaud, 1805) (Zonitidae). This small European land snail has been reported in British Columbia, with the suggestion that it could affect the native land snail fauna through predation (Forsyth *et al.* 2001). However, there is no evidence of this and it is not listed by Robinson (1999) as having been intercepted.

Pomacea diffusa Blume, 1957 (Ampullariidae). We include all other species of *Pomacea* Perry, 1810, but this species, which is often referred to incorrectly as *Pomacea bridgesii* (Reeve, 1856) (Rawlings *et al.* 2007), has been considered a microherbivore (feeding on algae) (Howells 2002) and therefore not a potential pest, although its food preferences may be wider (Aditya and Raut 2001). It is also widely used as a domestic aquarium snail. Regulatory changes have banned live *Pomacea* spp., with the exception of *P. bridgesii* (*i.e.*, *P. diffusa*), from any United States trade.

Potamopyrgus antipodarum (Gray, 1853) (Hydrobiidae). This freshwater species may outcompete native species and change stream ecology but is probably already too widespread in the United States to be eradicated or contained, having been found in ten western states, as well as in the Great Lakes (Kerans *et al.* 2005, Hall *et al.* 2006, Bersine *et al.* 2008).

Thiaridae. Within this freshwater family, the two most invasive species, *Melanoides tuberculata* (Müller, 1774) and *Tarebia granifera* (Lamarck, 1816), are already too widespread in the United States, the former having been reported from at least 15 states, the latter from seven (Dundee and Paine 1977, Burch and Tottenham 1980, Mitchell *et al.* 2007, NatureServe 2008).

Triculinae (Pomatiopsidae). Some of these freshwater taxa transmit *Schistosoma* and most triculines can transmit *Paragonimus*, helminth parasites infecting people (Davis *et al.* 1999). However, none of them is a threat, as their ecological requirements probably cannot be met in the United States (G. M. Davis, pers. comm.).

Consultation with the malacological community

Having developed a preliminary version of this list we disseminated it widely over the Internet, primarily through the MOLLUSCA listserver, with an explanation of the purpose of the project and a request for comments and suggestions of additional or alternative species to include on it. The MOLLUSCA listserver has approximately 1,000 members throughout the world. The message was also sent to the AMS membership of about 340 malacologists although many of these are also subscribers to MOLLUSCA. Responses were received from over 20 people. The first author also presented a talk at the 2002 annual meeting of the AMS, outlining the progress of the project and again requesting input. A number of helpful comments were made by various conference attendees. All these comments were considered when developing the final prioritized list.

Scoring taxa and prioritizing the list

Following this consultation phase we evaluated each of the species or species-groups in the list according to 12 non-exclusive attributes that are generally thought to correlate with a species' invasiveness and that seemed particularly pertinent to non-marine molluscs (*e.g.*, Veltman *et al*. 1996, Goodwin *et al*. 1999, Lockwood 1999, Duncan *et al*. 2001, Kolar and Lodge 2001, Sakai *et al*. 2001, Daehler *et al*. 2004, Leung *et al*. 2004, Marchetti *et al*. 2004, Theoharides and Dukes 2007, Alonso and Castro-Díez 2008, Bomford *et al*. 2008, Hayes and Barry 2008). Our evaluations were based on information obtained via a thorough search of the literature.

Species and species groups were scored by giving them a '1' if the data suggested that an attribute would enhance their pest potential and a '0' if the data suggested it would not do so. If an attribute was mixed or would enhance pest potential only somewhat, we scored it as '0.5', and if the data were insufficient, we did not assign a score. We were conservative in using 0.5 or not assigning a score if there was any question about giving 1 or 0.

For each species or group we summed the scores to obtain S, a simple measure of the pest potential of each species or group. This measure, however, downplays a species' pest potential when fewer attributes can be scored (*i.e.*, when we had less knowledge). We therefore also divided each value of S by the total number of attributes scored, to obtain P, a proportional measure of pest potential not influenced by the number of scores, and ranging from 0 to 1, least to greatest concern. The species/groups were then ranked from highest to lowest based on the values of S and P.

The attributes scored included both biological attributes of the species and attributes related to their interaction with people. The biological attributes evaluated were as follows.

Range. If a species has a wide natural climatic range, it could invade a larger area within the United States. For example, among the Ampullariidae, one or more species of *Pomacea* occur from temperate Argentina to the Amazon basin and have the potential to spread widely in the United States (scored as 1), contrasting with the two species of *Marisa* (scored as 0), which are more restricted in South America and thus probably less likely to become widespread in the United States (Rawlings *et al*. 2007, Hayes *et al*. 2008). Similarly, among Helicidae, *Otala punctata* is confined to the western Mediterranean, primarily close to the coast, a limited climatic range (scored as 0), whereas *Theba pisana* occurs from the southwest of the British Isles to the eastern Mediterranean, a much wider geographic span, but nonetheless almost exclusively close to the coast (Cowie 1990), and therefore *T. pisana* was scored as 0.5 rather than 1. The extent of the natural ranges of some species has been confounded by human-mediated spread, *e.g. Archachatina marginata* and *Achatina fulica* (Raut and Barker 2002), or by misidentification, *e.g.*, *Achatina achatina* (Bequaert 1950), and are probably smaller than sometimes supposed. Nevertheless, *A. fulica* may have the potential to spread widely within the United States (Smith 2005). Ranges were determined by scanning the literature, web sites, and from our personal knowledge. Detailed data for many species are unavailable, and while those with very wide or very narrow ranges are easy to assess, others are more difficult. Our scoring of range size was thus in some cases somewhat subjective.

Phylogenetic relationships. If a species is closely related to known pests (pest status assessed below), the likelihood of it becoming a pest is greater (Hayes *et al*. 2008, examples in Barker 2002a). We scored taxa as 1 if in the same or a very closely related genus as a known serious pest, 0.5 if in a less closely related genus or in the same or a very closely related genus as a less serious pest, and 0 if more distantly related to any known pest. Species known themselves to be serious pests were scored as 1.

Adult size. Larger species are favored for deliberate introductions (Mead 1979, Smith 2005, Thiengo *et al*. 2007) but for inadvertent introductions smaller species have a greater chance of evading quarantine (Cowie and Robinson 2003). For species we knew to be introduced predominantly deliberately, we scored large size (maximum shell dimension of snails and maximum extended length of slugs roughly >2 cm) as increasing invasive potential (1), whereas for species introduced primarily accidentally we scored small size (roughly <1 cm) as increasing invasive potential. Deliberately introduced taxa <1 cm and accidentally introduced taxa >2 cm were scored as 0. Intermediate-sized snails (1-2 cm), regardless of mode of introduction, were scored as 0.5. Assessments were based on information from basic field guides and the taxonomic literature, augmented by our knowledge of probable modes of introduction (*e.g.*, Cowie 1998a, Cowie and Robinson 2003).

Egg/juvenile size. Production of smaller and therefore more readily dispersed offspring could lead to a species' more rapid and wider dispersal once introduced (cf. Vagvolgyi 1975, Paulay and Meyer 2002). Egg size is reflected by hatchling size and is broadly correlated with adult size (Heller 2001). Heller (2001) tabulated known egg sizes for terrestrial species and we augmented those data with information for additional species from other published sources: Barrientos (1998) (*Ovachlamys fulgens*); Staikou and Lazaridou-Dimitriadou (1991) (*Xeropicta*); Thompson (1957) (*Euglandina*); Turner and McCabe (1990) and Barnes *et al*. (2008) (*Pomacea*); Liang (1974), Liang and van der Schalie (1975), O'Keeffe (1985), Parashar *et al*. (1986), Raut *et al*. (1992), and Saha (1993)

(Planorbidae); Chi and Wagner (1962) (*Oncomelania*). For a few taxa we relied on our personal experience (*Otala punctata*, *Cochlicella* spp., *Succinea tenella*), and for one, *Limicolaria aurora*, on data for a congeneric (Ergonmwan 2007). We could not find information for other species. We scored eggs <3 mm in diameter as small (1), those >7 mm as large (0), and those between these sizes as intermediate (0.5). Heller (2001) gave ranges of sizes for some species and we have combined some species into groups (*e.g.*, *Pomacea*, *Helix*) for our analyses. Thus, for the few taxa in which egg size data straddled these categories, we were conservative and scored them as 0.5.

Reproductive potential. In general, larger snails produce more eggs over their lifetime (Heller 2001) although there is great variation in both longevity and productivity among species. However, if a species produces large numbers of young in a short period of time, *e.g.*, an annual reproductive season, the chances of it being more invasive may be greater (Keller *et al.* 2007). Annual productivity data were obtained from: Hodasi (1979) (*Achatina achatina*); Raut and Barker (2002) (*Achatina fulica*); Plummer (1975) (*Archachatina marginata*); Barrientos (1998) (*Ovachlamys fulgens*); Cowie (1984) and Baker (1991) (*Theba pisana*, *Cernuella virgata* (da Costa, 1778)); Baur and Raboud (1988) (*Arianta arbustorum*); Lazaridou and Chatziioannou (2005) (*Xerolenta obvia*); Baker and Hawke (1991) (*Cochlicella acuta*); Rueda *et al.* (2002) (*Sarasinula plebeia*, *Leidyula moreleti*); Cowie (2002b) (*Pomacea*); Keller *et al.* (2007) (*Marisa cornuarietis*, *Biomphalaria glabrata*); Dillon (2000; annualized from data in his table 4.1) (*Biomphalaria*, *Bulinus*). For *Limicolaria aurora* we used data from a congeneric (Ergonmwan 2007). We scored mean per snail annual production of >1,000 eggs as 1, of 500-1,000 eggs as 0.5, and of <500 eggs as 0. In some cases productivity appears highly variable among regions, straddling categories (*e.g.*, *Achatina fulica*; Raut and Barker 2002); we scored these as 0.5.

Semelparous or iteroparous. Semelparous species put all their reproductive effort into a single reproductive event (or season), a life-history trade-off that results in a shortened life-cycle. Semelparity is probably correlated with high reproductive potential so semelparous species may be more invasive than iteroparous species (Dillon 2000, Heller 2001, Barker 2002b). We treated species with an annual (or shorter) life-cycle as semelparous, scoring them as 1. Other species were scored as semelparous if they breed only during one season before dying, regardless of their overall life-cycle, which may be biennial or longer (Heller 2001). Iteroparous species, including some that reproduce more or less continuously over multiple years (Dillon 2000), were scored as 0. We based our scores on the following: Raut and Barker (2002) (Achatinidae); Txurruka *et al.* (1996) (*Arion ater*); South (1992) (Arionidae, *Tandonia budapestensis*); Barrientos (1998) (*Ovachlamys fulgens*); Baur and Raboud (1988) (*Arianta arbustorum*); Cowie (1984), Baker (1989, 1991, 2002), and Baker *et al.* (1991) (*Theba pisana*, *Cernuella virgata*, *Cochlicella* spp.); Heller (2001), Staikou *et al.* (1988), and Staikou and Lazaridou-Dimitriadou (1991) (*Helix*, *Xeropicta*); Lazaridou and Chatziioannou (2005) (*Xerolenta obvia*); Barker (2002b) (*Tandonia sowerbii*); Cowie (2002b) (Ampullariidae); Dazo *et al.* (1966), Sturrock (1973), and Loreau and Baluku (1987) (*Biomphalaria*, *Bulinus*); Yapi *et al.* (1994) (*Indoplanorbis exustus*); Remais *et al.* (2007) (*Oncomelania*). *Eobania vermiculata* is "marginally iteroparous", with most individuals reproducing only once but a significant number reproducing for at least one additional season (Lazaridou-Dimitriadou and Kattoulas 1991); we scored it as 0.5. In some cases we generalized from information for one or a few species, *e.g.*, *Xeropicta* in our list: information for *Xeropicta vestalis* (Pfeiffer, 1841) (Heller 2001) and *Xeropicta derbentina* (Krynicki, 1836) (Staikou and Lazaridou-Dimitriadou 1991, Kiss *et al.* 2005).

Breeding system. Selfing or parthenogenetic rather than outcrossing species may be better invaders (Foltz *et al.* 1984, Baur and Bengtsson 1987, Dybdahl and Kane 2005). All ampullariids and pomatiopsids were scored as outcrossing (0) as they have separate sexes and no records of parthenogenesis (Dillon 2000, Cowie 2002b). All other species on the list are hermaphrodites. None exhibits parthenogenesis (Jordaens *et al.* 2007), but selfing may occur to a greater or lesser degree in most species, along something of a continuum of strategies. Many normally outcrossing species may self under rare circumstances, especially if kept in isolation (Duncan 1975), though usually producing eggs/young at a very much reduced rate. For example, achatinids, helicids, and hygromiids are generally considered obligate outcrossers (*e.g.*, Duncan 1975, Barker 1999, Raut and Barker 2002) although limited selfing may be possible (*e.g.*, *Arianta arbustorum*; Heller 2001); all were scored as outcrossing. *Arion lusitanicus* is predominantly, if not exclusively, outcrossing (Foltz *et al.* 1982). Some species adopt either strategy although in some cases selfing only in isolation, *e.g.*, *Arion ater* (Foltz *et al.* 1982), *Sarasinula plebeia* (Rueda *et al.* 2002) and *Laevicaulis alte* (Duncan 1975); they were scored as 0.5. Most planorbids are capable of outcrossing and selfing although preference for one mode or the other differs among species (Jarne *et al.* 1993, Dillon 2000, Jordaens *et al.* 2007). Even in a preferential outcrosser, *Biomphalaria glabrata* (Say 1818), there is little loss in productivity when forced to self (Paraense 1959). However, planorbids were scored as 0.5, since although the potential in some species to self without loss of fecundity is equivalent, from the current perspective, to being selfers, it is not known how widely this applies in the taxa considered. The capacity to self is widespread in Succineidae, but whether important in natural situations and in our listed taxa is not known (Barker 2001); they were not assigned a score. *Ovachlamys fulgens* selfs readily with no loss of fecundity and this may be the predominant mode (Barrientos 1998), as it is in *Tandonia budapestensis* and *Tandonia sowerbii* (Foltz *et al.* 1984); these were scored as 1.

The human-interaction attributes evaluated were as follows.

Introduction pressure. Frequent interception implies higher introduction pressure and hence greater likelihood of establishment (Cowie and Robinson 2003). Species listed by Robinson (1999: table 3) were the species most commonly intercepted by USDA-APHIS-PPQ during 1993-1998; those on our list we scored as 1. Robinson (1999) also mentioned *Helix pomatia*, *Cantareus apertus*, *Achatina* spp., and *Archachatina marginata* as being frequently intercepted; they also were scored as 1. Others scored as 1 include *Xeropicta* spp., based on Kiss *et al.* (2005, reporting on *Xeropicta derbentina*), *Succinea tenella*, based on Cowie *et al.* (2008), *Pomacea* spp. and *Marisa* spp. because of their worldwide popularity in the aquarium trade (Rawlings *et al.* 2007, Hayes *et al.* 2008), and a number of taxa based on data (D. G. Robinson, unpubl. data) accumulated since 1998 (Robinson 1999). We scored other species as 0.5 if they were listed by Godan (1983) or Robinson (1999) as having been intercepted entering the United States or Canada. Others were scored as 0, and no score was assigned if we were unsure of their introduction pressure.

Invasion history. Invasiveness elsewhere in the world suggests a greater likelihood of becoming invasive in the United States. Species known to be invasive (as opposed to simply recorded as present, *e.g.*, *Macrochlamys indica*: Robinson 1999; Barker and Efford 2004) elsewhere in the world (including Hawaii, as being distinct from the continental United States) were scored as 1 based on the literature, including the following: Mead (1979), Raut and Barker (2002), Smith (2005), and Thiengo *et al.* (2007) (*Achatina fulica*); Grimm (2001) and Shoaib and Cagáň (2004) (*Arion lusitanicus*, *Xerolenta obvia*); Hollingsworth *et al.* (2007) (*Parmarion martensi*); Robinson and Fields (2004) (*Zachrysia provisoria*); Robinson (1999) and Cowie *et al.* (2008) (*Ovachlamys fulgens*); Baker (1989, 2002, 2008) (*Theba pisana*, *Cernuella virgata*, *Cochlicella* spp.); Kiss *et al.* (2005) (*Xeropicta*); Barker (1999, 2002a) (*Tandonia budapestensis*, *T. sowerbii*); Cowie *et al.* (2008) (*Succinea tenella*); Cowie (1998b) and Cowie *et al.* (2008) (*Laevicaulis alte*, *Sarasinula plebeia*, *Veronicella cubensis*); Cowie (2002b), Rawlings *et al.* (2007), and Hayes *et al.* (2008) (*Pomacea* spp.); Coelho da Silva *et al.* (1997), Pointier *et al.* (2005), Majoros *et al.* (2008) (*Indoplanorbis exustus*, *Biomphalaria* spp., with *Bulinus* spp. explicitly not considered invasive). *Pila* was scored as 0.5 on the basis of its localized but serious invasive status on one of the Hawaiian Islands (Tran *et al.* 2008), as was *Limicolaria aurora* because of its invasive status in Martinique (Raut and Barker 2002). *Cantareus apertus*, a Mediterranean species, is invasive in southern Germany (Godan 1983); *Eobania vermiculata*, another Mediterranean species, is locally established in California (Roth and Sadeghian 2003) and Japan (Ueshima *et al.* 2004), and may be invasive; *Tandonia rustica*, a central European species is arguably invasive in Western Europe, where it is widespread (*e.g.*, Philp 1987); all were scored as 0.5. Species that appeared not to have become invasive anywhere or that were explicitly stated to be only minimally invasive, were scored as 0. Species for which we were unsure were not scored.

Major pest elsewhere. If a species is a major pest elsewhere of a crop grown in the United States, or causes other major problems elsewhere (*e.g.*, environmental damage, human disease), there is a greater likelihood that it will cause serious problems in the United States. Species scored as having a history of invasion (above) are often considered invasive on the basis of being major pests where introduced. The two attributes are closely linked. Some species, however, lack an extensive history of invasion but are pests (perhaps relatively minor pests) within their native ranges (*e.g.*, *Arion ater*, *Mariaella dussumieri*). Many, if not most, snails and slugs can act as intermediate hosts of human and livestock parasites (Godan 1983, Grewal *et al.* 2003). Assessment of whether a species causes sufficient problems to be categorized as a major pest is somewhat subjective. We have been conservative in scoring as such only those taxa that are explicitly referred to in the literature as causing substantial problems. Many species have been reported as pests although many of them may cause little loss. Numerous crops have been listed as susceptible to damage by certain species but with no indication of the severity of the problem (*e.g.*, Raut and Barker 2002: table 3.1). And some species have been reported as pests but only on the basis of occasionally being found in association with a particular crop, as we suspect is the case for many of the instances listed by Godan (1983). Our assessments were based primarily on the following: Raut and Barker (2002) (Achatinidae); Frank (1996) and Grimm (2001) (*Arion lusitanicus*); Godan (1983), South (1992), and Barker (2002b) (Arionidae, Milacidae); Kumar and Ahmed (2000) (*Macrochlamys indica*); Godan (1983) (*Mariaella dussumieri*, *Parmarion martensi*); Hollingsworth *et al.* (2007) (*Parmarion martensi*); Robinson and Fields (2004) (*Zachrysia* spp.); Sanderson and Sirgel (2002) (*Theba pisana*); Godan (1983) (*Helix*, *Arianta* [as '*Helicigona*'] *arbustorum*, *Cantareus apertus*, *Eobania vermiculata*, *Otala punctata*, *Xerolenta obvia*); Baker (1989, 2002, 2008) and Coupland (1996) (*Theba pisana*, *Cernuella virgata*, *Cochlicella* spp.); Kiss *et al.* (2005) (*Xeropicta*); Cowie *et al.* (2008) (*Succinea tenella*); de Jager and Daneel (2002) (*Elisolimax flavescens*); Godan (1983), Raut (1996), Hata *et al.* (1997), Rueda *et al.* (2002), Fields and Robinson (2004), USDA-APHIS-PPQ (2006), Hollingsworth *et al.* (2007), Naranjo-García *et al.* (2007), and Cowie *et al.* (2008) (Veronicellidae); Stange (2006) (*Zachrysia provisoria*, *Ovachlamys fulgens*, *Veronicella sloanii*); Cowie (2002b), Joshi and Sebastian (2006), and

Rawlings *et al*. (2007) (Ampullariidae); Stevens (2002) and Pointier *et al*. (2005) (Planorbidae); Davis *et al*. (1999) (*Oncomelania*).

A "multi-pest". The severity of the problems caused has been scored above, according to whether a species is a major pest. Here we score species as 1 if they cause problems in more than one of agriculture (including livestock health), environment, human health, and commerce, regardless of degree. Thus, for example, *Achatina fulica* is not only a serious plant pest but also an important vector of parasitic diseases, as well as a major public nuisance (Mead 1979, Civeyrel and Simberloff 1996, Raut and Barker 2002, Smith 2005, Thiengo *et al*. 2007); *Veronicella cubensis* is an important parasitic disease vector (Hollingsworth *et al*. 2007) as well as an agricultural and garden pest; *Pomacea* spp. are major crop pests (Cowie 2002b, Joshi and Sebastian 2006) and important parasite vectors (Hollingsworth and Cowie 2006). Other species may cause serious problems in one area but only minor problems in another. For instance, *Parmarion martensi* is a plant pest in Malaysia (Godan 1983) and a possibly serious human disease vector in Hawaii (Hollingsworth *et al*. 2007). Other taxa cause problems in more than one area but they are not severe in either. For example, *Arion ater* is a minor crop pest and also causes environmental damage by feeding on young tree seedlings (South 1992); *Pila* spp. are local or minor crop pests (Cowie 2002b, Levin *et al*. 2006) and recognized parasite vectors (Hollingsworth and Cowie 2006), as are *Indoplanorbis exustus* (Stevens 2002), *Thelidomus aspera* (Lindo *et al*. 2002), and *Diplosolenodes occidentalis* (Rueda *et al*. 2002); *Laevicaulis alte* is a disease vector, although not as important as *Veronicella cubensis* or *Parmarion martensi* (Hollingsworth *et al*. (2007), and a relatively minor plant pest (Raut 1996). All were scored as 1.

Economic potential. We evaluated whether the problems a species could cause would be likely to result in major economic loss in the United States, including costs of control or eradication. This attribute overlaps with the attribute of being a major pest elsewhere, but is explicitly focused on economic cost. Our evaluation was based on the likelihood of the taxon becoming widespread in the United States and on either quantified assessments of costs in other regions, *e.g*., Baker (1989) (*Cernuella virgata*, *Cochlicella* spp., *Theba pisana*), Andrews (1989) (*Sarasinula plebeia*), Cheng (1989), Naylor (1996), and Levin *et al*. (2006) (*Pomacea*), or unquantified statements of the pest's economic importance, *e.g*., Mead (1979) and Raut and Barker (2002) (*Achatina fulica*), Frank (1996) and Grimm (2001) (*Arion lusitanicus*), South (1992) (*Tandonia budapestensis*), de Jager and Daneel (2002) (*Elisolimax flavescens*). If we found no report in the literature explicitly indicating major economic costs or only highly localized costs, or found explicit statements that a species/group was not a major economic problem we scored it as 0, *e.g*., *Archachatina marginata* and *Limicolaria aurora* (Raut and Barker 2002). Others, for which the economic literature was limited or equivocal, or for which we considered the potential economic costs unlikely to be widespread were scored as 0.5, *e.g*., *Achatina achatina* (Raut and Barker 2002), *Zachrysia provisoria* (Robinson and Fields 2004), *Ovachlamys fulgens* (Stange 2006, Cowie *et al*. 2008), *Tandonia* spp. (South 1992), *Veronicella cubensis* (USDA-APHIS-PPQ 2006), *Veronicella sloanii* (Stange 2006), *Pila* spp. (Cowie 2002b, Levin *et al*. 2006).

Validating the model

We assessed the appropriateness of the model by scoring the following representative suite of species that have already been introduced to the United States and determining whether it would accurately predict their invasion status. We excluded information from the United States when scoring the species' attributes, to avoid circularity. We selected a non-random sample of taxa that (1) have been subject to relatively substantial amounts of research in the United States, so that there is an appropriate level of knowledge of their distributions and impacts, (2) are already widespread in the United States, and (3) represent a range of impacts. Scores of attributes were obtained as follows.

Deroceras reticulatum (Müller, 1774) (terrestrial slug, Agriolimacidae): native range (Kerney and Cameron 1979, Barker 1999), adult size (Kerney and Cameron 1979), egg size, reproductive potential, and semelparity/iteroparity (Heller 2001), breeding system (Foltz *et al*. 1984), introduction pressure (Robinson 1999), invasion history (Barker 1999), pest status, and economic damage (Barker 2002a).

Cepaea nemoralis (Linnaeus, 1758) (terrestrial snail, Helicidae): native range, adult size, and invasion history (Kerney and Cameron 1979), phylogenetic relationships (scored as 0.5 since *Cepaea* is somewhat closely related to *Cornu*), egg size (Heller 2001), reproductive potential and semelparity/iteroparity (Cowie 1984), breeding system (helicids in general are outcrossers: Duncan 1975), introduction pressure (Robinson 1999), pest status, and economic damage (Godan 1983, Henderson 1989, 1996, Barker 2002a).

Cornu aspersum (Müller, 1774) (terrestrial snail, Helicidae): native range and adult size (scored as 0.5 because it is probably introduced both deliberately and accidentally: Barker 1999) (Kerney and Cameron 1979), egg size (Heller 2001), reproductive potential (Desbuquois *et al*. 2000), semelparity/iteroparity (R. H. Cowie, pers. obs.), breeding system (Selander and Hudson 1976), introduction pressure (Robinson 1999), invasion history (Barker 1999), pest status, and economic damage (Godan 1983, Sanderson and Sirgel 2002).

Potamopyrgus antipodarum (Gray, 1853) (freshwater snail, Hydrobiidae): native range, adult size, reproductive potential, breeding system, invasion history (Alonso and Castro-Díez 2008, Radea *et al*. 2008), juvenile size (Radea *et al*.

2008), semelparity/iteroparity (Winterbourn 1970), invasion pressure (Robinson 1999, Alonso and Castro-Díez 2008), and pest status (Alonso and Castro-Díez 2008, Holomuzi and Biggs 1999).

Milax gagates (Draparnaud, 1801) (terrestrial slug, Milacidae): native range and adult size (Kerney and Cameron 1979), egg size (Heller 2001), semelparity/iteroparity (South 1992), breeding system (Foltz *et al.* 1984), introduction pressure (Robinson 1999), invasion history (Barker 1999), pest status, and economic damage (Godan 1983, Henderson 1989, 1996, South 1992, Barker 2002a).

Rumina decollata (Linnaeus, 1758) (terrestrial snail, Subulinidae): native range (Batts 1957), phylogenetic relationships (scored as 0 as it is not known as a pest nor closely related to a known pest), adult size (scored as 0.5 because it is probably introduced both deliberately and accidentally: Cowie 2001a), invasion history (De Francesco and Lagiglia 2007), egg size (Heller 2001), reproductive potential (extrapolated from Batts 1957, Selander and Hudson 1976, Fisher and Orth 1985), semelparity/iteroparity (Dundee 1986), breeding system (Batts 1957, Selander and Hudson 1976, Fisher and Orth 1985), pest status, status as a "multi-pest", and economic damage (Cowie 2001a).

Melanoides tuberculata (Müller, 1774) (freshwater snail, Thiaridae): native range (not assigned a score because it is now so widespread that its true region of origin and its extent is not known), phylogenetic relationships (scored as 1 as it is itself a minor pest), adult size (Dudgeon 1986, Pointier *et al.* 1994) (scored as 0.5 because it is probably introduced both deliberately and accidentally: Cowie and Robinson 2003), juvenile size (Dudgeon 1986, Pointier *et al.* 1992), reproductive potential (Berry and Kadri 1974), semelparity/iteroparity (Berry and Kadri 1974, Dudgeon 1986, Pointier *et al.* 1992), breeding system (Berry and Kadri 1974, Dudgeon 1986, Ben-Ami and Heller 2007), introduction pressure (Robinson 1999), invasion history (Berry and Kadri 1974, Dudgeon 1986, Pointier *et al.* 1994, Pointier 1999, Cowie 2001b), pest potential, status as a 'multi-pest', and economic damage (Berry and Kadri 1974, Dudgeon 1986, Pointier 1999, Ben-Ami and Heller 2001).

RESULTS AND DISCUSSION

The prioritized list

We created a ranked list of 46 species or groups of species representing 18 families (Table 1). Ranks based on simple (S) and proportional (P) values for each taxon were generally similar. However, some species exhibited relatively large disparities between the two scores although none reflected grossly different placement of these species in the overall rankings, for instance from the top to the bottom third. Nevertheless, we argue that the rank based on P values probably captures the true pest potential better, as it is less biased by the number of attributes it was possible to score for a particular species. The S rank will inevitably increase as more attributes are scored (unless they are all scored as 0), which is not the case for the P rank. The data for the individual attributes on which these scores and ranks are based are provided (Appendix 1). The evaluated species/groups belong to 18 families (Table 2). The top-ranked 12 species or groups fell in eight families, and these eight families included 28 of the 46 taxa evaluated (Table 2).

The top-ranked potential pest groups were the Ampullariidae and Hygromiidae (Table 2). The former ranked highly because of *Pomacea* spp. These freshwater snails have become major pests of rice and other crops in southeast Asia and Hawaii (Joshi and Sebastian 2006). Four species of *Pomacea* have been introduced to the continental United States, where they threaten rice crops and natural ecosystems (Rawlings *et al.* 2007). Cowie and Thiengo (2003) recognized 117 nomenclaturally valid species, many of which may have a similar pest potential to those already introduced. Hygromiids ranked highly because of *Cernuella* spp. and *Xeropicta* spp. *Cernuella virgata* has become a major cereal and pasture pest in Australia (Baker 2002). These and many other hygromiids are especially prone to being introduced in association with domestic tiles imported to the United States from southern Europe (Robinson 1999). Some of them also occur in temperate localities in their native Europe (Kerney and Cameron 1979) and collectively they thus have the potential to invade large parts of the United States.

Helicidae and the closely related Cochlicellidae ranked immediately below the ampullariids and hygromiids (Table 2). Helicids ranked highly essentially because of the value for *Theba pisana* (Table 1, Appendix 1). The value for cochlicellids (Appendix 1) was based on information for *Cochlicella acuta* (Müller, 1774) and *C. barbara* (Linnaeus, 1758). Both *T. pisana* and these cochlicellids have become pests in various parts of the world where they have been introduced, notably in Australia where they are major cereal and pasture pests (Baker 2002). *Theba pisana* is also a pest of grape vines in South Africa (Sanderson and Sirgel 2002) and was formerly an important citrus pest in California but was thought to have been eradicated (Armitage 1949). It has now reappeared but is not widespread (Roth and Sagedhian 2003).

Veronicellid slugs ranked next highest (Table 2). Veronicellids are large slugs. *Sarasinula plebeia* and *Veronicella cubensis* especially can become extremely abundant and are important pests in numerous crops, horticultural facilities, and gardens, and can become a public nuisance in urban/suburban areas (Rueda *et al.* 2002, Naranjo-García *et al.* 2007, R. H. Cowie, pers. obs.). *Laevicaulis alte* is less well recognized

Table 1. List of mollusc species and species-groups of potential major pest significance to the United States, ranked according to their pest potential from greatest (1) to least (46). S and P denote Simple and Proportional values and the ranks based on them (see methods).

Species/species-group	Family[a]	S score	P score	S rank	P rank
Cernuella Schlüter, 1838	Hygromiidae	9.5	0.79	1	1
Pomacea Perry, 1810[b]	Ampullariidae	9.5	0.79	1	1
Cochlicella Férussac, 1821	Cochlicellidae	9.0	0.75	3	3
Theba pisana (Müller, 1774)	Helicidae	9.0	0.75	3	3
Sarasinula plebeia (Fischer, 1868)	Veronicellidae	6.5	0.72	9	5
Xeropicta Monterosato, 1892	Hygromiidae	6.5	0.72	9	5
Laevicaulis alte (Férussac, 1822)	Veronicellidae	5.5	0.69	12	7
Succinea tenella Morelet, 1865[c]	Succineidae	5.5	0.69	12	7
Veronicella cubensis (Pfeiffer, 1840)	Veronicellidae	5.5	0.69	12	7
Achatina fulica Bowdich, 1822	Achatinidae	7.5	0.68	5	10
Indoplanorbis exustus (Deshayes, 1834)	Planorbidae	7.5	0.68	5	10
Biomphalaria Preston, 1910[d]	Planorbidae	7.0	0.64	7	12
Bulinus Müller, 1781	Planorbidae	6.5	0.59	9	13
Ovachlamys fulgens (Gude, 1900)	Chronidae	7.0	0.58	7	14
Zachrysia provisoria (Pfeiffer, 1858)	Pleurodontidae	4.5	0.56	22	15
Tandonia budapestensis (Hazay, 1881)	Milacidae	5.5	0.55	12	16
Xerolenta obvia (Menke, 1828)	Hygromiidae	5.5	0.55	12	16
Arion lusitanicus Auct., *non* Mabille, 1868[e]	Arionidae	5.5	0.50	12	18
Elisolimax flavescens (Keferstein, 1866)	Urocyclidae	4.0	0.50	24	18
Marisa Gray, 1824	Ampullariidae	5.0	0.50	18	18
Parmarion martensi Simroth, 1893	Ariophantidae	4.0	0.50	24	18
Pila Röding, 1798	Ampullariidae	5.0	0.50	18	18
Tandonia sowerbii (Férussac, 1823)	Milacidae	5.0	0.50	18	18
Cantareus apertus (Born, 1778)	Helicidae	4.5	0.45	22	24
Eobania vermiculata (Müller, 1774)	Helicidae	5.0	0.45	18	24
Veronicella sloanei (Cuvier, 1817)	Veronicellidae	3.0	0.43	30	26
Diplosolenodes occidentalis (Guilding, 1825)	Veronicellidae	2.5	0.42	35	27
Macrochlamys indica Godwin-Austen, 1888	Ariophantidae	2.5	0.42	35	27
Succinea s.g. *Calcisuccinea* Pilsbry, 1948[f]	Succineidae	2.5	0.42	35	27
Arion ater (Linnaeus, 1758)	Arionidae	4.0	0.40	24	30
Oncomelania Gredler, 1881	Pomatiopsidae	4.0	0.40	24	30
Enidae Woodward, 1903	Enidae	3.5	0.39	29	32
Achatina achatina (Linnaeus, 1758)	Achatinidae	4.0	0.33	24	33
Thelidomus aspera (Férussac, 1821)	Pleurodontidae	2.5	0.31	35	34
Zachrysia auricoma (Férussac, 1821)	Pleurodontidae	2.5	0.31	35	34
Euglandina Crosse and Fischer, 1870[g]	Spiraxidae	2.5	0.28	35	36
Tandonia rustica (Millet, 1843)	Milacidae	2.5	0.28	35	36
Helix Linnaeus, 1758	Helicidae	3.0	0.27	30	38
Limicolaria aurora (Jay, 1839)	Achatinidae	3.0	0.27	30	38
Otala punctata (Müller, 1774)	Helicidae	3.0	0.27	30	38
Archachatina marginata (Swainson, 1821)	Achatinidae	3.0	0.25	30	41
Mariaella dussumieri Gray, 1855	Ariophantidae	2.0	0.25	43	41
Arianta arbustorum (Linnaeus, 1758)	Helicidae	2.5	0.21	35	43
Acusta touranensis (Souleyet, 1842)	Bradybaenidae	1.5	0.19	44	44

(continued)

Table 1. (continued)

Species/species-group	Family[a]	S score	P score	S rank	P rank
Leidyula moreleti (Crosse and Fischer, 1872)	Veronicellidae	1.5	0.19	44	44
Zachrysia trinitaria (Pfeiffer, 1858)	Pleurodontidae	1.0	0.13	46	46

[a] All assignments to family from Robinson (1999), except for Wilke *et al.* (2001) for Pomatiopsidae and Vaught (1989) for Ariophantidae, while accepting that some are in flux (*e.g.*, Wade *et al*. 2007).

[b] All species of *Pomacea* except *P. diffusa* Blume, 1957, which is often referred to, incorrectly (Rawlings *et al*. 2007, Hayes *et al*. 2008), as *P. bridgesii* (Reeve, 1856), and the native *P. paludosa* (Say, 1829).

[c] May also include the similar *Succinea horticola* Reinhardt, 1877.

[d] All species of *Biomphalaria* except the native *B. obstructa* (Morelet, 1849).

[e] *Arion lusitanicus* Auct., *non* Mabille is now referred to as *Arion vulgaris* Moquin-Tandon, 1855 by many workers. *Arion lusitanicus* Mabille, 1868 is increasingly acknowledged as a species of *Mesarion* Hesse, 1926, restricted to Spain and Portugal. The issue is not satisfactorily resolved.

[f] Only species of *Succinea* (*Calcisuccinea*) not native to the United States.

[g] Only species of *Euglandina* not native to the United States.

as a major pest, but some of its other attributes resulted in a high ranking (Table 1, Appendix 1). This may be an instance in which differential knowledge of the attributes scored among these veronicellids resulted in a higher ranking of a species (*L. alte*) than its potential may warrant, relative to other species (*S. plebeia* and *V. cubensis*), and reflects the need for caution when interpreting the results of analyses of this kind when based on limited knowledge.

The succineids, achatinids, and planorbids included the remaining taxa in the top ranked 12 (Table 1). In general, succineids have not been considered significant pests until recently as a number of species, notably *Succinea tenella*, are increasingly transported around the world in the horticultural trade (Cowie *et al*. 2008). What their impacts will be is not entirely clear. *Achatina fulica* has often been thought of as one of the world's worst land snail pests (Mead 1979, Raut and Barker 2002) and was the driver of the high ranking of the achatinids (Table 2). Like most snails and slugs, it can act as a vector of human and animal diseases and, with its large size and potential for explosive population growth following introduction, can become a major public nuisance (Poucher 1975, Civeyrel and Simberloff 1996). Other achatinids ranked much lower. However, complacency about them would be misplaced, as little is known about the biology of most of them and many are difficult for untrained specialists to distinguish. Quarantine officials should be vigilant of any achatinids. The planorbids' biological attributes make them potentially highly invasive (Appendix 1). The planorbids role as potential pests is primarily in the arena of human disease, as they are major parasite vectors. However, in this regard their potential is more difficult to evaluate than the more straightforward agricultural potential of most of the other taxa evaluated and it may be that sanitary conditions and people's behavior may minimize the chance of the parasites cycling in the United States (D. S. Woodruff, pers. comm.). The potential of planorbids may be overestimated by our model.

Table 2. Families ranked according to the highest rank achieved by a species or group of species in each family, with the number of species or groups ranked in the top 12 (based on P rank) for each family, and the total number of species or groups that we assessed in each family.

Family	Highest species or group rank (P/S)	Number of species or groups in top 12	Total number of species or groups assessed
Ampullariidae	1/1	1	3
Hygromiidae	1/1	2	3
Helicidae	3/3	1	6
Cochlicellidae	3/3	1	1
Veronicellidae	5/9	3	6
Succineidae	7/12	1	2
Achatinidae	10/5	1	4
Planorbidae	10/5	2	3
Chronidae	14/7	0	1
Pleurodontidae	15/22	0	4
Milacidae	16/12	0	3
Arionidae	18/12	0	2
Ariophantidae	18/24	0	3
Urocyclidae	18/24	0	1
Pomatiopsidae	29/24	0	1
Enidae	31/29	0	1
Spiraxidae	36/35	0	1
Bradybaenidae	44/43	0	1

Validation of the model

To test the validity of our model, we scored a number of additional species and compared the outcome with their known status in the United States. Their attribute scores are available (Appendix 2).

Deroceras reticulatum (Agriolimacidae) scored 7.5 (S value) and 0.68 (P value), ranking it 5 and 10, respectively, among the more serious 'potential' invaders, and appropriately predicting its wide distribution and major pest status in the United States (chapters in Barker 2002a).

Cepaea nemoralis (Helicidae) scored 3.5 (S) and 0.29 (P), ranking it 29 and 36, respectively, toward the bottom of the list. While it is widespread in the eastern United States (Brussard 1975, Whitson 2005), it appears not to be a pest and although a role as a competitor of native snail species has been suggested (Whitson 2005), it has not been demonstrated. The prediction of the model, especially the P rank, which we deem more appropriate, concurs with the essentially non-pest status of this species in the United States.

Cornu aspersum (Helicidae) scored 7.0 (S) and 0.58 (P), ranking it 7 and 14, respectively, among the top-ranked one third. While it is widely distributed in the United States (Roth and Sadeghian 2003), it is only a major agricultural pest, notably of citrus, in California (*e.g.*, Sakovich 2002). Elsewhere it may be more of a garden nuisance. Nevertheless, its status as invasive in the United States is unquestionable and its ranking may reflect the relatively lesser relevance of its biological attributes (which included relatively few 1 scores) as opposed to its human interaction attributes (see discussion below). Thus, the model, at least regarding the P rank, may have underestimated its potential.

Potamopyrgus antipodarum (Hydrobiidae) scored 7.5 (S) and 0.63 (P), ranking it 5 and 13, respectively, among the top third. This ranking is reflected appropriately in its increasing spread through much of the western United States and increasing but as yet somewhat limited documentation of its ecological impacts (Kerans *et al.* 2005, Hall *et al.* 2006).

Milax gagates (Milacidae) scored 7.0 (S) and 0.58 (P), ranking it 7 and 14, respectively, also in the top third. Although widely distributed in the United States (Pilsbry 1948, Roth and Sadeghian 2003), the relative lack of literature (*e.g.*, Godan (1983) reports it as damaging Brussels sprouts; it is not mentioned in the chapters of Barker (2002a) dealing with the United States) suggests that it has not yet become a major widespread pest. In this case the model (at least the S value) may have overestimated this species' potential, although given its pest status in Europe, it would be unwise to assume this. However, simply changing the multi-pest score from 0 to 1 on the basis of its damaging endemic plants in Hawaii (Cowie 1997), changes its scores to 8.0 (S) and 0.73 (P), thereby ranking it 5 (both S and P ranks) and illustrating both the sensitivity of the ranking system to minor changes in the scores and perhaps the serious potential of this species as both an agricultural and environmental pest.

Rumina decollata (Subulinidae) scored 5.0 (S) and 0.42 (P), ranking it 18 and 27, respectively. Having been initially introduced accidentally, it has now been spread deliberately as a putative control agent for *Cornu aspersum*, and is now found widely in southern states from the east coast to California (Cowie 2001a). It has not been considered a serious agricultural pest although it may occasionally become sufficiently abundant in domestic gardens to be considered a nuisance (Fisher and Orth 1985, Cowie 2001a). As a facultative snail predator, it has been suggested that it could affect native, including endangered, snail species, but any such impacts have not been documented (Cowie 2001a). Thus, its wide distribution but low, though not negligible, effects are reflected appropriately in its ranking in the middle third.

Melanoides tuberculata (Thiaridae) scored 6.5 (S) and 0.59 (P), ranking it 9 (S) and 13 (P), among the top third. This ranking of its invasive potential is reflected in its presence in 15 states (Mitchell *et al.* 2007). Almost no studies have attempted to demonstrate any negative effects. However, it can reach high densities and acts as a vector of various trematode parasites. Thus it may have serious ecological impacts as a result of both competition with other freshwater organisms (including native snails and mussels) and transmission of parasites to fish (including endangered species) and indirectly to birds; it potentially may also have a human health impact as a result of the indirect transmission of trematodes to people (Mitchell *et al.* 2007).

Broadly, the model appropriately predicted the invasive pest status of this range of species, suggesting that it works at a gross level. Nevertheless, it is clearly sensitive to minor scoring changes and to the scoring algorithm used, and because some of the scores, especially the human attribute ones, are somewhat subjective, the model can only provide a rather general categorization.

Alternative models

In addition to the uncertainty in an analysis of this kind resulting from a lack of adequate basic knowledge of the attributes scored, subjectivity in scoring some of them, and choice of ranking algorithm, one could arguably include other attributes or weight the attributes differentially, as certain ones may be more important than others in determining potential invasiveness. Notably, climate/habitat match, introduction pressure, and being invasive elsewhere seem to be especially important (*e.g.*, Kolar and Lodge 2001, Theoharides and Dukes 2007, Bomford *et al.* 2008, Hayes and Barry 2008). However, weighting some attributes more than others would involve even more subjectivity than is already inherent in our model and we preferred to take the more objective approach of not weighting. Nevertheless, some of the categories are strongly related to each other (*e.g.*, invasion history, major pest elsewhere, economic potential) and by including scores for each of them we are in a sense positively weighting the more fundamental underlying attribute. Also, many of the biological attributes scored do indeed seem to be generally correlated with the human interaction attributes. Furthermore, by scanning Appendix 1, it is possible to identify those species that, for instance, are frequently intercepted, that are invasive/pests elsewhere, and so on, and to emphasize certain attributes in order to fine-tune or re-evaluate the ranking of a particular species or group of species. By doing so, it may be possible to tailor quarantine interventions to the threats from individual species or groups. In simplest terms, however, if a species is an invasive pest elsewhere and occurs in habitats/climates represented in the United States, in the absence of any more sophisticated risk assessment, the simplest approach is to assume that it also has that pest potential in the United States.

CONCLUSIONS

Our extensive review of the pest snail and slug literature and consultation with the malacological community, combined with our testing of the model against known alien pests in the United States, makes us confident that our prioritized list does indeed include those taxa most likely to become pests in the United States if they breach quarantine and/or if they cannot be contained locally. The ampullariid genus *Pomacea*, hygromiids, *Cochlicella* spp., helicids (notably *Theba pisana*), veronicellids, succineids, achatinids (primarily *Achatina fulica*), and planorbids topped the list. However, while the ranks, particularly the P ranks, assigned to these species/groups may be reasonable approximations of the relative seriousness of their threats, they should not be adhered to rigidly. Similarly, paying strict attention to the relative rankings of the other taxa that constitute the remainder of the list is also probably not warranted, especially as these species rank as potential pests for a variety of reasons in addition to their potential specifically as agricultural pests.

Other snail and slug species not listed may well have pest potential of which we are currently unaware or may develop pest potential as a result of future environmental changes, changes in agricultural practice, and changes in commercial activities including import/export routes and societal preferences. Notable among these are the numerous hygromiid species from around the Mediterranean, where the group exhibits immense diversity, exemplified by the long list of hygromiids given by Robinson (1999: 438) and of '*Helicella*' species given by Godan (1983: 272).

A key need, however, is better knowledge of the basic biology of many of these potential pests, and rigorous documentation of the levels of damage they cause (including economic data) rather than statements such as 'is a pest of legumes' or 'causes damage to fruit trees', which do not permit assessment of the severity of damage caused. Also, the relative lack of study of their environmental as opposed to agricultural impacts means that the potential of some species to cause serious environmental harm may be underestimated in studies such as this, since with little knowledge, it may not be possible to assign a score for their environmental pest status and potential economic impact on the environment.

Nevertheless, we consider this prioritized list of potential pest snails and slugs of quarantine importance to the United States to be a good approximation that we hope will be used as a basis for further development and more detailed evaluation of the pest potential of the taxa included.

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Appendix 1. Scores of each of the 46 taxa evaluated against the 12 attributes related to potential invasiveness (see text for explanation).

Taxon	Present in USA[a]	Native range	Phylogenetic relationships	Adult size	Egg/ juvenile size	Repro- ductive potential	Semelparous/ iteroparous	Breeding system	Intro- duction pressure	Inva- sion history	Major pest	Multi- pest	Economic damage
Land snails and slugs													
Achatinidae													
Achatina achatina	N	0	1	1	0	0	0	0	1	0	0.5	0	0.5
Achatina fulica	R	-	1	1	0	0.5	0	0	1	1	1	1	1
Archachatina marginata	N	0	1	1	0	0	0	0	1	0	0	0	0
Limicolaria aurora	N	0	0	1	0.5	0	-	0	0.5	0.5	0.5	0	0
Arionidae													
Arion ater	N	-	1	0	0.5	-	1	0.5	0.5	0	0	0.5	0
Arion lusitanicus	N	0	1	0	0.5	-	1	0	0	1	1	0	1
Ariophantidae													
Macrochlamys indica	N	-	1	0.5	-	-	-	-	0	0.5	0.5	0	-
Mariaella dussumieri	N	0	1	0.5	-	-	-	-	0	0	0.5	0	0
Parmarion martensi	R	0	1	0.5	-	-	-	-	0	1	0.5	1	0
Bradybaenidae													
Acusta touranensis	N	0	0.5	0.5	-	-	-	-	0.5	0	0	0	0
Cochlicellidae													
Cochlicella	N	1	1	1	1	0	1	0	1	1	1	0	1
Chronidae													
Ovachlamys fulgens	R	0	1	0	1	0	1	1	1	1	0.5	0	0.5
Enidae													
Enidae	N	0.5	1	0.5	1	-	-	-	0.5	0	0	0	0
Helicidae													
Arianta arbustorum	N	0.5	0	0.5	0.5	0	0	0	0.5	0	0.5	0	0
Cantareus apertus	R	0	1	1	-	-	0	0	1	1	0.5	0	0
Eobania vermiculata	R	0.5	1	1	0.5	-	0.5	0	1	0.5	0	0	0
Helix	R	0	0.5	1	0.5	-	0	0	1	0	0	0	0
Otala punctata	R	0	1	1	0.5	-	0	0	0.5	0	0	0	0
Theba pisana	R	0.5	1	0.5	1	1	1	0	1	1	1	0	1
Hygromiidae													
Cernuella	R	1	1	0.5	1	1	1	0	1	1	1	0	1
Xerolenta obvia	R	1	-	0.5	1	0	1	0	0.5	1	0.5	0	-
Xeropicta	N	1	-	0.5	1	-	1	0	1	1	1	0	-
Milacidae													
Tandonia budapestensis	R	0	1	0.5	-	-	1	0	0.5	1	1	0	0.5
Tandonia rustica	N	0	1	0.5	0.5	-	-	-	0	0.5	0	0	0
Tandonia sowerbii	N	0	1	0.5	0.5	-	1	0	-	1	0.5	0	0.5
Pleurodontidae													
Thelidomus aspera	N	0	1	0	-	-	-	-	0.5	0	0	1	0
Zachrysia auricoma	N	0	1	0	-	-	-	-	0.5	0.5	0.5	0	0
Zachrysia provisoria	R	0	1	0	-	-	-	-	0.5	1	1	0	1
Zachrysia trinitaria	R	0	1	0	-	-	-	-	0	0	0	0	0
Spiraxidae													
Euglandina [b]	N	0	1	0	1	-	-	-	0.5	0	0	0	0
Succineidae													
Succinea (Calcisuccinea) [c]	N	0	1	0.5	-	-	-	-	1	0	-	0	-
Succinea tenella [d]	R	0	1	1	1	-	-	-	1	1	0.5	0	-

Appendix 1. (continued)

Taxon	Present in USA[a]	Native range	Phylogenetic relationships	Adult size	Egg/ juvenile size	Repro- ductive potential	Semelparous/ iteroparous	Breeding system	Intro- duction pressure	Inva- sion history	Major pest	Multi- pest	Economic damage
Urocyclidae													
Elisolimax flavescens	N	0	1	0.5	-	-	-	-	0.5	0	1	0	1
Veronicellidae													
Diplosolenodes occidentalis	N	-	1	0	-	-	-	-	0.5	-	0	1	0
Laevicaulis alte	R	1	1	0	-	-	-	0.5	0.5	1	0.5	1	-
Leidyula moreleti	N	0	1	0	-	-	-	-	0.5	0	0	0	0
Sarasinula plebeia	R	-	1	0	-	0	-	0.5	1	1	1	1	1
Veronicella cubensis	R	0	1	0	-	-	-	-	1	1	1	1	0.5
Veronicella sloanii	N	0	1	0	-	-	-	-	0.5	-	1	0	0.5
Freshwater snails													
Ampullariidae													
Marisa	R	0	0.5	1	-	1	0	0	1	0.5	1	0	-
Pila	R	1	0.5	1	-	-	0	0	0.5	0.5	0.5	1	0
Pomacea [e]	R	1	1	1	0.5	1	0	0	1	1	1	1	1
Planorbidae													
Biomphalaria [f]	N	1	1	1	1	0.5	0	0.5	0	1	1	0	-
Bulinus	N	1	1	1	1	1	0	0.5	0	0	1	0	-
Indoplanorbis exustus	R	0	1	0.5	1	1	0	0.5	0.5	1	1	1	-
Pomatiopsidae													
Oncomelania	N	0	1	1	1	-	0	0	0	0	1	0	-

[a] Not present (N) or locally restricted (R).
[b] Only species of *Euglandina* not native to the United States.
[c] Only species of *Succinea* (*Calcisuccinea*) not native to the United States.
[d] May also include the similar *Succinea horticola*.
[e] All species of *Pomacea* except *P. diffusa* (often referred to, incorrectly, as *P. bridgesii*) and the native *P. paludosa*.
[f] All species of *Biomphalaria* except the native *B. obstructa*.

Appendix 2. Scores of each of the seven species already present in the United States that were used to validate the model for assessing invasive potential.

Taxon	Native range	Phylogenetic relationships	Adult size	Egg/ juvenile size	Repro- ductive potential	Semelparous/ iteroparous	Breeding system	Introduction pressure	Invasion history	Major pest	Multi- pest	Economic damage
Agriolimacidae												
Deroceras reticulatum	-	1	0	1	0.5	1	0	1	1	1	0	1
Helicidae												
Cepaea nemoralis	1	0.5	0.5	0.5	0	0	0	0.5	0.5	0	0	0
Cornu aspersum	1	1	0.5	0.5	0	0	0	1	1	1	0	1
Hydrobiidae												
Potamopyrgus antipodarum	0	1	1	1	0	1	1	0.5	1	1	0	0
Milacidae												
Milax gagates	0.5	1	0	1	-	1	0	0.5	1	1	0	1
Subulinidae												
Rumina decollata	0.5	0	0.5	1	0.5	1	0.5	0	1	0	0	0
Thiaridae												
Melanoides tuberculata	-	1	0.5	1	0	0	1	0.5	1	0.5	1	0